THE USE OF URINE MARKING IN THE SCAVENGING BEHAVIOR OF THE RED FOX (*VULPES VULPES*)

by

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(With 2 Figures)
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INTRODUCTION

The use of experiments to investigate scent marking behavior in mammals has greatly expanded in recent years, although mainly captive animals have been studied (*e.g.*, MYKYTOWCZ *et al.*, 1962, 1969, 1970; SCHULZE-WESTRUM, 1965; MÜLLER-SCHWARZE, 1971, 1974).

Well-controlled, manipulative experiments on mammals free-ranging in their natural environment have seldom been carried out, even though the ultimate reference point of ethology is the behavior of the animal in its natural environment. Where large mammals are concerned, so few manipulative field experiments have been done that we may question if this reference point to ethology is not beyond the reach of the experimental techniques of the science. We may ask whether the behavior of large mammals in a natural environment can indeed be studied by experimentation. The following study explores this question by experimentally investigating the scent marking behavior of free-ranging red foxes.

To begin, certain definitions of scent marking behavior must be made clear. Scent marking is usually described as the behaviors used to deposit secretions or excretions on environmental objects (see JOHNSON, 1973). More rigorously stated, scent marking occurs when a substance (secretion

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or excretion) is deposited on an environmental object or conspecific and where some of these substances (but not necessarily all of them) will be perceived and responded to by conspecifics, including the animal that deposited the mark (after SCHENKEL, 1966).

Mammals can scent mark with skin glands or with urine or feces. EWER (1968), MYKYTOWYCZ (1970, 1971), RALLS (1971), and JOHNSON (1973) offer good reviews of mammals that scent mark with skin glands. Urine marking, on the other hand, needs clarification.

Urine marking behavior in mammals.

The first problem is to differentiate between urination and urine marking behavior. Urination implies a simple elimination of waste products. On the other hand, urine marking implies an elimination of waste products, where glandular secretions may or may not be added to the urine, and where some of these substances are perceived and responded to by conspecifics.

Urine marking has evolved to serve a diverse number of functions in mammals. For example, urine marks are probably used to mark territories (HEDIGER, 1949; HORNOCKER, 1969; LAWICK-GOODALL, 1970), although much of the evidence here is anecdotal or interpreted with preconceived notions of functions in mind (RALLS, 1971; EISENBERG & KLEIMAN, 1972; JOHNSON, 1973). Urine marking is used as a dominance display in many species (see RALLS, 1971, for a review). Urine marks are also used for following trails (SEITZ, 1969), as an alarm substance in order to warn conspecifics (MÜLLER-VELTEN, 1966), and to inhibit aggression (DIXON & MACKINTOSH, 1971). During sexual behavior, urine marks are used for many different functions, for example, as a sexual isolating mechanism (MOORE, 1965), to locate remote females and evaluate their estrus status (BEACH & GILMORE, 1949), to synchronize the reproductive physiology of females (MARSDEN & BRONSON, 1964), to block pregnancies in recently inseminated females (BRUCE, 1959; DOMINIC, 1966), as a social releaser (Auslöser) for copulatory behavior (MICHAEL & KEVERNE, 1968), and to reinforce the pair bond by making the mate smell more familiar (KLEIMAN, 1971). In summary, urine marks and urine marking behavior in mammals appear to serve at least eleven different behavioral functions.

One partial explanation for this diversity is that urine marking makes extensive use of metabolic waste products (WICKLER, 1968). Mammals may urine mark many different points on their home range; and yet, because waste products are used, these marking substances cost the animal very little in terms of energy expenditure (MONTGOMERY, 1974).

Clearly, urine marking is not associated with the same behavioral function every time it appears. Indeed, SCHULTZE-WESTRUM (1965) points out that one urine mark may serve several different functions depending upon which conspecific animals perceive it. Thus, urine marking might indeed be viewed as an olfactory communications system that transmits many different messages, perhaps even several simultaneously (see EISENBERG & KLEIMAN, 1972).

Field observations suggest that urine marking may also serve a purpose in the red fox's scavenging behavior. Before this hypothesis can be understood, however, the urine marking behavior of the red fox must be described.

Urine marking behavior in the red fox.

In Prince Albert National Park, Saskatchewan, Canada, I observed free-ranging red foxes for long periods of time in a natural boreal forest-aspen parkland ecotone (see ROWE, 1959; GIMBARZEVSKY, 1973). The study ran from April to December in three consecutive years, 1971 to 1973, and also during October, 1974. However, a majority of the field observations were collected during autumn because the foxes were most tolerant of humans during this season.

These observations were possible because certain foxes scavenge for food around the human settlements in the park. As a result, these foxes soon habituate to man and can be observed for long periods of time both around the settlements and in the natural environment.

With practice, foxes can be sexed by spotting the genitals and can be individually recognized from natural markings. In total, I observed urine marking behavior over a thousand times in fifteen different foxes (although the experiments of this study only use five of these foxes). These fifteen foxes included three yearling males, three adult males, two yearling females, three adult females, and four foxes of undetermined age and sex. The following general description of urine marking behavior was constructed from numerous field notes and movie films of these foxes.

Before a red fox urine marks a tree, an object, or a spot on the forest floor, it always investigates it (see Figure 1). The fox approaches, lowers its nose, and smells or visually scans the object and the ground immediately around it. This investigation may last from several seconds to well over a minute. Then the fox frequently urine marks the spot (see Figure 2). Specifically, it urine marked the spot in 42% of the investigations (255 times out of 613 recorded instances). The fox usually puts the urine within 15 cm. of the investigated spot and frequently directly on it (see Figure 2). I identified nine different urine marking postures in the red fox. For example, in order to urine mark vertical objects, male foxes lift a leg and assume either the elevated or raised posture (see SPRAGUE & ANISKO, 1973). In order to urine mark the ground, male foxes lower the inguinal region towards the ground (see Figure 2) and assume either the lean, flex, or flex-raised posture (SPRAGUE & ANISKO, 1973). Female foxes urine mark vertical objects from the face-away posture (see KLEIMAN, 1966). Finally, female foxes urine mark the ground by lowering the anal region towards the ground and assuming either the squat posture or squat-raised posture (see SPRAGUE & ANISKO, 1973).

Urine marking behavior in the red fox is a very brief behavior, lasting only 2.25 $\pm$ 0.48 seconds (mean duration and its standard deviation; N = 40). When snow was on the ground, I estimated the volume of urine released during a urine marking behavior. Two hundred urine marks were checked, and the volume of urine released always appeared less than 20 ml. Furthermore, during the four years of observation, I never saw a fox release a large volume of urine. They always urinated in 20 ml. or less quantities. Thus, the red fox appears to eliminate all its nitrogenous wastes during urine marking behavior.

With snow on the ground, I could also check for pseudourinations in the red fox. SPRAGUE & ANISKO (1973) report that the domestic dog frequently assumes one of the urinating postures but that no urine is released. I checked the snow 200 times after the foxes showed a urine marking posture, and there was always urine on the snow. Thus, pseudourinations are apparently rare or non-existent in the red fox.

Most urine marking in the foxes appeared during scavenging behavior. In fact, while scavenging, the foxes were observed to urine mark up to 70 times per hour.

Scavenging behavior in red foxes can be identified from the following characteristics: the fox walks back and forth a number of times within the same area of woods, with its nose lowered, apparently scanning the ground. It frequently stops and investigates many spots on the forest floor. While scavenging, the fox seldom travels along trails. On the other hand, while hunting or when travelling, the fox frequently follows trails (for example, animal runs, hiking paths, or the edges of roadways). During scavenging behavior, the fox appears to be searching for certain types of food-items such as slow moving invertebrates, bird eggs, carcasses, or food caches made by it or a different fox (see also TINBERGEN, 1965). What function is being served by the urine marking during scavenging behavior?

Canidae have been reported to urine mark their territories (LAWICK-GOODALL, 1970; FOX, 1971), to urine mark as a dominance display

(HEIMBURGER, 1959), and to use urine marks in order to locate remote females (BEACH & GILMORE, 1949). However, most of my observations on the foxes were made during autumn when the breeding season of the red fox was still five months away. Also only a few of the urine marks were made during social encounters. These few urine markings did appear to serve as dominance displays because they were made by the dominant animal towards the end of the agonistic encounters.

FOX (1971) suggests that most canid species, whether territorial or not, urine mark specific points on their home range and that these urine marks serve as a social record of what animals have recently passed by this spot. TINBERGEN (1965) and BURROWS (1968) describe this type of urine marking in red foxes. For example, TINBERGEN (1965) located an old rubber boot on the Ravenglass sand dunes and observed that red foxes repeatedly urine marked this boot over a three year period. Common sites were identified in Prince Albert Park where several different foxes repeatedly urine marked. Urine marks at these places probably did serve as a social record, but these sites accounted for only about 12% of the urine marks.

Thus, urine marks made by the red foxes could at times be serving territorial and "social record" functions, but field observations clearly suggested that another function was also being served, one relevant to the fox's scavenging behavior. For instance, many urine marks that the foxes made appeared to be elicited by food remains. For example, the foxes consistently urine marked inedible food remnants such as bones, feathers, or dried out carcasses. Other researchers have also observed foxes to urine mark or defecate on food remnants. For example, EGOSCUE (1962) stated that the kit fox, *Vulpes macrotis*, frequently urine marked bird wings and rabbit feet and occasionally left scats near bits of bone or other animal remains. KORYTIN *et al.* (1969 a, b) reported that foxes consistently urine marked food remnants and feeding places (see also TEMBROCK, 1957; TINBERGEN, 1965; and BURROWS, 1968). This consistent urine marking of food remnants led to the formation of the following hypothesis.

HYPOTHESIS

During scavenging behavior, a fox stops and investigates up to 220 spots per hour on the forest floor, and it scavenges for approximately 35% of its active time, or approximately five hours per day (ABLES, 1969). Thus, while scavenging a red fox investigates an extremely large number of spots on the forest floor, many more than it could probably remember without some external signal. Secondly, I have observed the same fox, or several different foxes, scavenging in the same area several times within a two day period.

Thus, urine marking may function as a type of "book keeping system" during scavenging behavior. The hypothesis is that a fox urine marks places where food has already been eaten, but where food odor or inedible food remnants remain. When the same or a different fox re-investigates this spot, the scent of fox urine signals 'no food', and the fox will investigate this spot for only a short period of time.

This use of urine marking might increase the efficiency of the red fox's scavenging behavior so that more food items are found per hour of scavenging. Efficiency of scavenging behavior may be particularly important during periods of food shortage. The ten-year cycle among red foxes in the boreal forest (KEITH, 1963) suggests that these foxes, at least, are regularly subjected to periods of severe food shortage.

I shall now proceed to test this "book keeping" hypothesis with three different experiments.

RESULTS

Experiment I.

Do red foxes urine mark inedible food remnants?

Many researchers have observed red foxes to urine mark food remnants. However, the odor of a fox could already be on these food remnants. Perhaps it is the conspecific's odor, rather than the food remnant itself, that causes the urine marking behavior. This is a point that should be checked. Furthermore, HEIMBURGER (1959) documented that certain odoriferous substances trimethylamine, gasoline, oil) are rubbed, rolled on, and sometimes urine marked by certain canid species. Consequently, in this first experiment, I wish to test if urine marking in red foxes can actually be elicited either by inedible food remnants or by these odoriferous substances.

The experiment consisted of placing seven different substances on the ground: trimethylamine, gasoline, oil, synthetic urea, soft dogfood, dry dogfood, and water. Once every hour while I was observing a fox, one of these substances was chosen at random and some of it was placed on the ground. The first four substances presented the fox with strong non-food odors (HEIMBURGER, 1959). Water was included in the experiment as a control. Two types of dogfood were also set out, a dry granular type and a soft, moist, canned type. Both types of dogfood were placed on the ground in 30 gms. piles. These small piles are termed 'baits'.

Whenever I placed a substance on the ground, the fox approached, investigated the substance, and ate any food that was present. I then recorded if the fox urine marked the substance. I realized that by occasionally putting food down I was reinforcing the fox to investigate any substance that I put on the ground. Thus, I was rewarding the fox for taking part in the experiment. I did not feel, however, that I was reinforcing the urine marking behavior. The fox got the food whether or not it urine marked the spot, and got an equal amount of food whether it was dry or soft dogfood.

When the fox ate the dry dogfood, few crumbs and very little food odor were left behind on the ground. When the fox ate the soft dogfood, visual and olfactory food stimuli did remain behind on the ground. To insure that this happened, whenever I set out a soft dogfood bait, I smeared a corner of it over a hard surface on the ground (rock, root of a tree). Direct observation confirmed that some soft dogfood did remain on the ground after the fox ate the bait. This smeared dogfood created a food remnant that the fox could not eat; and I observed whether or not the fox urine marked it.

I continued the experiment until each substance had been set out 30 different times (see Table 1). The experiment was conducted during October, 1974, on three different foxes (two adult male foxes and a young female fox). The way that the foxes urine marked these substances showed some individual variation, but all these foxes showed identical trends. Thus, the data from the individual foxes were combined before being presented in Table 1.

TABLE 1

The results of Experiment I. The number of times a fox urine marked the ground after investigating each substance

	Urine marked	Not urine marked
Soft Dogfood	23	7
Dry Dogfood	4	26
Trimethylamine	1	29
Gasoline	0	30
Oil	3	27
Synthetic Urea	0	30
H_2O	1	29

An examination of Table 1 shows that only one substance — the soft dogfood — consistently released urine marking behavior in the foxes. The foxes did not usually urine mark the dry dogfood spots, nor did they urine mark any of the other substances. Clearly, the soft dogfood — the only substance that left visual and olfactory food stimuli on the ground — was the only substance that elicited urine marking behavior.

Fig. 1. A male red fox investigates a spot on the ground.

Fig. 2. The same fox then urine marks that spot. (The white arrows indicate the same spot on the ground in both pictures.)

In conclusion, this experiment confirms that inedible food remnants are urine marked by red foxes. It also shows that certain odoriferous non-food substances are not urine marked. Red foxes, therefore, specifically tend to urine mark inedible food remnants.

Experiment II.

Does urine marking serve a function in scavenging behavior?

It is clear that foxes urine mark inedible food remnants. A second more complex experiment was conducted to test if urine marking functions as a type of "book keeping system" in the fox's scavenging behavior.

To test this point, I mimicked the caching behavior of the red fox. A fox makes a cache by burying a single food-item in a shallow hole. The fox digs a hole so that it corresponds to the size of the food-item but deep enough so that the food-item can be covered by 5 to 8 cm. of dirt. The fox then stuffs the food-item into the hole, covers it with dirt, packs the dirt, and finally disguises the cache with leaves and other litter. It usually scatters its caches so that only one food-item is placed in each hole and the holes are well separated from each other (see TEMBROCK, 1957; KRUUK, 1964; TINBERGEN, 1965).

During scavenging behavior the red fox retrieves these buried food caches (see TINBERGEN, 1965), eats the food-item, smells the hole, and frequently urine marks it. These observations provide a basis for the following experiment.

In this experiment I tested if two foxes (an adult female and an adult male) investigate for a shorter time period places with both the odors of food and urine as compared to places with just the odor of food. The experiment consisted of creating four different types of spots on the forest floor. Each type of spot presented a different set of stimuli to the fox; and the fox's investigation time at each spot was recorded. Table 2 outlines the stimuli that were presented a each different type of spot.

Type I spots were created by mimicking the caching behavior of the red fox. I dug an 8 cm. deep hole and placed a 30 gm. bait of soft dogfood in that hole. I then smeared a corner of the bait over a hard surface in the hole (rock, root, or hard packed soil) to insure that the odor of food remained in the hole after the bait had been eaten. The bait was then covered with 5 to 7 cm. of dirt, and the dirt was packed down with 15 strokes of the fingertips. The spot was then disguised with leaves and other litter.

Type II spots were created by digging an 8 cm. deep hole and then

TABLE 2

Summary of the types of spots that were created in Experiment II

Type of spot	*How the spot was created*	*Stimuli presented to the fox*
Type I	Thirty grams of dogfood buried in 8 cm. deep hole. Hole filled with dirt and disguised with leaf litter.	Odor of food.*
Type II	Two grams of dogfood smeared on bottom of 8 cm. deep hole.	Odor of food. Open hole.
Type III	A fox investigated one of the above two types of spots and did not urine mark spot.	Odor of food. Open hole. Odor of a fox.
Type IV	A fox investigated one of the above three types of spots and urine marked the spot.	Odor of food. Open hole. Odor of a fox. Odor of fox's urine mark.
Type V	Spot not manipulated in any way.	No food was ever found at these spots. Foxes usually did not urine mark spots.

* The odor of a human was probably also present at Type I - IV spots. This was an unintended stimulus that could not be eliminated. Any effect of human odor on the foxes, however, should have been equal throughout the four types of spots.

smearing approximately 2 gm. of dogfood on a hard surface in the hole. A thin layer of dirt was then sprinkled over the dogfood. The hole was not filled in with dirt, nor was the place disguised with leaves or litter. Type II spots were supposed to mimic a dug out caching hole where there was the odor of food but where the caching hole had not been urine marked by a fox.

Type III and IV spots were created by the activities of foxes at Spots I and II. Periodically a fox came onto the experimental plot and began to investigate the spots that I had created. The fox usually dug out and ate the bait at the Type I spots. They investigated and even dug at the Type II spots but usually found little or nothing to eat at these places (that is, they showed little licking and chewing behavior at these places).

After investigating Type I and II spots, the fox usually urine marked them (see Table 3). This changed them into Type IV spots. Table 2 outlines the stimuli present at Type IV spots. Sometimes the fox left without urine marking the spots. This converted them into a Type III (see Table 2).

TABLE 3

The percentage of times the foxes urine marked after investigating the five different types of spots

	Female fox		Male fox
Type I spots.	73%	63%	80%
Type I spots with markers.	63%	—	77%
Type II spots.	53%	60%	63%
Type III spots.	66%	—	57%*
Type IV spots.	10%	20%	23%
Type V spots.	0%	3%	0%

(Sample size for each cell is 30. An *indicates the one cell where the sample size is 14).

Type III spots were less frequently created because the foxes usually urine marked after investigating the Type I and II spots (see Table 3). I do not know why the fox did not urine mark these spots. Perhaps they were simply temporarily out of urine. There definitely was the odor of food at these spots. This was confirmed by spotting dogfood in the holes. Later when the foxes investigated these Type III spots, they frequently urine marked them (see Table 3). This action changed them into Type IV spots.

Type V spots were altogether different. On the experimental plot, the fox investigated many spots that I had not manipulated in any way. These spots were classified as Type V spots. The fox frequently investigated such places. I do not know what attracted the fox to these spots initially, but it usually smelled these spots very briefly and walked on. Because it never licked, chewed, or dug at these places, I assume the fox never found any food there. Furthermore, the fox rarely urine marked these spots (see Table 3). Thus, Type V spots are interpreted as places where the fox was attracted by some feature, but where no food stimuli appeared to be present.

The field procedure for this experiment was as follows: Each day, a new 1,000 m^2 experimental plot was set up in the woods. Early each day, I chose thirty different locations on the plot and randomly assigned fifteen Type I spots and fifteen Type II spots to these locations. The spots were approximately five meters apart and usually remembered from natural features or infrequently from a painted stone placed a meter away from the spot.

Eventually a fox came onto the plot. With a stop watch, I timed its investigation of each spot, specifically from the moment it stopped or turned towards the spot until its head came up signaling the end of the investigation. I also recorded whether or not the fox urine marked the spot. Since the fox changed Type I and II spots into Type III and IV, after the fox left, I created some new Type I and II spots on the plot until I again had thirty of each. Usually after an hour or more, the same or a different fox (see Tables 3 and 4) came back on the plot and began investigating the spots once again. I continued the experiment until twilight each day.

In order to obtain a sample size of thirty for each cell in Tables 3 and 4, the experiment was run for fifteen days during October, 1972. (Cell #16 is the only exception; here the sample size is fourteen. This cell is excluded from the statistical analysis). Table 3 gives the percentages of the times the foxes urine marked after investigating each spot. Table 4 summarizes how long the foxes investigated the spots by giving the mean investigation time and standard deviation for each cell.

TABLE 4

The means and standard deviations of the investigation times recorded in Experiment II

	Sample #	Female fox			Sample #	Male fox
Type I spots.	≠ 1	9.16 ± 2.97	2	7.35 ± 1.73	11	7.62 ± 2.28
Type I spots with markers.	3	8.21 ± 3.63		——	12	7.38 ± 2.78
Type II spots.	4	6.82 ± 3.09	5	7.35 ± 3.36	13	6.68 ± 2.29
Type III spots.	6	5.91 ± 4.15		——	16	6.40 ± 4.45
Type IV spots.	7	1.24 ± 0.51	8	1.45 ± 0.61	14	1.57 ± 0.57
Type V spots.	9	1.75 ± 1.30	10	1.22 ± 0.73	15	1.40 ± 0.62

In this experiment, two foxes investigated the five different types of spots. (Sample # refers to the numbers in Table 5.)

From these data, I wanted to test if mean investigation times for spots that were urine marked differed significantly from those that were not urine marked. To do this, I analyzed the data with the non-parametric Simultaneous Treatment Procedure that allows for multiple comparisons between pairs of samples (SOKAL and ROHLF, 1969). The results of this statistical analysis are given in Table 5.

The analysis consisted of fifteen samples, each having a size of thirty. A critical point for the Mann-Whitney U-value was calculated at α = 0.001 and equalled 748. Then U-values for every possible pair of samples were calculated and are reported in Table 5. If the U-value for a pair

TABLE 5

The statistical analysis of the data in Table 4

Sample ≠	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	—	617	557	650	574	725	900 *	900 *	891 *	900 *	592	628	693	900 *	900 *
2		—	488	539	453	625	900 *	900 *	880 *	899 *	459	482	573	900 *	900 *
3			—	569	499	653	900 *	899 *	881 *	898 *	474	506	589	900 *	900 *
4				—	504	541	899 *	897 *	875 *	891 *	553	519	475	900 *	897 *
5					—	583	885 *	877 *	861 *	865 *	452	461	496	873 *	881 *
6						—	864 *	836 *	813 *	858 *	644	616	559	821 *	842 *
7							—	576	607	501	900 *	899 *	899 *	606	527
8								—	471	609	900 *	898 *	898 *	500	496
9									—	627	883 *	879 *	874 *	487	487
10										—	899 *	897 *	897 *	650	563
11											—	492	554	900 *	900 *
12												—	545	900 *	898 *
13													—	893 *	897 *
14														—	545
15															—

An (*) marks the pairs of samples that are significantly different ($P<0.001$).

exceeds 748, the two samples are concluded to be from two distinct populations. If the U-value is $\leqslant 748$, the two samples are concluded to be from the same population.

There are significant differences in the data (see Table 5). The samples can be partitioned into two sets:

(#1, #2, #3, #4, #5, #6, #11, #12, #13)
(#7, #8, #9, #10, #14, #15)

A comparison of any two samples from *between* these two sets always results in a significant difference. A comparison of any two samples from *within* one set always results in no significant difference.

This analysis allows the following statements:

1. The average investigation time for a fox to find a piece of dogfood buried 8 cm. deep in the forest floor is 9.16 ± 2.97 seconds (Sample #1, Table 4). This investigation time did not change significantly with repeated sampling (Sample #1 = Sample #2, Table 5), nor did it change for different individual foxes (Sample #1 = Sample #11).

2. The painted stone markers did not appear to influence the investigation times of the foxes (Sample #1 = Sample #3; Sample #11 = Sample #12).

3. A fox investigated a Type II spot for an average of 6.82 ± 3.09 seconds (Sample #4, Table 4). This investigation time remained constant over repeated sampling (Sample #4 = Sample #5) and for different individual foxes (Sample #4 = Sample #13). The investigation times for Type I and II spots showed no significant differences (Sample #1 = Sample #4; Sample #11 = Sample #13). Thus, the open hole in Type II spots did not elicit a short investigation time in the foxes.

4. The foxes investigated Type III spots for as long as they investigated Type I or Type II spots (Sample #1 = Sample #4 = Sample #6). The stimuli of Type II and III spots were similar, but Type III spots had in addition the odor of a fox associated with them. Thus, the odor of a fox at a spot not elicit a short investigation time.

5. The presence of a urine mark greatly modified the behavior of the foxes. A fox investigated a Type IV spot on the average of 1.24 ± 0.51 seconds (Sample #7, Table 4). This investigation time remained constant over repeated sampling (Sample #7 = Sample #8) and also for different individual foxes (Sample #7 = Sample #14). Foxes investigated Type IV spots for significantly shorter periods of time than they investigated any of the first three types of spots (Sample #1 = Sample #4 = Sample #6 > Sample #7; Sample #11 = Sample #12 = Sample #13 > Sample #14). Thus, the presence of a urine mark at Type IV spots appeared to elicit a much shorter investigation time in the foxes.

6. What was the specific message content of a urine mark at a Type IV spot? To answer this question, Type V spots must be examined. As explained earlier, Type V spots were places where no food appeared to be present (see p. 92). Foxes investigated these spots for an average of 1.75 ± 1.30 seconds (Sample #9, Table 4). Thus, foxes investigated Type IV and Type V spots for the same amount of time (Sample #7 = Sample #9; Sample #14 = Sample #15). In short, foxes thoroughly investigated places with the odor of food (Type I, II, III spots) but investigated only briefly

places with no food stimuli (Type V spots). Spots that had both the odor of food and urine were investigated as if no food stimuli were present (Type IV = Type V spots). This suggests that the message content of a urine mark at a food remnant is equivalent to "no edible food present".

At this point I would like to eliminate two alternative explanations for the shorter investigation times at the Type IV spots. Two foxes were involved in this experiment, a male and a female. Could some of the shorter investigation times be a sexual response when one fox investigated the other's urine marks? This seems unlikely. First, one would expect urine marks to elicit greater interest and longer investigations, not shorter, if sex were involved. Secondly, I never observed any sexual behavior between these foxes, and the breeding season was still five months away when this experiment was conducted. Thus, the short investigations at the urine marks did not appear to occur for a sexual reason.

Neither can the shorter investigation times be completely explained by memory. The female fox came onto the experimental plot more frequently than did the male, and usually was the first fox on the plot each day. When the male fox came onto the plot for the first time each day and investigated Type IV spots, I knew he was investigating spots that had been urine marked by the female: he could not have used memory cues at these places. Yet, he investigated these spots for only 1.55 ± 0.57 seconds ($N = 15$ timings). Thus his short investigation at these places must have been a reaction to the presence of the urine mark. (His investigation of Type I, II, and III spots during these times averaged 7.11 ± 2.53 seconds, $N = 32$ timings).

Thus I conclude that foxes spend less time investigating places on the forest floor if the odor of urine has been added to the odor of food. A dug out hole and the odor of a fox at these places did not elicit the short investigation. In this experiment, a urine mark was the key stimulus that elicited the brief investigation.

This experiment supports the "book keeping" hypothesis. It might be objected, however, that the investigation times were somehow influenced by the experimental setting. The experiment should be verified in a more natural environment. To do this, I collected the following observations.

Before any experiment was conducted, I observed the foxes for long periods of time while they scavenged in their natural environment. It was during these long exploratory observation periods that the "book keeping" hypothesis was formulated. During this time, I recorded how long foxes investigated many spots on the forest floor and whether they urine marked each spot. Urine marked spots were remembered from natural features, or from a painted stone that was placed a meter west of the spot. If a fox investigated this urine marked spot again within 48 hours, this second investigation was also carefully recorded. Second investigations were recorded only for 48 hours because urine is probably an effective olfactory signal for only two or three days (see HEIMBURGER, 1959).

The first type of spot I will consider is any place where a fox investigated and subsequently urine marked. For a large sample (N = 90), the mean investigation time and its standard deviation for this type of spot were 3.68 ± 3.98 seconds (range: 0.5 to 22.2 seconds). I knew very little about what stimuli were present at these spots. Probably they varied from spot to spot. It is even possible that some of these spots were recently urine marked. Thus, the average investigation time here is expected to be less than for the unmarked spots (Type I, II, and III) in the experiment.

The second type of spot was any place where a fresh urine mark was known to be present before a fox investigated. The average investigation time and standard deviation for this type of spot were 1.48 ± 0.97 seconds (range: 0.4 to 4.5 seconds; N = 60).

I tested the two means using a Student's t test that was corrected for unequal sample sizes and unequal variances (SOKAL & ROHLF, 1969). The critical t value (one tailed test, $\alpha = 0.001$) was 3.21. The t value for the two samples was $t_s = 4.96$; thus, the two means differ significantly. The consistent presence of a urine mark at the second type of spot appeared to elicit a short investigation time in the foxes. Thus, these observatons, collected before any experiment was made and while the foxes were scavenging in the natural environment, tend to verify Experiment II and support the "book keeping" hypothesis.

Experiment III.

Do the foxes ever ignore the urine marks?

The previous experiment shows that when a fox encounters a urine mark at a food remnant, the urine mark appears to signal that no edible food is present, and the fox investigates the spot for a very brief period of time. It is important to probe the relationship between the amount of food stimulus that is present at a spot and the fox's reaction to the urine mark. For example, if the amount of food odor at a spot is increased, will the fox's reaction to the urine mark change? This question is examined in the following experiment.

During October, 1973, I was able to follow a young male fox for long periods of time as it scavenged in its natural environment. This was a different individual from the older male fox in Experiment II. During scavenging behavior, this young fox urine marked many places on the forest floor. At each urine mark, I carefully placed painted stones on each side of the mark so that it could be precisely relocated at a later time. When the fox left the area, I returned to these urine marks. I then randomly chose and buried one of two types of baits at each spot. Specifically, at half of the urine marks, I dug an 8 cm. deep hole that was located approximately 10 cm. from the urine mark. (Foxes frequently urine marked that far away from spots they had investigated, see p. 84). In that hole I placed a 30 gm. bait of soft dogfood. The hole was then filled with dirt, packed down, and the spot was disguised with leaves and litter. In doing this, I took great care not to disturb the urine mark. The stones were then removed and the spot was remembered from natural features. At the other urine marks, the same procedure was followed except that a 3 gm. bait of soft dogfood was buried instead of a 30 gm. bait. It is assumed that the 30 gm. bait would give off more food odor than the 3 gm. bait. Thus the experiment examines if a fox's reaction to the urine mark changes when the amount of food odor is increased.

During the next two days, it the fox investigated these spots again, I recorded how long he investigated each spot and if he dug out and ate the buried bait. Only spots that had been urine marked within 48 hours of the fox's re-investigation were included in the experiment. Also, if the spot had been disturbed prior to the fox's re-investigation of it, the spot was excluded from the experiment. I soon found that it was necessary to attract the fox to the vicinity of these spots. Specifically, for 65% of the spots (39 out of 60), I dropped a small amount of dry dogfood 2 m. away from the spot when the fox was nearby. The fox then walked over, ate the dry dogfood, and then usually investigated the urine marked spot where the bait was buried. If the fox left the spot without digging out the bait, I then dug the bait out in order to verify that it was still present. The experiment was continued for nine days until 30 places with each type of bait had been investigated. The results are presented in Table 6.

TABLE 6

The results of Experiment III. The number of times the fox dug out a bait that was buried near a urine mark

	Baits dug out	Baits not dug out
30 gm Bait	24	6
3 gm Bait	2	28

Regarding the 30 gm. baits, the fox smelled the area on the average of 5.7 ± 4.9 seconds (range: 0.6 to 26.3 seconds) and then began to dig. The fox dug out 24 of the 30 large baits, ate them, or carried them off and cached them in a new place. Thus, the fox was not 'deceived' by the urine mark that was present at these places. The fox appeared to respond to the strong odor of food instead of the odor of the urine mark and dug out the bait that was present at these spots.

Regarding the 3 gm. baits, the fox smelled the area on the average of 2.3 ± 3.5 seconds (range: 0.4 to 12.8 seconds), occasionally urine marked the spot again, and walked on. The fox dug out only 2 of the 30 smaller baits.

This experiment shows that the fox's reaction to the urine mark is highly dependent on the amount of food odor that is concomitantly present. In fact, there appears to be a hierarchy of stimuli that determines the fox's reaction to a spot. A hierarchy of stimuli determining different responses has also been observed in the behavior of other carnivores (see RASA, 1973b). The hierarchy of stimuli in the fox's scavenging behavior can be ranked: strong odor of food > odor of a urine mark > weak odor of food. The highest stimulus of this hierarchy that is present appears to determine what the fox's reaction to that spot will be. For example, if the weak odor of food is the only stimulus present, the fox thoroughly investigates the spot (see Type II and III spots of Experiment II). If there is both the weak odor of food plus the odor of a urine mark, the fox usually investigates the spot for a short period of time and walks on. This reaction was observed both in Experiment II as well as in this experiment. Finally, if the fox encounters a spot where there is a strong odor of food plus the odor of a urine mark, the strong odor of food takes precedence, and the fox thoroughly investigates the spot. Thus this experiment shows that a urine mark elicits a short investigation in the fox only when it is in combination with the weak odor of food.

DISCUSSION

This study shows that manipulative experiments can be used to investigate the behavior of free-ranging large mammals; yet, this has seldom been done. TINBERGEN (1965) was one of the first to demonstrate the feasibility of this approach when he experimentally investigated the caching behavior of wild foxes. It is unfortunate that manipulative experiments have so seldom been used in mammalian field studies. Their use is one of the best ways to test theories not only about the behavior but also about the management of wildlife species.

Alternative hypothesis.

KORYTIN & SOLOMIN (1969) present an alternative explanation for why foxes urine mark food remnants. They observed wild foxes urine marking many places where food was obtained and suggest that foxes will later use these urine marks in order to locate areas where caches or other food-items have once been found. To experimentally test this hypothesis, they buried 10 pieces of meat at a time in a round enclosure (700 m^2) and marked five of these baits with fox urine. Captive foxes let into the enclosure found 70% of the marked baits (42 out of 60) but only 59% of the unmarked baits (35 out of 60). KORYTIN & SOLOMIN conclude that the foxes used the urine marks as orientation cues in order to locate the buried baits.

Their experiment, however, is weak on several points. Although the data from one fox, Yashka, did show significant differences, an analysis of their data using a χ^2 Contingency Table (SOKAL & ROHLF, 1969) showed that their overall results, as given above, were not significant at the 0.05 level of confidence ($\chi^2 = 1.776$; 1 d.f.).

Furthermore, their experiment does not mimic the natural behavior of the red fox in my area. Foxes in Prince Albert Park rarely made a cache and then urine marked on it. Out of 225 caches that I saw the foxes make, they urine marked on or near the cache only twice. However, after retrieving the cache and eating the food-item, the foxes frequently urine marked the dug out, empty hole (see p. 89).

In addition, a prediction from KORYTIN & SOLOMIN's hypothesis is that the foxes should frequently show scavenging behavior after smelling a fresh urine mark. I have explained at the end of Experiment II (see p.   ) how I kept track of when two foxes in their natural environment were smelling fresh urine marks. I also recorded what behavior they showed immediately prior to and following this action. Scavenging behavior preceded smelling a fresh urine mark 44% of the time (25 out of 57 recorded instances), but scavenging behavior followed this action on only 39% of the instances (22 out of 57). Thus there was no increase in scavenging behavior as a result of smelling the fresh urine marks. In short, urine marks did not seem to elicit scavenging behavior in these red foxes.

These criticisms do not disprove KORYTIN & SOLOMIN's hypothesis. In the introduction, I have stressed that a urine mark may serve several different functions. Thus, it is conceivable that both their hypothesis and mine could be correct; that is, a fox may urine mark to indicate that no food is present at a particular spot but also to indicate the general areas where caches or other food-items have been found. However, because of the above criticism, I suggest that KORYTIN & SOLOMIN's hypothesis needs to be further tested before it is accepted.

Scent marking behavior.

JOHNSON (1973) and RASA (1973a) state that one area that has never been experimentally investigated is an animal's response to its own scent marks. In Experiment II of this study, the female fox frequently investigated her own urine marks at food remnants and responded by investigating these food remains for a brief period of time. This response may increase the efficiency of scavenging behavior. Thus, it appears that in some circumstances an animal may use its own scent marks in a way that could have adaptive value.

The male fox in Experiment II also responded to the female's urine marks by investigating these food remnants for a brief period of time. This suggests two things: As mentioned earlier (see p. 95), it suggests that the foxes' short investigation times were elicited, not by memory cues, but by the presence of the urine marks. Second, it suggests there is a degree of social behavior in the scavenging behavior of red foxes (see below).

Limitations.

There are, however, some limitations to this study that should be kept in mind. First, the experiments involved only five different foxes. The other ten foxes in which urine marking was observed did not habituate to me sufficiently to take part in the experiments. Second, all the foxes in this study were from the same geographic region. Thus, I am not able to state how applicable my findings will be to foxes of other areas. However, other researchers (TEMBROCK, 1957; TINBERGEN, 1965; BURROWS, 1968; KORYTIN *et al.*, 1969) have described foxes in other areas urine marking or defecating on food remains. These observations suggest that the use of scent marking in scavenging behavior may be a widespread phenomenon in the red fox, and may also occur in other closely related canid species (see EGOSCUE, 1962; OZOGA & HARGER, 1966).

In Prince Albert Park, urine marking was the most frequent way of scent marking food remnants; however, the foxes did occasionally *defecate* on food remnants, particularly on durable ones, such as pieces of bone. However, foxes also defecated on places where no food remnant appeared to be present and without first investigating the ground. Thus, it appears that defecation is only sometimes used as a scent mark during scavenging behavior.

A third limitation to this study is that I was clearly visible to the foxes during all the experiments. Thus, there is a possibility that my behavior influenced the behavior of the foxes. I do not think this is likely, but it should be checked in future research. It seems unlikely because, in none of the experiments, did the foxes receive the food rewards directly from me; and, in none of the experiments, did the foxes receive a food reward only after they had shown the appropriate behavior. For example, in Experiment I, the foxes got the dry dogfood even though they did not urine mark these spots. In Experiment II, the foxes thoroughly investigated Type II and Type III spots and usually urine marked these places even though they received no food reward at these spots (see Table 3). Thus, the food rewards were given to encourage the foxes to take part in the experiments, but they were not given as reinforcements for certain behaviors.

A fourth limitation to the study is that the majority of my fox watching and experimentation was done during autumn. However, I was able to verify that foxes do urine mark food remnants in every month from April through December, but I cannot say whether they do so during the breeding season. This question remains to be examined.

The concept of pheromone.

An important principle of scent marking behavior is that scent marks serve several different functions. It is even possible that an animal may derive several different messages from the same scent mark. For example, a fox may learn from a single urine mark, first, that a certain female has recently passed by, second, that she is not in estrus, and third, that there is no edible food present at the spot. This possibility leads us to re-examine the traditional concept of pheromone.

KARLSON & LÜSCHER (1959) state that a pheromone is a specific chemical substance that releases a specific reaction in conspecifics, for exemple, a definite behavior or a developmental process. Thus, their concept of pheromone implies a one secretion-one response relationship. However, recent evidence for mammals suggests that this is frequently not the case.

SCHULTZE-WESTRUM (1965, 1968) has completed a thorough study of olfactory communication in the flying phalanger (*Petaurus breviceps*). In one series of experiments, he collected secretions on filter paper from a dominant animal's frontal, sternal, and anal glands. He then presented these filter papers one at a time to a series of conspecific animals. The results of the experiment clearly documented the wide range of reactions that these animals give to a single secretion from a single gland. None of the secretions released the same, consistent reaction in all the animals. Thus, a one secretion-one reaction relationship was never observed. SCHULTZE-WESTRUM, furthermore, showed that such factors as age, sex, rank, and colony membership of the animal were as important in determining what response was shown to an odor as was the odor itself.

GLEASON & REYNIERSE (1969) and WHITTEN & BRONSON (1970) also argue against a narrow definition of pheromone. BRONSON (1971) suggests that there is a pheromone in the urine of male house mice that appears to elicit several different responses. This pheromone attracts females to males, but it also elicits aggression between strange male mice. The pheromone may also play an important role in causing estrus synchrony among female mice (the WHITTEN effect), as well as blocking pregnancies in recently inseminated females (the BRUCE effect). Again this species demonstrates that such factors as age, sex, and the physiological conditions of the animals involved may be as important in determining what response is shown to a pheromone as the pheromone itself.

Solitary animals.

LEYHAUSEN (1965) stresses that we do not understand the social life of solitary animals. Solitary species are assumed to represent the primitive state of social organizations. Solitary species are also assumed to show few mechanisms for social interactions. LEYHAUSEN (1965), however, points out that this view may be due to an anthropomorphic bias: Man is a highly social species. Thus we find it more interesting to study highly social species rather than solitary species. LEYHAUSEN states that little effort has been made to understand the ecological strategies and social adaptations of solitary species.

The red fox definitely appears to be a solitary species. For example, an adult red fox is normally sighted alone over most of the year; and during this time it usually appears intolerant of conspecifics. Yet, this study shows that there may be a dimension of social behavior in its scavenging activities. Experiment II showed that a urine mark on a food remnant elicited a short investigation time not only from the fox that originally marked the spot but also from other foxes that investigated there. Thus, red foxes may use each other's urine marks to increase the efficiency of their scavenging behavior.

It is possible that future research will discover other mechanisms for social interaction in the red fox (BARASH, 1974; MONTGOMERY, 1974). Thus, as LEYHAUSEN (1965) indicates, the social life of solitary animals may be much more complex than we realize. Clearly, the social evolution and ecological advantages of solitary species deserve to be studied in greater detail. It may emerge that a solitary organization does not always represent a primitive state, but rather in many cases may represent a highly evolved strategy that is ingeniously adapted either to utilize dispersed food resources or to occupy certain niches where a highly social species could not be maintained.

SUMMARY

The eleven different functions for which mammals use urine marking are reviewed in this paper, and the urine marking behavior of the red fox (*Vulpes vulpes*) is described in detail.

A new hypothesis is advanced that urine marking may serve as a "book keeping system" in the red fox's scavenging behavior. Foxes consistently investigate and urine mark inedible food remnants (*e.g.*, bones, bird wings, and dried out pieces of hide). When a fox re-investigates a marked remnant, the urine mark signals "no food present," and the fox investigates this object for only a brief period of time. This use of urine marking may increase the efficiency of its scavenging behavior, *i.e.* more food-items found per hour of scavenging. This efficiency may be particularly important during periods of food shortage.

The hypothesis is tested in three different experiments, using free-ranging red foxes as subjects. Experiment I establishes that fox do urine mark food remnants. Experiment II shows that foxes investigate for a significantly shorter period of time ($P<0.001$) food remnants exhibiting both the odor of food and the odor of urine as compared to remnants exhibiting just the odor of food. Experiment III suggests that there a hierarchy of stimuli which determines different responses in the fox's scavenging behavior.

The experiments also suggest that there is a degree of social behavior in the scavenging activities of red foxes. Foxes appear to use each other's urine marks to increase the efficiency of their scavenging behavior. Thus this study definitely support LEYHAUSEN's (1965) statement that the social life of solitary animals is frequently more complex than we realize. Solitary species probably show many ingeniously adapted mechanisms for occupying niches where highly social species could not be maintained. The social evolution and ecological advantages of solitary species deserve to be the focus of future research.

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ZUSAMMENFASSUNG

Elf verschiedene Funktionen der Säugetierharnmarkierung sind in dieser Arbeit diskutiert. Das Harnmarkieren des Rotfuches, *Vulpes vulpes,* ist im einzelnen beschrieben.

Nach der hier entwickelten Hypothese bedeutet das Harnmarkieren für den Fuchs eine Art „Buchführung". Füchse markieren alle ungeniessbaren Futterreste wie etwa Knochen, Vogelflügel und ausgetrocknete Haut mit Harn. Wenn ein Fuchs auf ein so markiertes Überbleibsel stösst, signalisiert der Harn „nicht essbar". Der Fuchs hält sich dann nicht länger auf dieser Stelle auf. Die Harnmarke erhöht also die Erfolgsaussichten der Futtersuche. In anderen Worten: Der Fuchs findet mehr essbare Objekte je Suchstunde. Dies kann zu Mangelzeiten von grosser Bedeutung sein.

Diese Hypothese wurde in drei verschiedenen Versuchen mit freilebenden Füchsen überprüft. Der erste Versuch bestätigte, dass Rotfüchse Futterüberreste mit Harn markieren. Der zweite Versuch zeigte, dass Füchse Stellen untersuchen, die einen Geruch von Futter und Harn haben; jedoch halten sie sich dabei bedeutend kürzer auf als an Stellen, die nur nach Futter riechen. Das dritte Experiment beweist dass die

Reize „Futtergeruch" und „Harngeruch" je nach Intensität verschiedene Verhaltensweisen des Rotfuchses auslösen.

Ferner deuten die Experimente darauf hin, dass die beschriebenen Verhaltensweisen des Fuches auch soziale Bedeutung haben. Es scheint, als ob die Füchse gegenseitig auf ihre Harnmarkierungen achten und in dieser Weise sich gegenseitig die Futtersuche erleichtern. Die Arbeit bestätigt LEYHAUSEN's (1965) Annahme, das Sozialleben von solitären Tieren sei oftmals komplizierter als man früher meinte. Höchstwahrscheinlich besitzen solitäre Arten viele sinnreiche Anpassungsmechanismen für ökologische Nischen, die für soziallebende Arten ungeeignet wären. Weitere Studien über die Sozialevolution und die ökologischen Vorteile der solitären Arten sind sehr zu wünschen.