Scent-Marking in Wolves: Radio-tracking of wolf packs has provided definite evidence that olfactory sign is used for territory maintenance and may serve for other forms of communication within the pack as well

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Source: *American Scientist*, Vol. 63, No. 6 (November-December 1975), pp. 628-637
Published by: Sigma Xi, The Scientific Research Honor Society
Stable URL: https://www.jstor.org/stable/27845779
Accessed: 02-02-2019 19:32 UTC

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Scent-marking in mammals—the application of an animal's odor to its environment—has long intrigued researchers from various disciplines. However, because of a dearth of detailed knowledge about the behavior of free-ranging mammals, most research has been restricted to captive animals. Lack of adequate tracking and measurement techniques and the intrinsic difficulties in studying olfaction have also greatly hindered such investigations. Thus little is known about the ecological and sociological context and implications of scent-marking under natural conditions, and detailed descriptions of the frequency and distribution of scent marks in the wild are available for only a few species.

Mykytowycz (1974), working with captive and free-ranging European rabbits (*Oryctolagus cuniculus*), and Thiessen (1973), whose subjects were captive Mongolian gerbils (*Meriones unguiculatus*), have gained remarkable insight into the scent-marking systems of these two species. Through histological, neurological, endocrinological, and biochemical studies, they have learned that (1) the development and use of scent glands are related to sexual maturity and the presence of gonadal hormones, (2) dominant males tend to scent-mark most frequently, and (3) scent-marking is related to possession of territory. Other researchers have postulated that some of these findings were true for other species under natural conditions, and there seems to be general intuitive agreement on these three points (Ralls 1971; Ewer 1973). However, few actual data from field studies have been available to confirm or elaborate these concepts.

In canids, scent-marking is a well-known phenomenon, commonly observed in domestic dogs, and there has been much speculation about its functions. Investigators—from Schenkel (1947) through Mech (1970)—who have studied the social behavior of wolves (*Canis lupus*) and its ecological context have assumed that scent-marking is associated with territory maintenance. Mowat (1963), in a widely read fictionalized account of his interactions with wolves, popularized the notion that wolves produce a line of scent marks around their territory which neighboring packs do not dare cross.

Despite the history of speculations, assumptions, and conjecture linking scent-marking in wolves to territory maintenance, it has only recently been possible to gather hard data on the subject. This possibility arose as a result of intensive radio-tracking studies of wolves (Fig. 1) in the Superior National Forest of northeastern Minnesota (Mech and Frenzel 1971; Mech 1972, 1973, 1974). From 1968 through 1973, 96 wolves were radio-tagged, and the interactions of 13 contiguous packs were studied. Radio-tagged wolf packs provide three critical advantages for gathering data on scent-marking: (1) each pack can be identified, (2) each pack can be located at any time so that it can be tracked in the snow, and (3) a history can be developed for each pack, including number of members, sex and age of at least some members, and size and location of the pack's territory.

Wolf packs in the Superior National Forest are basically territorial, and most stable territories range in size from 125 to 310 km^2. Territories seem to be stable and exclusive from year to year under normal conditions, but over several months they may overlap about 2 kilometers along the borders. Interpack contact, however, is rare or nonexistent along the overlap.

Figure 1. Radio-tagging of wolves has made it possible to track them and study pack behavior. Here a radioed pack has killed a deer, and its members clean up the remains while scavenging ravens appear hopeful for the wolves' early departure. (Photo by L. David Mech.)

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The authors wish to acknowledge the help of Steve Kaplan, George B. Rabb, William W. Cochran, Jeff Renneberg, Fred Harrington, and Robert Himes. The following agencies and organizations provided financial and logistical support: The Danforth Foundation, U.S. Fish and Wildlife Service, U.S.D.A. North Central Forest Experiment Station, Ober Charitable Foundation, World Wildlife Fund, and Superior National Forest. *Address for Dr. Peters: Psychology Department, Fort Lewis College, Durango, CO 81301; Dr. Mech: North Central Forest Experiment Station, Folwell Ave., St. Paul, MN 55108.*

The basic members of each pack are a dominant male and female—the "alpha pair." Generally the alpha male is the pack leader, and he takes the initiative in leading attacks on prey and intruders and directs the movements and activities of the pack (Mech 1970). The remaining pack members usually are the offspring of the alpha pair, from several litters. If an alpha animal perishes, one of the mature offspring probably takes its place.

Within the pack a definite social hierarchy develops below the alpha pair. The youngest litter of pups are subordinate to the other pack members, and among littermates some are dominant to others. Thus a pack can be viewed as a group of related, interacting individuals with various social ranks that keep them compatible. However, as younger members mature, they may not accept their position. If they are low ranking, they may not tolerate being subordinate to the other members. Or, if they are high ranking, they may not accept domination by the alpha animals. In either case, the resulting disruption of the social order may lead to the dispersal of the individual from the pack.

Whatever the behavioral reason underlying the process, some, but not all, young wolves are forced to leave the pack and become loners (Fig. 2). They may wander far from the pack territory and become nomadic in an area as much as twenty times the size of a territory (Mech and Frenzel 1971). If during their wanderings they cannot avoid resident packs, they may be chased and attacked (Mech 1970). If the lone wolves can find a suitable vacant area and a member of the opposite sex, they may mate and start their own pack. They probably determine that a territory is vacant and find a mate by reading scent marks as they travel.

The scent-marking study

Scent-marking was studied during the winters of 1971–72, 1972–73, and 1973–74 to help determine the role it plays in the information flow that is integral to maintaining the organization of the wolf population. The basic method was to track identified wolf packs in the snow and record the spatial and temporal frequency and distribution of the scent marks. Tracks were located by aerial or ground radio-tracking of the wolves. Observations of captive wolves supplemented the three winters of field studies.

During 1972–73 and 1973–74, we concentrated on two adjacent packs near our field headquarters, because we could correlate aerial observations of behavior with ground investigations of their sign. After watching the wolves from the air, we could follow their tracks on the ground to the area where we had observed them, which provided a check on both the aerial observations and the interpretations of sign.

Data were recorded on a detailed sketch keyed to a topographic map. A "sample" of data was defined as a set of tracks examined along the entire length of a given stretch, and 110 samples, totaling 240 km of ground tracking, were analyzed.

Wolves scent-mark in several ways that make the odors they apply to the environment especially apparent (Kleiman 1966). We considered four kinds of scent-marking: (1) raised-leg urination (RLU), (2) squat urination (SQU), (3) defecation (scats), and (4) scratching. During all snow tracking, we recorded the frequency and distribution of these four types of sign. Because raised-leg urination involves the frequent delivery of small amounts of urine, it can be considered primarily a scent-marking behavior rather than elimination. In contrast, defecation and squat urination may be for both elimination and scent-marking. Thus, although we recorded all eliminations, we regarded RLUs as providing the most unambiguous information about scent-marking.

Our observations at both the Brookfield Zoo and the St. Paul (Como) Zoo indicate that only mature, dominant wolves, primarily the alpha male or female, urinate with raised leg (cf. Woolpy 1968). For example, 22 of 27 RLUs observed in the Brookfield pack, which contained several mature wolves, were performed by the alpha animals, 20 of them by the alpha male. Furthermore, over 60 percent of the RLUs were associated with self-assertion, snarling, growling, or biting, whereas this was not true of SQUs (Table 1). Twice in the field, we established by radio-location that the tracks we followed were those of pups. We found several SQUs, but no RLUs, in over 6 km of tracks, which supported the captivity observations that pups do not usually produce RLUs.

We could not measure the exact amount of urine excreted in an RLU, but we could simulate the mark by squirting snow with 5 cc of colored water. We recorded 584 RLUs in the 240 km of ground tracking, an average of one RLU per 450 m, with a range from none in 7 km to 20 in 1 km. All but 4 RLUs were directed at particular objects, such as blocks of snow, trees, shrubs, rocks, snowbanks—and even a plastic bag. The objects marked were always conspicuous, either because they protruded from the snow near the wolves' route or because they lay on or across the route. Once marked, of course, they also bore an olfactory stimulus.

Table 1. Relative frequencies of various behaviors associated with different types of scent-marking in captive wolves

Type of scent-marking	*Type of behavior*				
	Assertive[1]	*Agonistic*[2]	*Sexual*[3]	*Disturbed*[4]	*Friendly*[5]
RLU	8	2	5	1	0
Scratching	9	4	7	1	0
SQU	4	3	5	1	11
Defecation	2	4	1	2	0

1. Staring, standing over
2. Snarling, growling, biting
3. Mounting, vulvar blood
4. Barking, whining
5. Making a "playface," or "happy," "friendly" demeanor

Figure 2. Lone wolves disperse from packs, for unknown reasons, and circulate about the population until they find a mate and available space in which to begin a pack of their own. (Photo by L. David Mech.)

In more than 70 instances we noted that wolves traveling on roads had left a nose-shaped indentation in the snow, suggesting that they had sniffed snowbanks at the height of a typical RLU. Under about 30 percent of the indentations we verified that an RLU was present by blowing away a layer of snow to reveal traces of urine, but in the rest of the cases we could not be sure. Many of the indentations were associated with a fresh RLU mark.

The characteristics of an RLU mark imply that its major function is the production of a prominent, long-lasting olfactory and visual signal. Depositing urine well above ground, on a snowbank or tree, for example, facilitates dispersal of odor by wind, increases the evaporating surface as the urine trickles downward, and minimizes chances that the mark may be covered by snow or washed away by rain. In winter, when an RLU contrasts clearly against the snow, it is visible several meters away. Placing only a small quantity of urine on many different objects increases the total effectiveness of the amount.

A pattern of signs frequently observed in the field during the breeding season was a combination of an SQU and an RLU. One observation from the air and six in captivity suggest that this pattern results from an SQU by a female, investigated by a male, which then performs the RLU.

Like RLU and scratching, defecation is often associated with certain kinds of behavior under conditions that suggest it has significance beyond elimination. The ability of wolves to deposit scats on prominent objects and in particular places indicates a degree of autonomic and central control. Furthermore, defecation by wild and captive wolves often occurs in emotional contexts. It is often difficult to classify scats as marks or eliminations, because neither the defecation posture nor the product has a characteristic marking form, as is the case with the RLU. Scats can be classified as marks when they are deposited on prominent objects (e.g. snowbanks, stumps, shrubs, and empty beer cans), when they are found in large concentrations accumulated over several months, and when they are marked with scratching or urine by the same wolf that deposited the scat.

Scats in the immediate vicinity of kills, in the absence of RLUs and scratching, are probably primarily eliminative, but of course they have prominent visual and olfactory properties as well. Scats found where wolves crossed a road, or at trail junctions, may have been deposited as marks, but it is difficult to be sure since elimination is always a factor in all scats.

The distribution of scats around "rendezvous sites" also suggests

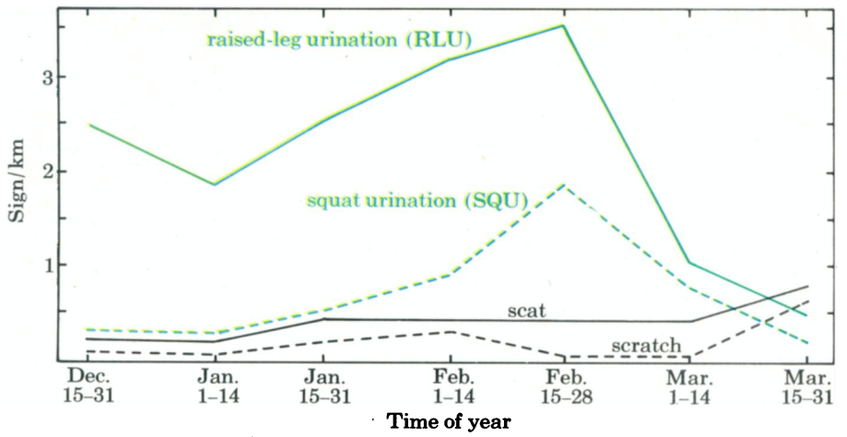

Figure 3. The mean frequency of four types of scent marks as a function of the time of year reveals a significant increase in the number of RLUs and SQUs during the breeding season in late February.

Table 2. Summary of tracking data from three wolf packs (sign within 20 m of kills excluded)

	Harris Lake pack	*Jack-pine pack*	*Perch Lake pack*
Average size of pack	3	5	2
Number of samples	42	14	5
Distance tracked (km)	114	30	15
Total number of signs	380	241	76
Sign/km	3.3	8.0	4.9
RLUs/km	2.3	5.0	3.8
SQUs/km	0.3	0.8	0.6
Scats/km	0.5	1.3	0.4
Scratches/km	0.2	1.0	0.2

Table 3. Average frequency of wolf sign (in number per kilometer) in various environments (signs within 20 m of kills excluded)

	Type of sign			
Environment	*RLU*	*SQU*	*Scat*	*Scratch*
Roads and trails	3.4	0.3	0.5	0.3
Bush	1.7	0.7	0.6	0.2
Frozen waterways	0.4	0.6	1.0	0.2

Table 4. Comparison of rate of RLU marking within a pack's territory

Area	*No. samples*	*Kilometers*	*No. RLUs*	*Mean RLUs/km*
Edge of territory	43	102.7	276	2.67
Center of territory	32	78.3	100	1.27

that scats are sometimes left as marks. Rendezvous sites are places where growing pups are left while adults hunt during July, August, and September. Large scats are sometimes deposited at strategic points around the site, on trails leading into the central area, and especially at nearby junctions. Such deposits evidently are left by adults, and they often contain as many as six separate scats, indicating repeated or multiple visits to a location.

Wolf scats, whether deposited as marks or not, are powerful sources of odor, sometimes detectable by humans up to 10 m away, even when the air is still and the temperature below −20°C. They may also bear the odor of secretions from the anal sacs, which empty on both sides of the anal opening and which may give the scats an individual identity. Therefore it is not surprising that wolves are at least as interested in scats as in urine and scratching. We noticed that wolves walking along roads frequently veered to sniff at scats, many of which lay beneath several centimeters of snow.

Scratching, which may release odors from the glands in the paws, may, like RLU marks, be both an olfactory and a visual signal as well. It is often preceded by RLU or by orientation to an olfactory stimulus, and like RLU, it varies in intensity. When scratching at high intensity, a wolf paws the ground with alternate motions of the stiffened right and left forelegs, each combined with a similar movement of the rear leg on the opposite side. Although scratching is usually associated with elimination, a wolf generally takes several steps away from the urine or scat before scratching, and the material thrown behind is almost never directed toward the excreta. Furthermore, only high-ranking wolves scratch, another indication that this activity is primarily autonomic rather than eliminative.

Distribution of olfactory sign

Our descriptions of the spatial and temporal distributions and contingencies of various forms of wolf sign are based on 240 km of ground tracking and 40 km of aerial tracking, primarily of three wolf packs (Table 2). In the ground tracking, in snow fresh enough to ensure observation of all sign, we recorded 1,006 possible marks: 584 RLUs, 193 scats, 170 SQUs, and 59 scratches. RLUs, by far the most widely distributed strong-smelling and long-lasting form of wolf sign found, can be considered the most important form of indirect olfactory communication.

Wolves make all types of marks and eliminations throughout the year, but the relative frequencies of marking during various seasons has been unknown. Because of the lack of lasting snow in our study area during the warmer months, we could obtain data by snow tracking only from December through March. Nevertheless, during this period, which includes the breeding season in late February (Mech 1970), we discovered some interesting differences (Fig. 3). The average rate of RLUs increased throughout winter from about 2.5/km in December and January to a peak of 3.5/km in late February, and then dropped to about 1/km in March. Although we do not know the rate for spring and summer, sometime before December there is a strong increase in the RLU rate. The SQU rate does not increase until late January. Like the RLU rate, it peaks in late February and drops to its base level in late March, which strongly suggests that both SQUs and RLUs are related to breeding. In contrast, the rates of defecation and scratching remained constant from December through March. All figures agree with those

we have obtained from observing wolves in captivity.

The distribution of tracks reflects the major occupation of the wolf—travel in search of prey. The main features of wolf movements are an extensive, complex network of regularly used travel routes, including frozen waterways, roads, and trails, and concentrations of prey often more than 10 km apart. The distributions of wolf sign in different types of environment and in the centers and edges of territories are important in trying to interpret the significance of these signs.

A high proportion of all four kinds of sign left along roads and trails was found at junctions, as also noted by Seton (1909) and Mech and Frenzel (1971). Both tracks and aerial observations show that wolves rarely loiter at junctions any longer than the few seconds necessary to sniff a bush or two or to leave an RLU or other sign. Yet, on roads and trails, about 40 percent of the RLUs and scratches and 50 percent of the SQUs and scats were found at junctions.

The type of travel route also influenced the proportion of different kinds of wolf sign found. The average frequency of the various signs was recorded (1) for regular travel routes such as roads and trails, (2) for cross-country or "bush" tracks, and (3) for those on frozen lakes and waterways (Table 3). We divided 104 samples of tracks into 140 segments, each composed of a continuous set of tracks in one of the three environments. Comparison of the RLU rate for 73 segments on roads and trails (3.4 RLU/km) with the rate for 55 segments in bush (1.7 RLU/km) revealed a significantly greater tendency toward RLUs on roads and trails than in bush ($t = 2.3$, $df = 126$, $p < 0.02$). Although speed varied in the two environments, the gait for almost all samples was "walking."

Of 28 segments of tracks that went through both environments, the number of RLUs/km was greater on the road and trail parts than in the bush parts in 18 of them, and in only 8 cases was the reverse true; in 2 cases they were equal. A sign test on the 26 samples showed that the wolves increased their rate of RLU when traveling along an established route and decreased it when cutting cross-country through the bush ($z = 1.98$, $N = 26$, $p < 0.05$).

The mean number of RLUs/km is much lower on frozen waterways (0.4/km) than in the other two environments. This low rate is easy to understand: almost all waterways on which tracks were followed were iced-over lakes, where there are few vertical objects to serve as targets. In fact, all 7 RLUs recorded were on rocks or weeds protruding above the ice, or on the shoreline.

This effect of target availability makes the difference between rates of RLU on regular travel routes versus bush routes even more striking, for targets are far more available in bush than on roads. (The rate of RLU was high even on unplowed roads, where there was no bank to invite marking.) Clearly, availability of targets does not explain the greater rate of marking along roads and trails.

Probably the most important areal difference found was that between the rate of scent-marking in the centers of wolf territories and at the edges. Each tracking sample was classified as to whether it lay in a narrow strip about a kilometer wide along the edge of a territory or whether it fell in the center. A few samples which had segments in both were deleted from the analysis. The samples along the edges averaged 2.67 RLUs/km, whereas the samples in the centers averaged 1.27 (Table 4). The average length of track sample (2.4 km) was the same for both edges and centers, but there were 6.5 RLUs per sample at the edges and 3.1 in the centers, a highly significant difference ($z = 6.3$; $N = 376$; $p \ll 0.001$).

The number of wolves making the tracks we followed was, predictably, a major determinant of the rates of sign production, although it did not correlate similarly for each of the four kinds of sign (Fig. 4). There

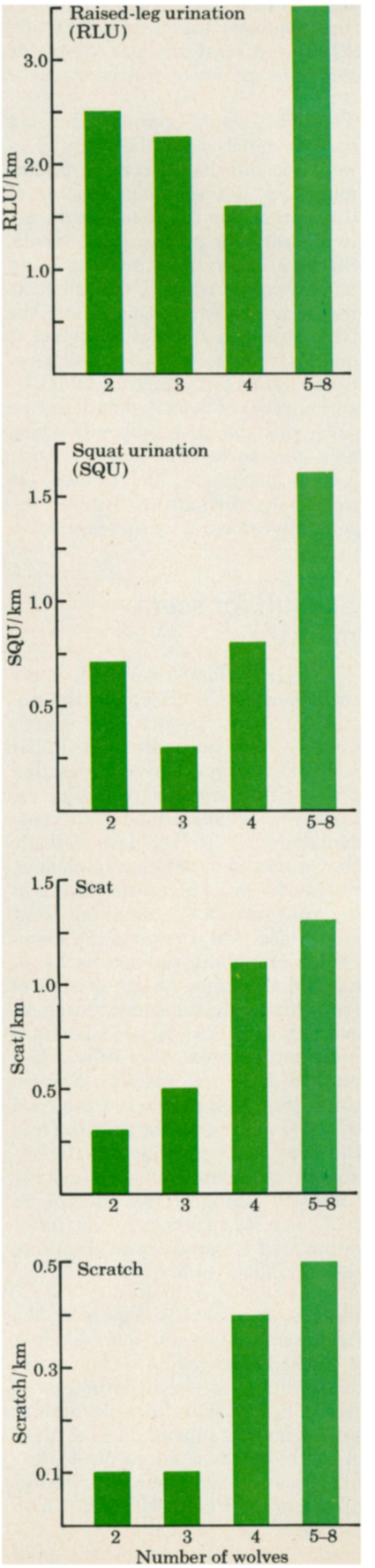

Figure 4. When the frequency of four types of scent marks was plotted against the number of wolves in the pack, a high correlation was apparent between number of marks and number of wolves for all types of sign except RLUs, which are made primarily by the alpha male in each pack.

was a linear relationship between the average numbers of scats, SQUs, and scratches per kilometer and the number of wolves tracked.

The RLU rate, however, did not vary as much with the number of wolves as did the other rates. Spearman's r's, a measure of degree of correlation, for the relationship between rates of production of scats, SQUs, and scratches and the number of wolves are 1.0, 0.8, and 1.0, respectively, while the r for the RLU rate and number of wolves is only 0.2. The lack of correlation between rate of production of RLUs and number of wolves should not be surprising: because only one alpha pair dominates each pack, regardless of pack size, the number of wolves that urinate with raised leg generally does not increase with pack size.

Stimuli for scent-marking

The conventional view of canid scent-marking is based on the notion of von Uexküll and Sarris (1931, cited in Scott and Fuller 1965) that stimuli from unfamiliar conspecifics are the primary "releasers" for scent-marking, especially for RLUs. Our data indicate that although scent marks of alien wolves do evoke high rates of marking, they are not the usual releasers. On at least ten occasions the members of one of our radioed packs remarked the same 2.4-km stretch of road, including the same junctions, even though our daily inspections indicated that no other wolves had marked it in the interim. Several times this pack re-marked the road while the odor of the RLUs from the previous visit was still detectable by a human. Evidently neither complete fading of the odor of an RLU nor its masking by an unfamiliar wolf is necessary to stimulate re-marking.

In fact, as shown in Figure 5, the fresher an RLU is, the more likely it is to elicit further RLUs. The major determinant of the distribution of RLUs is not sign from unfamiliar wolves but the repeated use of travel routes by the resident pack. Regular use of scent-marked routes produces positive feedback, which increases the probability of remarking, with the result that sign of

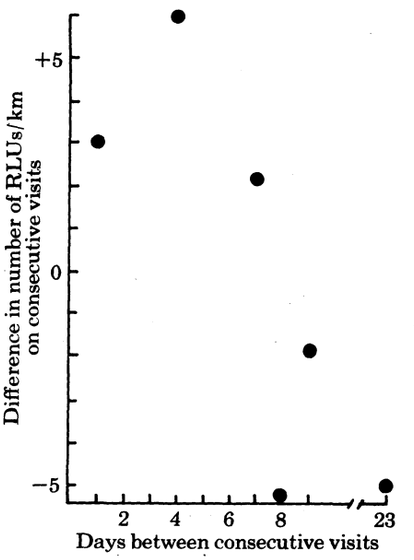

Figure 5. The difference between the number of RLUs deposited on a certain stretch of road by a wolf pack on one visit and the next, in the absence of visits by other wolves, is plotted against the intervening time. A positive difference indicates a higher frequency of RLUs on the subsequent visit, and a negative difference, a lower frequency. The pronounced, significant negative correlation (Pearson's $r = -0.76$, $t = 2.5$, $df = 4$, $p < 0.05$) between these differences and the number of days between visits indicates that fresh marks stimulate more re-marking by the same pack than old ones.

the resident pack is especially dense in areas visited frequently.

The data in Figure 5 also allow us to estimate the length of time during which an RLU stimulates more RLUs under winter conditions. Assuming that the y-intercept of the regression line corresponds to equal tendencies to mark on initial and subsequent visits, the base rate is reached after the marks are approximately a week old. The rate of response continues to decline as scent marks age, but we have recorded marking in response to familiar sign as much as 23 days old, although the rate was low, indicating that the stimulus value of familiar scent marks probably drops to zero sometime soon after 23 days of age. Of course weather conditions could cause considerable variation in these figures.

Responses to neighboring packs

Our findings indicate that each pack's territory is well marked throughout with its own scent and that the marks are renewed through positive feedback. But what is the response of a resident pack to the marks of a neighboring pack? Data on this subject are difficult to gather because human beings cannot identify by odor the marks of different packs; however, we have no doubt that wolves can detect such differences. In four instances we were able to track a pack of wolves when it encountered fresh sign of a neighboring pack. Twice we found that there was an abrupt and immediate increase in the rate of scent-marking by the pack when it encountered the alien sign—from no scent marks in over 2 km to approximately 10 scent marks, including at least 6 RLUs, in the first kilometer after the encounter. In the other two instances, the rate of scent-marking was the highest we have recorded, but it was impossible to determine a base rate of marking just before the encounter.

The result of such high rates of marking in response to sign of neighboring packs is that a concentration of marks accumulates along the borders of each territory. Some of the marks are those of one pack, and some those of its neighbors, while many marks are made by both groups alternately superimposing their own scent. In effect, each territory is an olfactory "bowl" with the edges composed of high rates of the resident pack's marking interspersed with high rates of the neighbor's marks.

Functions of scent-marking

The picture that emerges from the description of scent-marking in free-ranging wolves is that each pack of wolves travels about its 125 to 310-km^2 territory irregularly but reaches most parts of it at least every 3 weeks and probably sooner. The wolves travel mostly on game paths, old logging trails, dirt roads, and other established routes with which each territory is interlaced and, at least in winter, encounter (and leave) a sign every 240 m on the average, including an RLU each 450 m (Fig. 6).

At their usual rate of travel—8 km per hour (Mech 1970)—wolves would encounter and produce an olfactory sign about every 2 minutes, including an RLU every 3 minutes.

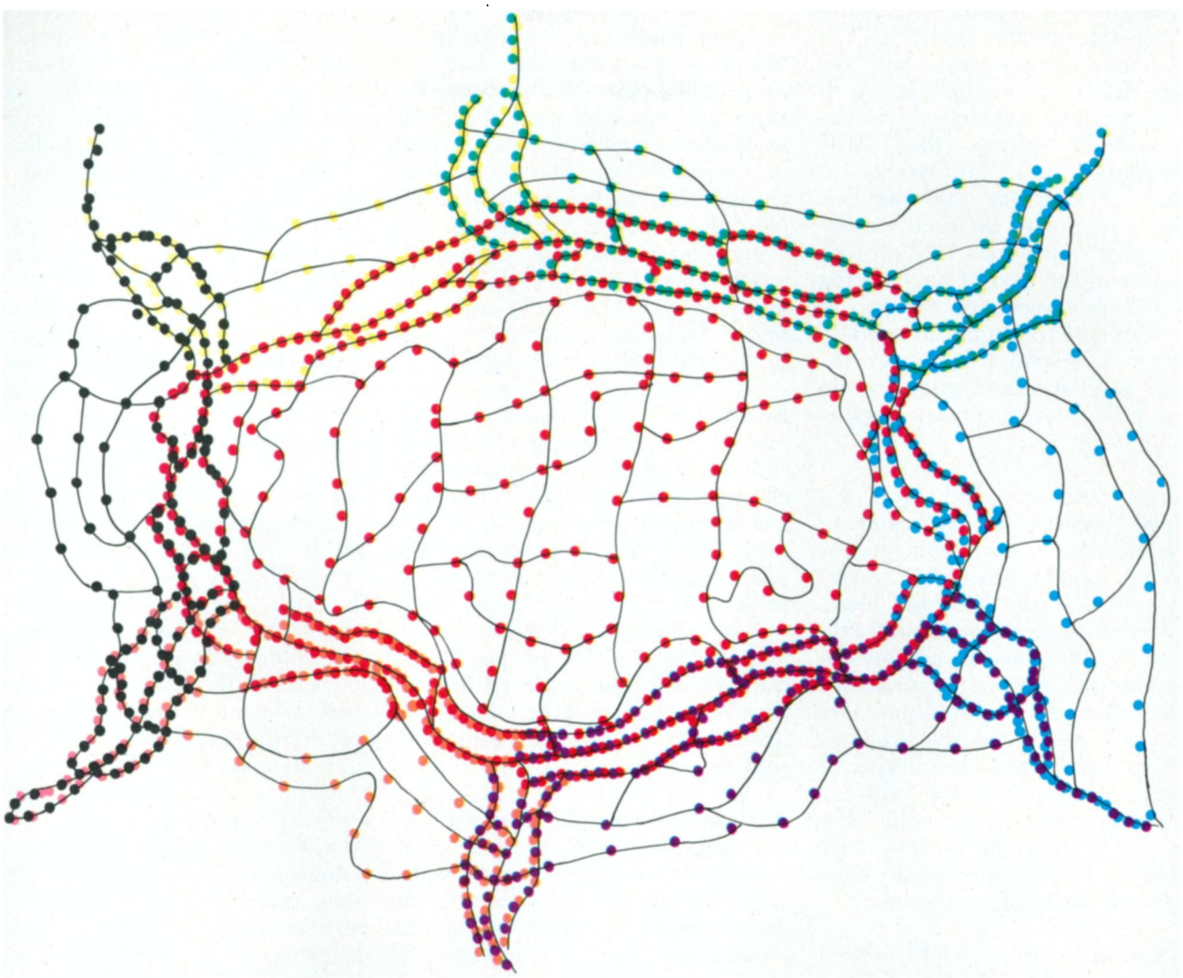

Figure 6. In this model of the distribution of RLU scent-marks, RLUs are indicated throughout the territory of one wolf pack (*red*) and for the areas where six neighboring packs border this territory. Travel routes are simulated, but mean density and territory size are to scale, on a range approximately 20 km wide. Note the bowl-shaped effect caused by heavier scent-marking by both the resident pack and its neighbors at the edges of the territory.

Even if they strike out cross-country to pursue prey or to take a short-cut, they leave sign frequently, although the RLU rate is depressed. This means that the entire territory is studded with olfactory "hotspots," and wherever a wolf is, it can tell whether or not it is in its own territory. The concentration of scent marks around junctions further ensures that any traveling wolf will detect a mark in a minimum of time no matter what route it uses. Each pack can also quickly detect when it reaches another pack's territory, and the nomadic lone wolves know just where they are in relation to the various packs' territories—on the border of two packs, in the center of a territory, etc.

Because wolves seem to respond differently to scent marks of different ages, it appears that they can detect the time elapsed since they were last in any particular area. And perhaps the accumulation of a certain density of marks triggers travel to another part of the territory. At the border of the territory they probably also can tell approximately when their neighbors have passed through.

No doubt squat urination and defecation also carry such information. However, since they are basically eliminative in function and show few significant seasonal or spatial differences in distribution, and since all pack members, including pups, perform them, their scent-marking significance may apply primarily within the pack.

We have often seen pups and other pack members temporarily separated from the main pack. During summer, subordinates may spend days away from the den when the alpha pair attends the pups. Various pack members often hunt separately, especially during this period. By reading the urinations and defecations of their associates, they may be able to determine whether an area has been hunted recently, if an associate is nearby, or who is traveling with whom. This would ensure that efficient use is made of all parts of a pack's territory. Scratching, although usually done by alpha animals, particularly the male (as determined by our observations of animals in captivity), shows no seasonal or distributional variation, so its primary function might also be intrapack, perhaps as assertion of the alpha animal's continuing status.

It is raised-leg urination that is

probably most effective in maintaining the pack's territory. The well-established relationship between RLUs and dominance, breeding, and territorial defense is circumstantial evidence that RLU scent-marking is intimately involved in territory maintenance. What is necessary for proof is evidence that one pack's RLUs cause aversion on the part of neighboring packs. Direct evidence for this is most difficult to obtain under field conditions, Mowat (1963) notwithstanding. What observations we do have, however, are highly suggestive.

In one instance we found tracks of a pack of seven to nine wolves along the northwest edge of their territory. Their tracks proceeded southwest onto a frozen lake and along the northwest shore for about 2 km. The wolves remained several meters from land but made 13 approaches to the northwest shore of the lake; each time they turned back before reaching land. The only type of aversive agent perceivable this far out on the lake which could have been distributed for such a long stretch along the shore would have been scent marks of another pack.

In a second instance, eight wolves approached the east edge of their territory and crossed the tracks made by a neighboring pack of five wolves two weeks earlier. They scent-marked at the junction of the trails, some members followed the tracks for a short distance, and others continued eastward. Much scent-marking ensued, and after going about one kilometer, the pack turned around and headed back into its own territory. If the aversive agent was not the odor of the neighboring pack, the most likely alternative explanation other than coincidence would be the lack of visual or olfactory familiarity with the area. This does not seem plausible, however, because each winter when the large lakes (some several kilometers across) in the study area freeze, the wolves venture far out onto the ice, even though this must also be unfamiliar ground.

A third observation involved a river boundary between two packs. Soon after the river froze we found tracks of seven members of the pack north of the river crossing to the south shore and then returning. The next day, the south pack approached to within 50 m of the river; one wolf approached the south shore five times and made RLUs and scratches at the northern extreme of each excursion. Where the south pack encountered the tracks of the north pack there was a network of wolf trails, covering 300 × 600 m, in which there were 30 RLUs, 10 scratches, 2 SQUs, and 1 scat. The south pack went no further, but turned and headed back south.

In another, rather telling instance involving these two packs, tracks showed that the north pack had chased a deer across the frozen river and wounded it severely. When the deer proceeded farther into the south pack's territory, the north pack did not persist after it as wolves usually do. Instead, the members scent-marked heavily in the area and then returned to their territory. A day later, the south pack located the deer and consumed it.

Obviously more such observations are necessary, and attempts must be made to watch the animals actually responding to the marks of their neighbors. Nevertheless, the present evidence is sufficient to allow us to formulate a hypothesis concerning the manner in which scent-marking (especially RLU), as the main information medium, helps hold together the spatial organization of the wolf population.

We do not regard scent-marking as an isolated system functioning independently of other behavioral traits and mental processes. Wolves appear to have well-organized memories for routes, points, junctions, and their juxtaposition (Peters, diss. 1973). These "cognitive maps" with which they travel their territories probably also help them recognize territorial edges. In the four instances of avoidance just mentioned, cognitive maps, as well as unfamiliar sign, were probably involved. It is difficult to separate the effects of sign and terrain, since scent marks are found along all the major routes and at all important points in the territory.

Aversion to unfamiliar territory therefore may be involved in aversion to unfamiliar marks, and responses to foreign scent marks may depend on whether the wolves that encounter them are in their own area. Aversion to foreign odors probably is not innate; captive wolves we have observed did not avoid the odors of unfamiliar conspecifics. Nor is the response to foreign scent marks stereotyped, as the four examples cited above demonstrate. The aversion to unfamiliar sign and territory may be acquired through rare agonistic encounters between packs or may be learned by exposure to emotional responses of adults who have been involved in such encounters.

At present the wolf population has reached the saturation point in our study area, with no land left unoccupied by the wolves (Mech 1973). In such a situation, we postulate that frequent scent-marking and aversion to strange marks hold each pack in its territory and that a system of positive-feedback stimulus ordinarily keeps each territory adequately marked.

Several questions can be asked. What would happen if, because of unusual environmental conditions such as the reduction of prey in part of the territory, a pack neglected marking all of its territory every three or four weeks? Or what would happen if a pack were exterminated? Presumably, the scent marks would eventually lose their stimulus value. Would this mean that the returning pack, or some other pack, would never again scent-mark the territory because of the lack of scent-mark stimuli? How are new territories set up?

There must be some sort of "setting" or "resetting" of the feedback system. Presumably, where there are no scent marks or when the stimulus value of scent marks reaches zero, merely the absence of marks must be a stimulus for wolves in the appropriate physiological and behavioral condition to mark. These wolves could be resident pack members returning belatedly to an unused part of their territory or perhaps a neighboring pack extending its own territory. They may also be a newly formed pair of loners that had perceived the olfactory (territorial) vacuum.

Loners could easily locate each

other by their scent marks. Since the SQUs of an alpha female are probably usually accompanied by the RLUs of the alpha male during the breeding season, each lone animal would be able to determine that the other was unmated. Just as within an established pack, the newly formed pair could then carry on a courtship, in which frequent scent-marking probably plays an internal role, could mate, bear young, and begin their own pack. Such a system would tend to ensure that all available habitat is occupied and that, if any territory were too large to be patrolled frequently enough, "surplus" animals would detect and colonize it. The ultimate result would be full use of available space and resources by a population that would in turn be regulated by the size of the colonizable area.

There are many gaps yet to be filled in our knowledge of the wolf scent-marking system. However, this basic description and hypothesis provides a good first approximation of the underworkings of a complex social organization, much like those proposed for other species (Thiessen 1973; Mykytowycz 1974), and also an excellent framework within which to pursue other detailed studies.

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"Just between you and me, where does it get enriched?"