

**The Humane Society Institute for Science and Policy**  
**Animal Studies Repository**

5-1981

# An Observational Study of Coyote (*Canis latrans*) Scent-marking and Territoriality in Yellowstone National Park

Joseph J. Allen

Marc Bekoff  
marc.bekoff@gmail.com

Robert L. Crabtree

Follow this and additional works at: [http://animalstudiesrepository.org/acwp\\_ena](http://animalstudiesrepository.org/acwp_ena)

 Part of the [Animal Studies Commons](#), [Behavior and Ethology Commons](#), and the [Comparative Psychology Commons](#)

---

## Recommended Citation

Allen, J. J., Bekoff, M., & Crabtree, R. L. (1999). An Observational Study of Coyote (*Canis latrans*) Scent-marking and Territoriality in Yellowstone National Park. *Ethology*, 105(4), 289-302.

This Article is brought to you for free and open access by the Humane Society Institute for Science and Policy. It has been accepted for inclusion by an authorized administrator of the Animal Studies Repository. For more information, please contact [eyahner@humanesociety.org](mailto:eyahner@humanesociety.org).

# An Observational Study of Coyote (*Canis latrans*) Scent-marking and Territoriality in Yellowstone National Park

Joseph J. Allen, Marc Bekoff, and Robert L. Crabtree

## ABSTRACT

*Free-ranging coyotes (Canis latrans) living in neighboring packs were observed in the Lamar Valley of Yellowstone National Park, Wyoming, from Jan. to May 1997. Through direct observation, we recorded the location of coyote scent marks and information regarding the identity of the marking animal. Patterns of scent-marking were then analyzed spatially and demographically. All of the evidence from the present study supports a strong relationship between scent-marking and territoriality in these coyotes, and all predictions were met. A preponderance of scent marks was found in the periphery of territories. Most of those marks were raised-leg urinations (RLUs) and forward-lean urinations (FLUs), postures associated very strongly with males, particularly dominant individuals. Ground-scratching was also closely associated with these types of marks and was performed more on the periphery of territories than in the interior. A complete lack of overlap of adjacent territories and very limited overlap of movements into territories fits classic definitions of territory and home range. Scent-marking seems to be strongly associated with the establishment and maintenance of these boundaries between packs of coyotes competing for the same resources in a limited space.*

## **Introduction**

While there has been a good deal of interest in elimination patterns and scent-marking in canids (e.g. Kleiman 1966; Peters & Mech 1975; Henry 1977; Rothman & Mech 1979; Barrette & Messier 1980, Bekoff & Wells 1980, 1986; Bowen & Cowan 1980; Harrington 1981, 1982; Wells & Bekoff 1981; Paquet 1991; Gese & Ruff 1997), there have been few studies in which the majority of data come primarily from direct observations of individual animals (Wells & Bekoff 1981; Gese & Ruff 1997). Kleiman (1966) distinguished scent-marking behavior from mere elimination by: 1. its directional quality; 2. the deposition of scent on objects that are novel or familiar (having been previously marked); and 3. patterns of scent deposition being repeated frequently in response to the same stimulus. Mykytowycz (1968) was one of the first to propose evidence for scent-marking as a mechanism of territoriality in wild mammals. Gender, age, and individual differences in scent marks also indicate that scent-marking is related to behaviors other than territoriality (Müller-Schwarze 1971; Ralls 1971; Johnson 1973; Jones & Nowell 1973; Gorman 1976; Harrington 1976; Stoddart 1976; Barrette 1977) Other possible functions of scent marks include their role in laying trails, signaling alarm, signaling dominance, identifying individuals, recognizing group

or species members, attracting sexual partners, and producing 'priming' pheromones influencing reproductive processes.

Several detailed studies of the mechanisms and functions of marking and its importance to the social behavior of mammals are available (Gorman & Trowbridge 1989; Gosling & McKay 1990; Swihart et al. 1991; Johnston et al. 1994; Johnston & Jernigan 1994; Gosling et al. 1996). The major proposed functions are those regarding identification, reproduction, territoriality, and social status. These possible functions overlap and a single scent mark could accomplish more than one of these tasks. In wolves (*Canis lupus*), Peters & Mech (1975) observed a pattern of scent-marking that seemed to correspond with predictions of wolves marking their territorial borders with urine; that is, more marks were found around the periphery of the territory than in the center. Also, lone wolves marked less frequently and less conspicuously than paired wolves with territories, and newly established pairs marked most frequently, suggesting that the new pair was trying to establish its territorial boundaries (Rothman & Mech 1979).

Field studies of coyotes (*C. latrans*) have also demonstrated that while all animals in a group may leave marks, dominant individuals (especially dominant males) scent-mark more frequently and with more stereotypically dominant postures. Similar differences were seen between established, territory-holding coyotes and solitary individuals (Bowen & Cowan 1980; Barrette & Messier 1980). These data were gathered by snow-tracking coyotes and by chance observations over one or two winters. Wells & Bekoff (1981) conducted a primarily observational study of coyote scent-marking behavior for two full years. Their results were similar to earlier studies, but they found that snow-tracking resulted in underestimation of scent-marking activity when compared with data gathered by direct observation. They also showed an association between areas of high rates of urine-marking and areas of high rates of intrusion by neighboring coyotes. Recently, Gese & Ruff (1997) found a higher rate of marking by coyotes in the periphery of a territory than in its interior (based on 574 marks for one pack). They also found that resident animals and dominant individuals, in particular, marked more frequently than other coyotes. Gese & Ruff (1997) did not examine adjacent packs, so no direct comparisons can be made with some of the results reported here.

The present study focused on the role of scent-marking in territorial maintenance and defense, and re-examined patterns of scent-marking (specifically urine-and feces-marking) within coyote home ranges and territories. If the 'signpost' theory of territorial scent-marking (in which it is proposed that scent marks serve as boundary markers to potential intruders) holds true, we would expect to see not only a higher density of marks at the boundaries of territories, but also aversive or avoidance reactions to these marks by neighboring coyotes. If the purpose of scent-marking is primarily for self-orientation of resident animals, it is hypothesized (see Johnson (1973)) that there would be a more even distribution of marks within the territory (when controlling for the amount of time spent in each area), because outlying areas of the territory should not be more important than the interior.

## **Methods**

### *Study Area*

Research was conducted in a 40 km<sup>2</sup> area in the Lamar River Valley, Yellowstone National Park, Wyoming (44°52'N, 110°11'E). The elevation of the valley is ≈ 2000 m above sea level. Summers are short and cool, winters are long and cold. The mean annual temperature and precipitation in the Lamar Valley are 1.8°C and 31.7 cm, respectively. Most of this precipitation falls as snow (Houston 1982). Several habitat types have been identified in this area: forest, riparian, grassland, sage-grassland, mesic meadow, mesic shrub-meadow, and road (Gese 1995).

### *Data Collection*

Data were collected from Jan. to May 1997. Most data were collected by direct observation, although some snow-tracking was carried out, and radio telemetry was used to establish animal locations. Observations were made with the naked eye, with binoculars, or with a Nikon SpotterXL 16-47 x spotting scope. Telemetry was conducted with an AVM LA-12 receiver and an AF Antronics 148 kHz antenna.

The unique topography of the Lamar Valley and the fact that the Northeast Entrance Road passes along the valley floor, facilitates direct observation of the coyotes. Observation points (Ops) on hills along the length of the valley provide a wide range of view, usually of more than one coyote pack territory. The road is maintained year round and the OPs are easily accessible from the road. Because the coyotes under investigation generally limited their activities to the valley, which lacks dense vegetation, many of their daily activities were readily observable.

Individual coyotes were identified by physical characteristics and several of the coyotes were marked with ear tags and/or radio collars. The identification of individual animals and observation of their movements were beneficial to the understanding of scent-marking behavior. By knowing which animals were marking where, how often, and with which postures, a clearer picture of coyote territoriality and the dynamic interactions among coyotes was established.

For analysis of scent-marking patterns, we recorded the following information, whenever possible, for each observed instance of marking behavior: date/time, location on a Universal Transverse Mercator (UTM) grid, type of mark, posture used, identity of marking animal(s), whether the mark appeared to be directed in some way, if there was ground-scratching associated with the mark, and any unique circumstances surrounding the behavior. The location and movement patterns of any identified animals were recorded ad libitum to determine home range areas. Coyote tracks discovered incidentally were also followed and any marks along these paths recorded.

All coyotes observed in the valley were members of one of the resident packs. Seven packs were observed, but analyses were performed only on the data from the five packs of the central valley. These were the groups most easily observed, and they had adjacent or nearly adjacent ranges.

### *Data Analyses*

Data were analyzed several ways to examine the distribution, density, orientation, relative frequency, demographics, and temporal variations of the marks. Polygons were constructed around the scent marks of each pack, such that the polygon encompassed all marks of that pack yet occupied the minimum possible area. Pearson's correlations were used to assess the relationship between territory and pack size. Percentages of marks in the interior, vs. periphery, of the territories were compared with predicted percentages (based on a uniform distribution over the territory area) by Chi-squared tests.

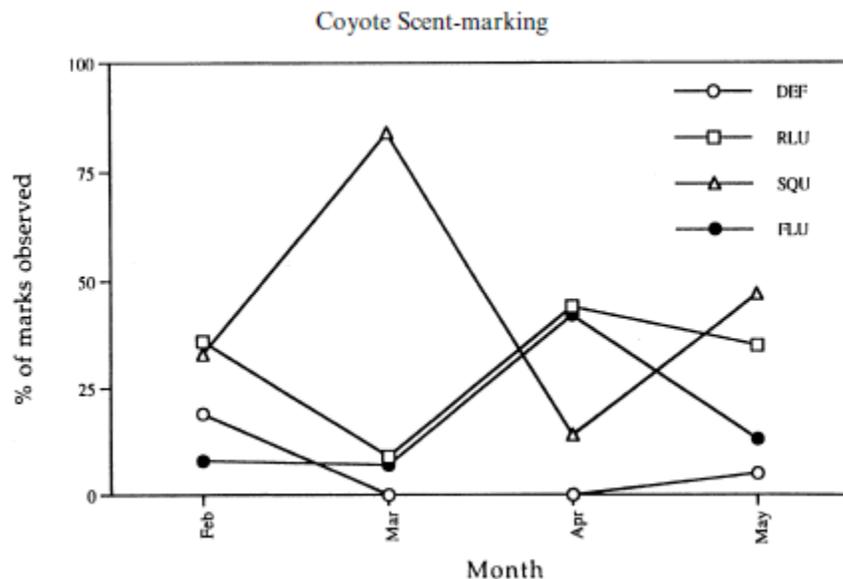
### **Results**

Data were collected for five packs of coyotes in the Lamar Valley. These packs varied in size from three to eight individuals (Table 1). We observed five types of marking behaviors ( $n = 147$  marks). Most marks were urinations, and these were categorized according to the posture of the marking animal: raised-leg urinations (RLU;  $n = 47$ ), squat urinations (SQU;  $n = 66$ ), and the forward-lean urination (FLU;  $n = 15$ ). Also observed were defecations (DEF;  $n = 10$ ), body rubbing ( $n = 2$ ), and the combination of DEF and urinations ( $n = 6$ ). In the lattermost category, four instances were DEF with a SQU, two were with a FLU. The relative frequencies of these marks also changed over the course of the study (Fig. 1).

**Table 1. Pack size (n), composition, and territory size of the observed packs of coyotes in the Lamar Valley, Yellowstone National Park, Wyoming**

Pack name	Composition	Territory size (km <sup>2</sup> )
Lamar Canyon	n = 3+ 1 male, 1 female, ?, ?	?
Jackson	n = 5-6 α male, 2 females, ?, ?, ?	1.59
Druid	n = 3 α male, α female, β male	1.59
Bison	n = 5 α male, female, β female, ?, ?	2.35
Amethyst	n = 5-8 α male, α female, 2 females 1 male, 3 female yearlings	3.34

**Fig. 1. Relative frequency of coyote scent-marking postures as a function of season, Lamar Valley, Yellowstone National Park, Wyoming, 1997. DEF, defecation; RLU, raised-leg urination; SQU, squat urination; FLU, forward-lean urination**



### Spatial Distribution

A plot of all scent marks leads to a distribution such that when polygons are drawn to encompass all scent marks of each pack, there is no overlap (Fig. 2). When similar plots are made encompassing all observed movements, however, interpack overlap is observed (Fig. 3). The scent mark polygons, for the four packs for which complete polygons could be made, varied in size from 1.59 km<sup>2</sup> to 3.34 km<sup>2</sup> ( $\bar{X} \pm$  standard deviation (SD) = 2.22  $\pm$  0.83 km<sup>2</sup>), and this size was correlated with the average pack size ( $r = 0.82$ ,  $p = 0.058$ ; Table 1). Thus, the scent mark polygons will hereafter be referred to as territories (see discussion below).

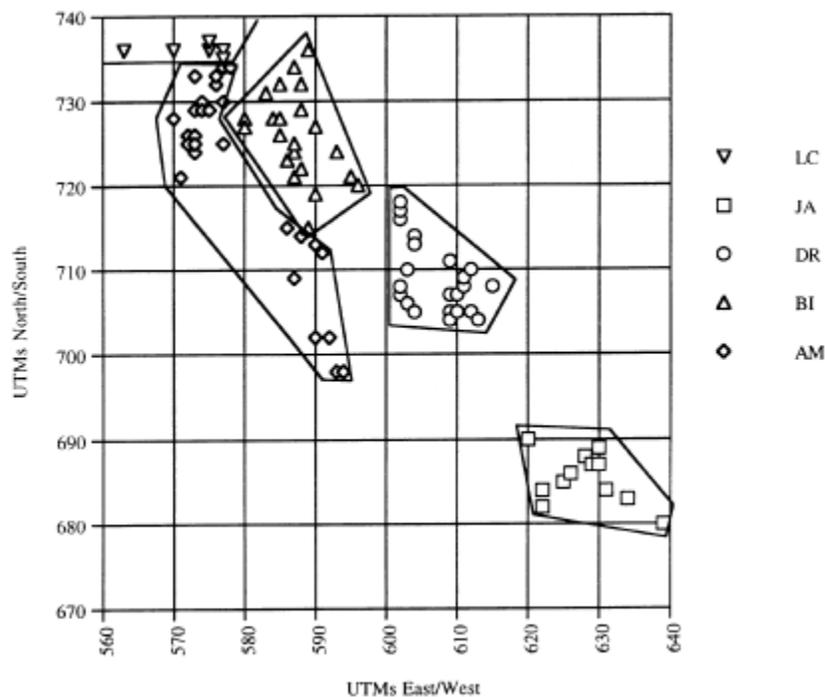
When comparing marks on the periphery vs. the interior of the territory, we measured the percentage of marks that were deposited in the interior of the territory as compared with a 0.1 km band along the edge of the territory. While this band accounted for a small part of the territory area (24.5%), 37% of the marks were found in this border portion. This distribution of marks was significantly different from an even distribution ( $\chi^2 = 8.45$ ,  $df = 1$ ,  $p < 0.01$ ). When the relative frequency of mark postures was compared for these two parts of the territory, we found an increase in frequency of RLUs ( $\chi^2 = 12.2$ ,  $df = 1$ ,  $p < 0.001$ ) and

FLUs ( $\chi^2 = 20.0$ ,  $df = 1$ ,  $p < 0.001$ ) in the perimeter, and a corresponding decrease in the relative frequency of SQUs (Fig. 4). The distribution of SQUs did not differ significantly from a uniform pattern ( $\chi^2 = 2.5$ ,  $df = 1$ ,  $p > 0.05$ ).

### Demographic Associations

For the one pack (Druid) in which the gender and status of all members were known, urination postures were highly associated with gender and dominance rank. The alpha male performed only RLUs. The alpha female performed only SQUs. The beta male exhibited a combination of RLUs (50%), FLUs (33%), and SQUs (17%)

**Fig. 2. Distribution of coyote scent marks, by pack, in the Lamar Valley, Yellowstone National Park, Wyoming, 1997. Axes are Universal Transverse Mercator (UTM) coordinates. Pack abbreviations: LC, Lamar Canyon; JA, Jackson; DR, Druid; BI, Bison; AM, Amethyst**



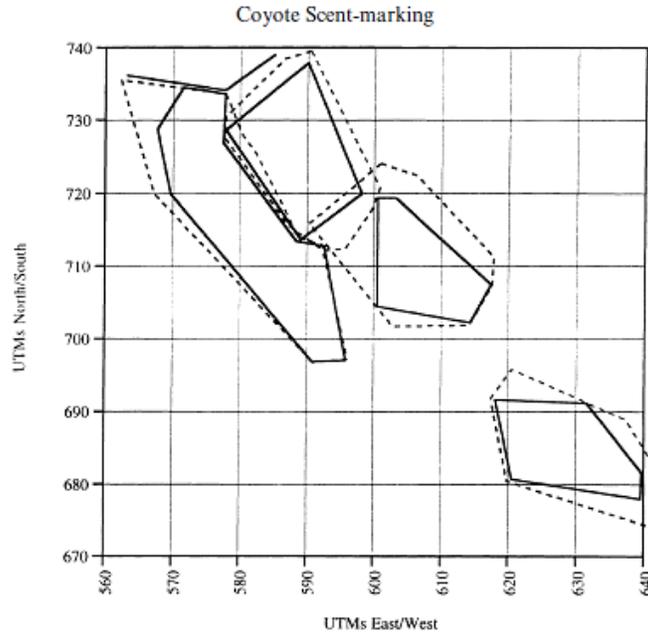
### Directional Qualities

When examining the directional qualities of the marks, the three urination postures were all categorized as 'directed'  $\approx 50\%$  of the time, with DEFs being oriented much less frequently (Fig. 5). Ground-scratching, however, was most highly associated with RLUs, approximately twice as frequently as with the SQUs, FLUs, or DEFs (Fig. 5). The combinations of ground-scratching and orientation also varied among the different mark types (Fig. 5). There was also seasonal variation in the directionality of urine marks, with an increase in Apr. followed by a sharp decrease in May. Examinations of the individual postures showed no discernible trend in the directionality of FLUs or RLUs, but a clear trend, parallel to the overall trend, for SQUs.

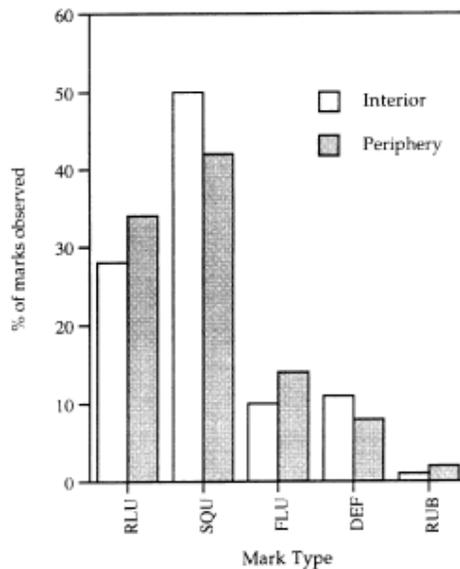
Marks were considered directed based on several criteria, which were seen with different frequencies. Most (50.5%) directed marks were oriented towards spots where another animal had marked previously. These were often made in succession (multiple marks). The next most frequent objects of orientation

were carcasses or foraging locations (27%). Other marks were oriented at points of unknown identity that the animals sniffed before marking (12%), on trails or roadways (9%), or on conspicuous objects (1.5%). There were no differences in the proportions of directed-only marks in the interior vs. the periphery of the territories ( $\chi^2 = 2.87$ ,  $df = 1$ ,  $p > 0.05$ ), but there were significantly more marks in the periphery that were associated with ground-scratching ( $\chi^2 = 28.0$ ,  $df = 1$ ,  $p < 0.001$ ) or both associated with ground-scratching and directed ( $\chi^2 = 6.30$ ,  $df = 1$ ,  $p < 0.025$ ; Figs 6, 7).

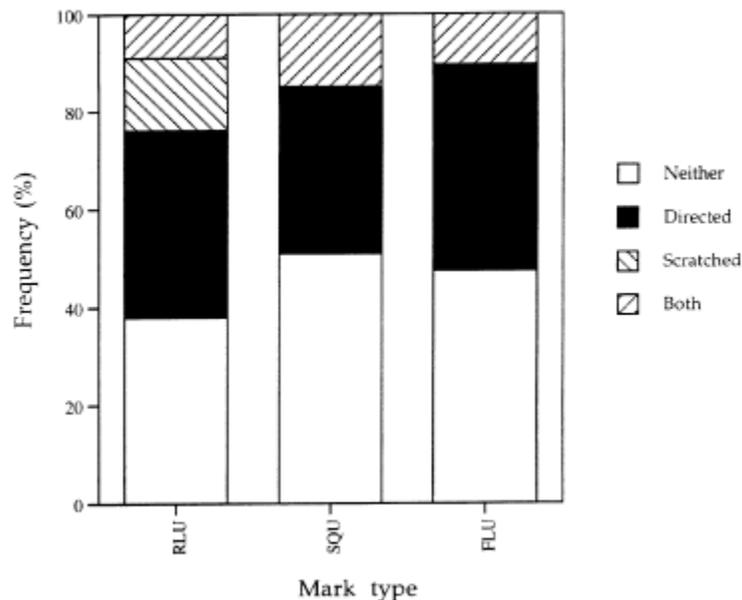
**Fig. 3. Coyote pack territories and movement ranges in the Lamar Valley, Yellowstone National Park, Wyoming, 1997. Territories are solid lines\ movement ranges are dashed lines. Axes are Universal Transverse Mercator (UTM) coordinates**



**Fig. 4. Relative frequency of different coyote scent mark types in interior vs. periphery of coyote territories, Lamar Valley, Yellowstone National Park, Wyoming, 1997. Abbreviations are the same as Fig. 1**



**Fig. 5. Combinations of directionality and ground-scratching associated with the three urination postures of observed coyotes, Lamar Valley, Yellowstone National Park, Wyoming, 1997. Abbreviations are the same as Fig. 1**



### Multiple Marks

Multiple marks were observed on 27 different occasions. Two (7.4%) of these were cases of one animal marking twice on the same carcass. All others were different animals marking in sequence. Of these 25, there were an approximately equal number of females marking after males ( $n = 12$ ) and males marking after females ( $n = 10$ ). On three occasions more than two coyotes marked in sequence on the same location. More multiple marks (40% of observations) occurred in the perimeter of the territory than would be expected by an even distribution ( $\chi^2 = 12.98$ ;  $p < 0.001$ )

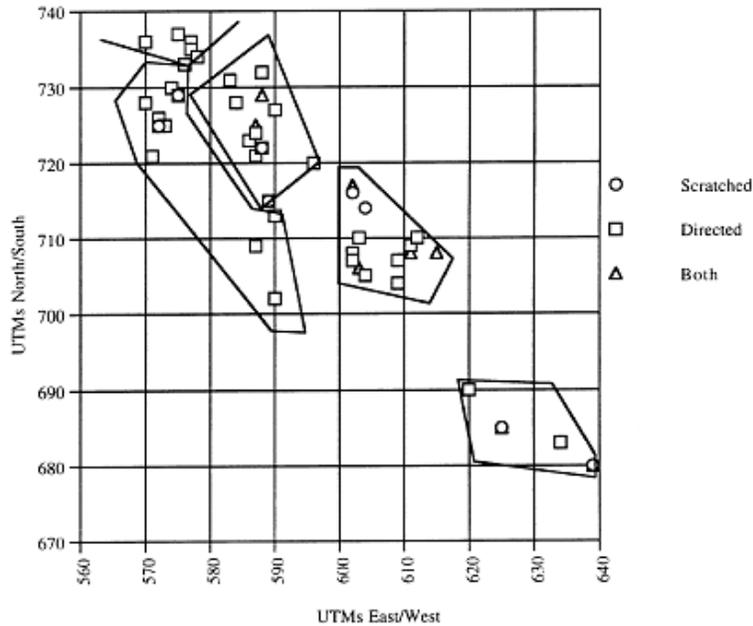
### Discussion

The present results provide strong evidence for a territorial function of scent-marking in five packs of coyotes. Spatial distribution and density, temporal variations, demographic associations and information on directional qualities of marks are all in accordance with predictions based on scent-marking as a mechanism of territory maintenance and defense. Our results agree with those of Gese & Ruff (1997) for the single pack of coyotes they observed. However, they did not study adjacent packs and, therefore, provide no information on territorial overlap between different packs.

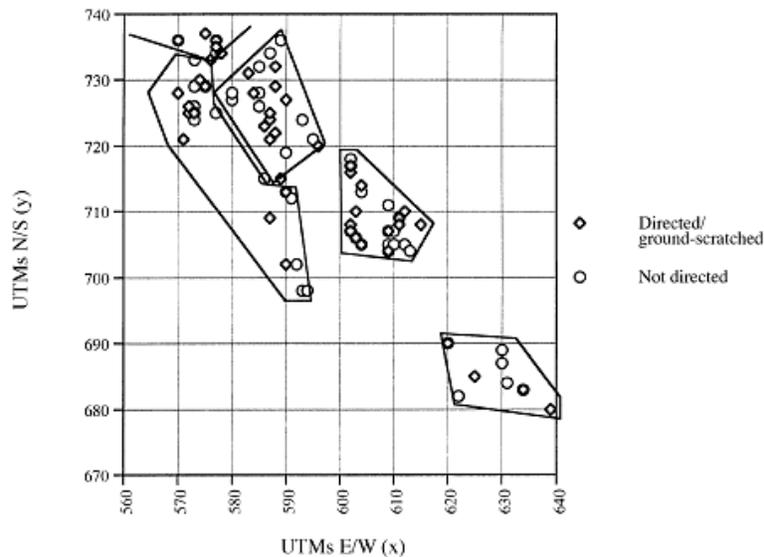
While direct aversive effects of one animal's urine on another's behavior, especially in regard to movement patterns, have been demonstrated in a few animals (Jones & Nowell 1973; Gosling & McKay 1990; Gosling et al. 1996), these data have come from laboratory studies of animals who regularly come in contact with their neighbors in their natural environments. Camenzind (1978) argued that because direct confrontations were rare in coyotes (see also Bekoff & Wells (1986)), indirect means of territory maintenance (scent-marking and vocalizations) were possibly more important. Vocalizations can provide a long-range signal that is short lived, whereas odors provide a local but long-lasting mark of territory ownership. White & Harris (1994) found that direct encounters, although almost always aggressive, were uncommon in red foxes (*Vulpes vulpes*), and therefore a relatively unimportant means of territory defense. The importance of possessing and maintaining a territory for social animals, particularly those

with more altricial young, is clear. Protection for the developing offspring and a resource base from which to feed them are essential to their survival (Messier & Barrette 1982). And while the exact mechanism of what information is transmitted and how that information is used to maintain territories are still poorly understood, available data strongly suggest that scent-marking can be an efficient way to achieve this end and avoid costly interactions for both territory holders and intruders (Gosling 1982).

**Fig. 6. Spatial distribution of coyote scent marks that were either directed\ had ground-scratching associated with them, or both. Lamar Valley, Yellowstone National Park, Wyoming, 1997. Axes are Universal Transverse Mercator (UTM) coordinates**



**Fig. 7. Spatial distribution of coyote scent marks that were directed or had ground-scratching associated with them, vs. marks that were neither directed nor had ground-scratching associated with them, relative to coyote territorial boundaries. Lamar Valley, Yellowstone National Park, Wyoming, 1997. Axes are Universal Transverse Mercator (UTM) coordinates**



### *Evidence of Territorial Function for Scent-marking*

The most significant support for the role of scent-marking in territoriality is the novel observation that there was no overlap of scent marks by adjacent packs of coyotes. There was also an increased density of marks in the periphery of the territories. The increased density of marks in the territory edges is consistent with the findings of Gese & Ruff (1997), but they did not examine adjacent packs. In the present study, the scent mark polygons were congruent with standard definitions of territory in that they did not overlap, they were areas which contained important resources (den sites), and other pack members generally did not enter them ('exclusive use'). It can be seen that when movement ranges are compared, there is in fact overlap of where the coyotes go throughout the day (Fig. 3). But the areas defined by the scent mark polygons were intruded upon very little, adding support to their being viewed as territories.

The fact that group size and territory size were correlated also suggests an importance of this area to the pack as a social unit. The more coyotes in the pack, the more resources they need to defend in order to survive (Bekoff & Wells 1986). This correlation of pack size and territory size fits well into the model of a territory, and is further evidence that the areas circumscribed by scent marks can accurately be called 'territories'.

If scent-marking is associated with the maintenance of territorial boundaries, how does it function? The 'signpost' theory predicts an 'olfactory bowl', with a greater density of marks in the periphery of the territory than the interior (Peters & Mech 1975). This is precisely what was seen in the distribution pattern of marks by the Lamar coyotes. Overall marks, and specifically RLUs and FLUs, were seen in significantly greater density in the perimeter of the territory than would be expected if there was a uniform distribution. While there was no such disparity in the distribution of SQUs, this could be explained in two ways: 1. territorial scent-marking is a behavior performed mostly by dominant males, so no disparity in the density of SQUs would be expected; or 2. females were denning during the study period, and so had a disproportionate number of marks near the den sites, which were in the interior of the territory, thus eliminating any periphery/interior disparity that might normally exist. The latter theory is supported by the temporal variation both in observations of SQUs (Fig. 1.), and their directional qualities. Regardless, the overall trend was that many more marks were observed in this boundary area than in the interior, as predicted by the {signpost} model of territorial marking.

As mentioned above, there were differences in the distributions of the different urination postures, which are generally associated with gender and dominance status in coyotes (see also, e.g. Bekoff & Wells (1980) Bowen & Cowan (1980), Wells & Bekoff (1981) and Gese & Ruff (1997)) This trend was also observed in the members of the Druid pack. Most theories of territorial defense, at least in polygamous species, suggest that this is performed most frequently by dominant males. The fact that the most conspicuous posture was only performed by males, and that the male-associated postures were seen with increased frequency at the territory perimeters, both strongly support this idea.

All urination postures had a 'directional' quality in approximately the same percentage of cases. However, RLUs were most frequently observed to have these qualities and had by far the greatest association with ground-scratching. Ground-scratching, although possibly scent-related, is a visual signal that is conspicuous both at the time of the behavior and after it is performed. The fact that it was most often seen in association with RLUs again supports the role of these marks as intentionally placed signals, as would be expected if they serve to delineate territorial boundaries. Ground-scratching, unlike the 'directional' criterion, was observed significantly more often in the territorial periphery than would be expected by a uniform distribution throughout the area of the territory. This supports similar findings in domestic dogs (*C. familiaris*; Bekoff 1979a,b) and the idea of its use as a signal, along with the accompanying scent mark, to mark the boundaries of a pack's territory.

Multiple marks also seem to be important socially for coyotes, and the fact that this unique type of scent-marking was also observed at a higher frequency along the edge of the territory suggests that all members of the pack may participate in territorial marking, even if it is predominantly performed by the alpha male.

#### *Urine-marking and Food*

Urine-marking has also been shown to be associated with food and food caches in wolves and coyotes (Harrington 1981, 1982) as well as in red foxes (Henry 1977). In these studies, marks were left after the cache had been recovered, which suggested a 'book-keeping' system for keeping track of the pack's various food stores. Again, the use of marks for information valuable to the sender (as would be expected for self-orientation within one's territory) is implied. Aversive effects might also be seen in these situations, however. The intruding coyote may smell less of its own scent, and more of others as it ventures into an adjacent territory, and return to familiar ground. A higher density of marks on the perimeter of the territory does not necessarily exclude this hypothesis however and the self-orientation and 'signpost' theories are not mutually exclusive, as both functions could be achieved by the same mark. Whether one or the other, or both, of these functions apply to wild canids remains the subject of debate, and further research will be necessary to obtain a more definitive answer.

**Table 2. Comparison of various field studies of canid scent-marking**

<b>Species</b>	<b>Study length</b>	<b>Primary methods</b>	<b>No. of marks</b>	<b>Types of information Collected</b>
Coyotes (this study)	1 winter/spring	observations	146	L G P (I) U B
Coyotes (Gese & Ruff 1997)	2.5 yr	observations (574 for territories)	3493	(L) G P (I) U B
Coyotes (Wells & Bekoff 1981)	2 yr	observations	562	L G P (I) U B
Coyotes (Bowen & Cowan 1980)	2 winters	snow-tracking	1047	L (G P U B)
Coyotes (Barrette & Messier 1980)	1 winter	snow-tracking	949	L (G P I U B)
Wolves (Peters & Mech 1975)	3 winters	snow-tracking	697	L (G) P (I U B)
Wolves (Rothman & Mech 1979)	2 winters	snow-tracking	225	L (G) P (I U B)
Wolves and coyotes (Paquet 1991)	4 winters	snow-tracking	3606	L U
Domestic dogs (Bekoff 1979b)	5 yr (opportunistic)	observations	1716	L G (P = n/a) I U B

L, location; G, gender; P, pack; I, individual; U, posture; B, associated behaviors.

Parentheses mean data were collected for only some marks.

In the present study, the degree of association of directed marks with food (27% of directed marks) suggests that the 'book-keeping' hypothesis may also apply in some instances. More detailed examinations of these types of marks would be needed to clarify this potential function, but it reminds us

that many of the proposed functions of marking behaviors are not mutually exclusive, and all should be explored through detailed field and laboratory studies.

While the total number of scent marks observed in this study was not as large as in some previous works on the subject, that the data were gathered by direct observation allows some strong inferences to be made about urination patterns in coyotes. With the exception of Wells & Bekoff (1981) and Gese & Ruff (1997), all other examinations of coyote (and other canid) scent-marking have relied almost exclusively on snow-tracking. Sample size may be increased in this fashion, but information about each scent mark must be inferred, and is often indiscernible or inaccurate (see Bekoff (1980)). By making direct observations of these animals, we were able to obtain definitive information about not only the marks, but the animals that left them, and the circumstances surrounding the behavior. Table 2 is a comparison of the time frames, sample sizes, methods, and types of information collected by this study and those made previously (also see Table X in Wells & Bekoff (1981)).

Although it seems clear that scent-marking plays a role in the maintenance of coyote territories, the question remains concerning what information in the mark is used by the coyotes. While the distribution and directionality of the scent marks support the idea of their acting as a signpost to potential intruders, how that information is gathered and processed by such animals is unknown. Field experiments, although very difficult to perform, are needed. The olfactory capabilities of coyotes and the role of other ecological factors, such as interspecific interactions, also play important roles in the highly dynamic patterns of coyote scent-marking, and should be examined in greater detail in the future. The present results provide yet another step towards the goal of understanding how these animals use and partition space among themselves. While more data are needed, for coyotes and other canids, the consistency in the findings among different studies, using different methods, supports the notion that there are many possible functions of scent-marking, in addition to its use in territorial behavior.

### **Acknowledgements**

We would like to thank the William H. Burt Memorial Fund and the Department of EPO Biology, University of Colorado, Boulder, for financial support of this research. AVM Instruments and Moonstone Mountaineering provided technical support. We also thank the National Park Service for their cooperation and support. Carl Bock, David M. Armstrong, and Eric Gese provided comments on earlier drafts, as did three anonymous reviewers.

### **Literature Cited**

- Barrette, C. 1977. Scent-marking in captive muntjacs, *Muntiacus reevesi*. *Anim. Behav.* 25, 536-541.
- Barrette, C. & Messier, F. 1980. Scent-marking in free-ranging coyotes, *Canis latrans*. *Anim. Behav.* 28, 814-819.
- Bekoff, M. 1979a. Ground scratching by male domestic dogs: a composite signal. *J. Mammal.* 60, 847-848.
- Bekoff, M. 1979b. Scent-marking by free-ranging domestic dogs: olfactory and visual components. *Biol. Behav.* 4, 123-139.
- Bekoff, M. 1980. Accuracy of scent-mark identification for free-ranging dogs. *J. Mammal.* 61, 150.
- Bekoff, M. & Wells, M. C. 1980. The social ecology of coyotes. *Sci. Am.* 242, 130-148.
- Bekoff, M. & Wells, M. C. 1986. Social ecology and behavior of coyotes. *Adv. Study Behav.* 16, 252-338.
- Bowen, W. D. & Cowan, I. McT. 1980. Scent marking in coyotes. *Can. J. Zool.* 58, 473-480.
- Camenzind, F. J. 1978. Behavioral ecology of coyotes on the National Elk Refuge, Jackson, Wyoming. In: *Coyotes: Biology, Behavior, and Management* (Bekoff, M., ed.). Academic Press, New York, pp. 267-296.

- Gese, E. M. 1995. Foraging ecology of coyotes in Yellowstone National Park. PhD Thesis, Univ. of Wisconsin, Madison.
- Gese, E. M. & Ruff, R. L. 1997. Scent-marking by coyotes, *Canis latrans*: the influence of social and ecological factors. *Anim. Behav.* 54, 1155-1166.
- Gorman, M. L. 1976. A mechanism for individual recognition by odour in *Herpestes auropunctatus* (Carnivora: Viverridae). *Anim. Behav.* 24, 141-145.
- Gorman, M. L. & Trowbridge, B. J. 1989. The role of odor in the social lives of carnivores. In: *Carnivore Behavior, Ecology, and Evolution*, 1 (Gittleman, J. L., ed.). Comstock, Ithaca, pp. 57-88.
- Gosling, L. M. 1982. A reassessment of the function of scent marking in territories. *Z. Tierpsychol.* 60, 89-118.
- Gosling, L. M., Atkinson, N. W., Collins, S. A., Roberts, R. J. & Walters, R. L. 1996. Avoidance of scent-marked area depends on the intruder's body size. *Behaviour* 133, 491-502.
- Gosling, L. M. & McKay, H. V. 1990. Competitor assessment by scent matching: an experimental test. *Behav. Ecol. Sociobiol.* 26, 415-420.
- Harrington, F. H. 1981. Urine-marking and caching behavior in the wolf. *Behaviour* 76, 280-288.
- Harrington, F. H. 1982. Urine marking at food and caches in captive coyotes. *Can. J. Zool.* 60, 776-782.
- Harrington, J. E. 1976. Discrimination between individuals by scent in *Lemur fulvus*. *Anim. Behav.* 24, 207-212.
- Henry, J. D. 1977. The use of urine marking in the scavenging behavior of the red fox (*Vulpes vulpes*). *Behaviour* 56, 82-105.
- Houston, D. B. 1982. *The Northern Yellowstone Elk: Ecology and Management*. Macmillan, New York.
- Johnson, R. P. 1973. Scent marking in mammals. *Anim. Behav.* 21, 521-535.
- Johnston, R. E., Chiang, G. & Tung, C. 1994. The information in scent over-marks of golden hamsters. *Anim. Behav.* 48, 323-330.
- Johnston, R. E. & Jernigan, P. 1994. Golden hamsters recognize individuals, not just individual scents. *Anim. Behav.* 48, 129-136.
- Jones, R. B. & Nowell, N. W. 1973. Aversive effects of the urine of a male mouse upon the investigatory behavior of its defeated opponent. *Anim. Behav.* 21, 707-710.
- Kleiman, D. 1966. Scent marking in the Canidae. *Symp. Zool. Soc. Lond.* 18, 167-177.
- Messier, F. & Barrette, C. The social system of the coyote (*Canis latrans*) in a forested habitat. *Can. J. Zool.* 60, 1743-1753.
- Müller-Schwarze, D. 1971. Pheromones in black-tailed deer (*Odocoileus hemionus columbianus*). *Anim. Behav.* 19, 141-152.
- Mykytowycz, R. 1968. Territorial marking by rabbits. *Sci. Am.* 218, 116-126.
- Paquet, P. C. Scent-marking behavior of sympatric wolves and coyotes in Riding Mountain Park. *Can. J. Zool.* 69, 1721-1727.
- Peters, R. P. & Mech, L. D. 1975. Scent-marking in wolves. *Am. Sci.* 63, 628-637.
- Ralls, K. 1971. Mammalian scent marking. *Science* 171, 443-449.
- Rothman, R. J. & Mech, L. D. 1979. Scent-marking in lone wolves and newly formed pairs. *Anim. Behav.* 27, 750-760.
- Stoddart, D. M. 1976. *Mammalian Odours and Pheromones*. Edward Arnold, Southampton.
- Swihart, R. K., Pignatello, J. J. & Mattina, M. J. I. 1991. Aversive responses of white-tailed deer, *Odocoileus virginianus*, to predator urines. *J. Chem. Ecol.* 17, 767-777.
- Wells, M. C. & Bekoff, M. 1981. An observational study of scent-marking in coyotes. *Anim. Behav.* 29, 332-350.
- White, P. C. L. & Harris, S. 1994. Encounters between red foxes (*Vulpes vulpes*): implications for territory maintenance, cohesion and dispersal. *J. Anim. Ecol.* 63, 315-327.