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Recommended Citation

Wells, M. C., & Bekoff, M. (1981). An observational study of scent-marking in coyotes, *Canis latrans*. *Animal Behaviour*, 29(2), 332-350.

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An Observational Study of Scent-Marking in Coyotes, *Canis latrans*

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ABSTRACT

Urination and defaecation patterns of free-ranging coyotes (Canis latrans) were studied in the Grand Teton National Park, Jackson, Wyoming, for two years. The vast majority of urinations by adult males and females were involved in 'marking,' and differentiating between 'marking' and 'elimination' may not be necessary. Our results may be summarized as follows: (1) Raised-leg urinations (RLU) performed by males were most frequently used in marking. (2) Females marked throughout the year using the squat (SQU) posture. (3) Snow tracking and reading snow sign resulted in a gross underestimate of the relative frequency of SQU's and a large overestimate in the relative frequency of defaecations (DEF) when compared to results obtained by direct observation. (4) There was sexual dimorphism for the contexts in which marking occurred. Overall, marking by males was associated with courtship and mating, with travelling, and with aggression. Marking by females was associated with the acquisition and possession of food and with the denning season. (5) Marking rates per coyote increased in groups larger than two animals. (6) RLU marking rates were greatest in areas of high intrusion when compared to denning areas and areas in which non-group members infrequently trespassed. SQU marking rates were highest in denning areas and high-intrusion areas. We suggest that scent odours are important in orienting individuals in space but do not represent in and of themselves barriers to movement.

Studies of mammalian olfactory communication have generated considerable interest in recent years (Ralls 1971; Eisenberg & Kleiman 1972; Johnson 1973; Mykytowycz 1974; Mech & Peters 1977; Brown 1979), especially concerning the use of urine, faeces, or glandular secretions to mark environmental objects or specific areas. Within the family Canidae, few detailed field data are available (Peters & Mech 1975; Mech & Peters 1977; Bekoff 1979a; Macdonald 1979a, b; Rothman & Mech 1979; Barrette & Messier 1980; Bowen & Mech. Cowan 1980). However, the bulk of these data stem from studies in which marking patterns were inferred from an analysis of the design that resulted from the deposition of (mainly) urine on snow-covered ground ('yellow snow'; Peters & Mech 1975; Rothman & Mech 1979; Barrette & Messier 1980; Bowen & McT. Cowan 1980) and not from direct observation of the animals themselves. While these seminal studies have demonstrated that yellow snow does, indeed, have biological importance, there remains an element of uncertainty associated with reading urine sign in snow (Bekoff 1980a).

In canids (and other mammals), urine marking is thought to be closely associated with the acquisition and maintenance of individual or group territories (Peters & Mech 1975; Camenzind 1978; Macdonald 1979a; Rothman & Mech 1979; Bowen & McT. Cowan 1980). However, the generality of the relationship between marking and territorial behavior may be limited (Scot 1967; Eisenberg & Kleiman 1972; Bekoff

1979a; Barrette & Messier 1980) and in coyotes (*Canis latrans*) at least, variations in life-style (Bekoff & Wells 1980; Bowen 1978; Camenzind 1978) and the difficulty of determining the land-tenure system of local populations (Gipson & Sealander 1972; Bekoff 1980b) warrant cautious acceptance of the association between marking patterns and territoriality. Scent-marking in canids may also function to label depleted food caches (Henry 1977; Harrington 1981), to aid in long-distance sex recognition (Dunbar 1977; Bekoff 1979a), to express social status and or reproductive condition (Golani & Mendelssohn 1971; Golani & Keller 1975; Peters & Mech 1975; Bekoff & Diamond 1976; Lamprecht 1979; Macdonald 1979b; Rothman & Mech 1979; Barrette & Messier 1980), to promote the reproductive synchrony (Rothman & Mech 1979), and to direct dispersing individuals into unoccupied areas (Rothman & Mech 1979).

The purpose of the present study was to describe quantitatively patterns of scent-marking in directly observable free-ranging coyotes. Emphasis was placed on (1) providing descriptions of various marking behaviours and differentiating among the postures using univariate and multivariate analyses, (2) differentiating between marking patterns of males and females using univariate and multivariate techniques, (3) describing the behavioural contexts in which various types of elimination occurred, (4) documenting seasonal patterns in marking, (5) assessing the effects of social factors on the marking behaviour of identified individuals, and (6) analysing the relationship between the spatial distribution of urine marks and known territorial boundaries. Furthermore, we compare the results of 'yellow snow' analyses in coyotes (Barrette & Messier 1980; Bowen & McT. Cowan 1980) with our data gathered from direct observation. Such a comparison is useful for assessing the degree of agreement between the two approaches, because in some cases, reading snow sign is the only practical method of data collection.

Methods

Data were collected by direct observation of individual coyotes between September 1977 and August 1979 in the area of Blacktail Butte (approximately 50 km²) in the southeast corner of the Grand Teton National Park, about 20 km north of the town of Jackson, Wyoming. Coyotes were observed for 426 h. The average number of coyotes in view at any one time was 1.57. Therefore, the total number of 'coyote-hours' was 668 (1.57 × 426). In addition, snow-tracking was conducted during winter 1978 in the same area. These data were only used to compare marking frequencies recorded by direct observation with those estimated by snow-tracking (Table 3). Approximately 50 coyotes were observed using focal animal (or group) sampling; 32 were previously fitted with coloured ear-tags (Rototags) and/or radio-collars (AVM suppliers). Standard procedures were used for deodorizing, setting, and baiting the Victor 3N traps (Gipson & Sealander 1972; Hawbaker 1974) used to capture coyotes. From the butte (about 8 km²), which rises 300 m off the valley floor, coyotes were easily observed using Bushnell Spacemaster II spotting scopes equipped with 20 m lenses, with low-power binoculars (7-1 ×), or with the naked eye as they roamed in the open habitat consisting of short grasses and sagebrush (*Artemisia* spp.; see Cole 1969 and Oswald 1966 for details about vegetation) or travelled on snow-covered ground. All measures of time were taken with digital stopwatches (Cronus II or Fisher). Observations were spoken into a Sony microcassette recorder (model 101) and later transcribed. Included in the recorded data were the coyote's identity (if known), its ongoing activity, the type of posture used to deposit urine or faeces, the location of the marking coyote, the number and identities of nearby coyotes, whether or not the focal coyote or other individuals had previously been observed marking, and the presence of food or other objects.

Elimination and Marking

Although it has been suggested that scent-marking should be differentiated from simple elimination (Kleiman 1966; Barrette 1977), some investigators have considered all urine sign encountered in snow to be potential scent-marks (Barrette & Messier 1980). The latter clearly was not the case for domestic dogs (*C. familiaris*; Bekoff 1979a) but might not be a grossly misleading assumption for coyotes (see below).

Indeed, the possibility exists that all bodily excretions are potential marks to the recipient, regardless of the sender's intent (Dunbar 1978; Bekoff 1979a). Also, the chemical composition (and consequent effects) of urine used in marking and that deposited during simple elimination is not known to differ.

One main criterion for marking that seems to apply in most cases is that the stream of urine is directed at some conspicuous object (directional quality; Kleiman 1966; Peters & Mech 1975; Bowen & McT. Cowan 1980). However, use of this criterion alone is insufficient. First, there is a high probability that the detectability of snow sign by a human is related to the conspicuousness of the object on which the scent was originally deposited. Second, that which was conspicuous was so defined because the sign was located by the investigator(s). Therefore, other criteria are needed to make a more rigorous distinction between marking and simple elimination, and the importance of seeing animals excrete is increased.

Marking criteria. The following criteria were used to differentiate marking from simple elimination. Not all criteria were necessarily present at any one time. We considered an animal to be marking if it performed at least one of the behaviours. We then used multivariate methods to assess the relative importance of each criterion singly as well as in combination with all other actions. Marking criteria included: (1) The coyote was observed to sniff a spot and then eliminate directly over the spot. (2) Ground-scratching after urinating or defaecating; this behaviour never occurred before an elimination (the same was true for domestic dogs; Bekoff 1979a, b). Camenzind (1978) used this criterion solely. (3) The stream of urine was directed at a previously known urination deposited by the same or another individual. Another criterion that is difficult to assess during observations, but one that is useful when doing snow-tracking studies, is that typically less urine is expelled during marking than during simple elimination (Peters & Mech 1975; Barrette 1977; Henry 1977; Bekoff 1979a; Bell 1980; Macdonald 1980).

Results

Elimination Postures

Four types of postures were observed, accounting for a total of 562 eliminations. Urination postures included the raised-leg urination (RLU; $N = 181$), or leg-lift; the squat urination (SQU; $N = 242$), and the forward-lean urination (FLU; $N = 85$, see Sprague & Anisko 1973; Beach 1974; Peters & Mech 1975; Bekoff 1979a for descriptions). When defaecating (DEF; $N = 54$), the posture assumed by the coyotes resembled the SQU. However, the DEF squat lasted significantly longer than the SQU posture (DEF squat, $N = 12$, $\bar{X} = 7.14$ s, $SD = 3.12$; SQU posture, $N = 21$, $\bar{X} = 1.64$ s, $SD = 0.45$; $t = 4.12$, $df = 31$, $P < 0.001$).

Differentiation of elimination postures and their association with marking criteria. The major questions here were (1) could the various elimination postures be differentiated from one another and by what criteria, and (2) how closely was each posture associated with marking criteria? These data are presented in Tables 1 and 2. The proportion of RLU's associated with prior sniffing, subsequent ground-scratching, and the direction of the urine stream or faeces at a previously observed mark was significantly greater than that for the other three types of elimination ($t_b > 1.96$, $P < 0.05$ for all paired comparisons) with the exception of DEF followed by ground scratching (see Sokal & Rohlf (1969), pages 607 ff. for discussion of the t_b statistic; critical values of t_b and levels of significance are presented in Table 1; all paired t_b comparisons in this study were performed only after doing the χ^2 analysis for testing the differences among three or more proportions as suggested by Snedecor (1956)). Sniffing preceded SQU's proportionately more than FLU'S ($P < 0.001$) or DEF's ($P < 0.001$), but ground-scratching followed SQU's, FLU's, and DEF's with about equal frequency. SQU's were directed at previously observed marks proportionately more than were DEF's ($P < 0.001$) but not more than were FLU's ($P > 0.05$).

Table 1. The Relationship between Urination Postures and Defaecation and the Criteria Used to Differentiate Marking from Simple Elimination*

Criteria	RLU†	SQU	FLU	DEF	Total
Sniffing preceded	168 (92.8%)‡	211 (87.2%)	44 (51.8%)	22 (40.7%)	445
Ground scratching followed	46 (25.4%)	31 (12.8%)	5 (5.9%)	8 (14.8%)	90
Directed at previously observed urination	72 (39.8%)	30 (12.4%)	13 (15.3%)	0	115
Total observed	181 (32.2%)	242 (43.1%)	85 (15.1%)	54 (9.6%)	562

* See text.

† RLU = raised-leg urination; SQU = squat urination; FLU = forward-lean urination; DEF = defaecation.

‡ Proportions test, Sokal & Rohlf 1969, pp. 607 ff; $t_b > 1.96$, $P < 0.05$; $t_b > 2.58$, $P < 0.01$; $t_b > 3.3$, $P < 0.001$; See text.

In addition to looking at marking criteria singly, it was also useful to study the ways in which they were interrelated. These data are presented in Table 2 for RLU's and SQU's. A significantly higher proportion of SQU's were performed in the absence of any of the defining criteria, while a significantly greater percentage of RLU's incorporated all three criteria. A significantly higher proportion of RLU's (171/181 = 94.5%) than SQU's (213/242 = 88.0%) were marks according to the criteria used to differentiate marking from simple elimination ($t_b = 2.37$, $P < 0.05$). Sniffing (in the absence of the other two criteria) preceded SQU's a significantly greater percentage of the time than it preceded RLU's; prior sniffing and subsequent ground-scratching were about equally associated with RLU's and SQU's. The correlation between sniffing and ground-scratching was not significant ($r = 0.19$, $N = 45$). Sniffing and then urinating on a previously known urination occurred proportionately more with RLU's than with SQU's. Overall, sniffing and then urinating on a previously known urination were highly correlated with one another ($r = 0.83$, $P < 0.001$). Because subtle movements of the head or muzzle may not have been detected and sniffing could, in fact, have taken place in the absence of any observable motion, the actual frequency of occurrence of sniffing may be underestimated. Also, obviously not all previous urinations were observed. Because such a high percentage of RLU's and SQU's were 'marking' by our criteria, and because this may be an underestimate, the term 'marking' is herein used synonymously with 'eliminating'. The same assumption is inherent in snow-tracking studies.

A discriminant function analysis (DFA; see Aspey & Blankenship (1977) and Bekoff (1977) for applications of this method to behavioural data) was performed in order to identify those variables that were most important in differentiating RLU's from SQU's. The variables considered included all those listed in Table 1 plus the season, (breeding, December to February, and non-breeding, March to November) and the number of coyotes present near the coyote that was urinating. This multivariate analysis showed that RLU's and SQU's were different ($\chi^2 = 57.6$, $df = 5$, $P < 0.001$; the distance between the mean discriminant values (centroids), $D^2 = 0.78$), and these two types of signs could be separated from one another about 70% of the time. The most important discriminating variables were the frequencies with which urine was directed at a previously known urination (discriminant weight = 0.45) and the number of coyotes present (discriminant weight = 0.65). RLU's were directed significantly more frequently at previously known urinations; and when RLU's were performed, there were more coyotes present than when SQU's were performed.

Table 2. The Relationship between Raised-Leg and Squat Urinations and Single and Combined Marking Criteria

Posture	Sniff only	GS† only	Directed at previous urination only (DPU)	Sniff plus GS	Sniff plus DPU	DPU plus GS	None	All
RLU (N = 181)	74 (40.8%)***	2 (1.1%)‡	1 (0.6%)‡	23 (12.7%)‡	50 (27.6%)***	0	10 (5.5%)*	21 (11.6%)**
SQU (N = 242)	159 (65.7%)	2 (0.8%)	0	22 (9.1%)	20 (8.3%)	0	29 (12.0%)	10 (4.1%)

† GS = ground search.

Significant differences between RLU and SQU: * $P > 0.05$; ** $P < 0.01$; *** $P < 0.001$ (Proportions test; for critical values of t_b see footnote to Table 1.

‡ $P < 0.05$.

Relationship between elimination postures and the sex and age of the performer. Adult males ($N = 4$) performed the RLU posture over 78% of the time (91/116), never squatted, and assumed the FLU position about 22% of the time. Adult females ($N = 4$) performed the SQU 97.5% of the time (159/163), and only on four occasions were females observed in the RLU posture (2.5%). Females never performed FLU's. Juveniles ($N = 3$, five to nine months of age) never exhibited the RLU posture and were observed performing SQU's (46.7%; 7/15) and FLU's (53.3 %; 8/15) about the same proportion of time.

We used two multivariate techniques in analyzing these data: principal components analysis and discriminant function analysis. Variables included in the analyses were sex (when known) and other variables used in the discriminant function analysis above. Sex and posture were highly correlated ($r = 0.94$, $P < 0.001$). In the principal components analysis the first three factors accounted for 77.9% of the variance. Factor scores for the first two factors were plotted (Fig. 1) and showed that the sexes were clearly separable. The first factor, which accounted for 40.1 % of the variance, could not be labelled specifically (this is not uncommon; Sneath & Sokal 1973), but the second factor, which accounted for 23.4% of the variance, could be labelled 'sex' (factor loading = 0.80). It is important to mention that ground-scratching was not important in the separation of the sexes by the principal components analysis; only 16% of the variance of ground-scratching was accounted for by sex. For all of the other variables, over 75% of the variance was accounted for by sex (posture = 95%). An ANOVA indicated that posture was the only variable separating males from females ($F = 419.9$, $df = 1, 59$; $P < 0.001$). A principal components analysis was also performed in which sex was omitted from the list of variables. In this analysis, the percentage of variance in posture that was accounted for fell to 45 %, a drop of about 50% from the principal components analysis in which sex was included. Therefore, posture was not important without considering sex.

Figure 2 shows the plot (range) of linear discriminant function value cast on a female/male discriminant axis. All urinations by known males were classified correctly as having been performed by males, but in two instances (6.1%) females overlapped with males. The centroids of both groups were clearly separate ($D^2 = 5.47$). When posture (discriminant weight = 2.91) was removed from other discriminant function analyses, all showed non-significant differences between males and females. That is, the sexes could not be discriminated on the basis of variables other than posture, though there were important seasonal differences in marking rates (see below).

Fig. 1. A two-dimensional plot of factor scores from a principal components analysis showing that there was no overlap between male and female coyotes with respect to urination patterns (see text for variables included in analysis; N = number of urinations by known males and females).

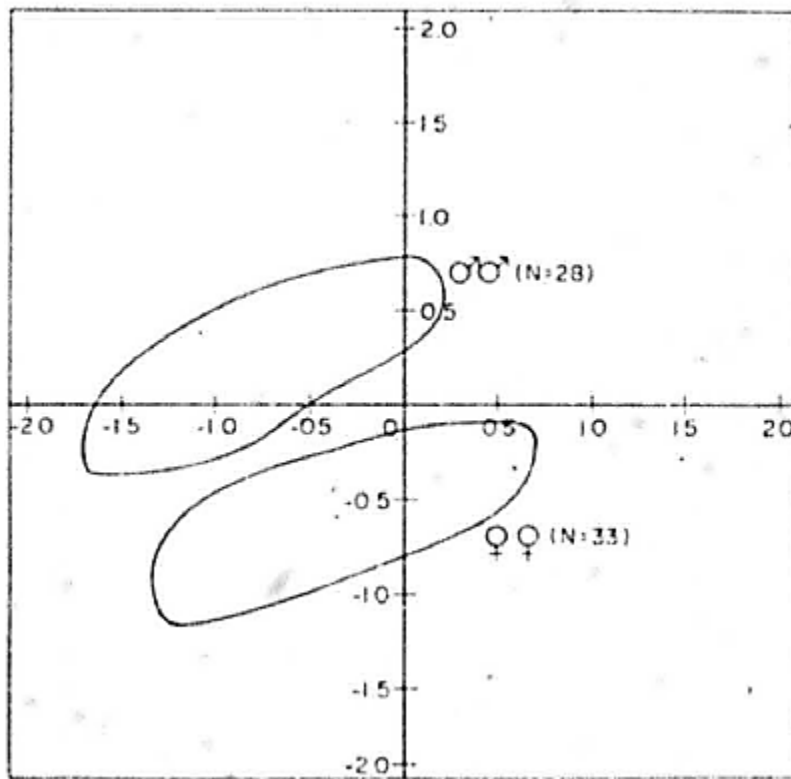
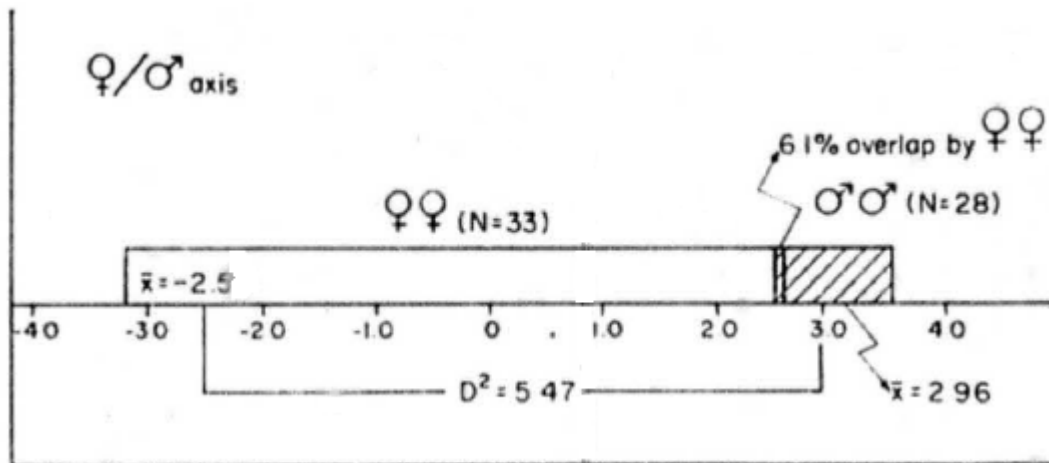


Fig. 2. The range of linear discriminant values for female and male coyotes cast on a female/male discriminant axis. Urinations by known males ($N = 28$) were all classified correctly; two urinations (6.1%) by known females fell within the range of male discriminant scores (see text).



Reading snow sign versus direct observation. About the same proportion of RLU's and FLU's were identified by reading snow sign (using criteria set forth by Peters & Mech 1975 and Rothman & Mech

1979) as by all direct observations ($t_8 = 0.91$ and 0.20 , respectively, $P > 0.05$; see Table 3). However, a significantly lesser proportion of SQU's ($t_8 = 4.19$, $P < 0.001$) and a significantly greater proportion of DEF's ($t_8 = 6.17$, $P < 0.001$) were found by snow-tracking than by direct observations. When snow-tracking data for winter 1978 were compared with observations for the same period of time, SQU's still were underestimated and DEF's were overestimated by reading snow. However, RLU's were also underestimated (14.9%) by snow-tracking when compared to winter observations.

Table 3. Comparisons of Relative Elimination Frequencies Inferred from Reading Snow Sign and from Direct Observations

Method	RLU*	SQU	FLU	DEF	Total
Snow sign	37 (28.0%)	31 (23.5%)	19 (14.4%)	45 (34.1%)	132
Observation	181 (32.2%)	242 (43.1%)	85 (15.1%)	54 (9.6%)	562
Percentage of difference using observation as standard	+4.2	+19.6	+0.7	-24.5	

*See Table 1 for legend

Behavioural Context of Marking

The frequencies of marking during different ongoing activities (described in Bekoff & Wells, 1981) are presented in Table 4. While at carrion, a coyote could engage in other activities; all other categories were mutually exclusive. Marking frequency was standardized to account for the frequencies with which the different activities were observed. The corrected values were then ranked. Of the six top-ranking activities, behaviours directly associated with food accounted for four (hunting, digging (usually for carrion or rodents), at carrion, and eating). Marking during travelling ranked first and marking during aggressive interactions ranked fourth.

A similar analysis was performed for the relationship between marking frequency and the cumulative duration of the 11 activities. Among the five top-ranking activities for which the time span between marks was less than 1 h were digging, aggression, eating, and travelling. While resting (lying, sitting), coyotes stood up and marked infrequently.

The frequencies with which each urination posture and DEF were observed in association with ongoing activities are presented in Table 5. The results can be summarized (critical values for t_8 can be found in Table 1): (1) RLU's, FLU's, and DEF's were observed the greatest proportion of time in association with travelling ($P < 0.05$ when compared to the second highest percentage). (2) SQU's were performed about the same proportion of time during hunting and travelling. (3) RLU's and FLU's were associated with travelling proportionately more than were SQU's ($P < 0.001$). (4) SQU's were performed in conjunction with hunting proportionately more than either RLU's ($P < 0.001$) or FLU's ($P < 0.001$), and more with eating ($P < 0.001$) than RLU's. (5) A significantly higher proportion of RLU's were associated with aggression than were SQU's ($P < 0.05$) or FLU's ($P < 0.01$). (6) DEF's were performed proportionately more at carrion and interspersed more with lying down than any of the three urination postures ($P < 0.05$ in all cases).

We also determined the frequency with which scent-marks were deposited directly on food objects (e.g. bones, ungulate carrion, dead rodents). SQU's were directed more frequently (18.5%; 45/242) toward a

food item than were any of the other types of eliminations ($t_8 > 2.13$, $P < 0.05$ in all cases). RLU's were directed at food items 10 (5.5%) times.

Table 4. The Frequency of Marking and Intervals (Min) between Marks*

Activity†	Number of marks	Frequency of activity	Marks/activity frequency	Rank	Duration (min)	Min between marks	Rank
Travel	307	389	0.79	1	7 976	26.0	4
Hunt	109	268	0.41	2	8 439	77.4	8
Dig	15	39	0.38	3	149	9.9	1
Aggression	25	72	0.35	4	339	13.6	2
At carrion	46	142	0.32	5	3 264	71.0	7
Eat	38	145	0.26	6	815	21.4	3
Play	8	65	0.12	7	510	63.8	6
Lie	24	353	0.07	8.5	16 784	699.3	11
Roll on ground	2	30	0.07	8.5	67	33.5	5
Vocalize	3	48	0.06	10	386	128.7	9
Sit	2	77	0.03	11	314	157.0	10

*Data were standardized to account for the frequencies with which the different activities were observed.

†Activity patterns as described in Bekoff & Wells (1981).

The last behavioural context analysis involved examining the frequencies with which various activities were observed before and after marking (Table 4). About 25% of the time the activity before marking was different from the activity that followed marking. Of particular note is that scent-marking occurred significantly more often after eating, digging, and aggression and significantly more often before rolling on the ground.

Seasonal Trends in Marking

Figure 3 presents monthly marking rates for RLU's and SQU's plotted against the proportion of time during which coyotes were active (not resting or sitting). The marking rates have been standardized to account for the actual time that coyotes were in view (coyote-hours) during each month. Marking rates greatly increased as the percentage of active time decreased. RLU and SQU rates were significantly negatively correlated with duration of active periods from September to March ($r = -0.99$, $P < 0.001$). When these marking rates were plotted against resting and active hours combined (Fig. 4), other seasonal trends that were previously -masked became apparent. First, FLU's and DEF's were performed at a relatively low and stable rate throughout the year. Second, RLU's were performed at a relatively high and stable rate between November and February that subsequently decreased steadily to a low and stable rate during the summer and early fall. The overall marking rate for RLU's between November and April was significantly higher than that observed between May and October ($t_8 = 9.02$, $P < 0.001$). The rate of SQU varied throughout the year, showing a moderate winter increase followed by a large increase in April and May. SQU rates fell during summer and fall. The difference in SQU marking rates between March and April was significant ($t_8 = 2.69$, $P < 0.01$). Finally, ground-scratching was performed at its highest rate during January, decreased in February and March, and increased once again in April. The April peak was due to the fact that ground-scratching and SQU's were performed in conjunction most frequently during this period.

Table 5. The Frequencies with which Urination Postures and Defaecation Were Observed in Association with Ongoing Activity

Activity	RLU*	SQU	FLU	DEF	Total
Hunt	12 (6.6%)†	78 (32.2%)	7 (8.2%)	12 (22.2%)	109 (19.4%)
Travel	127 (70.2%)	94 (38.8%)	58 (68.2%)	28 (51.9%)	307 (54.6%)
Eat	4 (2.2%)	28 (11.6%)	5 (5.9%)	1 (1.8%)	38 (6.8%)
Roll on ground	1 (0.6%)	1 (0.4%)	0	0	2 (0.3%)
Dig	3 (1.7%)	9 (3.7%)	2 (2.3%)	1 (1.8%)	15 (2.7%)
Lie	6 (3.3%)	8 (3.3%)	3 (3.5%)	7 (13.0%)	24 (4.3%)
Play	2 (1.1%)	2 (0.8%)	4 (4.7%)	0	8 (1.4%)
Aggression	14 (7.7%)	8 (3.3%)	1 (1.2%)	2 (3.7%)	25 (4.4%)
Vocalize	1 (0.6%)	1 (0.4%)	1 (1.2%)	0	3 (0.5%)
Sit	1 (0.6%)	0	1 (1.2%)	0	2 (0.3%)
At carrion	12 (6.6%)	18 (7.4%)	5 (5.9%)	11 (20.4%)	46 (8.2%)

*See Table 1 for legend.

†See text; critical values of t_b are presented in Table 1.

Group Effects on Marking

The mean overall group size observed during this study was 1.57; mean group size when marking occurred was 2.30. The data in Table 7 show the frequency of marking per coyote in groups of different sizes. A significantly higher marking frequency per coyote was observed in groups of three than for solitary individuals ($t_b = 6.40$, $P < 0.001$), pairs ($t_b = 6.30$, $P < 0.001$), and groups of four coyotes ($t_b = 2.09$, $P < 0.05$). There was no difference in marking frequency between solitary animals and pairs. Both solitary coyotes and pairs marked at lower frequencies than individuals in groups of four ($t_b = 4.37$ and 5.18 , respectively, $P < 0.001$). Ground-scratching also showed a significant increase in groups of three compared to solitary coyotes ($t_b = 2.84$, $P < 0.01$), but there were no significant differences among all other group sizes. However, when the percentage of ground-scratching for solitary animals was compared to the overall percentage of ground-scratching for groups of two to four coyotes, a significant difference was noted ($t_b = 2.01$, $P < 0.05$). Groups of five and six coyotes were observed too rarely to determine marking or ground-scratching rates.

A total of 76 group scent-marks, during which more than one coyote marked in succession, was observed. Forty-six series marks involved two animals, 25 involved three coyotes, and 5 involved four

coyotes. The percentage of group marks (number of group marks/total number of marks) observed on a monthly basis is presented in Fig. 5. The highest percentage of group marks was observed between December and March (winter). A winter increase also was evident when the percentage of group marks was corrected to account for monthly differences in coyote group sizes (which also increased during the winter; Bekoff & Wells 1980).

Table 6. Frequencies with which Various Activities were Observed Before and After Marking

Activity	Frequency before marking	Frequency after marking	Difference	t_b^*
Hunt	109	124	15	NS†
Travel	307	344	37	2.23
Eat	38	6	32	5.35
Roll on ground	2	11	9	2.70
Dig	15	5	10	2.33
Lie	24	30	6	NS
Play	8	9	1	NS
Aggression	25	1	24	5.71
Vocalize	3	1	2	NS
Sit	2	6	4	NS
Scent-mark	29	25	4	NS
At carrion	46	36	10	NS
Total	608	608	156 = 25.7%	

*Proportions test; critical values of t_b are presented in Table 1.

† $P > 0.05$.

Fig. 3. Monthly marking rates for urinations performed using the raised-leg (RLU) and squat (SQU) urination postures. The percentage of time that coyotes were active during each month is also indicated. Marking rates were standardized to account for the actual time that coyotes were in view (coyote-hours; see Methods) and active each month. December to February was the breeding season; pups were born in late April.

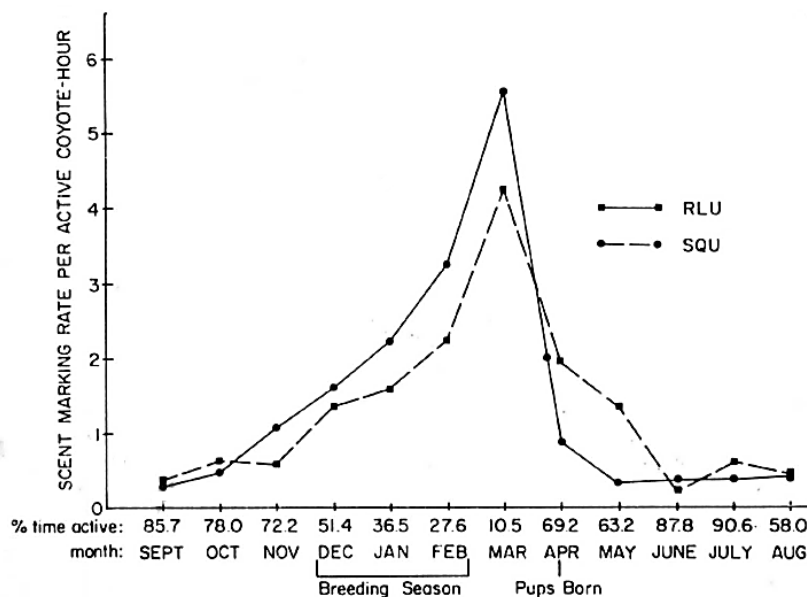


Fig. 4. Monthly marking and ground-scratching rates corrected for the actual total time that coyotes were in view (coyote-hours; see Methods) each month when active and when resting. GS = ground scratching, RLU = raised leg urination, SQU = squat urination, FLU = forward lean urination, DEF = defaecation. December to February was the breeding season; pups were born in late April.

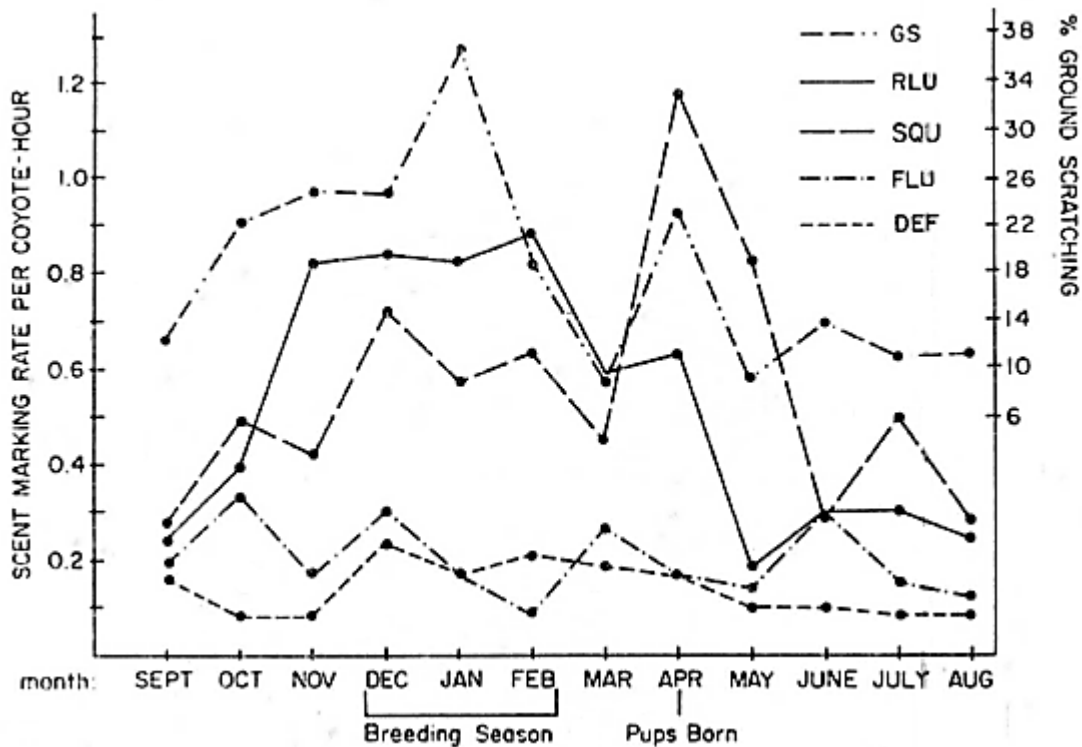


Table 7. The Relationships among Coyote Group Size, Rates of Marking per Coyote, and Ground-Scratching

Group size	Frequency observed	Number of marks	Marks/coyote	GS*	Percentage of marks followed by GS
1	505	194	0.38	20	10.3
2	160	107	0.33	18	16.8
3	78	167	0.71	35	21.0
4	39	91	0.58	17	18.7
5	14	1	0.01	---†	---
6	6	2	0.06	---	---

*GS = ground-scratching frequency.

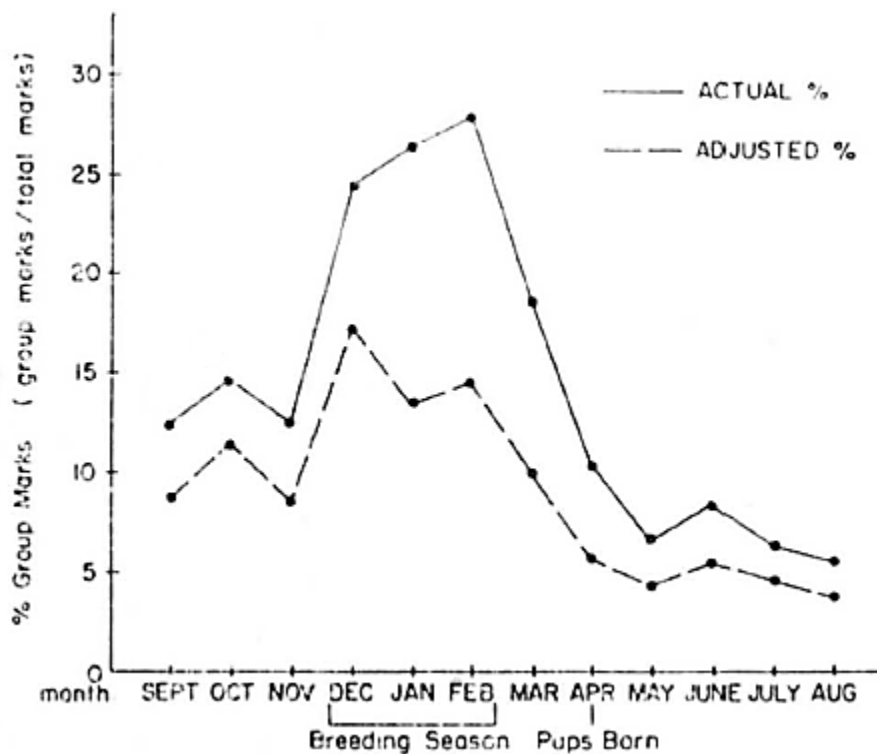
†Insufficient data.

Series Marking by Known Individuals

We collected detailed information on marking during the winter of 1978-1979 for one group of coyotes, called the 'Gang of Four'. This group consisted of a four- to six-year-old female, her six- to eight-year-old mate, a two-year-old male offspring (helper) born in 1977, and a juvenile male born in 1978 (see Bekoff & Wells (1980) for details). The juvenile male died in February 1979. Before and after his death the coyotes were a unified, closely knit group.

A total of 120 urine marks were observed for the Gang of Four when they were together as a group. On 34 occasions, more than one animal marked in succession (series marking). Twenty-three (67.7%) of the series marks involved two coyotes, 10 (29.4%) involved three animals, and 1 (2.9%) involved all four group members. The number of marks observed for each individual and the places in line that each individual marked during series marking are presented in Table 8. The two parents scent-marked the most and proportionately the same ($t_b = 0.39$, $P > 0.05$), followed by the helper, who marked proportionately more than the juvenile ($t_b = 2.61$, $P < 0.01$). The two parents marked equally frequently and were most often first, again followed by the helper and the juvenile, the latter of whom was never observed to mark first. The two parents and the helper were all last in line about the same proportion of time. Note that there were as many as six places in line, because one individual could have marked more than once during a series. The two parents marked twice during a series on six occasions and were first and last each time. The helper and juvenile were never observed to do this. Ground-scratching was performed equally and most often by coyotes first (42.3%) or last (65.4%) in line and significantly less in other positions during series marking ($t_b = 2.55$; $P < 0.05$ in all cases).

Fig. 5. The percentage of group marks observed on a monthly basis (actual %) and the monthly percentage of group marks adjusted to account for monthly differences in group sizes (adjusted %). December to February was the breeding season; pups were born in late April.



Spatial Distribution of Marks by the Gang of Four

We calculated the frequencies of marking in known denning areas, in areas of high intrusion by non-group members (there was an actively defended boundary), and in areas of low intrusion by outsiders. The home range of the Gang of Four was divided into six 2.59-km² (1-mile²) quadrats whose boundaries were obvious landmarks such as roads and irrigation ditches. Table 9 presents the frequency distributions of group marks, RLU's, SQU's and ground-scratches in each of the six quadrats. Group marks, RLU's,

and SQU's were non-randomly distributed throughout the group's home range. SQU's occurred most frequently in quadrat 2, which coincided with the major denning area, and in high-intrusion areas (quadrats 3, 4, and 5); RLU's were mainly observed in areas of high intrusion by other coyotes.

In order to be more precise, we determined the amount of time that was spent in an area by 'the entire group in addition to analysing merely the frequencies of observed marking. About the same percentage of time was spent by the group in the den area (31.2%), the area of low intrusion (34.7%), and the area of high intrusion (34.2%). However, marking rates were significantly greater in the area of high intrusion (0.72 marks/h) than in the den area (0.08 marks/h; $t_8 = 6.50$, $P < 0.001$) or in the area of low intrusion (0.21 marks/h; $t_8 = 4.89$, $P < 0.001$). Marking rates were the same in the den area and the low-intrusion area.

Discussion

This is the first long-term study of scent-marking in coyotes or any other wild canids that is based on direct observation. Comparison with other studies may therefore be somewhat hampered because of different methodologies. Nonetheless, comparative analyses are useful and will elucidate both similarities and differences among available data. Table 10 presents comparisons between the results of the present study and those of some other investigations of scent-marking in free-ranging canids.

Table 8. Number of Urine Marks Observed for Each Individual In the Gang of Four (See Text) at a Particular Place In Line When Marking in Succession

Place in line	Mother	Father	Helper	Juvenile
1st	27 (56.3%)*	26 (51.0%)	4 (25.0%)	0
2nd	11 (22.9%)	16 (31.4%)	4 (25.0%)	3 (60.0%)
3rd	8 (16.8%)	5 (9.8%)	7 (43.8%)	1 (20.0%)
4th	1 (2.1%)	3 (5.9%)	0	0
5th	0	1 (2.0%)	1 (6.3%)	1 (20.0%)
6th	1 (2.1%)	0	0	0
Total	48	51	16	5
Last	21 (43.8%)	27 (52.9%)	9 (56.3%)	1 (20.0%)
1st and last	6 (12.5%)	6 (11.8%)	0	0

*Percentage of total marks observed for each individual.

Differentiation of Elimination Postures

Of the four postures considered, raised-leg (RLU) and squat (SQU) urinations were most involved in marking according to the criteria used to differentiate marking from simple elimination. About 95% of all

RLU's and 88% of all SQU's were considered 'marking'. The relative frequency of marking compared to simple elimination might actually have been higher because sniffing accompanied by slight (or no) head movements would have gone undetected. Also, not all previous urinations were observed. We therefore believe that almost all urine deposits might be marks with respect both to an individual's 'intent' in depositing urine and to subsequent effects on recipients of the odour. Similar assumptions have also been made in snow-tracking studies. It should also be stressed that our results suggested that SQU's were more important in marking than previous studies have indicated.

Table 9. The Frequency Distribution of Group Marks, Raised-Leg Urinations, Squat Urinations, and Ground-scratches in Each of Six Quadrats Comprising the Home Range of the Gang of Four (See Text)

Quadrat	Den area		High intrusion* area			6	Total	χ^2	P
	1	2	3	4	5				
Group marks	1	3	7	8	15	5	39	18.4	0.01
RLU†	5	10	19	23	24	9	90	21.5	0.001
SQU	34	68	10	18	38	7	175	71.9	0.001
GS	10	9	7	10	16	3	55	9.9	NS**

*Area in which non-group-member coyotes crossed into the defended territory of the Gang of Four; quadrat 6 was a low-intrusion area.

†See Table 1 for legend.

** $P > 0.05$.

RLU's and SQU's were clearly distinguishable visually and also could be differentiated when we examined their respective associations with marking criteria. RLU's were associated significantly more with prior sniffing, subsequent ground-scratching, and the proportion of time that urine was directed at a previous urine deposit. Also, significantly more RLU's than SQU's were associated with all three criteria. A multivariate analysis (discriminant function analysis) showed that RLU's could be differentiated from SQU's using two major variables. First, as indicated above, RLU's were directed more frequently (proportionately) at other known urine signs. Second, when RLU's were performed, there were more coyotes present than when SQU's were performed. The roles of forward-lean urinations (FLU) and defaecations (DEF) in marking by coyotes were not clear, but neither seemed to be particularly important. Defaecation was not used in territorial demarcation and faecal piles (latrines) were not constructed except around carrion (see below), in contrast to what has been observed in some populations of golden jackals (*C. aureus*, Macdonald 1979a), spotted hyenas (*Crocuta crocuta*; Kruuk 1972; Bearder & Randall 1978), civets (*Civettictis civetta*; Bearder & Randall 1978), and European badgers (*Meles meles*; Kruuk 1978).

Table 10. A Summary of Wild Canid Scent-Marking Patterns

Species	Raised-Leg Urinations	Squat Urinations	Ground-Scratching	Location	Rate†	Season	Group size**	Group marking
Coyotes (this study)	Mainly performed by adult males; most frequent mark; deposited on any surface	Mainly performed by females who marked throughout the year	Always in association with (after) another mark, mostly RLU's; randomly distributed	RLU rate highest in intrusion area; SQU rate highest at den; GS rate random	RLU's: 2.5/h; SQU': 2/h; All: 5.5/h	RLU's, SQU's, GS's increased with increasing group size; no difference between single individuals and pairs	RLU's, SQU's, GS's increased with increasing group size; no difference between single individuals and pairs	Adult male and female marked 1st and last about equally; males GS more; GS usually performed by last coyote to mark
Coyotes* (Bowen & McT. Cowan 1980)			Mainly performed by adult males on edge of territory	Marking highest at territory edge, including GS	Dominant male: 12, 7/h; Dominant female: 6.6/h.	No difference, November to March		
Coyotes* (Barrette & Messier 1980)			Always in association with another mark		All. 2.17/h	No difference, November to March	Marking rate increased in groups larger than one	
Wolves, <i>C. Lupus</i> * (Peters & Mech 1975)	Mainly performed by dominant male and female; most frequent mark; deposited on vertical surface	Unimportant in marking	Only performed by high-ranking individuals	RLU's most frequent at Territory edge	RLU: 30/h	RLU and SQU rates higher in winter; GS rate, no change	RLU's did not increase with increase in group size	Female usually marked 1st, male last
Wolves* (Rothman & Mech 1979)	Occasionally performed by young animals		Only followed RLU's or DEF's, not SQU's; not done by loners				Marking increased during heterosexual pairing	Female usually marked 1st, male 2nd
Golden jackals, <i>C. aureus</i> (Golani & Keller 1975)								Female usually marked 2nd, male 1st
Bat-eared foxes, <i>Otocyon megalotis</i> (Lamprecht 1979)	Mainly performed by males	Mainly performed by females		Marking occurred throughout territory				Female usually marked 1st, male 2nd
Domestic dogs (Bekoff 1979a)	Mainly performed by males; most frequent mark	Mainly performed by females	Usually followed another mark; followed RLU's and SQU's about same proportion of time	Marking rate highest in areas where spent least amount of time	Males: 34/h; Females: 13/h			

*Snow-tracking studies.

†November to March only, except dog (Bekoff 1979a).

**Rates are for marks/individual.

Sex, Age, and Posture

There was clear sexual dimorphism with respect to the use of RLU's and SQU's (see also Kleiman 1966; Sprague & Anisko 1973; Beach 1974; Peters & Mech 1975; Bekoff 1979a). Although any individual was capable of performing any of the elimination postures, we found that the frequency distribution was skewed in such a way that we could assign conditional probabilities for the relationships among sex, age, and posture as follows. For example, given that a RLU was observed, the probability that it was performed by an adult male was 0.96, the probability that an adult female performed the behaviour was 0.04, and the probability that a juvenile performed it was 0. On the other hand, if a SQU was observed, the probabilities that it was performed by an adult male, an adult female, or a juvenile were 0, 0.96, and 0.04 respectively. All FLU's were performed either by adult males or juveniles. A principal components analysis added strength to the univariate analysis by showing that posture was not important without consideration of sex. Furthermore, the discriminant function analysis demonstrated that males were completely separated from females on a female/male discriminant axis, while only two of 31 female were incorrectly classified as males. The men (centroid) discriminant scores for the sexes were clearly separated ($D^2 = 5.47$; a similar analysis done on data presented in Bekoff 1979a for domestic dogs showed $D^2 = 5.70$). Additional discriminant function analyses showed that the sexes could not be discriminated on variables other than posture, though there were significant seasonal differences in marking rates between males and females (see below).

The trends in marking discussed above do not mean that there is necessarily little or no variation in the relationship between sex and posture. Indeed, very few other field data are available. In fact, in one captive study, Mottus (1969) never observed male coyotes to perform RLU's. However, the high probabilities associated with the major scent-marking behaviours may allow a researcher to estimate age and assign sex based on observations of elimination postures. In addition, one may now go back to snow-tracking studies to determine with caution the relationship between sex and different observed marking patterns for RLU's and inferred SQU's.

Snow Sign Analyses versus Direct Observations of Elimination

A major difference between the current study and others with which we are able to compare results stems from the fact that our data come from direct observation while other field studies of coyotes and wolves have had to rely on indirectly inferring the source of given urine sign in snow (e.g. what posture was used to produce the yellow snow). We do not mean to be overly critical of these other studies; rather we are calling attention to the fact that different methods have been employed that may result in disparate, as well as similar, conclusions concerning elimination patterns in wild canids. The limitations to snow-tracking are obvious and have been recognized by other researchers (Barrette & Messier 1980). Besides the fact that such studies are restricted to seasons when snow is on the ground and to regions where it snows, there is a problem associated with accurate post hoc association of a given posture with a specific snow sign. In only about 75% of all instances was an investigator lacking knowledge of the posture used to produce a particular scent-mark (though knowledgeable about snow sign patterns) able to identify accurately the posture that was used by domestic dogs to produce a particular pattern of yellow snow (Bekoff 1980). Similar verification data are not available for other canids. However, the difficulty of identifying postures from snow sign evidently led Barrette & Messier (1980) and Bowen & McT. Cowan (1980) to forego such analyses.

Our comparison between snow-tracking results and those obtained from year-round observation showed that while the same relative percentage of RLU's and FLU's were accounted for using either method, SQU's were grossly underestimated, while DEF's were greatly overestimated, by snow-tracking. (A comparison of snow-tracking data with winter observations showed that RLU's were also underestimated

using the former method.) It was unlikely that SQU's and DEF's were confused during observation because coyotes assumed the squat position when defaecating for a significantly longer period of time than when performing SQU's, and faeces could frequently be observed falling to the ground. The differences between snow-tracking and observational results make sense in that SQU's typically were directed toward the ground and could simply be overlooked while walking through deep snow. On the other hand, faecal piles were much more evident on white snow-covered ground than they were on grass or dirt. The relative frequency of ground-scratching inferred by snow-tracking (Barrette & Messier 1980; Bowen & McT. Cowan 1980) and observed by direct observation (this study; Sonntag 1977) is consistently reported to occur after about 25 to 35% of all marks, invariably following elimination.

Behavioural Context of Marking

Coyotes marked at different frequencies and rates during ongoing activity. While travelling, coyotes marked almost twice as frequently (corrected for the actual frequency of occurrence of different activities) as they did while hunting. With respect to the number of minutes between successive marks, coyotes marked about every 26 min while travelling and about every 78 min while hunting. Marking was also performed frequently during other food-related activities such as digging for carrion or rodents, eating, and while coyotes were at carrion. While resting, coyotes infrequently stood up and marked.

Sexual dimorphism was also noted when looking at the frequencies with which the different urination postures and defaecations were associated with ongoing activity, a phenomenon observed by Peters & Mech (1975) as well. In captive wolves (*C. lupus*), Peters & Mech (1975) found that a higher proportion of RLU's than of SQU's was associated with aggression, whereas the opposite relationship held for 'friendly' actions. RLU's were also more strongly associated with aggression for coyotes than were SQU's. However, we do not know if males were more aggressive than females. Neither posture was strongly linked to play or vocalization, the only other highly social activities. SQU's were more associated than RLU's with food-related behaviours such as hunting, eating, and directly marking food objects. However, SQU's and RLU's showed the same frequency distribution when coyotes marked in succession. Defaecation was performed proportionately more at carrion than any of the urination postures, producing a latrine effect also observed by Camenzind (1978) and Bowen & McT. Cowan (1980). Clumped faeces were not found elsewhere in coyotes' home ranges. The close association between DEF and lying down may simply be the result of a need to defaecate after rising from rest or sleep.

Our data suggested that during marking females may have important functions that are different from those associated with male marking and which may easily be overlooked, especially in snow-tracking studies which possibly deemphasize SQU's because of the difficulty of finding them. The patterns of association of RLU's and SQU's with various activities and seasons do suggest major functional differences between male and female marking. In general, SQU's by females were associated with the acquisition and possession of food, with the denning season, and with the location of the den itself. Females also performed SQU's as frequently in high-intrusion areas as around the den. High rates of marking around the den site may serve to develop and maintain site-specific familiarity for developing pups (see also Buchler 1980). RLU's; on the other hand, were associated with courtship and mating, with travelling, and with aggression and were performed mostly in areas of high intrusion by non-group members (see below). Therefore, male marking may be important functionally in promoting reproductive synchrony, demonstrating mate possession, and providing olfactory (and/or visual) signs about territorial boundaries.

Scent-marking was also associated with a change in behaviour about 25% of the time. A number of alternative explanations are possible concerning the relationship between behavioural changes and marking. First, the cues that triggered marking may also have been responsible for eliciting new

behaviour, such as travelling (and rotting, see below). For example, after marking, a coyote may travel and search for stimuli similar to the ones that released the initial marking. Second, scent-marking may also be performed as part of the completion of a particular activity, such as fighting or threatening, eating, or digging. In several mammalian species including some canids, aggression often follows marking, and marking may also comprise part of a threat display (Ralls 1971; Peters & Mech 1975; Macdonald 1980). We found the opposite trend: in coyotes aggression only rarely occurred after marking. With respect to behaviours associated with food, Henry (1977) found that red foxes (*Vulpes vulpes*) marked depleted food caches, possibly to avoid digging them up unnecessarily in the future even though food odours might persist (see also Korytin & Solomin 1969; Harrington 1981). Marking the sites at which food was previously eaten may fulfil the same function for coyotes. Also, digging by coyotes often uncovers depleted carrion stores; marking these could prevent digging them up once again. Finally, marking may be performed prior to the onset of, or as part of, an activity such as rolling (or scent rubbing; Reiger 1979). Kleiman (1966) suggested that rolling served to deposit body odours on objects or on the substrate. However, rolling may also be important in transferring scent from the environment to the body (Reiger 1979). Coyotes roll in many odoriferous substances such as cow dung, carrion, urine, and artificial scents, many of which are stronger than their own body odours. These strong odours may serve to release marking and rolling in sequence. Rolling may also be a comfort behaviour.

Seasonal Trends in Marking

Seasonal changes in marking rates were observed. Females, as well as males, marked throughout the year. The negative correlation between marking rate and the percentage of active time (standardized to account for coyote-hours of observation) suggested that there was a baseline level of marking and that as active time decreased, marking frequency increased to attain this level. When marking rates were plotted as a function of total observation time (in coyote-hours), seasonal variations were also apparent. The winter increase in marking by RLU's was associated with the onset of courtship (December) and extended through actual mating (late February). Similar trends have been observed for captive coyotes (Mottus 1972; Bekoff & Diamond 1976). For SQU's, the spring increase correlated with whelping and early pup rearing. As discussed above, it is highly likely that there is sexual dimorphism in marking functions for coyotes.

Although Peters & Mech (1975) found increases in both RLU's and SQU's for wolves during the winter, snow-tracking studies of coyotes have not documented increases in marking between November and March (Barrette & Messier 1980; Bowen & McT. Cowan 1980). Rothman & Mech (1979) indicated that marking was important for synchronizing mating in newly paired wolves. Our data, in agreement with Bowen & McT. Cowan's (1980) and Barrette & Messier's (1980) results, indicated that as a function of total time, seasonal changes in marking rates were small during the period of November to March. Major changes in marking rates actually occurred before and after the winter (breeding) period. Snow-tracking studies are unable to document the annual change in marking that we have detected.

One major factor that may account for the differences between our results and those based on snow tracking has to do with the fact that in snow-tracking studies, marking rates are measured in marks per kilometre, which is not truly a rate measure unless speed of movement is taken into account and/or the actual amount of time spent in an area is considered (Barrette & Messier 1980). Indeed, snow-tracking results for areas of marking by coyotes presented in terms of number of marks found per kilometer of tracking vary greatly. Ozoga & Harger (1966) reported overall rates of 0.89 marks per kilometre, while Bowen & McT. Cowan (1980), Barrette & Messier (1980), and Gipson & Sealander (1972) reported marking rates of 1.43, 2.17, and 5.47 marks per kilometre, respectively. Therefore, variations between our results stemming from direct observation and those obtained by snow tracking are not surprising.

Group Effects on Marking

We found, as did Barrette & Messier (1980) and Bowen & McT. Cowan (1980), that group size affected marking rates. When coyote group size was greater than two, marking rates per coyote increased. This is contrary to what Peters & Mech (1975) reported for wolves, for which there was no relationship between the number of snow-tracked animals (inferred group size) and marking rates. In wolves, marking is usually performed mainly by dominant individuals, and therefore the number of marking individuals is independent of group size (Peters & Mech 1975). Mottus (1972) reported that in captivity, dominant coyotes did not mark more frequently than other individuals. Our observations indicated that all coyotes in a group may mark, albeit at different rates.

The fact that coyote pairs did not mark more frequently than solitary individuals (marks/coyote; Table 7) suggested that variables other than group size were also important. For example, groups composed of females with competing male consorts may show higher marking rates per coyote than pairs living alone. The increase in group marking observed during the pair-bonding and mating seasons supports this suggestion. Along these lines, it should be noted that Barrette & Messier (1980) recorded higher marking rates (measured as marks per kilometre) for pairs (2.8) than for solitary (1.25) coyotes.

Marking by individual coyotes in succession was also studied in the Gang of Four pack. The parents marked equally frequently and did so about the same proportion of time both first and last in line. The male helper (Bekoff & Wells 1980) marked less frequently than his parents. However, he marked last in line proportionately the same amount as his parents. In 1979 he courted his mother but did not mate with her.

Ground-scratching was also affected by group size. The increase in ground-scratching we observed in groups of two or more animals when compared to the ground-scratching rate for solitary coyotes is consistent with the findings of Barrette & Messier (1980). Often discussed as a visual display (Muckenhirn & Eisenberg 1972; Seidensticker et al. 1973; Peters & Mech 1975; Bekoff 1979a, b; Bell 1980) or as part of a composite signal combining olfactory and visual cues (Bekoff 1979b), the act of ground-scratching may stimulate other coyotes to do likewise. In fact, all visual components of scent-marking actions may be major releasers for marking by nearby individuals (Golani & Keller 1975; Bekoff 1979a) and may be one reason for increased-scent marking per individual in larger groups. Consistent with these ideas are the facts that Barrette & Messier (1980) did not detect any ground-scratching by solitary coyotes and Bowen & McT. Cowan (1980) noted increased ground-scratching at the edge of territories, where a coyote could be observed either scratching or leaving a slash on the substrate where it was more likely to be encountered by potential intruders.

Spatial Distribution of Marks by Pack Members

Foremost in the mind of many researchers working in the area of chemical communication and scent-marking has been the possible role of marking in territorial behaviour, as suggested by Hediger (1949) and others. However, a good deal of the evidence linking marking with territorial behaviour is anecdotal (e.g. Johnson 1973), and in many cases there has been an overemphasis on the territorial functions of marking and less attention given to other, perhaps more important functions of marking (Eisenberg & Kleiman 1972; Butler & Butler 1979).

In the present study, we attempted to account for two possible sources of error in determining the relationship between marking and territorial behaviour. First, in many studies, territorial boundaries are determined by observation of very few actual agonistic encounters between resident animals and intruders, or no mention is made of the criteria used to define a territory. Radio-telemetry studies can

provide very useful information. However, in some cases it has been difficult to determine whether or not coyotes were territorial (Gipson & Sealander 1972) on the basis of information gathered from radio-tracking, and frequently the degree of resolution is not fine enough to demarcate boundaries. Because we have seen only 30 aggressive encounters between resident coyotes and non-group members, we did not attempt to delimit specific boundaries. Rather, we looked at intrusion rates in specific areas in the pack's home range and measured rates of marking in these locales. Second, as mentioned above, rate measures in other marking studies have been presented as marks per kilometre, which is not a measure of rate and does not account for time spent in a given area (Barrette & Messier 1980). We therefore measured the total amount of time (active and resting) spent by the pack in specific areas and calculated marking rates in these areas (marks/h).

We found that RLU's occurred most frequently in areas of high intrusion, which is in agreement with Peters & Mech's (1975) findings for wolves, and Camenzind's (1978) and Bowen & McT. Cowan's (1980) data for coyotes (see also Charles-Dominique (1977), Merti-Millhollen (1979) and Byers (1980) for comparative data). Although Bowen & McT. Cowan (1980) reported that ground-scratching occurred more frequently at the edges of territories, we found ground-scratching to be randomly distributed in space. No prior study determined the spatial distribution of SQU's; we found them to be about equally frequent in denning areas and in high-intrusion areas. Although we were unable to collect sufficient data on the amount of time spent by individual group members in a given area, unpublished data indicate that each coyote spent about the same amount of time in the three major areas. Therefore, RLU and SQU frequencies were not simply a reflection of time spent in a given locale.

Although there is some consistency among the results of snow-tracking and observational studies of coyote scent-marking, namely that there was a non-random distribution of RLU and group marks in areas of high intrusion (near territorial boundaries), the relationship between marking and territoriality in coyotes remains unclear. It is not known whether increased marking in high-intrusion areas was initially stimulated by the presence of other individuals or resulted in attracting them to these areas. Much has also been made of the use of scent-marks as an olfactory screen through which trespassers will not pass. Actually there is no solid evidence that this is the case (Scott 1967; Peters & Mech 1975; Bekoff 1979a; Rothman & Mech 1979; Bowen & McT. Cowan 1980). As noted by Owen-Smith (1977), scent-marks possess nothing in and of themselves to lead to avoidance of an area. Rather, it is the relationship between the individuals concerned that determines the response to marks. For lone wolves and trespassers, scent deposits may serve as signals to avoid a pack's territory (Peters & Mech 1975; Rothman & Mech 1979), but whether they are actually avoiding the pack's marks or the pack itself has not been determined. For coyotes, field observations (Bowen 1978; Camenzind 1978; Bekoff & Wells 1980) have indicated that neighbouring coyotes trespassed frequently, and there was no indication that scent deposits and/or areas around the deposits were avoided (urine sign may actually be attractive: Bowen & McT. Cowan 1980; this study). Rather, avoidance began when the resident coyotes themselves were encountered, and it is of importance that such encounters rarely lead to serious fights or injuries.

Based on our observations, we suggest that scent deposits do advertise territorial boundaries, but that the information may be used probabilistically in the following non-exclusive ways. First, odours may tell trespassers when they are trespassing and to avoid other coyotes when they are encountered. Second, odours may tell residents that they are in their own territory and to drive off other coyotes when encountered. Other cues such as environmental landmarks and vocalizations (Lehner 1978; Harrington & Mech 1979) also may be used for spatial orientation. Our conclusions are in agreement with those of Eisenberg & Kleiman (1972) and Walther (1978), who suggested that an important function of olfactory deposit is to help in orienting the movements of individuals in space.

Acknowledgments

This study was supported in part by NIMH (29571) and NSF (27616 and 23463) to M. Bekoff and by a Faculty Fellowship from the University of Colorado. We also wish to thank the administrators of the Grand Teton National Park for their cooperation during the course of our studies. V. Lipetz, A. Rathbun, C. Meaney, and J. Cook helped with observations. J. Mitton performed the principal component and discriminant function analyses. C. Barrette, P. Lehner, V. Lipetz, C. Meaney, and J. Byers provided helpful comments on an earlier draft of this manuscript; L. D. Mech suggested that we analyse the criteria associated with marking both singly and in a multivariate fashion. Katherine Thomas and Pat Holman typed the manuscript.

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