

## Scent-marking by coyotes, *Canis latrans*: the influence of social and ecological factors

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**Abstract.** We observed 49 coyotes, *Canis latrans*, from five resident packs for 2456 h and five transient coyotes for 51 h from January 1991 to June 1993 in the Lamar River Valley, Yellowstone National Park, Wyoming, U.S.A. During these observations we recorded 3042 urinations, 451 defecations, 446 ground scratches and 743 double-marks. The rate of scent-marking (via urination) was influenced by the social organization (resident versus transient) to which the coyote belonged, the social class (alpha, beta or pup) of the animal and the time of the year. Transient coyotes scent-marked at a lower rate than did members of a resident pack. Within the resident packs, alpha coyotes scent-marked at a higher rate than beta coyotes (adults and yearlings subordinate to alphas, but dominant over pups) and pups. Alpha coyotes increased their rate of marking during the breeding season; beta and pup coyotes performed scent-marks at a relatively constant rate throughout the year. There was no influence of social class or time of year on the rate of defecation. The rate of double-marking was highest among alpha coyotes with a peak during the breeding season. Alpha coyotes ground-scratched at a higher rate than did beta and pup coyotes. Alpha and beta coyotes scent-marked more than expected along the periphery of the territory compared to the interior; pups marked in the interior and edge in proportion to expected frequencies. Double-marking and ground-scratching were higher than expected along the periphery of the territory. The distribution of defecations was not different from expected along the edge versus the interior of the territory. Pack size did not influence the rate of scent-marking performed by individuals in the pack or by the alpha pair. We concluded that alpha coyotes were the primary members of the resident pack involved in scent-marking. The large coyote packs and the high rate of marking by the alpha pairs were parallel to the scent-marking behaviour displayed by wolves, *C. lupus*, to a greater extent than previously reported. Scent-marks appear to provide internal information to the members of the resident pack (internal map of territory, breeding condition, reproductive synchrony) and enhance demarcation of territorial boundaries.

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Scent-marking has been defined as the application of scented secretions and excretions by an animal to areas or objects in its environment (Barrette & Messier 1980; Bowen & Cowan 1980; Wells & Bekoff 1981). Among canids, scent-marking may serve as a mechanism for territory maintenance (Peters & Mech 1975; Rothman & Mech 1979; Bowen & Cowan 1980) or sex recognition (Dunbar 1977; Bekoff 1979), as a signal of empty food caches (Henry 1977; Harrington 1981, 1982),

as an indicator of sexual condition, maturity or synchrony (Bekoff & Diamond 1976), or as internal information to orient members of the resident pack (Wells & Bekoff 1981) and to dispersing animals entering occupied territories (Rothman & Mech 1979). Studies on scent-marking by coyotes, *Canis latrans*, have primarily been based upon interpretation of snowtracking (i.e. reading urine signs in the snow: e.g. Barrette & Messier 1980; Bowen & Cowan 1980). Only one study used direct observation of free-ranging coyotes (Wells & Bekoff 1981), showing that (1) males and females used different postures while marking, (2) rates of marking per coyote increased in packs larger than two coyotes, and (3) raised-leg urinations were deposited at a higher rate in areas of

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high intrusion. Wells & Bekoff (1981) concluded that differentiating between scent-marking and elimination was not necessary, that scent-marking by coyotes was important for spatial orientation of individuals and that, although scent-marking was greatest in areas of high intrusion, it does not restrict the movement of animals. Questions remain, however, regarding variations in scent-marking behaviour between different social organizations and among social classes within a resident pack.

Coyotes in Yellowstone National Park have not been persecuted since the late 1930s (Murie 1940). Hence, they are tolerant of a stationary observer, which has allowed unique behavioural observations to be made (Gese et al. 1996a, b, c). We analysed 2507 h of observation on 49 coyotes from five resident packs, as well as five transients, in Yellowstone National Park, Wyoming. In this study, we asked the following questions. (1) Is the rate of scent-marking influenced by sex, social class or the time of year? (2) Do coyotes of different social classes use different scent-mark postures? (3) Do coyotes of different social classes scent-mark the boundary disproportionately to the interior of the territory? (4) Do transients and residents scent-mark differently? (5) Does a division of labour exist among members of a coyote pack, and if so, does the rate of scent-marking by the alpha pair decrease in larger packs?

## STUDY AREA AND METHODS

The study area (70 km<sup>2</sup>) is in the Lamar River Valley in Yellowstone National Park, Wyoming, U.S.A. (44°52' N, 110°11' E), about 2000 m above sea-level. Long, cold winters and short, cool summers characterize the climate in the valley (Dirks & Martner 1982). Habitats within the study area are described in Gese et al. (1996a). Scent-marking behaviour was recorded during observations of coyote foraging ecology and predation (Gese et al. 1996a, b). Coyotes over 5 months of age were captured, weighed, sexed, ear-tagged and radio-collared, and the first vestigial premolar of the lower jaw was extracted for aging (Linhart & Knowlton 1967). Pups (8–12 weeks old) were captured at the den, ear-tagged, and surgically implanted with an intra-peritoneal transmitter. We classified coyotes by

age as pups (<12 months old), yearlings (12–24 months old) or adults (>24 months of age). Coyotes were also classified as residents if they displayed an affinity for one unique area or territory (Bowen 1978; Gese et al. 1988); otherwise, they were considered to be transients. Members of a resident pack were further classified by social classes, based upon the separate male and female dominance hierarchies observed in the pack (Gese et al. 1996a, b, c): alphas (dominant, breeding adults), betas (adults and yearlings that were subordinate to alphas, but dominant over pups) and pups (young-of-year that were subordinate to both alphas and betas).

The sampling design for the behavioural observations followed Gese et al. (1996a, b). We randomly sampled packs, and stratified individuals within each pack to allow for similar sampling of each sex and social class. We used focal-animal sampling (Lehner 1979), recording all behaviours for a single individual. Scent-marking events were recorded with a hand-held computer or on a tape recorder and transcribed later. We recorded the time and type of elimination event that the animal performed. All urinations and defecations were considered scent-marking events (Barrette & Messier 1980; Wells & Bekoff 1981) and were categorized as described by Wells & Bekoff (1981). Urination postures included raised-leg urination, squat urination, flexed-leg urination and standing urination, following the descriptions by Asa et al. (1985a; see also Camenzind 1978; Wells & Bekoff 1981; Bekoff & Wells 1986). We also recorded all defecations and ground-scratching (Kleiman 1966; Camenzind 1978; Wells & Bekoff 1981). We recorded whether the elimination occurred on the same site as scent-marking by another individual (i.e. a double-mark: Rothman & Mech 1979; Wells & Bekoff 1981), and whether the observed animal marked first or second. We defined a double-mark as a urination or defecation performed by two coyotes over the same site (usually within 10–15 s of one another). We standardized rates of scent-marking to the number of events per hour spent active (i.e. the coyote was considered active whenever it was not resting). Whenever possible, we recorded the location of scent-marking events to the nearest 10-m grid intersection using the Universal Transverse Mercator (UTM) grid system on a 1:24 000 U.S. Geological Survey topographic map.

**Table I.** ANOVA showing the influence of sex, social status, pack, and month on the rate of urinating, defecating, double-marking and scratching the ground, for resident coyotes in Yellowstone National Park, Wyoming, January 1991 to June 1993

Source	df	Rates of									
		Urination (No./h active)		Urination (No./h observed)		Defecation		Double-marking		Ground scratching	
		F	P	F	P	F	P	F	P	F	P
Sex*	1	0.95	0.330	0.11	0.741	0.44	0.506	0.30	0.584	4.00	0.047
Status†	2	51.12	<0.001	34.02	<0.001	1.67	0.19	32.43	<0.001	9.45	<0.001
Pack‡	4	1.81	0.130	1.31	0.266	0.46	0.768	0.66	0.619	1.68	0.156
Month§	9	3.18	<0.001	3.68	<0.001	0.99	0.445	6.28	<0.001	1.39	0.197
Error	158										

\*Male or female.

†Alpha, beta, or pup.

‡Bison, Druid, Fossil Forest, Norris or Soda Butte.

§October–July.

The sampling unit for all statistical tests was the individual coyote observed each month (Machlis et al. 1985). The influence of sex, social class within the dominance hierarchy, pack and season (months) on the rates of urination, defecation, double-marking and ground-scratching were analysed using multi-way analyses of variance (ANOVA) with mixed models examining only the main effects. An ANOVA with repeated measures was not used because many coyotes died, dispersed or were not observed in every month. All ANOVAs were performed using SYSTAT (Wilkinson et al. 1992) following a factorial design (Steel & Torrie 1980; Sokal & Rohlf 1981). A Tukey's test was performed where one-way ANOVA indicated differences between sexes, among social classes, packs, or months. Chi-square tests and Student's *t*-tests followed Steel & Torrie (1980).

## RESULTS

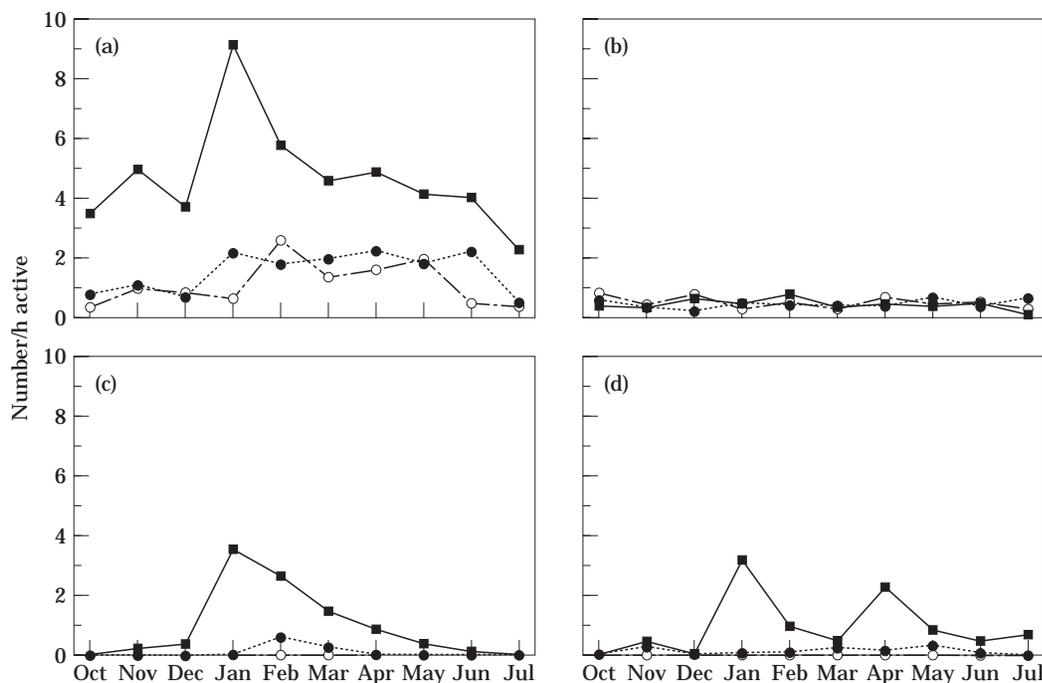
We observed 54 coyotes (49 residents from five packs, plus five transients) for 2507 h from January 1991 to June 1993. We observed 11 members of the Bison pack for 498 h, nine coyotes in the Druid pack for 432 h, 11 individuals of the Fossil Forest pack for 593 h, 10 members of the Norris pack for 463 h, and eight coyotes in the Soda Butte pack for 470 h. We observed five transient animals for 51 h. During this time, we observed 3042 urinations, 451 defecations, 446

ground-scratches and 743 double-marks. Of the urinations, we recorded 1448 squat urinations, 894 raised-leg urinations, 384 standing urinations and 316 flexed-leg urinations.

### Influence of Sex, Social Class and Season

The rate at which coyotes were observed scent-marking, via urination, was influenced by the social class of the coyote and the month of the year (Table I). Overall, alpha, beta and pup coyotes scent-marked at a rate of 5.1, 1.7 and 1.4 marks/h active, respectively. Alpha coyotes scent-marked at a higher rate than betas (Tukey's test:  $P < 0.001$ ) and pups (Tukey's test:  $P < 0.001$ ) throughout the year; betas and pups scent-marked at a similar rate (Tukey's test:  $P < 0.74$ ). Among alpha coyotes, we observed the highest rate of scent-marking during the breeding season (January; Tukey's test:  $P < 0.03$ ), and the lowest prior to breeding and in the summer (May–July; Fig. 1a). Beta and pup coyotes scent-marked at a similar rate throughout the year (betas:  $F_{9,57} = 1.02$ ,  $P = 0.43$ ; pups:  $F_{8,30} = 1.90$ ,  $P = 0.10$ ; Fig. 1a).

Behavioural budgets of coyotes varied under different environmental conditions (Gese et al. 1996a). Thus, we also examined whether seasonal (monthly) changes in the rate of scent-marking may be explained by differential time-activity budgets (i.e. whether coyotes scent-mark more during winter due to reduced activity). We found the same results and monthly pattern among the



**Figure 1.** The rate (number/h active) of (a) urinations, (b) defecations, (c) double-marks and (d) ground-scratches, for alpha (—■—), beta (—●—) and pup (—○—) coyotes from October to July, Yellowstone National Park, Wyoming, 1991–1993.

social classes using either the number of marks per hour active or per hour observed (Table I). We concluded that variation in coyote activity patterns did not explain the different rates of scent-marking among the social classes from October to July.

In contrast to the urination rate, the rate of defecation by coyotes was not influenced by sex, social class, pack or the time of the year (Table I). The defecation rate of coyotes remained relatively constant throughout the year between the sexes, and among the social classes and packs (Fig. 1b). Alpha, beta and pup coyotes defecated at a rate of 0.5, 0.5 and 0.8 defecations/h active, respectively.

The rate at which coyotes double-mark in their territory was influenced by the social class of the animal and the month of the year (Table I). Overall, alphas, betas and pups double-marked at a rate of 1.3, 0.1 and 0 double-marks/h active, respectively. For all months combined, alpha coyotes double-marked at a significantly higher rate than betas (Tukey's test:  $P < 0.001$ ) and pups (Tukey's test:  $P < 0.001$ ); betas and pups double-marked at a similar rate (Tukey's test:  $P = 0.82$ ).

Alpha coyotes double-marked at the highest rate in January and February (Tukey's test:  $P < 0.01$ ; Fig. 1c). Beta coyotes did not significantly change their rate of double-marking through the year ( $F_{9,57} = 1.64$ ,  $P = 0.12$ ). Pup coyotes were not observed double-marking (Fig. 1c). Of the 743 double-marks observed, 94% ( $N = 696$ ) were performed by alphas. The rate of double-marking was not influenced by the sex of the coyote, but the frequency of which sex scent-marked first did vary. Among the alpha coyotes, females initiated the double-mark 75.4% of the time, and alpha males initiated the double-mark 24.6% of the time ( $\chi^2_1 = 80.77$ ,  $P = 0.0001$ ). Among the beta coyotes, males and females initiated double-marking equally (males: 47.8%; females: 52.2%;  $\chi^2_1 = 0.04$ ,  $P = 0.83$ ).

The rate of ground-scratching following a scent-mark by coyotes was influenced by the sex and social class of the coyote (Table I). Alpha males ( $\bar{X} \pm \text{SD} = 1.6 \pm 3.3$ ) scratched the ground at a higher rate than did alpha females ( $0.6 \pm 0.6$ ; Tukey's test:  $P = 0.07$ ), particularly during April and May when the females whelped and began

**Table II.** Percentage of four urination postures among alphas, betas and pups for female and male coyotes, Yellowstone National Park, Wyoming, January 1991 to June 1993

Posture	Females			Males		
	Alpha	Beta	Pup	Alpha	Beta	Pup
Standing	0.8	0.7	4.1	14.5	41.0	51.8
Raised-leg	0.2	0	0	77.8	30.9	10.6
Squat	92.4	92.9	86.6	0.2	2.4	9.4
Flexed-leg	6.6	6.4	9.3	7.4	25.6	28.2

nursing pups (alpha males: 3.4 scratches/h versus alpha females: 0.8 scratches/h; Tukey's test:  $P=0.05$ ). Overall, alphas, betas and pups scratched the ground following a scent-mark at a rate of 1.1, 0.2 and 0 scratches/h active, respectively. Among the social classes, alpha coyotes scratched the ground following a scent-mark at a rate higher than betas (Tukey's test:  $P=0.001$ ) and pups (Tukey's test:  $P=0.001$ ); beta and pup coyotes did not significantly differ in the rate of ground-scratching (Tukey's test:  $P=0.86$ ). The time of year did not influence the rate of ground-scratching among alpha or beta coyotes, respectively ( $F_{8,60}=1.54$ ,  $P=0.16$ ;  $F_{9,57}=0.95$ ,  $P=0.48$ ; Fig. 1d). Pup coyotes were not observed scratching the ground following a scent-mark.

### Different Postures While Scent-marking

The proportion of different postures (squat urination, flexed-leg urination, standing urination and raised-leg urination) displayed while scent-marking via urination varied among the two sexes and three social classes (Table II). Males typically performed raised-leg urinations (59.7%) and standing urinations (24.7%); females usually displayed squat urinations (92.1%) and flexed-leg urinations (6.8%;  $\chi^2_3=2612.99$ ,  $P=0.0001$ ). Among males, the percentage of the four urination postures differed among the social classes. Alpha males usually performed raised-leg urinations, beta males typically displayed standing urinations, raised-leg urinations or flexed-leg urinations, while pups performed standing urinations or flexed-leg urinations ( $\chi^2_6=399.86$ ,  $P=0.0001$ ). Among the female coyotes, alphas, betas and pups all performed squat urinations most of the time, with female pups also using the flexed-leg

urination and standing urination postures more frequently than alphas and betas ( $\chi^2_6=12.67$ ,  $P=0.048$ ; Table II).

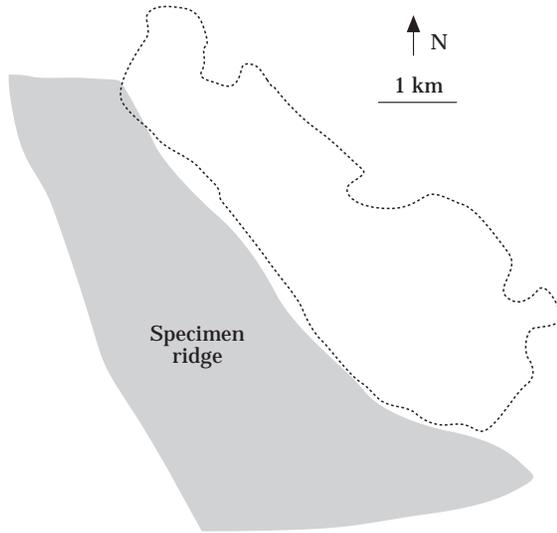
### Scent-marking on the Periphery Versus the Interior of Territory

We used the members of the Fossil Forest pack ( $N=574$  marks) to examine the frequency of scent-marking in the interior versus the periphery of a territory. The Fossil Forest pack occupied an area in the valley allowing for almost complete viewing of their entire territory (i.e. we maintained visual contact with a member of the pack 97% of the time during 593 h of behavioural observations). Their territory abutted Specimen Ridge, which is an escarpment of extremely steep terrain and cliffs unsuitable for occupation by coyotes (Fig. 2a); hence no adjacent coyote territory was present along their western border. We defined the periphery of the territory as a zone within 250 m of the territorial boundary (Bowen & Cowan 1980). This periphery or boundary zone comprised 26% of the area of the territory (i.e. 26% of scent-marks would be expected to be found in the periphery). Due to the lack of an interface with an adjacent pack along the western boundary, we did not classify this area as the periphery.

The frequency of scent-marks in the interior versus the periphery was influenced by the social class of the coyote (Fig. 2b–d). Alpha coyotes scent-marked along the periphery (49% of the marks) of the territory at a frequency greater than expected compared to the interior (51%) ( $\chi^2_1=113.57$ ,  $P=0.0001$ ). Beta coyotes also scent-marked along the periphery (48%) at a frequency greater than expected compared to the interior (52%) of the territory ( $\chi^2_1=26.61$ ,  $P=0.0001$ ). In contrast, pups scent-marked the periphery (24%) and interior (76%) as expected ( $\chi^2_1=0.06$ ,  $P=0.81$ ).

The frequency of different types of scent-marks also varied between the periphery and the interior of the territory. Double-marks were significantly more frequent along the periphery (66%) than in the interior (34%;  $\chi^2_1=144.72$ ,  $P=0.0001$ ; Fig. 2e). Ground-scratching was similarly more frequent along the periphery (74%) than in the interior (26%) of the territory ( $\chi^2_1=74.84$ ,  $P=0.0001$ ; Fig. 2f). The coyotes in the Fossil Forest pack did not ground-scratch along their western boundary where no adjacent pack existed (Fig. 2f), although they did urinate along the western border

(a) Fossil forest territory



(b) Alphas



(c) Betas



(d) Pups



(e) Double-marks



(f) Scratch ground



**Table III.** Daily rate (number/h active) of scent-marking events in the core and along the periphery of the territory for alpha, beta and pup coyotes of the Fossil Forest pack, Yellowstone National Park, Wyoming, January 1991 to June 1993

Social class	Rate of scent-marking						<i>t</i>	<i>df</i>	<i>P</i>
	Inside the core			Along the periphery					
	$\bar{X}$	SD	<i>N</i>	$\bar{X}$	SD	<i>N</i>			
Alphas	2.7	3.0	49	6.0	6.6	35	-3.039	82	0.003
Betas	1.7	1.7	26	1.2	2.3	19	0.834	43	0.409
Pups	0.5	0.9	31	0.9	1.6	14	-1.033	43	0.307

(Fig. 2b-d). Raised-leg urinations, mostly displayed by alpha males and to a lesser extent by beta males (Table II), were more frequent than expected along the periphery (48%) than in the interior (52%;  $\chi^2_1=35.12$ ,  $P=0.0001$ ). Squat urinations, displayed by all females, were also more frequent along the periphery (52%) than in the interior (48%;  $\chi^2_1=88.30$ ,  $P=0.0001$ ). In contrast, standing urinations, most commonly displayed by pup males and beta males, were not distributed differently from expected along the periphery and in the interior ( $\chi^2_1=1.01$ ,  $P=0.31$ ). Flexed-leg urinations, often displayed by beta males and pup males, were performed more than expected along the boundary (65%) than in the interior ( $\chi^2_1=29.05$ ,  $P=0.0001$ ). Defecations were not distributed differently from expected. The frequency of defecations along the periphery was 27% and in the interior was 73% ( $\chi^2_1=0.05$ ,  $P=0.82$ ).

In the previous analysis, we considered the amount of area as the expected value. We also examined whether the time spent in the core versus the periphery of the territory influenced the distribution of scent-marks. Members of the Fossil Forest pack spent 33% of their time along the periphery. Using 33% as our expected frequency, we found results similar to the findings using the percentage of the area. Based upon the time spent in the core versus periphery, alpha and beta coyotes both scent-marked more along the edge than in the interior (alphas:  $\chi^2_1=47.48$ ,  $P=0.0001$ ; betas:  $\chi^2_1=10.99$ ,  $P=0.0009$ ). The distribution of scent-marks by pups was as

expected ( $\chi^2_1=1.72$ ,  $P=0.19$ ). Ground-scratches and double-marks were distributed more than expected along the periphery ( $\chi^2_1=47.58$ ,  $P=0.0001$ ;  $\chi^2_1=86.13$ ,  $P=0.0001$ , respectively). Defecations were distributed along the edge and in the interior as expected ( $\chi^2_1=1.35$ ,  $P=0.24$ ). Among the different urination postures, raised-leg urinations ( $\chi^2_1=13.95$ ,  $P=0.0002$ ), squat urinations ( $\chi^2_1=41.29$ ,  $P=0.0001$ ), and flexed-leg urinations ( $\chi^2_1=16.99$ ,  $P=0.0001$ ) were distributed along the periphery more than expected. Standing urinations were distributed as expected between the time spent along the edge versus inside the core ( $\chi^2_1=0.26$ ,  $P=0.60$ ).

Not only did the distribution of scent-marks vary between the interior and periphery of the territory, but the rate of scent-marking also varied between the two areas. Alpha coyotes in the Fossil Forest pack scent-marked at twice the rate along the periphery of the territory compared to within the core area (Table III). The rate at which beta and pup coyotes scent-marked along the edge versus the periphery was not significantly different.

#### Scent-marking by Resident Versus Transient Coyotes

Due to a limited sample of behavioural observations on transient coyotes ( $N=51$  h), our analysis consisted of a direct comparison of all residents versus transients. We observed that

**Figure 2.** The location of (a) the Fossil Forest territory boundary, (b) scent-marks by alpha coyotes, (c) scent-marks by beta coyotes, (d) scent-marks by pup coyotes, (e) double-marks, and (f) ground-scratches, Fossil Forest pack, Yellowstone National Park, Wyoming, 1991-1993.

residents scent-marked at a higher average rate (3.0 marks/h active) than transient coyotes (0.2 marks/h active;  $t_{52}=3.502$ ,  $P=0.001$ ). Average defecation rates of resident (0.5 defecations/h active) and transient coyotes (0.3 defecations/h active) were not significantly different ( $t_{52}=1.778$ ,  $P=0.08$ ). Resident coyotes scratched the ground following a scent mark 0.5 times/h active; transients were not observed scratching the ground. Rates of double-marking for resident and transient coyotes were 0.4 and 0.03 double-marks/h active, respectively ( $t_{52}=1.532$ ,  $P=0.132$ ). The finding of no significant difference is due to low rates of double-marking by betas and to pups not double-marking. When we compared the three social classes within a resident pack versus transients, we found that transients double-marked at a rate significantly less than alphas (Tukey's test:  $P=0.007$ ), but not differently from betas (Tukey's test:  $P=0.99$ ) and pups (Tukey's test:  $P=0.99$ ). Female transients performed squat urinations, but male transients were not observed to perform raised-leg urinations; instead, they displayed either standing urinations or flexed-leg urinations similarly to resident betas and pups.

#### Scent-marking by Philopatric Versus Dispersing Coyotes

Gese et al. (1996c) found that dispersing coyotes, compared to philopatric individuals, were low-ranking individuals, had little access to carcasses, spent less time with other pack members and appeared to voluntarily leave their pack due to nutritional and social factors. Thus, we were also interested in examining whether dispersers, prior to their dispersal move, scent-marked less than philopatric individuals (i.e. if they were dispersing, would they contribute to the duties of scent-marking?). We compared the rate of scent-marking of both dispersers and philopatric coyotes, as identified by Gese et al. (1996c). The values reported for the dispersing coyotes are the rates of scent-marking during the 2 months preceding their dispersal move. Philopatric coyotes scent-marked at an average rate of 1.5 marks/h active, and dispersers marked an average of 1.6 marks/h active ( $t_{36}=0.105$ ,  $P=0.92$ ). We concluded that coyotes which later dispersed from their resident pack scent-marked similarly to animals that remained home.

#### Influence of Pack Size

The formation of large coyote packs allows for shared duties of territorial defence, food acquisition and the defence and care of offspring (Bowen 1978; Camenzind 1978; Bekoff & Wells 1986). Wells & Bekoff (1981) found that scent-marking rates per animal were higher in groups with more than two coyotes. Using regression analysis, we examined the rate of individual scent-marking versus pack size for each month of the year. Pack size included only coyotes over 4 months of age (pups were not mobile and hence were unable to contribute to scent-marking duties until 4 months of age). The rate of scent-marking by each coyote was independent of pack size ( $R^2=0.008$ ,  $F_{1,160}=1.265$ ,  $P=0.262$ ). We also examined this question from a different perspective: if duties of scent-marking are equally shared among pack members, then alpha pairs in large coyote packs should scent-mark less than alpha pairs in small packs. We have already demonstrated that the alpha members of a coyote pack scent-mark at a higher rate than beta and pup coyotes. We further examined the influence of pack size on scent-marking by the alpha pair by regressing the monthly pack size versus the monthly rate of scent-marking by the alpha pair. There was no relationship between the size of the coyote pack and the rate of scent-marking by the alpha pair ( $R^2=0.008$ ,  $F_{1,95}=0.773$ ,  $P=0.382$ ). We concluded that the rate of scent-marking by individuals in the resident pack, as well as by the alpha pair, was independent of pack size.

#### DISCUSSION

Scent-marking among carnivores probably serves to signal reproductive condition and maturity and may act as a mechanism for reproductive synchrony between the breeding pair. We found that the social class of the coyote and the time of the year influenced the rate of scent-marking. Breeding alpha coyotes scent-marked at a higher rate than both beta and pup coyotes. Among the alpha coyotes, the rate of scent-marking peaked during the breeding season when pair bonds are strengthened and breeding is initiated (Bekoff & Diamond 1976; Kennelly 1978). The lack of a similar change in the rate of scent-marking among the beta and pup coyotes suggests that scent-marking is strongly related to maintenance of the pair bond

and the synchrony of breeding behaviour between the alpha pair (Bekoff & Diamond 1976; Bekoff & Wells 1986). Urine from female coyotes entering proestrous became increasingly attractive to male coyotes (Bekoff & Diamond 1976), possibly conveying female reproductive condition and receptivity to the male. Many compounds deployed during scent-marking (Raymer et al. 1984, 1986; Asa et al. 1985b) convey information about the sender and elicit specific behavioural responses from the recipient (Asa et al. 1990). Among wolves, *C. lupus*, urine-marking by dominant wolves changed seasonally and was correlated with changes in testosterone during the breeding season (Asa et al. 1990). Rothman & Mech (1979) found an increase in scent-marking by newly formed pairs of wolves, which then declined in a few months to the level found in established pairs, suggesting that scent-marking played a role in establishing the pair bond.

The rate of double-marking was significantly influenced by the social class of the animal and the time of year. Alpha coyotes double-marked at a higher rate than both beta and pup coyotes, which peaked in January. The low rate of double-marking by betas and transients, and the lack of double-marks by pups, indicated that double-marking was important in pair bond formation and reproductive synchrony between members of the alpha pair. The finding that the alpha females initiated 75% of the double-marks, in contrast to the alpha males initiating 25%, also indicated that female scent-marks may attract males (Bekoff & Diamond 1976) and act as a mechanism for reproductive synchrony between the female and male. Similarly, Rothman & Mech (1979) concluded that the visual and olfactory stimulus of double-marking served to synchronize breeding behaviour and reproductive physiology among pairs of wolves. Double-marking between members of the breeding pair could also play a role in mate guarding. In one duetting bird species, initiation of a duet by the female acted as a message to other females of occupied territory, and the reply by the male served as a means of guarding their mate from other males (Levin 1996a, b). Perhaps double-marking plays a multifunctional role (reproductive synchrony, pair bond behaviour, territory defence and mate guarding) in the coyote social system.

Scent-marking by carnivores appears to influence demarcation of territorial boundaries and

provide internal information to members of the resident group or pack. Alpha and beta coyotes scent-marked more frequently along the periphery than in the interior of the territory; pups marked in the proportion expected. The finding that the pack members scent-marked inside the territory suggests that information was also conveyed via these internal marks. Double-marks and ground-scratching were also more frequent along the edge. However, defecations were not more frequent than expected along the edge. In contrast to our findings, Wells & Bekoff (1981) observed that ground-scratches were randomly distributed, but that scent-marking events were highest in areas of intrusion. We conclude that alpha and beta coyotes scent-marked more frequently in areas of high intrusion but still marked in the territory, and suggest that these scent-marks probably provided internal information for resident pack members. Although scent-marks may deter some coyotes from entering a territory, scent-marking along the edge does not completely prevent intrusion into the territory. Physical confrontation was also used when expelling intruders from the territory (E. M. Gese, unpublished data).

The rate of defecation was relatively constant among the social classes and throughout the year. Combined with the finding that defecations were distributed along the periphery and within the interior in proportion to the expected frequency, we conclude that defecations had relatively little value as an implement of scent-marking for coyotes in the Lamar Valley. Wells & Bekoff (1981) similarly concluded that defecations were not used in territorial demarcation. Asa et al. (1985a) speculated that urine may be a better implement for scent-marking because faeces may not be as available for deposition as urine due to the irregular feeding habits of wolves.

The rate of scratching the ground was significantly different among the three social classes. Alpha coyotes scratched the ground at a higher rate than both beta and pup coyotes. Alpha males ground-scratched at a higher rate than alpha females, similar to findings by Bowen & Cowan (1980). Ground-scratching by alphas peaked during January and April, similar to findings by Wells & Bekoff (1981). Increased ground-scratching during the breeding season apparently signals early stages of pre-copulatory behaviour in coyotes (Bekoff & Diamond 1976) and golden jackals, *C. aureus* (Golani & Mendelsohn 1971).

Ground-scratching also probably provides a visual cue of territorial boundaries to other coyotes. The finding that alpha males ground-scratched at a higher rate may be a mechanism of border enforcement. Alpha males lead most attacks when defending the territory against intruders (E. M. Gese, unpublished data). Perhaps scents dispersed by the alpha male during ground-scratching serve to identify that animal, allow other members of the pack to recognize the boundaries and inform intruders of territorial borders. Pups did not ground-scratch and were rarely observed evicting intruders by themselves, suggesting that ground-scratching conveys an element of social dominance to coyotes investigating that mark. Transient coyotes also did not ground-scratch and did not defend a territory.

As reported for other canid species (Kleiman 1966; Peters & Mech 1975), sexual dimorphism was evident with respect to urination postures. We recorded four urination postures, similar to those reported for wolves (Asa et al. 1985a); Wells & Bekoff (1981) reported three postures. Alpha males predominantly performed raised-leg urinations, and alpha females used squat urinations. Male betas and pups performed raised-leg urinations at a much lower frequency than the alpha males and typically performed standing urinations. Wells & Bekoff (1981) reported similar results for adult males, adult females and juveniles, but did not discriminate between the frequency of postures among various social classes. Although all individuals are capable of performing each of the postures, the reason for sexual dimorphism is not understood. Different postures appear to be correlated with certain behaviours: squat urinations by females were associated with food and denning, and raised-leg urinations performed by males were correlated with courtship, aggression and travel (Wells & Bekoff 1981).

Transient individuals scent-marked little compared to the resident coyotes, did not ground-scratch following a scent-mark and rarely double-marked. Furthermore, male transients were not observed to perform raised-leg urinations. Barrette & Messier (1980) similarly observed no ground-scratching among solitary coyotes and noted that packs scent-marked at twice the rate of non-territorial animals. Since scent-marking acts as a territorial marker, the finding that transients marked so little was not surprising. Transients

were typically lone individuals with no mate and did not defend a territory. Thus, double-marking and ground-scratching would serve little purpose among transient coyotes. The finding that transient males did not perform raised-leg urinations suggests that this posture may serve as an indication of social dominance, breeding condition and territorial enforcement. Rothman & Mech (1979) similarly reported that lone wolves rarely scent-marked by raised-leg urination.

Scent-marking by canids may also indicate empty food caches. Of 62 food caches emptied by coyotes, they urinated over 34 (55%) of them. In contrast, coyotes urinated on only one (6%) of 18 newly constructed food caches. Using urine to mark an empty food cache was very common among red foxes, *Vulpes vulpes* (Henry 1977), captive wolves and coyotes (Harrington 1981, 1982). Young & Jackson (1951) reported that coyotes often urinated on their food prior to consumption as a method of proclaiming ownership; we did not observe this behaviour.

Wells & Bekoff (1981) found that the group size of coyotes affected the rate of individual scent-marking. We found that the pack size did not influence individual rates of scent-marking. We also found no relationship between the pack size and the rate of scent-marking performed by the alpha pair. Thus, coyotes in the Lamar Valley behaved more similarly to wolves (Peters & Mech 1975), where the duties of scent-marking are performed mainly by the dominant animals. The coyote packs in Yellowstone ranged from three to 10 individuals, in contrast to the pack of four coyotes observed by Wells & Bekoff (1981); this difference in pack size may explain why the packs we observed behaved, with regard to scent-marking, more similarly to a wolf pack.

Observations of animals in the wild and in captivity have demonstrated the importance of chemical communication, and the relationships between scent-marking and social organization and space-use patterns (Ralls 1971; Brown & Macdonald 1986). We believe that, although the coyote has at times been viewed as a moderately social canid (Fox 1975), our results demonstrate the plasticity of the coyote social system. We observed large packs of coyotes in Yellowstone that showed scent-marking behaviour similar to wolves and other large, social carnivores. Studies of canids (Peters & Mech 1975; Henry 1977; Wells

& Bekoff 1981), felids (Schaller 1972; Smith et al. 1989) and hyaenas (Mills et al. 1982; Gorman & Mills 1984) have shown that, in general, (1) territorial carnivores will scent-mark more along the edge of their territory, (2) residents tend to perform the majority of the scent-marking in a population, (3) dominant members of social groups will scent-mark more frequently than subordinates, and (4) scent-marks consist of both odour and visual cues. We concur with conclusions that scent-marking in carnivores probably serves to establish reproductive synchrony between breeding individuals, provides internal cues and spatial orientation to members of the resident group or pack, and serves as an indicator of territorial demarcation to intruding animals (Eisenberg & Kleiman 1972; Ewer 1973; Gosling 1986). Scent-marks, in particular double-marks, may also act as messages to conspecifics and function in mate guarding, in a similar way to that reported for bird species that participate in duets (Levin 1996a, b). These scent-marks do not exclusively prevent the movement of other packs or intruding animals from crossing territorial boundaries (Peters & Mech 1975; Wells & Bekoff 1981; Smith et al. 1989). They still may, however, serve as subtle repellents eliciting avoidance by potential intruders.

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