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SCENT MARKING AND USE OF SPACE BY COYOTES IN A MIXED FOREST REGION OF MANITOBA

by

L. SCOTT MCKINLAY

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

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THE UNIVERSITY OF ALBERTA

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled SCENT MARKING AND USE OF SPACE BY COYOTES IN A MIXED FOREST REGION OF MANITOBA submitted by L. SCOTT MCKINLAY in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE.

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ABSTRACT

The scent marking behaviour of coyotes (Canis latrans), as it relates to habitat preferences and territorial defense, was examined during the winters of 1985-86 and 1986-87 in an area adjacent to Riding Mountain National Park, Manitoba. Data collected from 132.3 km of snow tracking revealed that coyotes deposited urine at an average rate of 3.0 scent marks per coyote per kilometer. Individual scent marks, multiple scent marks, scratches, and scats were deposited at least twice as frequently in coniferous as in non-coniferous habitats. These higher scent marking rates corresponded to a preference by coyotes for coniferous cover, and presumably resulted from a higher rate of encounter with previously deposited urine marks in these more heavily travelled areas.

Adult resident coyotes occupied home ranges of between 8.9 and 18.3 km^2. Although scent marking rates did not differ significantly between the peripheries and centres of these ranges, average rates were higher than those observed at territory edges in other studies. High annual mortality, of up to 72%, appears to have caused yearly shifts of home range boundaries, and is presented as a possible explanation for the observed deviation from previously reported patterns of territorial scent marking. All coyotes >1 year old that normally travelled in pairs or groups appeared to scent mark regularly. Individual scent marking rates did not change significantly during the winter months; however, multiple scent marks and scratches showed pronounced peaks during the mating season (January-February).

Coniferous stands had lower snow depths than any other habitat, and were the preferred habitat of coyotes. Deciduous woods and thickets were under-utilized by coyotes and had the deepest snow. Conifer stands were also the favoured habitat of white-tailed deer (Odocoileus virginianus), the primary winter food of these coyotes. Use of roadways, open areas, and frozen waterways declined after the formation of snow crusts in late winter, suggesting that these habitats were used primarily for ease of travel during periods of soft, deep snow. Bed sites were most common in coniferous areas and thickets. Shelter from the wind and exposure to solar radiation appeared to be of primary importance in the selection of bed sites by coyotes.

Environmental factors, such as habitat availability, snow conditions, and perhaps human predation, are important factors influencing the travel patterns of coyotes and, ultimately, the distribution of their scent marks.

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I. INTRODUCTION

Understanding how an animal communicates with conspecifics is basic to better our understanding of its behaviour. For instance, we can know very little about the spacing behaviour or mate acquisition of a song bird, without first examining the communicative role of its song(s) and brightly coloured plumage.

In coyotes (*Canis latrans*), as well as other canids, communication with conspecifics can be visual, auditory, tactile, or olfactory in nature (Lehner 1978). Unique among these modes of communication is scent marking; the message, in the form of urine, glandular secretions, or feces, persists in the environment long after the message sender has left the area. This type of communication allows a canid to be "present" throughout many parts of its home range simultaneously. Although most researchers agree that scent marking serves several functions, territorial defense has traditionally been considered the primary function of such behaviour (Schenkel 1947, Lorenz 1954, Kleiman 1966).

Despite widespread acceptance of the territorial defense hypothesis for scent marking, there was little quantitative data to support it until Peters and Mech (1975) conducted their snow tracking studies of radio-collared wolves (*Canis lupus*) in Minnesota. They discovered that wolves deposited urine more frequently per kilometer near territorial boundaries than in the central regions of their territories. Bowen and McTaggart Cowan (1980) followed with similar studies on coyotes, and reached the same conclusion. Wells and Bekoff (1981) quantified the distribution of scent marks by coyotes in marks per hour rather than marks per kilometer, but obtained results comparable with those of previous studies. Scent marks were most concentrated near territorial boundaries in areas where neighbouring conspecifics frequently intruded.

Such findings are not universal however. In Manitoba, Carbyn (1980) examined the spatial distribution of scent marking in wolves by dividing the territory into three concentric rings, corresponding roughly to the centre, mid-region, and periphery of the territory. The number of scent marks per kilometer did not differ between the peripheral and central zones, and was highest in the mid-region. Carbyn (1980) suggested that the differences in observed scent marking patterns between his and other studies may have resulted from frequent shifts in territorial boundaries of wolf packs within the Manitoba population. Clearly more studies are required to determine if marking of territorial boundaries is universal among canid populations living under various social and environmental conditions. The present study was designed to document the scent marking pattern of coyotes in a region of Manitoba with mixed forest and a high rate of coyote mortality.

Although the main thrust in this study was to examine the distribution of scent marks in relation to territorial boundaries, it became apparent that habitat had a significant role to play in the travel patterns and hence the scent marking regimes of coyotes. Consequently, habitat became an important aspect of this scent marking study, which I discuss in Chapter II. Moreover, it is a variable that has not been explored by previous researchers. The distribution of scent marks is also examined in relation to the following factors that have been previously examined elsewhere: pair bonding (Rothman and Mech 1979), group size (Barrette and Messier 1980), terrain (Peters and Mech 1975), and foraging efficiency (Henry 1977).

Information on habitat selection by coyotes in mixed forest regions of temperate North America is scanty; however, the evidence available suggests that coyotes in these areas utilize conifer-dominated cover more than expected (Ozoga and Harger 1966, Major 1983). Most studies suggest that the habitats preferred by carnivores are those containing the most prey (Ozoga and Harger 1966, Litvaitis and Shaw 1980, Parker 1980, Andelt and Andelt 1981, Whitman et al. 1986); however, some indicate that avoidance of deep snow may also be important in habitat selection (Parker 1980, Halpin and Bissonette 1988). In Chapter III I examine the habitat preferences of coyotes and attempt to distinguish between prey availability and ease of travel as causal stimuli for selection of habitats.

Chapter IV documents the spatial arrangements and population dynamics of the coyotes examined in my study. Such data were needed to determine the distribution of territorial scent marking by coyotes and to determine the degree of stability in territorial boundaries from year to year.

In summary, this study addresses seven major questions related to the scent marking distribution and habitat selection of coyotes adjacent to Riding Mountain National Park, Manitoba.

1) Do coyotes scent mark at a greater rate in preferred habitats, and, if so, what are the possible explanations for this difference?
2) Do coyotes living in unstable populations with high mortality rates exhibit the same territorial marking pattern as that documented in stable coyote populations?
3) What evidence can be found from the spatial and temporal distribution of coyote scent marks to support proposed functions of scent marks other than territorial defense?
4) What are the preferred winter habitats of coyotes in a northern mixed forest region of temperate North America?
5) Do coyotes select certain habitats during the winter because of the prey contained therein, or does snow depth also influence the choice of habitat?

6) What is the mortality rate of coyotes adjacent to Riding Mountain National Park?

7) How stable from year to year are territorial boundaries of coyotes adjacent to Riding Mountain National Park?

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II. PATTERNS OF COYOTE SCENT MARKING IN A MIXED FOREST REGION OF MANITOBA

INTRODUCTION

Canids deposit urine systematically on objects in their environment. This phenomenon, known as scent marking, has been credited with several communicative functions, including territorial defense (Peters and Mech 1975, Macdonald 1979*a*), spatial orientation (Peters 1979), pair bonding (Rothman and Mech 1979), improved foraging efficiency (Henry 1977), and assertion of dominance status (Mertl-Millhollen et al. 1986). The majority of studies, however, list territorial defense as the primary role of scent marking (see reviews by Eisenberg and Kleiman 1972, Brown 1979, Macdonald 1985).

Peters and Mech (1975) studied territorial marking in wolves (*Canis lupus*). They found that these canids created an olfactory "bowl" pattern over their territories by scent marking more frequently per kilometer at territorial boundaries than in the centre. Subsequently, Bowen and McTaggart Cowan (1980) obtained very similar results for coyotes. Other studies of coyotes have also emphasized the territorial aspect of scent marking (Camenzind 1978, Lehner 1978, Barrette and Messier 1980, Wells and Bekoff 1981); however, few of these studies have provided convincing evidence of increased scent marking at territorial boundaries (Wells and Bekoff 1981). In one study, (Barrette and Messier 1980), the authors questioned the validity of the olfactory "bowl" hypothesis.

Unlike the wolves in Minnesota (Peters and Mech 1975), wolves in Riding Mountain National Park, Manitoba (Carbyn 1980), scent marked as frequently per kilometer in the centre of their territory as near the edge. Carbyn (1980) suggested that observed shifts in territorial boundaries between years prevented establishment of traditional marking routes near the edge of wolf territories in the heavily exploited Manitoba population.

Macdonald (1979a) found that the number of urine sites per metre and the number of urine deposits per site decreased as domesticated red foxes (Vulpes vulpes) approached the edge of their marking range. He suggested that much of the intra-specific variation in the scent marking patterns of carnivores, is dependent on ecological factors, such as habitat, resource base, or social structure (Macdonald 1980). Although the studies reviewed by Macdonald (1980) presented some evidence on aspects of social structure and resource base, few, if any, examined the relationship between scent marking patterns and habitat.

This paper reports the spatial distribution of coyote scent marks with respect to cover type in a mixed forest region of Manitoba. Given that coyotes appear to select coniferous habitat when travelling in forested areas (Ozoga and Harger 1966, Major 1983, Chapter III), and assuming that scent marks are most effective in communicating information if deposited in the areas most utilized by coyotes, then coyotes should scent mark more frequently in coniferous than non-coniferous habitats.

The distribution of scent marks with respect to territorial boundaries was recorded to determine if an exploited population of coyotes in Manitoba would produce the same olfactory "screen" pattern of scent marking as was described by Bowen and McTaggart Cowan (1980) for a relatively protected population of coyotes in Jasper National Park, Alberta. Other factors such as group size, breeding season, and surface terrain, postulated by previous authors to influence scent marking patterns in either coyotes or wolves, were re-examined for their possible role in the context f a variable habitat.

STUDY AREA

The main study area, approximately 145 km^2, straddled the southern border of Riding Mountain National Park (RMNP) near the park's east end, 35 km north of Minnedosa, Manitoba (Fig. II-1). During the second winter of the study a 6.1-km section of snow-covered park road along the south shore of Clear Lake was also included in the study.

The vegetation of the main study area was dominated by either pure stands of aspen (*Populus tremuloides*) or mixed stands of aspen and white spruce (Picea glauca). Sloughs, small lakes, thickets and occasional black spruce (Picea mariana) bogs were scattered throughout. In the southwest part of the study area, lying adjacent to RMNP, the woodlands were interspersed with open fields, pastures and crop. The coniferous component of the woodlands increased slightly towards the northeast, whereas the number of openings decreased, particularly within the park. Privately owned land outside the study area was usually only sparsely wooded. For a description of vegetation and topographic features throughout the remainder of RMNP see Carbyn (1980).

Keck (1975) described the climate around RMNP as being characteristically continental. Summers were warm with a maximum mean daily temperature of 15.6°C in July and an average growing season of 72 days. Winters were long and cold with a minimum mean daily temperature of -20.6°C in January. Mean annual total precipitation was 47.6 cm.

Resident timber wolves in RMNP made sporadic visits of short duration to the study area. Human activities within the study area included hunting, trapping, snowmobiling, livestock grazing, and cultivation of feed crops.

METHODS

Coyotes were captured in late summer and autumn of 1985 and 1986 with either padded, #3 coil spring, "Softcatch," leg-hold traps or unpadded, #4 long spring, "Victor," and

"Newhouse," leg-hold traps with offset jaws. Modified snares were also used during the winter of 1985-86. Trapped animals, controlled with a forked stick and muzzle strap, were ear tagged, weighed, measured, and fitted with a radio collar. Photographs of the incisors were taken to assist in age determinations, which were based on tooth eruption and incisor wear patterns (Gier 1968). Coyotes were classified at the time of capture as juveniles (4-7 months), yearlings (16-19 months), or adults (≥ 28 months). Locations of radio-collared coyotes were obtained either from a fixed-wing aircraft fitted with "Yagi" antennae or by triangulation of two or more bearings from a hand held "H" antenna. Tracks of collared coyotes were located using radio signals, and then followed by back-tracking on snowshoes. When collared animals could not be found or tracked successfully, the tracks of unknown coyotes were followed, usually from their intersection with a snowmobile trail. Territorial boundaries were deduced by enclosing all non-extraneous radio fixes and mapped tracking routes within a minimum convex polygon (Chapter IV). Within each territory, a 0.5 km wide strip along the boundary was designated as the peripheral region. Because I did not observe direct evidence of territorial defense in this study, the term "home range" would actually be more appropriate to describe the area enclosed by the convex polygon. However, the term "territory" is utilized in this chapter to be consistent with other scent marking studies.

Using aerial photographs, I recorded each tracking session by mapping the travel route, the habitats and terrain types encountered, and the locations of urinations, defecations, scratch marks, beds, and kills. Distances were estimated in the field and then measured from aerial photographs along the mapped travel route. Habitat types were classed as follows: coniferous woods (≥50% conifer canopy), deciduous woods (>50% deciduous canopy), open areas, thickets (small marshes included), frozen waterways, and developed habitats (roads, farmyards, etc.). With the aid of 100-m grid overlays, I also determined habitat types within 500 m on either side of each coyote track followed. Hence, for each tracking session, there was an estimate of habitat composition for the area in general, as well as for the specific route chosen by coyotes.

Three terrain types were designated: established trails (roads, snowmobile trails, and established game trails), frozen waterways, and cross-country routes (coyote tracks not following established trails or water bodies).

I defined scent marks in this study as any urination directed at any object or feature in the environment, including previously deposited urine or other potential sources of odour (Kleiman 1966, Bowen and McTaggart Cowan 1980). Urinations without such orientation also qualified as scent marks if they were accompanied by a scratch mark

(Camenzind 1978). Otherwise, they were classed as simple eliminations. Each scent mark was referred to as an individual scent mark (ISM). When two or more scent marks were deposited within 1 m of each other during a single passing of one or more coyotes they were collectively called a multiple scent mark (MSM), but were also counted separately as ISMs.

Coyote tracks of unknown animals were assumed to be those of adults if there was a preponderance of raised-leg urinations (RLUs) with relatively few squat urinations (SQUs) (Kleiman 1966). Squat urinations also include the forward lean urination described for males (Kleiman 1966). Differences in posture between male and female coyotes for both RLUs and SQUs (Kleiman 1966, Camenzind 1978) were used as a basis for determining sex when an unknown single coyote was being followed. Where two or more coyotes were travelling together and at least two animals appeared to be performing RLUs, the group was assumed to include a mated pair (Barrette and Messier 1980).

Between 12 January and 29 March 1987, I also monitored the spatial and temporal distribution of coyote scent marks along a 6.1-km section of snow covered road outside the main study area. Each new urine deposit was recorded, marked with flagging tape on the nearest bush or tree, and subsequently checked on a daily basis for further coyote activity.

The scent marking frequencies observed for each habitat type, group size, territorial region, month, and terrain type were compared to expected values using G-tests for goodness of fit. Expected values for each comparison were calculated on the assumption that marks were evenly distributed along all coyote tracks. Hence, for every doubling of either length of coyote track or number of coyotes, twice the number of marks were expected.

Because the same marking data were used in five separate comparisons, critical values for P in statistical tests were adjusted to $a' = 1 - (1 - a)^{1/k}$, where a is the experimentwise critical value and k is the number of different comparisons made using the same data (Sokal and Rohlf 1981). Hence, for an experimentwise type I error rate of 0.05, and $k = 5$ comparisons, the critical probability for each test was $a' = 0.0102$. Unless otherwise stated, the probability levels listed in analyses of ISM, MSM, scratch, and scat frequencies will refer to the experimentwise error rate of 0.05. William's correction for sample sizes <200, was applied to G-values used in statistical tests (Sokal and Rohlf 1981).

RESULTS

Types of Marks

During the winters of 1985-86 and 1986-87, scent marking data were collected along 132.3 km or 199.5 coyote-km of coyote tracks (1 coyote-km = 1 coyote travelling 1 km;). Tracks of collared coyotes accounted for 54% of the total tracking distance. Of 598 urine deposits examined, 91% (543) qualified as ISMs; the remaining 9% (55) were deemed to be eliminations (Table II-1). For adult coyotes and groups known or believed to contain adult coyotes, 92.4% of urinations were ISMs, providing an average scent marking rate for this cohort of 3.0 ISMs/coyote-km (Table II-1). Although adults appeared to scent mark more frequently per kilometer than yearlings (G-test of goodness of fit, $\underline{P} < 0.01$) the data may be misleading. For example, one collared male yearling, which appeared to be living alone, did not scent mark once in 4.9 km of travel during December. During December and January, a second collared male yearling, which was frequently observed with a mated pair between December and April, scent marked while travelling alone at a rate almost identical to that of adults (3.1 ISM/coyote-km; $\underline{P} > 0.05$). Adults scent marked ten times as frequently as known juveniles ($\underline{P} < 0.001$; Table II-1).

Multiple scent marks were found only among pairs and groups of coyotes, and scratches were performed only by adults (Table II-1). All recorded scratches and all but two MSMs were observed during January and February; therefore analyses for these mark types were limited to these months. Analyses for scratches included only those individuals and groups of coyotes that produced this type of marking. As a group, juveniles and yearlings appeared to defecate more frequently than adults (*P* < 0.01; Table II-1); however, sample sizes were small.

Of 543 ISMs, 82% were found without either scratches or feces, 15% were accompanied by scratches, 2% were deposited with scats, and 1% were found with scratches and scats. Sixty-four percent of 83 scats were not accompanied by other marks, 25% were deposited with urinations (including elimination urinations), 8% were found with both scratches and ISMs, and 2% were associated with scratches but no urine. Scratches were never found alone.

In 272 cases in which marking posture was determined to be a raised-leg urination (RLU), 99% (270) were considered scent marks. A significantly smaller portion (57%) of 65 identified squat urinations (SQUs) qualified as scent marks (G-test of independence, $G = 89.88$, $P < 0.001$), the remainder (43%) being simple eliminations. Of 29 urinations deposited by known adult females, 34% were identified as RLUs, 28% as SQUs, and 38% were unclassified. The proportions for known adult males were significantly different than for females ($G = 14.21$, $P < 0.001$, $n = 51$), with 67% RLUs, 2% SQUs, and 31% unidentified. While travelling alone, the male yearling which was normally associated with a pack, performed four RLUs, one SQU, and six unclassified urinations. Single juveniles deposited one RLU, nine SQUs, and two unidentified urinations.

Statistical tests were not performed for yearlings or juveniles. Not all urine marks from single unknown coyotes could be classified as to gender, but enough were identified to determine which sex was responsible for each set of tracks. No attempt was made to examine changes in posture over the winter period.

Spatial and Temporal Distribution of Marks

Group Composition

When the ISM data from all adult coyotes (singles and groups) were partitioned according to coyote group size, sex, and year, the observed frequencies of ISMs varied significantly among the seven resulting data subsets ($G = 59.16$, $\underline{P} < 0.001$; Table II-2). Orthogonal comparisons demonstrated that the frequency of ISMs was significantly lower for pairs tracked in 1985-86 than for pairs tracked in 1986-87 (Table II-2). It is not clear whether the difference is biologically important or an artifact of a small sample size for the 1985-86 pairs ($n = 13$ ISMs). Without the 1985-86 pairs, no differences were detected among the six remaining data subsets ($G = 12.99$, $\underline{P} > 0.05$). Hence, the remaining data were combined across years, sexes, and group sizes for subsequent analysis.

As with ISMs, no differences were found between group sizes for frequencies of MSMs, scratches, or scats ($\underline{P} > 0.05$ in each case; Table II-2). Sample sizes, however, did not allow further partitioning between sexes, or years. Consequently, analyses are based on the assumption that MSMs, scratches, and scats are not greatly affected by these variables.

Habitat

Observed frequencies within four main habitat types were all significantly different than expected for ISMs, MSMs, scratches, and scats (G = 126.06, 36.87, 27.57, and 11.13, respectively; $\underline{P} < 0.05$ in each case; Table II-3). For each mark type, the observed deviations from expected resulted primarily from difference between coniferous and the combined non-coniferous habitats ($\underline{P} < 0.05$). In coniferous habitat, coyotes marked, on averaged, 2.6 times as often (ISMs/coyote-km) as in non-coniferous habitats. Likewise, MSMs, scratches and scats were produced 4.0, 3.0 and 2.1 times more often, respectively, in coniferous habitat than all others combined. There were no statistical differences in marking rates among the three non-coniferous habitat types ($\underline{P} > 0.05$ for each mark type).

Based on Spearman's rank correlation coefficients, the relationship between ISM rates and habitat was more a function of the immediate cover type than the nature of the surrounding habitat in general. Scent marking rates (ISM/coyote-km) for each tracking session were positively correlated with the proportion of coniferous cover directly over each tracking route ($r = 0.54$, $\underline{P} = 0.0013$, $n = 36$). However, marking frequencies were not related to the proportion of coniferous habitat within 500 m of either side of each tracking route, as determined from aerial photographs ($r = 0.23$, $\underline{P} = 0.1833$, $n = 35$). This distinction was evident despite a high degree of correlation between the two measures of coniferous cover ($r = 0.70$, $\underline{P} < 0.0001$, $n = 35$).

Because bed sites were also more numerous in coniferous than in deciduous or open habitats (Chapter III), it was important to know if association with bed sites could account for the more frequent occurrence of marks in coniferous habitat. G-tests of independence demonstrated that the various mark types were not equally associated with bed sites ($G = 28.36$, $\underline{P} < 0.001$). Scats and elimination urinations were three times more likely to occur within 50 m of a bed site than were ISMs, MSMs and scratches (orthogonal comparisons, $G = 26.23$, $\underline{P} < 0.001$; Table II-4). Scats and eliminations were equally associated with bed sites ($G = 0.291$, $\underline{P} > 0.05$), as were ISMs, MSMs, and scratches ($G = 2.115$, $\underline{P} > 0.05$). Of three multiple scats found while tracking coyotes, two were in close proximity to bed sites. In one instance, a known juvenile female had bedded down during a snow storm near the remnants of a deer carcass. Over a period of approximately 24 hours she rose three times to defecate and once to void a large volume of urine.

Territorial Boundaries

For coniferous habitats, observed frequencies of ISMs, MSMs, and scratches along coyote tracks were all slightly, but not significantly higher in the 0.5 km wide periphery of territories than in central regions ($P > 0.05$; Table II-5). This tendency for a higher frequency of ISMs in peripheral regions of coniferous habitat occurred for each of the three adult coyotes that were known to be paired, but showed the opposite trend for one adult male that was never observed or tracked with another coyote; however, these trends were never significant ($P > 0.05$ for each coyote). Rates for ISMs in non-coniferous habitats were marginally lower in peripheries than in the centres ($P > 0.05$). Small sample sizes precluded testing of MSMs and scratches in non-coniferous habitats, or of scats in either habitat type.

On a per unit area basis, the mean distance over which identified coyotes were tracked in the peripheral portions of territories was approximately equal to the mean tracking distance in central regions (periphery: 1.1 $km/km^2 \pm 0.19$, centre: 0.9 $km/km^2 \pm 0.26$; paired t-test, $t_s = 0.294$, $P > 0.5$, $n = 5$). Assuming that tracking distances reflect actual space use by coyotes, then it appears that coyotes use peripheral and central portions of their territory equally.

Breeding Season

Individual scent marking rates within coniferous habitat were marginally higher during the coyote breeding season (January, February) than in December and March, but were nearly identical throughout the winter for non-coniferous habitats ($\underline{P} > 0.05$ in both cases; Table II-6). By contrast, almost all MSMs and scratches were confined to January and February, resulting in significant peaks for these marks in both habitats (MSMs: G-test of goodness of fit, $\underline{P} < 0.05$; scratches: binomial exact test, $\underline{P} < 0.001$). Defecation rates did not differ significantly among winter months ($\underline{P} > 0.05$, Table II-6).

Terrain Type

At the 5% level of significance, rates for each type of scent marking did not differ significantly among the various types of terrain within either coniferous or non-coniferous habitats. There was a strong tendency in non-coniferous habitats, however, for both ISMs and scratches to be more common along trails than cross country routes (Table II-7). Frozen waterways were not included in statistical analyses of MSMs, scratches, and scats because the expected values in such tests were too low.

Possible Stimuli For Marking Behaviour

Three types of targets were used for 70% of all observed urine deposits left by adult coyotes or groups containing adults. These included standing or fallen vegetation, irregular snow surfaces, such as drifts and disturbed snow, and presumed food related items, such as inedible traces of prey and excavations made by coyotes (Table II-8). Other targets included previous canid sign, non-canid sign, protruding substrate material, and objects related to humans, such as litter and hay bales. Whereas 92% of urinations were directed at a recognizable target, only 44% of scats were so directed.

Of 90 inedible food related items found while tracking adult coyotes, 70% were marked or had been previously marked with urine. Seven small edible food items were found, including ungulate legs and pieces of flesh, but only one of these had been scent marked. Despite the small sample size, this difference was significant (G-test of independence, $G = 7.920$, $\underline{P} < 0.01$). Five of the edible items were cached beneath the snow, while two, including the one marked, were on the surface. These figures do not include large prey carcasses, because trampling and bird droppings at such sites made interpretation of sign virtually impossible.

Between 12 January and 29 March 1987, I detected 131 deposits of coyote urine distributed amongst 50 sites along 6.1 km of snow-covered road (Table II-9). Ninety-four percent of these sites were revisited at least once by a coyote during the observation period, but only 44% were re-marked. Sites at trail junctions were, on average, three times more likely to be re-marked by a passing coyote than sites not at trail junctions (G-test of independence, $G = 36.561$, $\underline{P} < 0.001$; Table II-9). There was also a tendency for re-marking to continue over a longer period of time at junction sites (Wilcoxon two sample test, $t_s = 1.844$, $\underline{P} < 0.1$; Table II-9).

Previous urine deposits, including eliminations, were re-marked at 14 different sites during January, 15 sites during February, but only six sites during March (Fig. II-2). Four sites, all at trail junctions (2, 4, 5, and 8; Fig.2), were marked with urine during all three months. Only three sites continued to be marked after 2 March. One of these (D) was marked on the first and last days of observation, but was not marked at all during the 78 day interim. Excluding this example, the longest observed period of time between marking and re-marking of a site by a coyote was 30 days (site 8, Fig. II-2).

DISCUSSION

Types of Marks and Postures

Scent marking in the Canidae is achieved primarily through the use of urine (Kleiman 1966, Peters and Mech 1975, Camenzind 1978, Macdonald 1979b, Barrette and Messier 1980, Wells and Bekoff 1981, this study). Definitions for scent marking have varied widely, but in most studies, with the exception of Camenzind (1978), the majority of recorded urine deposits were classified as scent marks. For wolves, Peters and Mech (1975) assumed that only RLUs qualified as scent marks. This definition may not be appropriate for coyotes, as 57% of the SQUs in my study and 88% of SQUs observed by Wells and Bekoff (1981) were categorized as scent marks under alternative criteria. Nevertheless, a larger proportion of RLUs than SQUs were identified as scent marks in both studies, suggesting that RLUs are more important than SQUs as scent marks, or that they are used in different contexts to convey different messages (Wells and Bekoff 1981).

Piles or middens of feces deposited along territorial boundaries or at trail junctions are believed to have communicative functions in golden jackals (*Canis aureus*) (Macdonald 1979*a*), dholes (*Cuon alpinus*) (Jonsingh 1982), spotted hyaenas (*Crocuta crocuta*) (Kruuk 1972), and several other carnivores (see review by Macdonald 1985). The role of feces, however, is less certain in coyote communication. In this study and others (Bowen and McTaggart Cowan 1980, Wells and Bekoff 1981), coyote feces were usually distributed singly, except where they accumulated around carcasses, bedding sites, and occasionally along trails or at other sites of repeated use. I observed a striking similarity between deposition of scats and eliminative urinations relative to bed sites (Table II-2). Macdonald

(1985) noted that red foxes also defecated near bed sites and suggested that, for both species, accumulations near beds may simply be a result of defecating after resting. That juveniles defecated more frequently than adults may indicate consumption of lower quality food by juveniles, as a result of scavenging kill remains.

Like Ozoga and Harger (1966), I frequently found coyote scats on conspicuous sites such as beaver lodges and squirrel caches; but, as in Bowen and McTaggart Cowan's (1980) study, the majority were not directed at any detectable target, and scats were seldom accompanied by a scratch unless urine was also present (see also Barrette and Messier 1980). In light of the above, and in the absence of any demonstrated relationship between scat deposition and season, territorial boundaries, or terrain, it appears that the spatial and temporal distribution of coyote feces is more a function of immediate physiological needs than any scent marking regime.

This does not preclude the possibility that once deposited, scats serve a secondary role in conveying information. The possibility also exists that only those scats anointed with anal gland secretions are intended as scent marks, while others are purely eliminative. In wolves, anal gland secretions accompany only a small proportion of feces (Asa et al. 1985), and there is some evidence that these may have communicative functions (Raymer et al. 1985). It would be of great interest to know whether scats deposited at conspicuous sites are more likely to be coated with anal gland secretions than those at less prominent sites.

Group Composition

In general, the total number of scent marks produced by a group of coyotes increases with the number of individuals present, which suggests that all coyotes in a group, including juveniles and subordinates, contribute to scent marking to some degree (Barrette and Messier 1980, Bowen and McTaggart Cowan 1980, Wells and Bekoff 1981, this study). It is known, for instance, that juveniles (Barrette and Messier 1980) and yearlings (this study), temporarily separated from their packs, scent mark at rates comparable with that of adults. Such animals may be somewhat inhibited, however, in the company of dominant animals. Indeed, three of the four studies above found that groups larger than two, marked at slightly, but not significantly lower rates than would be expected if all coyotes in a group marked equally. Even in the fourth study (Wells and Bekoff 1981), a yearling member of a free ranging pack of four coyotes marked at a lower rate than the dominant pair, but more frequently than its juvenile pack mate.

Bowen and McTaggart Cowan (1980), Wells and Bekoff (1981), and this study found no significant difference in the marking rate per coyote between singles and pairs. Conversely, Barrette and Messier (1980) found that individuals in pairs marked twice as frequently as lone animals. Single coyotes in that study included primarily juveniles and non-territorial individuals, whereas single coyotes in the other studies excluded non-adults from the analysis, and/or included largely group living individuals temporarily separated from their territorial groups. This is an important distinction in light of Barrette and Messier's (1980) findings that solitary living coyotes, regardless of age, marked much less frequently than single animals that normally lived in groups. Solitary wolves also mark infrequently until they find a mate and begin defending a territory (Rothman and Mech 1979).

As in coyotes, subordinate vixens in red fox groups scent mark frequently, but not as often as dominant vixens (Macdonald 1979b). Conversely, scent marking in highly social canids, such as wolves (Peters and Mech 1975, Mertl-Millhollen et. al. 1986) and wild dogs (Lycaon pictus) (Frame and Frame 1976) is restricted primarily to the alpha pair, regardless of the pack size. Hence, the effect of group size on marking rates may depend upon the degree of development of social hierarchies that are typical for each of these social species.

The Influence of Habitat on Scent Marking

If a scent mark is to have a communicative function, regardless of the message conveyed, it must first be encountered and perceived by the recipient. Thus, scent marks should be distributed through an animal's territory in such a way as to maximize the possibility that they will be encountered by conspecifics (Gosling 1982). In this study, and in other mixed forest regions of North America (see Chapter III), coyotes showed a clear preference for travelling in conifer-dominated habitat, and it was this habitat that was scent marked more frequently per coyote-km than any other.

One problem inherent in the study of scent marking in free ranging animals, is the definition of rate. Wells and Bekoff (1981) argued that scent marking rates should be measured on a unit-time basis. No one has documented the rates of travel of coyotes in various habitats. It seems reasonable that coyotes would travel slower in non-coniferous areas where deep snow impedes movement (Chapter III). Alternatively, coyotes may slow their pace in coniferous habitat because of more accessible food resources and more shelter (Chapter III). By measuring scent marking rates relative to time, Wells and Bekoff (1981) have emphasized the motivational state of the marker rather than the marking pattern perceived by the receiver. In my opinion, the message conveyed by scent marks depends primarily on how they are received, and therefore on their spatial distribution.

Similar arguments have been used in studies of wolves (Peters and Mech 1975, Carbyn 1980) and red foxes (Henry 1979, Macdonald 1979a) to explain significantly higher scent marking rates along established trails than along cross-country routes. In each case, trails were the preferred travel route, and consequently the most effective place for leaving messages in the form of scent marks.

Why then, did coyotes in the present study not mark trails more frequently than cross-country routes or frozen waterways? As demonstrated in Chapter III, the shallow snow associated with coniferous habitat reduces the importance of well packed trails as travel corridors (cf. Henry 1979). Coyotes seldom used distinct trails in coniferous habitat. Instead, their movements formed a diffuse network of tracks which often criss-crossed or parallelled one another. In non-coniferous habitats, where snow was deeper and trail use was more extensive (Chapter III), the trails were marked with ISMs and scratches at substantially, but not statistically higher rates than were cross country routes (Table II-4).

Apparently, part of the stimulus leading to high rates of scent marking along preferred travel routes is the previous deposition of urine. No distinction is made here between scent marks and eliminative urinations. Urine from canids can elicit scent marking by conspecifics for 3 weeks or more after being deposited (Peters and Mech 1975, Bowen and McTaggart Cowan 1980, this study). Urine and its volatile constituents have also been shown experimentally to elicit scent marking in domestic dogs (Graf and Meyer-Holzapfel 1974) and red foxes (Whitten et. al. 1980). Coniferous habitat may enhance the stimulus effect by sheltering scent marks from the elements, thereby prolonging the period over which they can be detected.

Not all urine elicits re-marking. In the present study, only 44% of sites previously marked with urine along a well used trail were re-marked by coyotes on subsequent visits. As in wolves (Peters and Mech 1975), the most frequently re-marked sites were trail junctions. By concentrating on trail junctions, coyotes ensured that their scent marks could be detected from either of the two intersecting trails.

Possible Functions of Scent Marking

Resource Defense

One function of scent marking frequently cited is territorial defense (canids: Kleiman 1966, Camenzind 1978, Peters and Mech 1975; other mammals: Mykytowycz 1968, Gosling 1982). Although opinions differ as to the mechanism by which scent marking confers territorial protection (Gosling 1982), there is a consensus that, to be effective, scent marks should be concentrated near the periphery of territories, such that trespassers, upon entering the area, encounter immediately a large number of the occupant's marks.

Several mammals which are known to distribute their feces and/or specialized gland secretions in this pattern include wild rabbits (Oryctolagus cuniculus) (Mykytowycz 1968), brown hyaenas (Hyaena brunnea) (Mills et al. 1980), pronghorn antelope (Antilocapra americana) (Kitchen 1974), and many others (Macdonald 1980). Similarly, studies of wolves (Peters and Mech 1975) and coyotes (Bowen and McTaggart Cowan 1980, Wells and Bekoff 1981), have reported that urine marks were deposited more frequently near territorial boundaries than centrally in the territory. I found only a non-significant trend towards this pattern of distribution of scent marks.

Gosling (1982) cites habitat as one factor that can influence the distribution of territorial scent marking. The dikdik (Rhynchotragus kirki) lives in dense brush, and, unlike plains dwelling ungulates, does not mark the entire periphery of its territory (Hendrichs and Hendrichs 1971, cited in Gosling 1982). Instead, it limits scent marking to trails, where travel is easier and intruders are more likely to enter. Coyotes near RMNP lived in a comparable situation where deep snow may have made travel difficult outside of coniferous habitat, except where there were well packed trails to follow. Hence, access by intruders was likely through coniferous habitat. This may explain why the observed tendency for increased scent marking and scratching in peripheral areas was limited to coniferous habitat (Table II-5).

Nonetheless, even in coniferous habitats, I did not observe significant differences in marking rates with respect to territorial boundaries as were described by Peters and Mech (1975), Bowen and McTaggart Cowan (1980), and Wells and Bekoff (1981). In each of the three studies listed above, territories were relatively stable from year to year, adult mortality was low, group sizes were predominantly or commonly larger than two, and the study areas suffered little from human disturbance (data published in Mech 1977, Rothman and Mech 1979, Bowen 1978, and Bekoff and Wells 1986). By contrast, my study population was less stable. Territorial boundaries changed significantly between years, mortality was high, even among adults, group sizes larger than two were observed for only two packs during the study period, and there was widespread trapping, hunting, cattle grazing and cultivation throughout the area (Chapter IV).

Carbyn (1980) has suggested that population instability might disrupt the normal scent marking behaviour of canids. He reported two major displacements of wolf packs in Riding Mountain National Park between 1975 and 1980 (Carbyn 1981, 1982), and observed no difference in scent marking rates between the centre and periphery of the territory (Carbyn 1980). Marking rates were highest mid-way between these two regions.

Repeated shifts in territorial boundaries could prevent establishment of traditional marking routes at the territory edge (Carbyn 1980). In addition, it would be difficult to detect increased marking in peripheral regions if these regions moved during the course of a winter. At least three adult resident coyotes died during the study period. New coyotes that moved in to fill these vacancies must have encountered many unfamiliar areas and odours, particularly those odours left by the previous occupant. Odours of unfamiliar conspecifics stimulate scent marking in dogs (Dunbar 1977), red foxes (Blizard and Perry 1979), coyotes (Fagre et al. 1980), and wolves (Brown and Johnston 1983). Consequently, high rates of scent marking would be expected through all regions of a new territory, not just at the edge. Assuming that newly formed coyote pairs scent mark at higher than normal rates, as do new wolf pairs (Rothman and Mech 1979), then the frequent loss of mates in my study is another factor that could mask the "olfactory bowl" pattern described by Peters and Mech (1975).

I am not implying that scent marks in this study served no territorial function, for even though I observed no significant differences in scent marking rates between peripheral and central regions of coyote territories, the average marking rate in my study (3.0 ISM/coyote-km) exceeded that observed by Bowen and McTaggart Cowan (1980) at territorial edges (1.7 marks/coyote-km). Unfortunately, Wells and Bekoff (1981) measured rate in marks per hour, making comparisons with their study impossible. Similarly, the average RLU rate recorded by Carbyn (1980) for wolves in RMNP (3.0 RLU/km), was higher than that observed by Peters and Mech (1975) along the territorial boundaries of a stable wolf population (2.7 RLU/km). These results suggest that the effectiveness of marking territorial boundaries is a function of how frequently an intruder encounters a scent mark, as opposed to the differences in marking rates experienced between central and peripheral regions.

Barrette and Messier (1980) challenged the "olfactory bowl" hypothesis on the grounds that the number of marks per kilometer do not reflect the true density of marks on a per unit area basis. They reasoned that if coyotes or wolves spent less time in peripheral regions of territories, then the resulting density of scent marks would actually be highest in central regions (cf. Mills et al. 1980). Judging, however, from data recorded by Peters and Mech (1975) and Bowen and McTaggart Cowan (1980), the wolves and coyotes in their studies travelled at least as frequently near territorial edges as in the centres. This was also the case in my study. In any case, coyotes and wolves do not move randomly through the environment, but select trails and habitats that provide for easy travel (Peters and Mech 1975, this study). Therefore, the number of marks encountered by an intruder will be a reflection of the linear density of scent marks along the chosen route, rather than the areal density of marks throughout the region as suggested by Barrette and Messier (1980).

Coniferous habitat was important not only for travel in this study, but it provided bedding areas for coyotes and shelter for white-tailed deer (Odocoileus virginianus), the coyote's major winter prey source (Chapter III). It has been argued that wild cats (Felis silvestris) and feral domestic cats increase their fecal marking rates in preferred hunting areas as a means of protecting food resources (L. Corbett, cited in Macdonald 1980).

It is difficult to determine conclusively whether coniferous areas were heavily scent marked in this study because they contained a valuable resource, or simply because they were frequently travelled, as described earlier. The limited data available suggests the latter. Despite the fact that deer are often associated with coniferous habitat during winter (Verme 1966, Armstrong et al. 1983, Chapter III), kill and carrion sites in this study were randomly distributed through all habitats (Chapter III). In addition, scent marking rates for individual tracking sessions were not correlated with the amount of nearby coniferous habitat, as would be expected if such areas contained valuable resources. Rather, the frequency of marking was more closely related to the extent of coniferous canopy directly overhead, and appeared, therefore, to be a function of snow depth and ease of travel.

Spatial Orientation

Peters (1979) reasoned that re-marking of traditional scent marking sites helps wolves to form "cognitive maps" of their home range by highlighting focal points and land marks used for spatial orientation. If canids can differentiate between urine odours belonging to themselves and mates, or familiar and unfamiliar conspecifics, as suggested by Dunbar (1977), Blizard and Perry (1979), and Brown and Johnston (1983), then urine odours distributed at focal points throughout the home range could provide coyotes with continuous feedback concerning their own movements and activities, as well as those of other pack members and intruders. Such information might be useful in regrouping separated individuals, for signalling that a hunting area has recently been used, or for alerting coyotes that they are leaving their territory and entering that of a neighbour. Again, it is the well used routes, such as coniferous corridors and established trails, that would provide the best sites for such a feedback system to operate.

Seasonality and Pair Bonding

Snow tracking studies of coyotes are limited in that they allow sampling of scent marking rates only during periods of snow cover, which, at temperate latitudes, extend generally from November or December to the end of March. Such studies (Barrette and Messier 1980, Bowen and McTaggart Cowan 1980, this study) have not demonstrated an increase in urine marking behaviour during the mating season, as was found by Peters and Mech (1975) for wolves. By contrast, year round captive and observational studies consistently demonstrate winter increases in scent marking rates for coyotes (Kleiman 1966, Wells and Bekoff 1981), red foxes (Macdonald 1979b) and wolves (Mertl-Millhollen et al. 1986), but these increases were not necessarily restricted to the stated mating season.

Estrous lasts only 4 to 15 days in coyotes, but its onset can occur from late January through mid-March, and may be preceded by two or three months of proestrous (Kennelly 1978). Hence, physiological changes associated with reproduction may often span the entire duration of the snow cover period. This probably accounts for the inability of most snow tracking studies to detect a general increase in scent marking during mating.

Despite relatively constant ISM rates during the winter months, ISMs were clumped together as MSMs at a much higher rate during January and February than during December or March. Wells and Bekoff (1981) also found a peak in MSM rates for coyotes during the mating season. Similarly, multiple marking has been linked to pair formation and breeding in wolves (Rothman and Mech 1979, Mertl-Millhollen et al. 1986) and red foxes (Macdonald 1979b).

Given that canids can distinguish between the urine of estrous and non-estrous females (Graf and Meyer-Holzapfel 1974, Dunbar 1977), that constituents of both male and female canid urine vary seasonally under hormonal control (Raymer et al. 1984, 1986; Shultz et al. 1988), and that the reproductive behaviour of certain animals are influenced by urine (Eisenberg and Kleiman 1972, Coopersmith and Banks 1983), it seems very probable that scent marks play an important role in canid reproduction. I support Rothman and Mech's (1979) suggestions that by investigating and marking over each other's scent marks during the mating season, as was observed in my study, canid pairs are able to familiarize themselves with each other's scent, assess each other's reproductive status, and synchronize physiological development of their reproductive systems prior to breeding.

Whereas peak scratch rates were observed during the mating season by Wells and Bekoff (1981) and myself, Barrette and Messier (1980) found the opposite pattern. They suggested that decreased visual effectiveness in deep snow resulted in mid-winter declines in this mark type. Deep snow was not a factor in Wells and Bekoff's (1981) study, and 94% of scratches in my study were restricted to coniferous habitat, established trails, or frozen waterways (Table II-7). Hence, the role of scratching in coyote reproduction may depend on the availability of suitable sites with shallow or well packed snow.

Scent Marking and Foraging Efficiency

Henry (1977) observed that 18% of red fox urinations were deposited on non-edible food items and exploited caches during winter. Similarly, 20% of coyote urinations were so directed in my study (Table II-8, includes prey sign, Henry 1977). According to Henry's "bookkeeping" hypothesis, such marks leave a "no food" message, thereby minimizing the time wasted during subsequent visits investigating unprofitable, residual food odours. Harrington (1981) extended Henry's hypotheses to captive coyotes and wolves. He demonstrated that urine marking never occurred during caching, rarely occurred while food remained in the cache, but usually occurred shortly after the cache had been exploited. These authors further demonstrated that foxes and wolves spent significantly less time investigating empty caches if the sites had been previously urine marked. The frequency with which non-edible food related items were scent marked by coyotes in my study, and the absence of marking at caches, suggest that "bookkeeping" also operates in free ranging coyotes.

Future Research

Several aspects of canid scent marking discussed in this paper deserve further investigation. In order to determine with greater certainty why coyotes increase their scent marking rates in coniferous habitats, it would be appropriate to manipulate the availability of either food resources or travel routes. An attempt should be made to compare rates of travel by coyotes in different habitats. Removal experiments should be used to focus on relationships between territorial stability and the spatial distribution of scent marks. Seasonal variations in scent marking patterns and postures observed in the field need to be compared more directly with fluctuations in the chemical composition of the urine.

CONCLUSIONS

Habitat, possibly by influencing ease of travel, seems to play an important role in determining the spatial distribution of coyote scent marks. Because coyotes in this study travelled more extensively in coniferous habitat than any other, these areas became important avenues for leaving information in the form of scent marks. This explains why preferential marking of territorial boundaries, if it occurred at all, seemed to be limited to coniferous areas. Not surprisingly, the highest marking rates outside of coniferous habitats occurred along well used trails, where the effects of deep snow were minimized and ease of travel probably increased.

Scent marks need not be arranged in the "olfactory screen" pattern as described by Bowen and McTaggart Cowan (1980) in order to establish territorial ownership. So long as intruders encounter sufficient scent marks at the territorial border to ascertain that the area is occupied, then the relative difference in scent marking rates between peripheral and central regions is apparently irrelevant. The exceptionally high scent marking rates observed within the interior of coyote territories in this study may have resulted from shifting territorial boundaries and/or establishment of new pair bonds in an unstable population.

A single scent mark may convey several messages. Thus, urine deposited on a food remnant in January, to increase future foraging efficiency, may also help in territorial defense or pair bonding if encountered by the appropriate individual. The social context, the physiological state of the participants, the location relative to other marks, and the type of substrate being marked all contribute to the multi faceted nature of the message.

Table II-1. Marking rates (mean number of marks/coyote-km) by coyotes of different ages during the winters of 1985-87 in southwestern Manitoba.

		EU[a]		ISM		MSM		Scratch		Scat	
Age class	Coyote-km	Rate	n	Rate	n	Rate	n	Rate	n	Rate	n
All Ages	199.5	0.3	55	2.7	543	0.4	81	0.4	82	0.4	83
Adult[b]	174.3	0.2	43	3.0	522	0.5	81	0.5	82	0.3	57
Yearling	8.1	0.4	3	1.2[c]	10	0.0	0	0.0	0	0.7	6
Juvenile	11.2	0.6	7	0.3[c]	3	0.0	0	0.0	0	1.6	18
Unknown	5.9	0.3	2	1.4	8	0.0	0	0.0	0	0.3	2

[a] EU = elimination urination, ISM = individual scent mark, MSM = multiple scent mark.

[b] Includes single adult males and females, and groups containing adults.

[c] Scent marking frequency less than for adults ($\underline{P} < 0.01$).

Table II-2. Marking rates (mean number of marks/coyote-km) by adult coyotes during winter for different group sizes, sexes, and years along coyote tracks in southwestern Manitoba, 1985-87.

	ISM[a]		MSM[ab]		Scratch[b]		Scat	
Data subsets	Rate	n	Rate	n	Rate	n	Rate	n
Single males 1985-86	2.3	39			1.1	13	0.7	11
Single males 1986-87	3.5	50					0.2	3
Single females 1985-86	3.4	32					0.3	3
Single females 1986-87	4.5	25					0.5	3
All singles combined	3.2	146			1.1	13	0.4	20
Pairs 1985-86[c]	0.7	13	0.1	2	0.1	2	0.0	0
Pairs 1986-87	3.4	320	0.8	69	1.0	60	0.3	28
Group of three 1985-86	2.4	43	0.8	8	0.6	6	0.5	9

[a] ISM = individual scent mark, MSM = multiple scent mark.

[b] Data from January-February only.

[c] Excluded from further analyses, ISMs fewer than expected ($\underline{P} < 0.001$).

Table II-3. Winter marking rates (mean number of marks/coyote-km) by adult coyotes in different habitats in southwestern Manitoba, 1985-87.

	ISM[a]		MSM		Scratch		Scat	
Habitat	Rate	n	Rate	n	Rate	n	Rate	n
Coniferous	5.8[b]	271	1.8[b]	46	2.1[b]	35	0.6[b]	27
Deciduous	2.4	95	0.5	10	0.5	13	0.4	15
Open	1.7	83	0.4	12	0.6	17	0.2	8
Other[c]	2.7	60	0.7	9	1.3	14	0.3	7

[a] ISM = individual scent mark, MSM = multiple scent mark.

[b] Marking rates in coniferous habitat are greater than those in other habitats ($P < 0.05$).

[c] Includes frozen waterways, thickets, and developed sites.

Table II-4. Association between bed sites and different types of marks left by adult coyotes during winters of 1985-87 in southwestern Manitoba.

Mark Type	Total number	Within 50[a] meters of beds n	%
Elimination of urine	43	10	23.3 A[b]
Scat	57	16	28.1 A
Individual scent mark	522	41	7.9 B
Multiple scent mark	81	6	7.4 B
Scratch	82	3	3.7 B

[a] Arbitrarily chosen

[b] Mark types with different letters are distributed differently relative to bed sites ($P < 0.01$).

Table II-5. Winter marking rates (mean number of marks/coyote-km) by adult coyotes at the peripheries and centres of territories in coniferous and non-coniferous habitats in southwestern Manitoba, 1985-87.

Habitat	ISM[a]		MSM[a]		Scratch	
Region	Rate	n	Rate	n	Rate	n
Coniferous						
Periphery	6.4[b]	121	2.4[b]	29	2.6[b]	19
Centre	5.3	79	1.3	12	1.5	9
Non-coniferous						
Periphery	1.6[b]	48	0.5[c]	8	0.3[c]	4
Centre	2.7	38	0.2	2	1.0	6

[a] ISM = individual scent mark, MSM = multiple scent mark.

[b] No difference between periphery and centre ($P > 0.05$).

[c] Sample size too small for statistical analysis.

Table II-6. Marking rates (mean number of marks/coyote-km) by adult coyotes in southwestern Manitoba, during the winter months of 1985-87.

Habitat Month	ISM[a]		MSM[a]		Scratch		Scat	
	Rate	n	Rate	n	Rate	n	Rate	n
Coniferous								
December	4.9	39	0.2	1	0.0	0	0.9	7
January	6.6	79	1.8[b]	17	2.5[b]	17	0.4	5
February	5.9	123	1.9[b]	29	1.8[b]	18	0.6	12
March	4.7	30	0.0	0	0.0	0	0.5	3
Non-coniferous								
December	2.1	23	0.0	0	0.0	0	0.7	8
January	2.1	74	0.4[b]	9	1.0[b]	28	0.2	6
February	2.3	110	0.5[b]	22	0.5[b]	16	0.3	12
March	2.0	31	0.2	1	0.0	0	0.3	4

[a] ISM = individual scent mark, MSM = multiple scent mark.

[b] Rates were higher during January and February (breeding season) than in other months ($p < 0.05$).

Table II-7. Winter marking rates (mean number of marks/coyote-km) by adult coyotes in different types of terrain within coniferous and non-coniferous habitats in southwestern Manitoba, 1985-87.

Habitat	ISM[a]		MSM[a]		Scratch		Scat	
Terrain	Rate	n	Rate	n	Rate	n	Rate	n
Coniferous								
Trails	6.3	98	2.1	21	2.4	12	0.3	5
X-country	5.5	173	1.7	25	1.9	23	0.7	22
Non-coniferous								
Trails	2.3[b]	148	0.4	18	0.7[b]	29	0.2	14
X-country	1.7	66	0.4	7	0.3	5	0.4	14
Waterways	2.8	24	1.0[c]	6	5.2[c]	10	0.2[c]	2

[a] ISM = individual scent mark, MSM = multiple scent mark.

[b] Differences between trails and cross country routes are marginally significant (ISM: $\underline{P} < 0.2$, scratch: $\underline{P} < 0.1$).

[c] Expected frequencies for waterways were too small for statistical analysis.

Table II-8. Targets marked with urine by coyotes of different ages in southwestern Manitoba, 1985-87.

	Adult		Yearling		Juvenile		Unknown	
Target	n	%	n	%	n	%	n	%
Vegetation	257	45.5	0		0		2	20.0
Raised snow & ice	75	13.3	0		0		0	
Food related item	61	10.8	5	45.5	1	8.3	2	20.0
Canid sign	55	9.7	4	36.4	2	16.7	0	
Non-canid sign	52	9.2	1	9.1	0		2	20.0
No apparent target	43	7.6	1	9.1	9	75.0	2	20.0
Scratch only	10	1.8	0		0		0	
Rocks, soil clumps	8	1.4	0		0		1	10.0
Human related	4	0.7	0		0		1	10.0
Total	565		11		12		10	

Table II-9. Re-marking of previous urine deposits by coyotes, at trail junctions and non-junction sites along a snow-covered road in RMNP, Manitoba, January - March 1987.

		Sites re-marked			Visits re-marked		Interval of marking (days)[b]	
Site type	Urination sites	n	%	Coyote	n	%	mean	± SE
Junction	14	8	[illegible]	[illegible]	49	32[c]	24[d]	7.4
Non-junction	36	14	39	324	30	9	8	2.7
Total	50	22	44	476	79	17	12	3.0

[a] Coyote visit = 1 coyote visiting 1 previous urine deposit.

[b] Number of days between first and last observed urine deposit.

[c] Junction sites elicited more re-marks per coyote visit than non-junction sites ($P < 0.001$).

[d] Junction sites tended to be marked over a longer period of time than non-junction sites ($P < 0.1$).

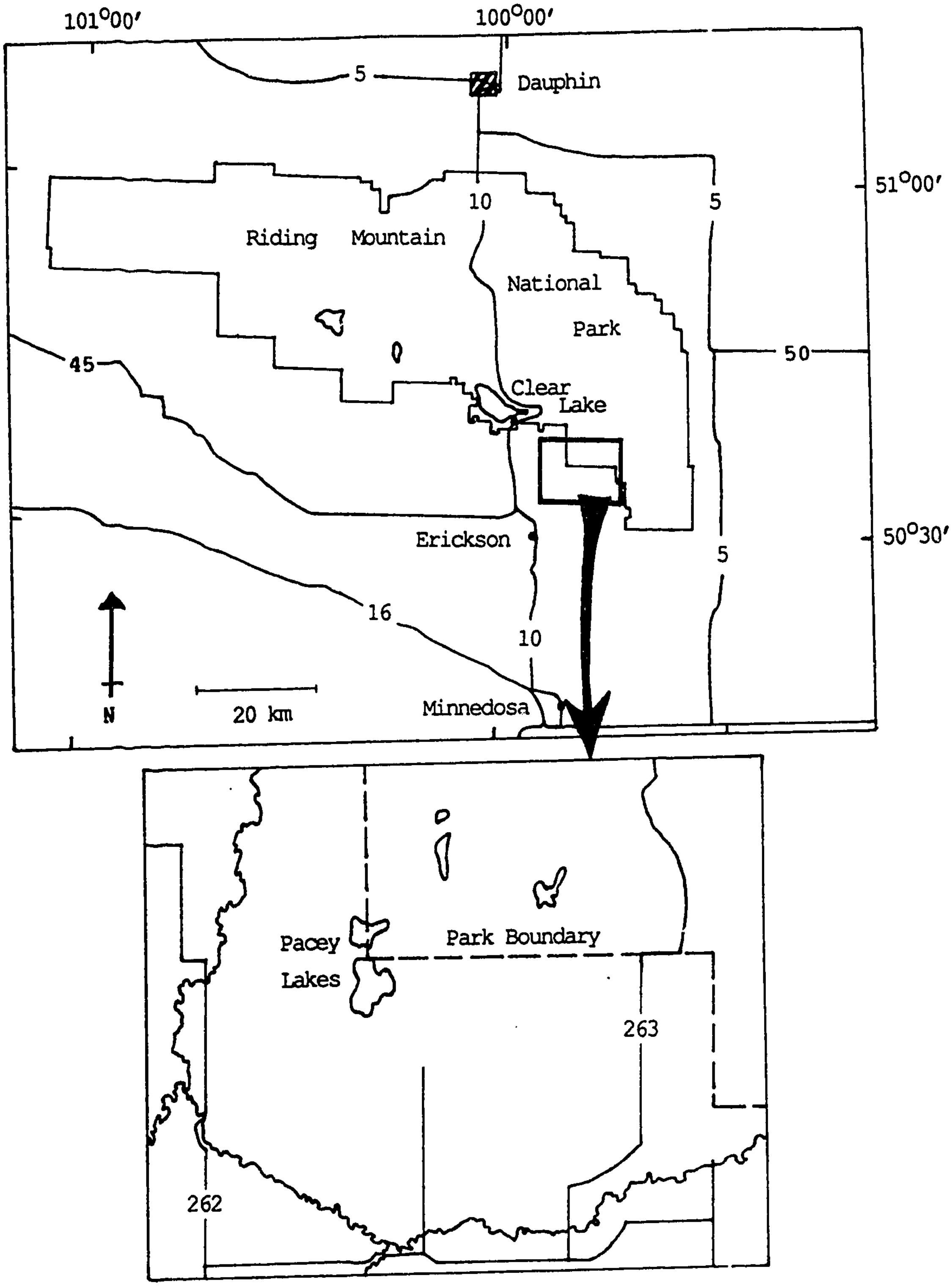

Fig. II-1. Map of the study area adjacent to Riding Mountain National Park, Manitoba, 1985-87. Numbers indicate highways.

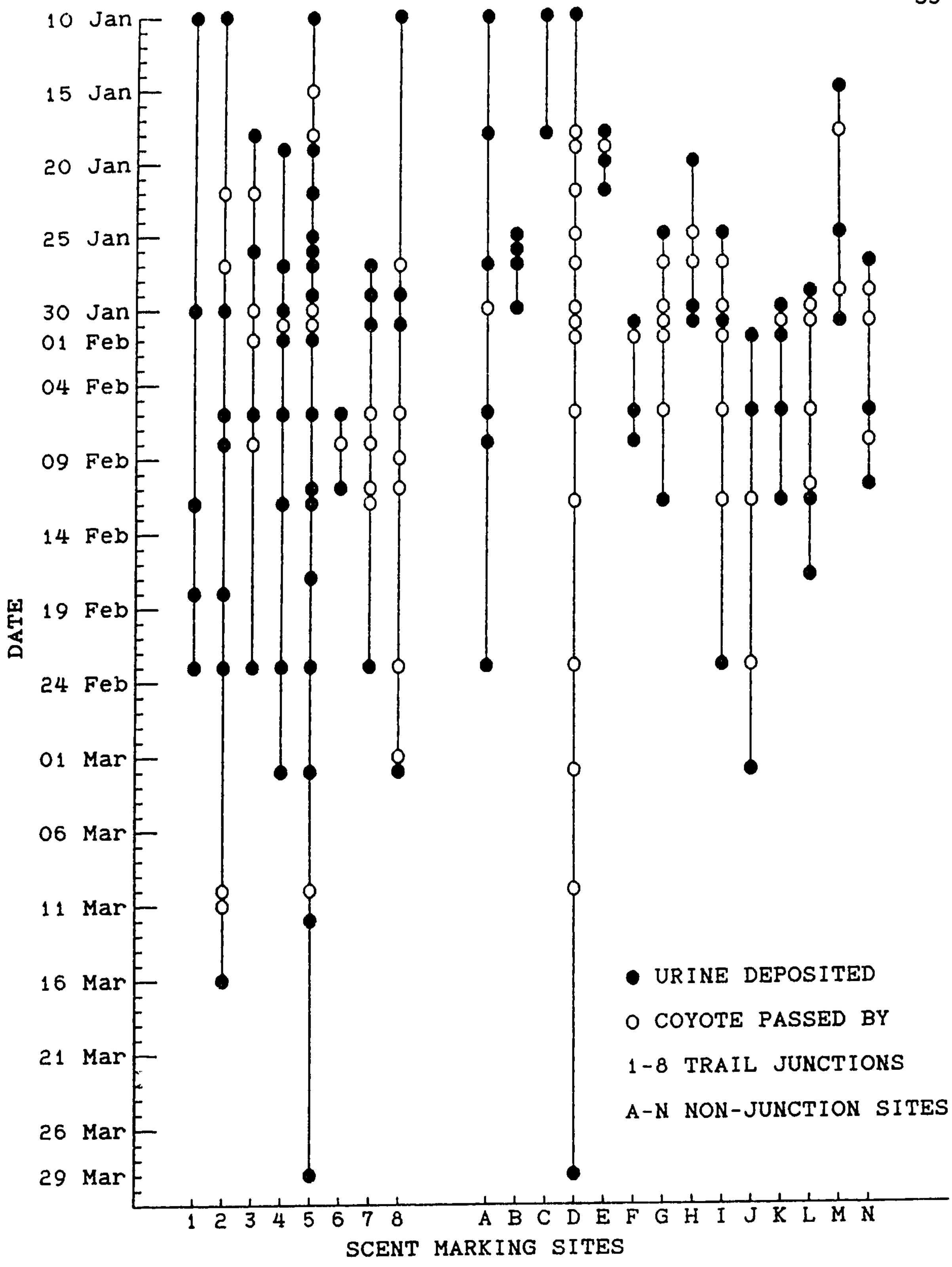

Fig. II-2. Marking activity of coyotes at urination sites along 6.1 km of snow-covered road in RMNP, Manitoba from 10 January to 29 March 1987. Only those activities occurring between the first and last recorded urine deposits are illustrated for each site. Sites marked only once are not included. Urine deposits recorded on 10 January are <48 hours old.

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III. WINTER HABITAT USE BY COYOTES: THE INFLUENCE OF SNOW CONDITIONS AND FOOD PREFERENCES

INTRODUCTION

In mixed forest regions of temperate North America, coyotes appear to favour conifer-dominated habitats during winter (Ozoga and Harger 1966, Major 1983). These authors suggest that such habitats are selected because they contain the coyote's main prey species. Many other studies have found similar relationships between habitat use by carnivores and habitat preferences of the major prey (Litvaitis and Shaw 1980, Parker 1980, Andelt and Andelt 1981, Todd et al. 1981, Whitman et al. 1986, Gese 1987, Halpin and Bissonette 1988). Other factors, such as ease of travel and protective cover have also been considered as possible determinants of habitat selection by predators (Henry 1979, Parker 1980, Litvaitis and Shaw 1980, Todd et al. 1981, Halpin and Bissonette 1988). With the exception of the red fox (_Vulpes vulpes_), however, quantitative data supporting such relationships have been limited (Henry 1979, Halpin and Bissonette 1988).

Coyotes are relatively new inhabitants of northern and northeastern forests of North America (Young and Jackson 1951, Richens and Hugie 1974, Hilton 1978). As such, they are physically ill-equipped to deal with deep and persistent snow cover (Todd and Keith 1976). Such morphological shortcomings in mammals may be compensated by behavioural adaptations (Telfer and Kelsall 1984). Selecting habitats with shallow or compact snow may be one way for coyotes in northern areas to cope. This study examines habitat use by coyotes in a mixed forest region of Manitoba, and attempts to determine the influence of prey availability and snow depth on coyote habitat selection.

STUDY AREA

Field studies were conducted within a 145 km^2 block of land 35 km north of Minnedosa, Manitoba on the southern border of Riding Mountain National Park (RMNP). Winters were typically long and cold, summers were short, warm, and dry (Keck 1975). Snow accumulations usually peaked in late February or early March, with maximum mean monthly snow depths often exceeding 40 cm (Meleshko 1986).

Forest cover was characterized by mixed and pure stands of trembling aspen (_Populus_ _tremuloides_) and white spruce (_Picea_ _glauca_). Beaked hazel (_Corylus_ _rostrata_) dominated the understory in deciduous woodlands. The southern portion of the study area formed a mosaic of grazed forest, open pastures, alfalfa fields, and cereal crops. Chokecherry (_Prunus_ _virginianus_) and service-berry (_Amelanchier_ _alnifolia_) were abundant along forest edges. The coniferous component increased slightly towards the northeast, particularly within RMNP, where openings were less common.

Sloughs, small lakes, willow (Salix sp.) thickets and occasional black spruce (Picea mariana) bogs were scattered throughout the region. For a description of vegetation and topographic features throughout RMNP see Carbyn (1980).

White-tailed deer (Odocoileus virginianus), snowshoe hare (Lepus americanus), cricetid rodents, porcupine (Erethizon dorsatum) and ruffed grouse (Bonasa umbellus) were among the winter prey species available to coyotes in the study area. Snowshoe hare numbers were just beginning to increase in 1985 following a population crash in 1982 (Carbyn et al. 1986). Within RMNP coyotes also had access to elk (Cervus elaphus) carcasses resulting from wolf (Canis lupus) predation (Meleshko 1986). Agricultural carrion was frequently available outside the park.

METHODS

Data pertaining to habitat use and food habits were collected by tracking coyotes through snow during the winters of 1985-86 and 1986-87. Both radio-collared and unmarked coyotes were tracked. Distances travelled in each habitat were estimated in the field and later measured from aerial photographs after the tracking sessions had been mapped. Six habitat types were recognized. Coniferous habitat included forest stands with greater than 50% coniferous canopy, whereas deciduous stands contained greater than 50% deciduous canopy. Open areas included pastures, crop fields, and forest openings. Thickets were characterized by willow (Salix sp.) and alder (Alnus rugosa) scrub, but also included marshes and ericaceous bogs. Any frozen water body or stream was classified as a frozen waterway. All roads, farmyards, and other developed sites were included in developed habitat.

Habitat availability was determined within 500 m on either side of each coyote track that was followed (see Chapter II for methods). This approach avoided problems associated with regional variation in habitat availability, by providing an estimate of available habitat in the area immediately accessible to coyotes. Wilcoxon's signed-ranks tests were then used to examine differences between the relative availability and corresponding use of each habitat. Expected frequencies for bed sites were based on the distances that coyotes were tracked in each habitat.

Food habits of coyotes were determined from scats collected along roads, trails, and coyote tracks. Procedures for collecting and analyzing scats were similar to those described by Meleshko (1986). As an additional precaution against infection from Echinococcus spp., scats were heated in an autoclave for 20 minutes at 110 C prior to processing. Prey hairs recovered from scats were identified using reference collections and keys by Kennedy and Carbyn (1981) and Moore et al. (1974). Remnants were expressed as relative frequencies of occurrence for each prey species, or group of species. Because individual scats frequently contained >1 prey item, the relative frequencies used in statistical tests were based on the total number of prey items rather than the total number of scats (Meleshko 1986). Weighted relative frequencies were also calculated (Appendix I). Such figures adjust for scats with >1 item, and probably reflected food habits more accurately (Meleshko 1986).

To determine habitat preferences of potential prey species, a track count was conducted on 3 March 1987, along 19.5 km of snowmobile trail, beginning approximately 36 hours after a 10 cm snowfall. The number of trail intersections observed in each habitat was tested against expected frequencies based on the proportion of snowmobile trail in each habitat. Tracks of animals that entered the snowmobile trail in one habitat and exited in another were counted once for each habitat.

Beginning in mid-winter of the first year, snow depths were measured almost every day by park staff at a permanent weather station near the study area. Habitat data collected prior to this period were not included in correlations with snow depths. For comparisons between habitats, snow depths were measured at numerous sites on 3 March 1987.

Where data were used in multiple, unplanned or non-orthogonal comparisons, critical values for G-tests were based on Sidåk's multiple inequality to account for the lack of independence among comparisons, therefore achieving the desired experiment-wise error rate of 0.05 (Sokal and Rohlf 1981). Binomial exact tests were used to analyze frequency data when values of zero or small expected values precluded use of a G-test.

RESULTS

Habitat Use and Snow Depths

Habitat data were collected along 130.9 km of coyote trail during 46 tracking sessions. The relative distances travelled by coyotes in different habitats did not match local availabilities. Coyotes travelled significantly more than expected in conifer-dominated areas and less than expected in deciduous forests and thickets (Wilcoxon's signed-ranks test, $\underline{P} < 0.01$ in each case, Table III-1). Coniferous habitat was selected both inside RMNP ($\underline{P} < 0.05$, $n = 9$) and outside ($\underline{P} < 0.01$, $n = 29$). Only those tracking sessions that were completely inside or outside the park were included in the latter analysis.

Although the preference value was slightly larger for open habitat than for coniferous habitat (Table III-1), use of open areas exceeded availability in only 50% of the tracking sessions, resulting in a non-significant rank test. This discrepancy occurred because coyotes tended to follow snowmobile trails when travelling through open areas (Table III-2). Coyote tracks on snowmobile trails were easier to follow than those on other snow surfaces; hence, tracking distances, and the resulting preference indices, were biased towards open habitat.

The preference value and rank test for developed habitat showed a similar discrepancy. When used, roads usually comprised a large portion of the tracking distance, however roads were travelled by coyotes in only seven of 46 sessions. Waterways were travelled by coyotes in roughly equal proportions to local availabilities ($p > 0.05$).

Single classification Model I analysis of variance showed that snow depths varied significantly between habitats ($p < 0.001$), and these differences parallelled the habitat preferences of coyotes (Table III-1). Snow depths in coniferous habitat were significantly lower than the combined average for open, deciduous, and thicket habitats ($p < 0.001$). Thickets and deciduous forests, which were used by coyotes less than expected, had significantly deeper snow than open areas ($p < 0.01$). There was no difference between snow depths in deciduous forest and thickets ($p > 0.05$).

The apparent relationship between snow depth and habitat selection by coyotes was further supported by Spearman rank correlations. As snow depths increased, so did the proportional distances tracked in coniferous habitat, whereas the use of deciduous cover by coyotes decreased (Table III-2). Travel in open habitat was not related to snow depth; however, it was correlated with the relative use of established trails by coyotes (Table III-2). Snowmobile trails were very common in open habitat and were frequently used by coyotes to cross fields.

Surprisingly, use of established trails did not increase with increasing snow depths (Table III-2). Trail use was, however, much greater along non-coniferous segments of tracking sessions than in the shallow snow of coniferous stands (Wilcoxon's signed-ranks test, n = 33, $\underline{P} < 0.01$). In non-coniferous habitats 57.8% of coyote tracks were along established trails or roads, versus 26.8% in coniferous areas. Sixty-nine percent of all coyote travel was either beneath coniferous canopy or along established trails. This is actually an underestimate, because snowmobile tracks on frozen lakes were not counted as established trails, even though coyotes often followed them.

Snow crusts capable of supporting coyotes first appeared on 6 March, 1986 and 24 February, 1987, and remained relatively intact until after the end of March each year. Use of deciduous habitat by coyotes increased dramatically after crusts formed, such that this habitat was travelled in near proportion to its availability (Table III-3). Decreased travel along established trails corresponded to less frequent use of open areas, frozen waterways, and developed habitats, all of which were extensively marked by snowmobile trails. The preference value for the latter two habitats switched from positive to strongly negative after crust formation (Table III-3).

No attempt was made to distinguish between travelling and hunting movements of coyotes. However, on five occasions during periods of fluffy snow, coyote tracks were examined that led away from a large mammal carcass at which feeding was believed to have occurred. Coyotes were assumed not to be hunting at such times, as they had just fed. For four of these tracking sessions, selection of coniferous habitat by coyotes exceeded availability by between 66 and 191%. For the remaining session, 37% (1 km) of the tracking distance was along the centre of a narrow, wind blown lake, where snow depths did not exceed 15 cm. Travel beneath coniferous canopy comprised an additional 33% of the route In contrast to these, were two sets of coyote tracks leading away from freshly-killed deer on heavily crusted snow. Coniferous habitat was not used at all in one instance and comprised only 3% of the trail in the other. Use of deciduous stands exceeded availability in each case.

Bed Site Selection

Coyote beds were not evenly distributed between habitats (G-test of goodness of fit, $\underline{P} < 0.001$, Table III-4). Bed site selection appeared to favour protection from wind and weather. Habitats without cover, such as open areas and frozen waterways, had significantly fewer bed sites per coyote-kilometer than wooded habitats ($\underline{P} < 0.001$). Beds were more common in low lying cover, which included coniferous habitat and thickets, than in upland deciduous forest ($\underline{P} < 0.001$). Finally, beds occurred more frequently along coyote trails [illegible] thickets than in coniferous regions ($\underline{P} < 0.001$). It is worth noting, however, that in absolute terms, more beds were located in coniferous stands than in any other habitat (Table III-4).

Orientation to the sun also appeared to be an important factor influencing bed site selection by coyotes. Only 25% of 112 beds were completely enclosed by dense (usually coniferous) vegetation. Cover was light or non-existent for 38%. For the remaining 37% (41), clear visibility of the sky was limited to primarily one direction. As a group, beds that opened in a southerly direction (southeast, south, or southwest) were more common than expected ($\underline{P} < 0.01$, Fig. III-1A). There were significantly fewer beds than expected with northerly or westerly openings ($\underline{P} < 0.01$ in both cases), and about as many as expected opening toward the east.

Bed sites on slopes comprised 24% (31) of recorded cases. Most of these (74%) were in deciduous habitat. South-facing slopes (southeast, south, or southwest) had significantly more beds (68%) than expected ($\underline{P} < 0.01$, Fig. III-1B). Beds occurred on predominantly east-, north-, or west-facing slopes slightly, but not significantly, less often than expected ($\underline{P} > 0.05$).

Food Habits

Between September, 1985 and April, 1987, 272 coyote scats were collected, containing 323 prey items. Of 226 prey items found in 202 winter scats (December - March), the most frequently occurring was white-tailed deer (30.1%), followed by elk (19.5%, Appendix 1). Small cricetid rodents, domestic cattle (*Bos* sp.), and unidentified bone chips represented 8.4, 7.1 and 6.6% of prey items respectively. However, when relative frequencies were weighted to account for scats containing >1 prey type, small cricetid rodents, which seldom occurred alone in a scat, dropped from a third to a fifth place ranking (Appendix 1).

All scats containing unidentified bone chips were located on agricultural land outside of RMNP, suggesting?that many, if not most, reflected coyotes scavenging on domestic cattle carcasses. Domestic carrion, therefore, was undoubtedly the third most important winter food of coyotes on the study area. The remaining prey items in winter coyote scats included vegetation (4.7%), porcupines (4.7%), snowshoe hares (2.5%), canids (2.5%), unidentified birds (1.2%), and unidentified remains (7.5%, Appendix I).

Large prey items were more prevalent in the winter diet of coyotes than were smaller items, whereas the opposite was true for the non-winter diet (G-test of independence, $\underline{P} <$ 0.01, Table III-5). Large prey items included white-tailed deer, elk, domestic cattle, unidentified ungulates, and unidentified bone chips. The latter was included because most chips appeared to be from large bones and because large prey, with a small surface area to volume ratio, were most likely to provide meals free of hair. Important non-winter coyote foods were chokecherries (40.3%), small cricetid rodents (16.9%), snowshoe hares (9.3%), and muskrats (Ondatra zibethicus) (6.3%, Appendix 1).

A change was apparent in coyote diets between the two winter seasons. Elk slightly overtook white-tailed deer as the main food item in the second winter; however, this difference is seen largely as a result of increased sampling effort within the park portion of the study area during the second year. Only 5.5% of samples came from the park during the first winter, versus 33.3% during the second. Elk remains were clearly more prevalent in scats collected inside the park (G-test of independence, $\underline{P} < 0.01$), whereas deer were more common in scats collected outside ($\underline{P} < 0.01$, Table III-5).

Deer was much more prevalent in coyote scats after crust formation in late winter than during periods without crusted snow ($\underline{P} < 0.01$, Table III-5). Coyote predation was known or believed to be responsible for 12 of 27 deer carcasses found on or near the study area. Ten of those killed by coyotes were killed during March after a crust had formed, one was killed during February, and one during October. Wolves killed one deer in each of October, November, January, February, and March. Four deer were shot by hunters and left in the field during November and December. Five deer died of undetermined causes in March, and another died in January. The frequency of elk in coyote diets did not change significantly as a result of crust formation ($G = 1.134$, $P > 0.05$), suggesting that availability of elk carcasses was not affected by snow condition.

Habitat and Food Relationships

Results from a track count along 19.5 km of snowmobile trail revealed that white-tailed deer were most common in coniferous habitat (G-test of goodness of fit, $P < 0.001$, Table III-6). Snowshoe hares also selected coniferous stands ($P < 0.05$), but not as much as they favoured thickets (binomial exact test, $P < 0.0001$). There was only a small bias towards coniferous habitat for small rodent tracks ($0.05 < P < 0.1$). All three of these prey groups showed a strong avoidance of open areas ($p < 0.001$ in each case), and deer also appeared to avoid deciduous forest ($p < 0.001$).

Only four of 17 deer carcasses found on the study area during winter were in coniferous cover. This is slightly less then the proportion of coyote trail found in that habitat. Domestic cattle carcasses were found at nine sites within the study area, five of which were dominated by conifers. Two were found in deciduous forest, and two were in the open. There were too few elk tracks or carcasses on the study area to interpret. However, unpublished data from a concurrent study in RMNP (Paquet 1989) demonstrated that wolf-killed elk were significantly less likely to be found in coniferous habitat than were coyote or wolf-killed deer (elk 13.9%, n = 72; deer 27.9%, n = 79; G-test of independence, $\underline{P} < 0.05$). The most common habitats for elk kills were frozen waterways (50.0%) and deciduous woods (36.6%). No estimates of habitat availability were provided.

Excluding carcasses, the number of food related remnants found along tracking routes was disproportionately high within coniferous stands (G-test of goodness of fit, $\underline{P} < 0.05$). Such remnants included bones, blood, clumps of hair, and bits of flesh, as well as holes dug in the snow by coyotes. These remnants need not have originated in the habitat where they were found, but may have represented food items carried to the site and/or deposited there as caches.

DISCUSSION

My results agree with the findings of Ozoga and Harger (1966) and Major (1983), that coyotes in temperate, mixed forests of North America use coniferous habitat during winter in a higher proportion than is locally available, and tend to avoid upland deciduous stands. Snow depths figured prominently in habitat selection. Not only did the preferred habitat provide the shallowest snow, but its relative use increased as snow accumulated through the winter. Halpin and Bissonette (1988) found similar relationships between snow depths and habitat use by red foxes. Open areas and softwood stands were the preferred habitats in that study, and also had the lowest snow depths.

Halpin and Bissonette (1988) stressed that snow conditions influenced habitat selection in foxes by affecting prey availability. As snow became deeper, the nu [illegible] ounce and dig marks in open habitat decreased, as did [illegible] consumption of small rodents. At the same time, use of dense understory and consumption of snowshoe hare by red foxes increased. Unfortunately, the authors did not report if foxes continued to travel in open areas despite the reduction in hunting efforts there.

Prey availability may also have influenced habitat choice in my study. Both coyotes and their prime food source, white-tailed deer, used coniferous-dominated stands more than expected based on availability. It is well known that deer congregate in coniferous areas to avoid deep snow and conserve energy (Verme 1966, Rongstad and Tester 1969, Armstrong et al. 1983), and deer are frequently the main winter food of coyotes in northern forests (Ozoga and Harger 1966, Hamilton 1974, Major 1983, Toweill and Anthony 1988).

Predators have been found to favour the habitats occupied by their main prey in other studies as well (Litvaitis and Shaw 1980, Parker 1980, Andelt and Andelt 1981, Todd et al. 1981, Whitman et al. 1986, Gese 1987).

Major (1983) observed that habitat differences between three species of sympatric predators in western Maine reflected differences in diet. During winter, red foxes and bobcats (Lynx rufus) travelled proportionally further in stands with softwood regeneration than did coyotes, and they consumed proportionally more snowshoe hares, which were common in that habitat. Foxes also ate more small rodents and ruffed grouse than did coyotes and made greater use of hardwood-dominated stands, which was a commonly used habitat for these two prey species.

Given that coyotes in my study area encountered not only shallow snow in coniferous habitat, but also their main food supply, it is impossible to say which factor, if any, is more important in determining habitat use. Several observations, however, cannot be readily explained in terms of prey availability alone, and suggest that coyotes sometimes select habitats primarily for ease of travel. For instance, even satiated coyotes selected coniferous habitat during times of deep, fluffy snow, but chose other habitats when snow crusts allowed less restricted movement. In addition, open habitat was used extensively outside of RMNP, and although probability levels were not significant, the preference value was very high. Yet, deer avoided open areas, and elk and cattle carcasses were found primarily in other habitats.

A similar discrepancy occurred in a coyote study north of Edmonton, Alberta (Todd and Keith 1976). Use of open habitat by coyotes and dependence on snowshoe hares both increased during periods of deep snow, despite a scarcity of snowshoe hares in open habitat. Rather than providing food, open areas in my study seemed to be important because of the ease of travel afforded by numerous snowmobile trails. Coyotes could travel quickly and easily along these routes between hunting, feeding, or resting areas.

The need for packed trails diminished after snow crusts formed in late winter, resulting in decreased use of open areas, frozen waterways and roads. Neither frozen lakes nor roads provided any appreciable food sources during winter, and were therefore of little value to coyotes except as travel corridors, or possibly for scent marking purposes (Major 1983, Peters and Mech 1975, Chapter II). Red foxes in Saskatchewan also switched from trails and wind blown lakes to previously under-utilized habitats after crusts formed in late winter (Henry 1979). Vulnerability to human predation may have been a further incentive for coyotes to avoid roads when possible (Todd and Keith 1976, Chapter IV).

During a study by Parker (1980), lynx (Lynx canadensis) on Cape Breton Island traveled through mature conifer stands proportionally more than expected, even though very few snowshoe hares occurred in that habitat. Hares formed the bulk of the lynx diet and were most abundant in advanced successional forest, a habitat that was also highly favoured by lynx. Parker (1980) concluded that lynx selected advanced successional forests because of food availability and used mature conifer stands for ease of travel between hunting areas. A similar selection process appeared to be operating for coyotes in my study. Coniferous habitats were selected by coyotes for both prey availability and ease of travel, whereas open areas, roads, wind blown lakes, and packed trails were used primarily to avoid deep snow.

Coyotes also differentiated between habitats when choosing bed sites. The intense selection of thickets in this regard is particularly interesting in light of the strong avoidance exhibited by coyotes for this habitat in general. Because thickets were often surrounded by dense coniferous stands they were usually well sheltered from the wind. However, unlike many coniferous sites, thickets also received direct solar radiation. Considering that coyotes rest at least as much during the day as they do at night, this may be of consequence (Laundré and Keller 1981, Andelt and Gipson 1979).

White-tailed deer in central Ontario were thought to be conserving energy when they selected winter day beds that were exposed to solar radiation (Armstrong et al. 1983).

Protection from wind, and radiant heat loss were thought to be more important in the selection of night beds. I could not distinguish between day and night beds in my study. Nonetheless, bed site selection by coyotes seemed to follow a similar pattern of minimizing wind exposure for some sites and maximizing sun exposure for others.

CONCLUSION

Without experimental manipulation of food resources, the relative influences of snow conditions and prey availability on habitat use by predators cannot be accurately assessed. Ideally, the habitat with the greatest food supply would also afford easy travel, which seems to have been the case for coyotes in my study. It is apparent, however, that deep, soft snow can lead to substantial use of habitats containing little or no food, provided such areas can improve travel efficiency between hunting, feeding and resting areas. Snow depth is not as important a consideration for bed sites, so long as the site can be easily reached. Because they are frequently associated with conifer stands, thickets are sheltered from the wind and are readily accessible to coyotes for use as bed sites. During the day, thickets also receive solar radiation, which should help to conserve energy when coyotes are resting. Shelter from wind, and exposure to the sun appear to be major factors governing the selection of bed sites by coyotes.

Table III-1. Relative use of different winter habitats by coyotes, and corresponding snow depths, based on 130.9 km of coyote tracks in southwestern Manitoba, 1985-87.

Habitat	% of coyote trail (r)	% of available areas (p)[a]	Index of preference (r-p/r+p)[b]	Mean Snow Depth (cm)[c]
Coniferous	25.6	17.3	0.19**[d]	36.8A[e]
Open	29.1	19.4	0.20	58.7B
Deciduous	31.9	48.8	-0.21**	65.7C
Thicket	3.3	9.0	-0.47**	68.5C
Waterway	5.7	5.0	0.06	[f]
Developed	4.4	0.4	0.84	[f]

[a] Grid counts for all tracking session were combined.

[b] positive values = selection, negative values = avoidance (Ivlev 1961).

[c] All measurements taken on the same day.

[d] Significance tests based on ranked differences between use and availability for each tracking session, **$\underline{P} < 0.01$.

[e] Snow depths with different letters are statistically different (single classification ANOVA, $\underline{P} < 0.05$).

[f] Not recorded.

Table III-2. Spearman rank correlations between snow depth, and coyote use of established trails and various habitats, for samples of coyote track in southwestern Manitoba, 1985-87.

	% Trail	% Coniferous	% Deciduous	% Open
Snow depth[a]	-0.003	0.46*[b]	-0.48**	-0.06
% Trail		-0.33*	-0.18	0.49***

[a] Snow depth measured daily at weather station.

[b] * $\underline{P} < 0.05$, ** $\underline{P} < 0.01$, *** $\underline{P} < 0.001$.

Table III-3. Differences in habitat and trail use by coyotes between periods of soft (December - February) and crusted (March) snow in southwestern Manitoba, 1985-87.

	Soft Snow[a]		Crusted snow[b]	
Habitat	% of coyote trail	Index of preference[c]	% of coyote trail	Index of preference
Coniferous	24.2	0.18	30.1	0.21
Open	31.2	0.22	23.1	0.14
Deciduous	29.0	-0.26	41.1	-0.07
Thicket	3.2	-0.48	3.5	-0.46
Waterway	6.8	0.17	2.2	-0.44
Developed	5.8	0.91	0.0	-1.00
Trails	51.6		22.8	

[a] 01/Dec/85 - 06/Mar/86 and 01/Dec/86 - 24/Feb/87

[b] 07/Mar/86 - 31/Mar/86 and 25/Feb/87 - 31/Mar/87

[c] Positive values = selection, negative values = avoidance (Ivlev 1961).

Table III-4. Distribution of 100 bed sites among various habitats along coyote trails in southwestern Manitoba during winters of 1985-87.

Habitat	Coyote-km[a]	Beds	Beds/coyote-km
Open	58.2	6	0.1A[b]
Frozen waterway	11.0	2	0.2A
Deciduous	65.6	26	0.4B
Coniferous	52.2	47	0.9C
Thicket	6.7	19	2.8D

[a] One coyote-km = one coyote travelling one kilometer.

[b] Different letters designate significantly different frequencies of occurrence (G-test of goodness of fit, $\underline{P} < 0.05$).

Table III-5. Relative frequencies of occurrence (%) of large prey items, small prey items, and two ungulate species in 272 coyote scats collected during winters of 1985-87 in southwestern Manitoba.

Criteria	Prey Items (n)	Large prey[a]	Small prey	Deer	Elk
Non-winter[b]	97	17.5	82.5		
Winter	226	66.8	33.2		
Soft snow[c]	160			20.0	21.3
Crusted snow[d]	66			54.5	15.2
Inside Park	42			9.5	57.1
Outside Park	169			37.3	11.8

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[a] Includes deer, elk, cattle, and unidentified bone chips.

[b] Comprised mainly of fall scats (September - November).

[c] 01/Dec/85 - 06/Mar/86 and 01/Dec/86 - 24/Feb/87

[d] 07/Mar/86 - 31/Mar/86 and 25/Feb/87 - 31/Mar/87

Table III-6. Density of tracks (crossings/km) for coyotes and potential prey species in different habitats along 19.5 km of snowmobile trail adjacent to RMNP, Manitoba, 1987.

		Track density[a]			
Habitat	Km	Coyote[b]	Deer	Hare	Rodent
Coniferous	3.2	1.3	20.3***[c]	4.4*	4.1
Deciduous	10.2	0.4	2.5***	1.6	2.2
Open	5.2	0.8	0.8***	0.0***	0.2***
Thicket	0.9	0.0	0.0	15.6***	5.6
All habitats	19.5	0.6[d]	4.9	2.3	2.1

[a] Tracks entering trail in one habitat and leaving in another were counted in both.

[b] Insufficient data for statistical tests.

[c] Observed frequencies deviated from expected, * $P < 0.05$, ** P <?0.01, *** $P < 0.001$ (G-test of goodness of fit).

[d] Bottom row represented expected track densities.

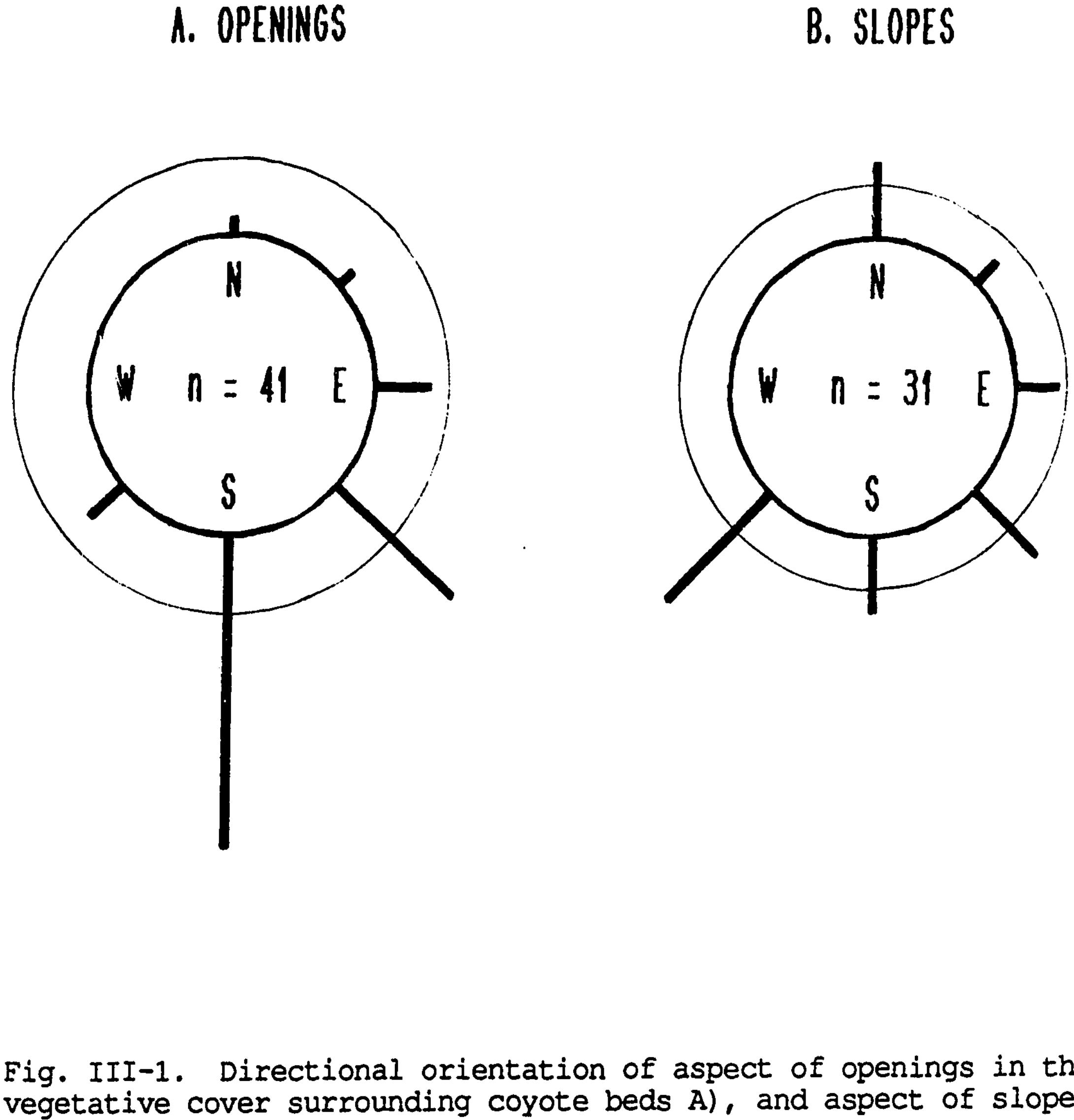

Fig. III-1. Directional orientation of aspect of openings in the vegetative cover surrounding coyote beds A), and aspect of slopes on which coyote beds are located B). Line lengths represent relative frequencies for each compass point. The outer circle indicates expected values.

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IV. HOME RANGE, DISPERSAL, AND MORTALITY OF COYOTES NEAR RIDING MOUNTAIN NATIONAL PARK, MANITOBA

INTRODUCTION

Estimates of home range size and mortality rates are of little value in understanding animal ecology unless they are interpreted in combination with other ecological factors. For example, Gese (1987) has linked differences in the size of coyote home ranges to regional variations in habitat, and ultimately to the density of food resources contained therein.

In this study, information on space use and population dynamics was required to assess the scent marking strategies of coyotes as described in Chapter II. The information is presented here as background to that chapter and to allow comparisons with studies of other coyote populations.

METHODS

Coyotes were captured using padded, steel leg-hold traps and modified snares, and were fitted with radio collars as described in Chapter II. Ages of trapped coyotes were estimated from tooth wear and eruption patterns (Gier 1968). When possible, age estimates were confirmed by counting cementum annuli in sectioned lower canine teeth after collared coyotes had died (Matson's Laboratory, Montana). Coyotes were classified at the time of capture as juveniles (4-7 months), yearlings (16-19 months), or adults ($\geq$ 28 months).

During winter (December - March), radio locations were obtained weekly from a fixed-wing aircraft and once or twice a week from the ground by triangulation of two or more bearings obtained with a hand-held antenna. Locations were less frequent during non-winter months. Home range determinations were based on the convex-polygon method. An outer point was included in the home range determination only if it lay within 1 km of where the boundary would otherwise have been without that point. Excluded points were considered excursions or "sallies" from the regular home range (Hibler 1977) and were not used in area-observation curves. Location data was augmented by tracking collared coyotes through the snow. Each mapped tracking route was included in the home range determination if it did not, on its own, result in a boundary extension of more than 1 km.

Dispersal was thought to have occurred when coyotes shifted their activities abruptly from one localized area to another, or if they began to range widely after a period of comparatively localized movement. When very few locations were obtained, coyotes were also suspected of having dispersed if their last known location was > 7 km from their point of capture. Seven kilometers was used because it exceeded the largest single dimension of an adult coyote home range in this study.

Mortality rates were determined by two methods. Confirmed mortality was based on animals located dead in the field, and on returns of collars and ear tags from trappers, hunters, and local residents. This method provided only a minimum estimate because animals that died of natural causes after their transmitters failed or after dispersing long distances would not have been recovered.

To estimate annual mortality, I first estimated annual survival using the equation $S_n = ((x-y)/x)^n$ described by Trent and Rongstad (1974) and Bowen (1978), where S is survival over n days, x is the number of coyote-days on which coyotes were wearing functional radio collars during period n, and y is the number of coyote-days on which a coyote died while wearing a functional transmitter. In this case n was 365 days. Annual mortality is simply $1-S_n$. Estimates of population age structure were obtained by counting cementum layers in sectioned canine teeth from coyotes harvested by local trappers.

RESULTS

During 2 years of field study, 30 coyotes were captured and 28 of these were fitted with radio collars. The proportions of captured coyotes in different age classes and sexes were similar to proportions found for a sample of 167 coyotes trapped, shot, or otherwise killed by humans in southwestern Manitoba during the study period ($\underline{P} > 0.05$ for both age class and sex, G-test of independence; Table IV-1). In both cases juveniles represented 50% or more of the sample. Only 11% of the coyotes killed had reached 3 years of age, the oldest being 6.5 years (Appendix 4).

Coyotes normally travelled in groups of one or two during the winter. Of 46 coyote trails followed during periods of snow cover, 50% involved single coyotes, 41% involved pairs, and the remaining 9% were left by groups of three. These estimates may be biased against lone animals, because known adult coyotes, which were frequently paired, were more often selected for tracking than juveniles. Three of the four trails left by groups of three coyotes were known to belong to the same pack, comprised of an adult collared female, her collarless mate, and a collared male yearling. Radio telemetry data suggest that these animals travelled together as late as 27 April 1986, after which radio contact with the yearling was lost.

Each of five adult collared coyotes, for which 15 or more locations were obtained, appeared to inhabit a well defined home range during winter. Three were frequently tracked or observed with another coyote believed to be a mate. The other two, although never observed together, occupied overlapping ranges and may have been a mated pair. Based on radio locations alone, the area-observation curve for home range size appeared to reach an asymptote in the case of only one coyote (AM8508; Fig. IV-1). When mapped tracking routes were superimposed over the radio locations, home range determinations increased by an average of 2.3 km^2 (Fig. IV-1). These latter estimates were thought to be relatively accurate for four adult coyotes (Fig. IV-2), producing a mean home range size of 13.0 $km^2 \pm 1.97$. With the inclusion of radio locations that were believed to be excursions, the average home range size increased to 27.3 $km^2 \pm 7.41$.

Home range was determined for only one non-adult coyote (YM8511; Fig. IV-1). This yearling male occupied a 6.2 km^2 area primarily within the range of an adult female (AF8503; Fig IV-2), which was known to be mated to another uncollared male. On 29 occasions both the yearling male and the female were located on the same day. They were located together four times and were within 1 km of each other on 12 occasions. They were associated with each other more often during December and March (eight of 13 same-day locations) than during the January-February mating season (four of 16 occasions) (G-test of independence, $\underline{P} = 0.05$). The yearling male was apparently in the company of the female during four of five excursions from his regular winter range. Inclusion of these excursions resulted in a winter home range of 49.1 km^2 for the yearling.

One other yearling and two juveniles also appeared to restrict their winter movements to a relatively localized area near their capture site. Too few locations were obtained for home range determinations, however, and associations with other animals were unknown (Appendix 5).

At least three of six yearlings and ten of 15 juveniles were believed to have dispersed within 1 year of being fitted with radio collars (Table IV-2). Dispersing coyotes included four of eight males and nine of 12 females. No adults dispersed. The distance from point of capture to site of death or last radio signal averaged 24 km ± 4.6. There was no significant difference in dispersal distance between males (20 km ± 4.8) and females (26 km ± 6.4; Mann-Whitney U-test, $\underline{P} > 0.2$).

Dispersals (n = 16) occurred primarily during autumn and early winter (n = 11) or late winter and spring (n = 3), and proceeded in a southerly direction (Table IV-2). These data may be misleading, however, as dispersing coyotes with inoperative transmitters were more likely to be recovered to the south, where trapping and hunting were prevalent, than to the north, where park regulations prohibited such activities. Four of six coyotes that dispersed with functioning transmitters, moved in a southerly direction. Early transmitter failures and trapping deaths resulted in more coyotes being monitored in the fall and early winter than any other time period. Nonetheless, of seven dispersing coyotes with functional transmitters during mid-winter, only one (YM8515) was known to disperse during this period. Five (JF8506, JF8510, YF8605, JF8607, and JM8610) were known to disperse before and/or after mid-winter, and the dispersal time of one (YM8512) could not be determined (Table IV-2).

Of 28 coyotes collared between September 1985 and October 1986, 69% (19) were known dead by 31 December 1988. Trapping and shooting accounted for 15 deaths, two coyotes were struck by vehicles and two (both adults) were killed by wolves inside the national park (Appendix 5). A minimum of 46% died within 1 year of being collared (Table IV-3). These figures do not include pups younger than 4 months of age.

Nine coyotes died while their transmitters were still functioning. Estimates based on these deaths revealed an annual mortality rate of 72% (Table IV-3). Regardless of which estimate was used, mortality appeared to be highest among juveniles between 0.5 and 1.5 years old. Only one of six yearlings was known to die within 1 year of being tagged, however, of six coyotes collared as juveniles three were killed between 12 and 18 months later. Hence yearling mortality was probably much higher than the 17% listed in Table IV-3. Annual mortality appeared higher for males than females. Sample size, however, did not allow any meaningful statistical comparisons.

Both of the adult resident coyotes (AF8503 and AM8508) studied in detail during 1985-86, were killed before the second winter of study. Parts of the previous ranges of these coyotes were taken over during 1986-87 by two newly collared coyotes (AM8601 and AM8613); however the two new ranges included only 30 and 35%, respectively, of the areas occupied by the previous residents (Fig. IV-2). Sixty-nine and 27% of the new ranges fell outside the home ranges of previous year's residents.

DISCUSSION

Estimates of average home range size for coyotes vary from 4.5 to almost 30 km^2 for those studies in which the minimum convex polygon method was used and where efforts were made to exclude coyote excursions from the calculation (Andelt and Gipson 1979, Bowen 1982, Messier and Barrette 1982, Laundré and Keller 1984, Pyrah 1984, Andelt 1985, Bekoff and Wells 1986, Gese 1987). The average value of 13.0 km^2 for coyotes in my study falls well within this range, and is typical for populations in forested habitats at similar latitudes (Bowen 1982, 13.8 km^2; Messier and Barrette 1982, 18.6 km^2).

Perhaps more important than the size of a home range is its stability over time. Whereas I observed substantial shifts in home range boundaries between years, other investigators, studying coyotes in relatively protected areas such as national parks and wildlife refuges, have found home range configurations to remain very similar year after year (Bowen 1982; Andelt 1985; Bekoff and Wells 1980, 1986; Gese 1987). Instability of home range boundaries may be a reflection of unstable populations and small group size. Coyote mortality was very high in my study (72%), even among resident adults, and group sizes were generally quite small (<17% of coyotes tracked were in groups > 2). In the relatively unexploited populations listed above, annual mortality was considerably lower (≤45%), and more coyotes (25 - 70%) belonged to packs with three or more members. The proportion of pack-living animals observed by Bekoff and Wells (1980) may actually have been <25%; however, some groups were known to contain up to seven individuals.

Pyrah (1984) also reported relatively consistent home range boundaries between years, despite high coyote mortality and frequent replacement of resident adults. Hence, factors other than mortality may also affect the stability of a home range over time. Bekoff and Wells (1980) suggested that only coyote groups larger than two are territorial. If this is true, lack of territoriality could explain the shifts in home ranges observed in my study. Although I observed no direct evidence of territorial defense by mated coyote pairs, territoriality cannot be ruled out. All residential adults in my study scent marked extensively throughout their home range (Chapter II), and other researchers have witnessed mated pairs defending their territory from intruders (Camenzind 1978).

The factors influencing the stability of home ranges and territorial boundaries over time clearly require further research. Population dynamics and territoriality are two factors which could potentially play an important role in determining site fidelity. Observations by Bekoff and Wells (1980) and Gese (1987) relating food distribution and abundance to home range size, suggest that changes in the availability of food resources may also be a rewarding area of investigation as it relates to home range stability.

Table IV-1. Age and sex composition of coyotes 1) captured during the study period and 2) killed by humans, in southwestern Manitoba, 1985-87.

	Juveniles		Yearlings		Adults		Males		Females	
Source	n	%	n	%	n	%	n	%	n	%
Study animals	15	50	6	20	9	30	14	47	16	53
Human-killed	103	62	33	20	31	19	80	52	75	48

Table IV-2. Timing, distance, and direction of suspected coyote dispersals in southwestern Manitoba, 1985-87.

Coyote	Date captured	Last radio signal	Time of movement	Distance (km) and direction[a]	
JM8502	29/Sep/85	N/A[b]	Oct	8.6	SE
JF8504	19/Oct/85	N/A	Oct	26.0	SE
YF8505	22/Oct/85	02/Nov/85	Nov - Dec	68.9	SE
JF8506[c]	24/Oct/85	29/Jun/86	Nov - Dec Mar - Jun	41.9	W-NW
JF8510	06/Nov/85	29/Jul/86	Mar - May	6.4	N-NW
YM8512	20/Nov/85	12/Jan/86	after Jan	28.1	E-SE
JF8515	09/Feb/86	26/Feb/86	Feb - ?	18.1	W
JF8603	26/Aug/86	30/Aug/86	Sep - Nov	18.4	SE
YF8605[c]	08/Sep/86	16/Jan/87	Oct, Dec	24.1	SE
JF8607[c]	14/Sep/86	04/Mar/87	Oct - Jan Mar - Dec	10.4	S-SE
JM8610	06/Oct/86	16/Jan/87	Nov	15.2	S-SE
JM8611	07/Oct/86	22/Nov/86	Oct - Nov	27.7	S-SW
JF8612	09/Oct/86	03/Nov/86	Nov - Jan	16.1	S-SW

[a] Measured from point of capture to site of last recorded signal or death.

[b] Not located by radio signal.

[c] Coyote shifted activity area on two separate occasions.

Table IV-3. Annual mortality of radio-collared coyotes in southwestern Manitoba, 1986-87.

		Confirmed		
	Coyotes tagged	n	%	Estimated (%)[a]
Total	28	13	46	72
Year				
1985-86	13	7	54	72
1989-87	15	6	40	72
Age				
Juvenile	14	8	57	80
Yearling	6	1	17	
Adult	8	4	50	64[b]
Sex				
Female	16	7	44	52
Male	12	6	50	87

[a] based on coyotes that died while wearing functional transmitters (Trent and Rongstad 1974).

[b] data for adults and yearlings combined.

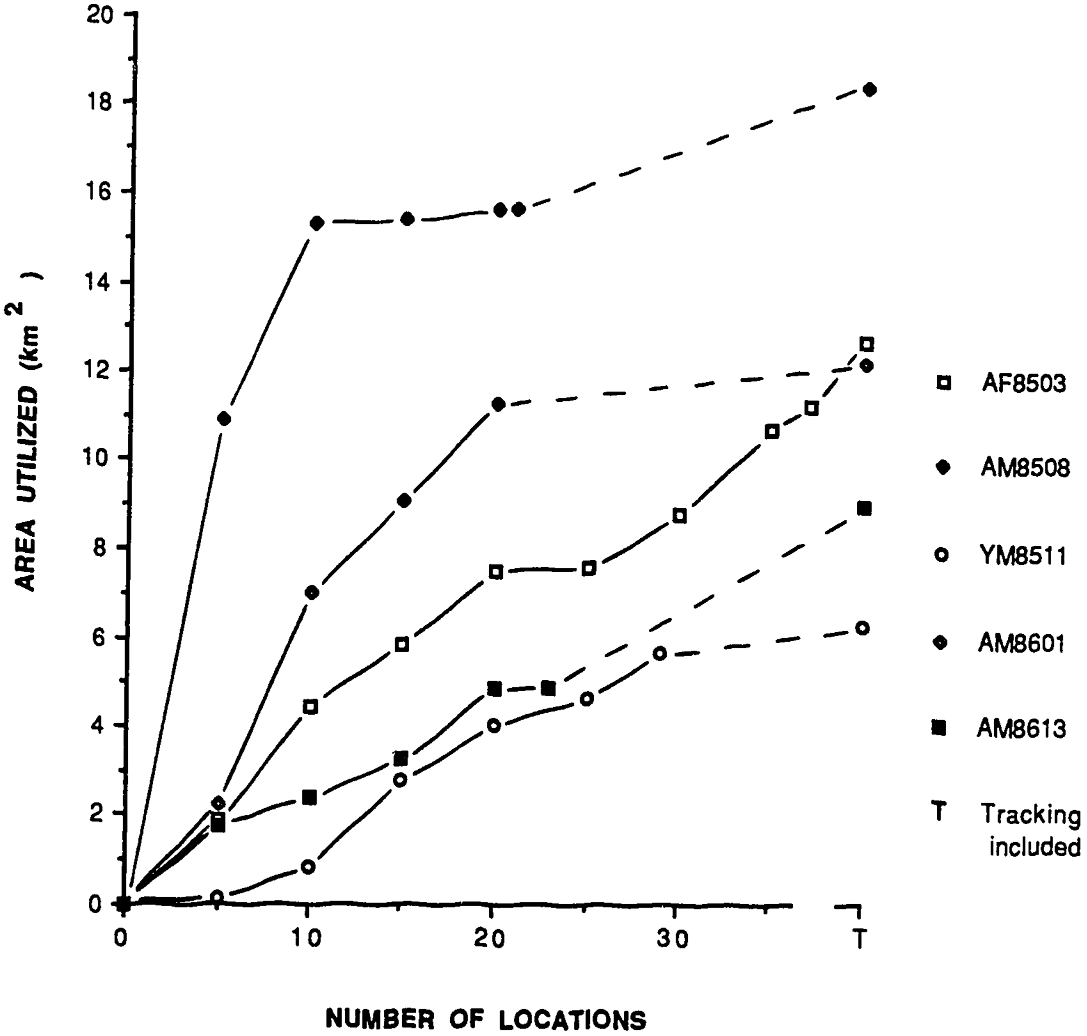

Fig. IV-1. Area-observation curves for winter home ranges, based on radio fixes of one yearling (Y) and four adult (A) coyotes in southwestern Manitoba, 1985-87. The cumulative area for every fifth location is plotted. The home range estimates indicated at the right side of the graph include mapped tracking routes.

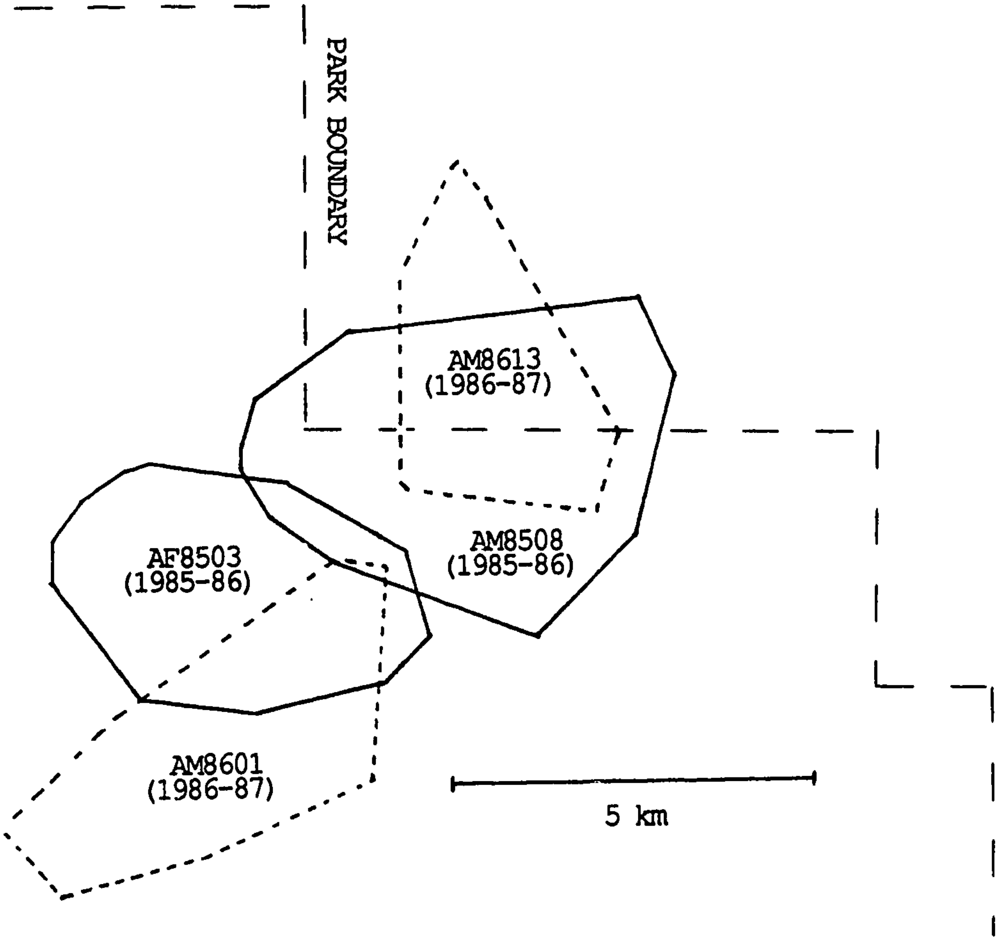

Fig. IV-2. Shifts in coyote home ranges between successive winters after the death of two resident adults in southwestern Manitoba, 1985-87.

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V. CONCLUSION

Of the factors examined in this study, habitat had the greatest influence on the spatial distribution of scent marks by coyotes. The higher incidence of scent marking within coniferous cover appeared to be linked to the coyote's preference for this habitat. Presumably, urine deposits accumulate more rapidly in the most frequently travelled habitats, resulting in a greater stimulus for scent marking during subsequent visits by coyotes. The same argument explains the tendency in non-coniferous habitats for greater scent marking rates along trails than cross-country routes. Trails were frequently used by coyotes for travel outside of coniferous cover. The result, in either case, is that scent marking rates were highest where they were most likely to be encountered in the future.

That coyotes did not scent mark more frequently per kilometer near the periphery of territories than in the centre, does not rule out the possibility of territorial scent marking. So long as intruders encountered sufficient scent marks at the periphery to ascertain that the territory was occupied, then the relative difference in scent marking rates between peripheral and central regions is irrelevant. Furthermore, high coyote mortality and yearly shifts in home range boundaries may have complicated territorial scent marking patterns. Nonetheless, observations suggested that scent marking served other important functions besides territoriality, such as pair bonding and improved foraging efficiency. Hence, scent marking by coyotes can convey messages at both the intra- and inter-pack level. The message depends on which coyotes encounter the mark and under what circumstances. The distribution of scent marks dictates which individuals are likely to encounter the marks.

The preference for coniferous habitat by coyotes in this study may have been influenced by both snow depth and abundance of food resources. Although it could not be ascertained which factor had the greatest influence on habitat selection in general, it was apparent that certain habitats and terrain types were used by coyotes primarily to avoid deep fluffy snow. Other considerations, such as protection from the wind and exposure to solar radiation seemed to govern which habitats were selected for bed sites.

In summary, coyotes seemed to prefer those habitats which provided the greatest amount of food and the greatest protection form harsh conditions and deep snow. The resulting travel patterns ultimately influenced the distribution of scent marks by coyotes and so played an important role in the communication system of these animals.

Appendix 1. Weighted[a] and unweighted relative frequencies of occurrence (%) of prey items in coyote scats during different seasons in southwestern Manitoba, 1985-87.

	Weighted			Unweighted		
Prey	Winter (202)	Non-winter[b] (70)	Total (272)	Winter (226)	Non-winter (97)	Total (323)
Deer	32.4	4.7	25.3	30.1	4.1	22.3
Elk	19.8	4.3	15.8	19.5	4.1	14.9
Unid. ungulate	3.7	2.9	3.5	3.5	3.1	3.4
Domestic cow	7.4	3.9	6.5	7.1	6.2	6.8
Unid. bone	7.4	0.0	5.5	6.6	0.0	4.6
Small cricetid	6.2	16.9	8.9	8.4	19.6	11.8
Porcupine	4.7	0.7	3.7	4.9	1.0	3.7
Vegetation	4.7	2.1	4.0	5.8	2.1	4.6
Snowshoe hare	2.5	9.3	4.2	2.7	8.2	4.3
Canid	2.5	1.9	2.3	3.1	3.1	3.1
Insect	0.0	2.1	0.6	0.0	3.1	0.9
Bird	1.2	0.0	0.9	1.8	0.0	1.2
Beaver	0.0	3.6	0.9	0.0	3.1	0.9
Muskrat	0.0	6.0	1.5	0.0	6.2	1.9
Chokecherry	0.0	40.3	10.4	0.0	35.1	10.5
Unidentified	3.0	0.0	2.2	2.7	0.0	1.9
No hair or bone	4.5	1.4	3.7	4.0	1.0	3.1

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[a] When two or more prey items occur in one scat, each item is given a weighted frequency of 0.5, 0.33, etc.

[b] Includes 59 scats from autumn, 7 from spring and 4 from summer.

Appendix 2. Weighted[a] and unweighted relative frequencies of occurrence (%) of prey items in winter coyote scats inside and outside of RMNP, Manitoba, 1985-87.

	Weighted			Unweighted		
Prey	Inside (37)	Outside (152)	Total (189)	Inside (42)	Outside (169)	Total (211)
Deer	10.8	40.1	34.4	9.5	37.3	31.8
Elk	59.5	11.8	21.2	57.1	11.8	20.9
Unid. ungulate	0.0	4.3	3.4	0.0	4.1	3.3
Domestic cow	2.7	7.9	6.9	2.4	7.7	6.6
Unid. bone	0.0	7.9	6.3	0.0	7.1	5.7
Small cricetid	16.2	4.3	6.6	19.0	6.5	9.0
Porcupine	0.0	4.6	3.7	0.0	4.7	3.8
Vegetation	2.7	5.6	5.0	2.4	7.1	6.2
Snowshoe hare	1.4	3.0	2.6	2.4	3.0	2.8
Canid	0.0	3.3	2.6	0.0	4.1	3.3
Bird	4.1	0.0	0.8	4.8	0.0	0.9
Unidentified	2.7	2.0	2.1	2.4	1.8	1.9
No hair or bone	0.0	5.3	4.2	0.0	4.7	3.8

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[a] When two or more prey items occur in one scat, each item is given a weighted frequency of 0.5, 0.33, etc.

Appendix 3. Weighted[a] and unweighted relative frequencies of occurrence (%) of prey items in coyote scats during different snow conditions in southwestern Manitoba, 1985-87.

	Weighted			Unweighted		
	Fluffy Snow	Crusted Snow		Fluffy Snow	Crusted Snow	
	Dec-Feb	March	Total	Dec-Feb	March	Total
Prey	(143)	(59)	(202)	(160)	(66)	(226)
Deer	21.3	59.3	32.4	20.0	54.5	30.1
Elk	21.3	16.1	19.8	21.3	15.2	19.5
Unid. ungulate	5.2	0.0	3.7	5.0	0.0	3.5
Domestic cow	9.4	2.5	7.4	8.8	3.0	7.1
Unid. bone	8.4	5.1	7.4	7.5	4.5	6.6
Small cricetid	5.6	7.6	6.2	7.5	10.6	8.4
Porcupine	6.3	0.8	4.7	6.3	1.5	4.9
Vegetation	4.9	4.2	4.7	6.3	4.5	5.8
Snowshoe hare	3.1	0.8	2.5	3.1	1.5	2.7
Canid	2.4	2.5	2.5	3.1	3.0	3.1
Bird	1.4	0.8	1.2	1.9	1.5	1.8
Unidentified	4.2	0.0	3.0	3.8	0.0	2.7
No hair or bone	6.3	0.0	4.5	5.6	0.0	4.0

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[a] When two or more prey items occur in one scat, each item is given a weighted frequency of 0.5, 0.33, etc.

Appendix 4. Age structure, as determined by counting tooth cementum layers, of 167 coyotes killed in southwestern Manitoba, 1985-87.

Age (years)	Number	Percent
0.5	103[a]	62
1.5	33	20
2.5	13	8
3.5	6	4
4.5	9	5
5.5	2	1
6.5	1	1

[a] The occurrence of open root canals made tooth sectioning unnecessary in the case of 38 juvenile coyotes.

Appendix 5. Duration of radio contact with study animals and their eventual fate in southwestern Manitoba, 1985-87.

Coyote	Date of capture	Last radio contact	Duration of contact (days)	No. of fixes	Fate of coyote[a]
JM8502	29/Sep/85	n/a	0	2	vehicle
AF8503	17/Oct/85	06/Jul/86	262	61	shot
JF8504	19/Oct/85	n/a	0	2	trapped
YF8505	22/Oct/85	02/Nov/85	11	8	trapped
JF8506	24/Oct/85	29/Jul/86	278	25	trapped
AF8507	25/Oct/85	29/Jan/86	96	18	unknown
AM8508	26/Oct/85	05/Mar/86	130	33	wolves
JM8509	05/Nov/85	13/Jan/86	69	13	trapped
JF8510	06/Nov/85	29/Jul/86	265	35	unknown
YM8511	06/Nov/85	27/Apr/86	172	44	unknown
YM8512	20/Nov/85	12/Jan/86	53	15	vehicle
AF8514	24/Jan/86	05/Mar/86	40	9	wolves
JF8515	09/Feb/86	27/Apr/86	77	9	trapped
AM8601	14/Aug/86	05/Feb/87	175	29	trapped
YM8602	17/Aug/86	30/Sep/86	44	6	trapped
JF8603	26/Aug/86	30/Aug/86	4	3	trapped
YF8604	29/Aug/86	30/Sep/86	32	4	unknown
YF8605	08/Sep/86	16/Jan/87	130	17	trapped
JM8606	09/Sep/86	17/Oct/86	38	5	trapped
JF8607	14/Sep/86	04/Mar/87	171	9	trapped
JF8608	17/Sep/86	17/Oct/86	30	3	unknown
AF8609	02/Oct/86	30/Dec/86	89	8	unknown
JM8610	06/Oct/86	16/Jan/87	102	15	unknown
JM8611	07/Oct/86	22/Nov/86	46	3	trapped
JF8612	09/Oct/86	03/Nov/86	25	5	trapped
AM8613	16/Oct/86	27/Feb/87	134	28	unknown
JF8614	23/Oct/86	13/Dec/86	31	5	trapped
AM8615	28/Oct/86	30/Dec/86	63	5	unknown

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[a] As of 31 December 1988.