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BEHAVIORAL ECOLOGY OF SYMPATRIC WOLVES (*CANIS LUPUS*) AND COYOTES (*C. LATRANS*) IN RIDING MOUNTAIN NATIONAL PARK, MANITOBA. ©

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN
PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

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THE UNIVERSITY OF ALBERTA
FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled BEHAVIORAL ECOLOGY OF SYMPATRIC WOLVES (*CANIS LUPUS*) AND COYOTES (*C. LATRANS*) IN RIDING MOUNTAIN NATIONAL PARK, MANITOBA submitted by PAUL C. PAQUET in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY.

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ABSTRACT

Although wolves and coyotes appear to be sympatric throughout portions of their geographic ranges little is known about their spatial interactions. Most researchers have implied that in regions where both species occur, coyotes either avoid the areas where wolves are most active or are displaced by wolves. Spatial segregation has been attributed to antipathy of wolves toward coyotes as well as inability of coyotes to compete successfully for essential resources such as food.

In Riding Mountain National Park wolves (*Canis lupus*) and coyotes (*C. latrans*) overlapped temporally and spatially. The movements of coyotes relative to wolves were not random. Coyotes sought out active wolf areas, and followed wolf tracks rather than avoiding them. The movements of wolves were not altered by the presence of coyotes.

Urine marking behavior of the two species was similar with both canids using the same scent mounds. Coyotes increased their rate of marking significantly in response to wolves. Wolves were less responsive to coyotes. Wolves did not use urine marks to demarcate territorial boundaries. The behavior does not appear to be a consequence of sympatry with coyotes.

Competition between wolves and coyotes was minimized by differential use of the available food resources. Wolves preyed primarily on elk (*Cervus elaphus*), and secondarily on white-tailed deer (*Odocoileus virginianus*), and moose (*Alces alces*) yearlings. Coyotes preyed on deer and rarely, young elk. Although wolves occasionally killed coyotes, coyotes followed wolves and scavenged at their kills. The benefits accrued from scavenging apparently compensated for the associated risks. This relationship could change if the nature of the food supply is altered.

A hypothesis is proposed that suggests the association, and therefore the distribution, of wolves and coyotes is influenced primarily by: a) the availability and use of large ungulate prey species by wolves, and b) the availability of wolf-provided carrion for coyotes to scavenge. It is concluded that the proximate reason why coyotes are excluded from some areas occupied by wolves is that they are unable to scavenge for food, and secondarily because of direct aggression by wolves.

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CHAPTER 1

GENERAL INTRODUCTION

There is a paucity of information concerning the ecological association of wolves (*Canis lupus*) and coyotes (*C. latrans*). Why the two closely related species successfully cohabit in some areas and not in others, and to what degree niche overlap occurs in areas where both canids exist remains unclear. Sympatry among carnivores is usually permitted through differences in diet, habitat, and escape behavior (Stanley et al. 1983). Therefore, wolf/coyote relations are likely characterized by niche segregation, because extreme overlap in hunting methods and food resources should result in competitive exclusion (Gause 1934).

C. latrans was present during the Pleistocene as a species distinct from *C. lupus* (Lane, 1948), and Gier (1975) concluded that the 2 species must have been separated geographically or ecologically rather than genetically or reproductively, otherwise interbreeding could not be so easily accomplished.

When Europeans first arrived in North America, the coyote occupied primarily the western half of the continent (Nowak 1978). The precise limits of its range, however, are unknown. Although Jackson (1951) recognized 3 distinct

Central American subspecies, Young (1951) believed that coyotes were originally found only as far south as Mexico, and that they later moved further south as livestock was introduced into the region. Nowak (1978) apparently supports this belief, stating that it is questionable whether 3 subspecies could have evolved in 400 years.

Prior to 1832, descriptions of wild canids in North America were vague (Young and Jackson 1951), but most evidence suggests that coyotes were precluded from much, although not all, of the range occupied by wolves (Gier 1975). About 1850, coyotes extended their range into Illinois and Michigan, Yucatan, northern California and the Pacific Northwest, and in the 1880s began a northward expansion. In the early 20th century, following extirpation of wolves, coyotes began to colonize the East and Northeast (Young and Jackson 1951, Pringle 1960, Mech 1970, Kolenosky and Standfield 1975), and eventually reached Hudson Bay and the Atlantic Coast. The eastern extension is known to have ranged into southern Wisconsin, northwestern Indiana, western Arkansas, and central Texas (Nowak 1978).

According to Young (1951) the coyote only recently became established in northwestern Canada and Alaska. As noted by Nowak (1978), this contrasts with Jackson's viewpoint that the species has been a long time resident of that area. Nonetheless, by 1950 much of the Yukon Territory and Alaska were inhabited (Gier 1975).

Western and northwestern extensions followed reduction of wolves, and were coupled with the clearing of forested areas. Eastern and northeastern extensions were concurrent with removal of wolves and conversion of forest to pasture (Gier 1975). Currently, the coyote is distributed throughout North America, including most of the former range of the wolf.

Because range extension of coyotes coincided with extensive environmental change, it is not clear whether movement into former wolf range was related to elimination of the wolf or to the creation of suitable habitat (Mech 1970). The issue is complicated by contradictory evidence concerning the role of the wolf in influencing coyote distribution. Coyotes often maintain densities in inverse relation to those of the wolf (Stenlund 1955, Berg and Chesness 1978, Carbyn 1982), and in extreme situations, wolves appear to displace or exclude coyotes completely (Mech 1970, Peterson 1974, Berg and Chesness 1978), which suggests that coyote distribution and numbers are affected by the presence of wolves. For example, in Minnesota, more bounties were paid for coyotes in areas of low wolf density than areas of high wolf density (Stenlund 1955), and in Algonquin Park, Ontario, where there is a high density of wolves, coyotes are seldom observed (Pimlott et. al. 1969, Theberge pers. comm.), although they are present around the periphery. The extirpation of coyotes on Isle Royale has been attributed to predation by colonizing wolves (Mech 1966, Krefting 1969, Wolfe and Allen 1973, Allen 1979), as well as to direct competition for food (Peterson 1977). Additionally, several telemetric studies suggest that coyotes avoid, or are excluded from, adjacent areas containing wolves (Berg and Chesness 1978, Fuller and Keith 1981, Carbyn 1982). Moreover, there are numerous published accounts of wolves killing coyotes (Seton 1929, Young and Goldman 1944, Munro 1947, Stenlund 1955, Berg and Chesness 1978, Carbyn 1982).

In contrast, wolves and coyotes are now, or were at one time, sympatric throughout a diverse range of North American habitat. Overlap was extensive from the Mississippi River, west into the Sierra Nevada Mountains, north to Alberta and south to southern Mexico (Gier 1975, p249). Both species were present in Yellowstone National Park, Wyoming (Murie 1940), and co-occurrence is still common throughout the Canadian Rocky Mountains (Cowan 1947, Carbyn 1975), the Yukon, and Alaska. In Riding Mountain National Park (RMNP), Manitoba and Prince Albert National Park, Saskatchewan substantial populations of both canids occur.

Both wolves and coyotes were present in RMNP in the middle 1800s and wolves were extirpated by about 1930. There is no evidence that coyote populations changed substantially following the elimination of wolves. Wolves began recolonizing RMNP in the early 1940s and were apparently well established by 1950. Again, there is no indication that coyote numbers were affected.

The results of studies in RMNP (Carbyn 1982) and Alberta (Fuller and Keith 1981) suggest that coyotes avoid wolves by surviving in "buffer zones" peripheral to wolf territories. However, mortality of radio-collared coyotes in RMNP showed that occupation of "buffer zones" did not guarantee protection from wolves. Nevertheless, coyote survival appeared to be greater in those areas than within core areas of wolf activity, particularly in years of moderate wolf densities. Generally, wolf-related coyote mortality in RMNP was greatest when wolf densities were high, regardless of coyote distribution relative to wolf territories. When wolf populations were moderate, chances of survival of at least a few coyotes appeared greatest at wolf pack territory edges. Overall, abundance indices obtained from howling surveys indicated that as wolf densities declined coyotes numbers increased (Carbyn 1982).

Chapter 1

OBJECTIVES

The objective of this study is to elucidate the mechanism(s) that allow for co-existence of wolves and coyotes in RMNP. The following questions pertaining to the behavioral and ecological relationship of the 2 species are asked:

I) What are the effects of wolves on the behavior, spatial distribution, and travel patterns of coyotes?

II) Wild canids have been shown to employ scent marks to delineate territory (Peters and Mech 1975), mark food caches (Harrington 1982) and to achieve reproductive synchrony (Rothman and Mech 1979). What, therefore, is the inter-specific behavioral significance of scent marks for sympatric wolves and coyotes; and are scent marks important for maintaining ecological separation?

III) Do sympatric wolves and coyotes both exploit ungulate prey species (moose, elk, deer), and if so, do they use the species differently, thereby reducing interspecific competition?

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CHAPTER 2

Spatial Relationships of Wolves (*Canis lupus*) and Coyotes (*C. latrans*) in Riding Mountain National Park, Manitoba

INTRODUCTION

Previous studies of parapatric or sympatric populations of wolves (*Canis lupus*) and coyotes (*C. latrans*) have noted that coyotes tend to be situated outside areas of intense wolf activity, implying that the relative geographic distribution of the 2 species is a consequence of active avoidance of wolves by coyotes (Hoskinson and Mech 1976, Berg and Chesness 1978, Fuller and Keith 1981, Carbyn 1982). It cannot be reasonably assumed, however, that avoidance has occurred, or that the presence of wolves has influenced coyote distribution, wherever coyotes and wolves are allopatric. It is possible, for example, that coyotes select living areas solely on the basis of habitat or prey base, or some combination of habitat and prey base, and that preferred areas differ from those used by wolves. Wolves could then indirectly affect coyote densities by altering the distribution of prey species (see Mech 1977 for Buffer Zone concept), but not by stimulating active avoidance.

Alternatively, coyotes and wolves may prefer similar environments. Spatial segregation could then result from wolf predation on coyotes. Survival of coyotes should be better in peripheral zones than wolf core areas. In such circumstances coyotes might, over time, learn to recognize the risks associated with living in close proximity to wolves (Carbyn 1982). Allopatric distribution would then be attributable to avoidance resulting from aggression.

In Riding Mountain National Park, coyote mortality appears to be lowest along the edges of wolf territories (Carbyn 1982), although coyotes travel throughout wolf territories. Analysis of distances between radio-collared wolves and coyotes indicated that coyotes do not consistently avoid wolves (Carbyn 1982). Moreover, Carbyn (1982) noted that coyotes in RMNP, as well as in the Canadian Rocky Mountains, often track wolves through thick snow. He speculated that it was either for convenience of travel or in anticipation of scavenging on wolf kills, and commented " . . . that even though coyotes may avoid wolves [in time], they may actually trail them at a safe distance in search of food".

One of 3 spatial relationships must exist between sympatric wolves and coyotes in RMNP: 1) coyote movements are random, with respect to the presence of wolves; 2) coyotes are attracted to areas used by wolves; or 3) coyotes avoid areas of wolf activity. The objective of this study was to assess movements of both canids to determine which of the 3 interspecific relationships best describes conditions in RMNP. I hypothesized that coyotes would avoid areas where wolves were active and that mutual use of trails would occur randomly, for no other reason than ease of travel.

Chapter 2

STUDY AREA

RMNP is a 2974 km^2 nature reserve located in southwestern Manitoba. The eastern slopes of the park are an extension of the Manitoba escarpment, elevated 422 m above the adjacent prairie. From the escarpment westward, the park is a gently rolling plateau. Elevations range from 319 m to 756 m.

The park occupies a transition zone between prairie grasslands to the south and boreal forests to the north. Vegetation reflects topography, drainage and fire history. The dominant cover is poplar-forest (*Populus tremuloides, P. balsamifera*), interspersed with sedge-willow wetlands, upland fescue (*Festuca* sp.) prairie, and mixed coniferous forest. Agricultural practices have drastically modified the surrounding landscape so that the area is now an isolated segment of the once expansive aspen parkland region.

The weather is dry continental, typical of the prairie provinces (Carbyn 1982). July is the warmest month with a mean daily temperature of 16° C (range 13.8° to 18.4°) and January the coldest month with a mean daily temperature of -20.4° C (range -13.8° to -26.4°) (Environment Canada, Atmospheric Environment Service). Microclimates throughout the park are influenced by updrafts from the lowlands, which are affected by the steep relief of the eastern escarpment. Snow accumulation is moderate with maximum thickness usually not exceeding 50 cm.

Moose (*Alces alces*) and elk (*Cervus elaphus*) are common throughout the park. White-tailed deer (*Odocoileus virginianus*) are seasonally abundant but appear to concentrate along the park periphery, particularly during winter. Other mammalian carnivores include black bear (*Ursus americanus*), lynx (*Lynx lynx*), and several mustelids. Red foxes (*Vulpes vulpes*) are extremely rare within the park interior but common in adjacent agricultural areas.

Chapter 2

METHODS

Information about wolf and coyote travel patterns was collected by means of snow tracking from 1982-83 to 1985-86. In 1982/83 and 1983/84 snow tracking was supplemented, for coyotes only, by aerial and ground radio-telemetry of individuals captured near the park periphery.

Trails were haphazardly selected (Lehner 1979) on an opportunistic basis. Five successive kilometers of tracking constituted a "tracking session", and each tracking session was divided into units of 100 m. Distances were measured by pedometer if tracking on foot, or odometer if tracking was by snow machine. Fresh canid tracks (0 - 2 days after snowfall) were classified as wolf only (WO), coyote only (CO), wolf on coyote (WOC), and coyote on wolf (COW). When tracks of both species were evident, overlapping prints were examined to determine which species used the trail first and which secondarily, and the direction of travel of each species. The categories WOC and COW were subdivided according to whether both species were travelling in the same direction (WOC> and COW>) or in opposite directions (WOC< and COW<).

To avoid biases arising from the influence of trail conditions, tracking data were subdivided into ESTABLISHED and NEW trails. New trails were defined as routes that had not been previously travelled, or routes on which at least 20 cm of snow had accumulated. Established trails were defined as previously travelled or routes where there was evidence of a definite path, and less than 20 cm of accumulated snow.

The following data were recorded during each 5 km tracking session:

A. Estimated number of both species tracked.

B. Number of 100 m units of independent WO and independent CO tracks.

C. Units of WOC and COW including directions of movements

D. The number of times 2 trails approached, joined, or crossed. The following possibilities were recognized, whether both trails had been used by the same species or if each trail had been used by a different species:

1. junctions, at which a canid intercepted a trail and followed it in the direction of the preceding user for a minimum distance of 1 unit.
2. junctions, at which a canid intercepted a trail and followed it in the direction opposite to that of the preceding user for a minimum distance of 1 unit.
3. approaches, at which a canid avoided an intercepted trail by not crossing it and not moving parallel to it for at least a minimum distance of 1 unit.
4. crossings, at which a second traveler crossed the first trail and continued on the same course for at least 1 unit; i.e. ignored the trail.

Trapping and Instrumentation of Coyotes

Coyotes were trapped in 1982/83 and 1983/84 along roads and trails intersecting the boundary of RMNP. Number 14 Victor jump and Number 4 Newhouse traps were used in blind sets, with lures, or near carcasses of domestic livestock. Traps were modified to reduce injuries, and the capture of non-target species.

In 1982-83 captured animals were immobilized with equal proportions (1 mg/kg body weight) of phencyclidine hydrochloride (Sernalyn®) and promazine hydrochloride (Sparine®). Drugs were administered intramuscularly by jabstick.

In 1983-84 captured animals were restrained with a forked stick, muzzled and then bound by the back legs. The muzzle was attached to a wrist strap to pull the muzzle off if the animal escaped.

Captured animals were sexed, weighed, and measured. Age was estimated from tooth eruption, tooth replacement, and tooth wear (Bekoff and Jamieson 1975, Parks 1979). Colored plastic ear tags (Rototags®) were affixed to the left ear of females and the right ear of males. Selected individuals were equipped with radio collars (Telonics Inc., Mesa, AZ; Austec, Edmonton, AB).

Radio-collared coyotes were located from the air using a portable receiver (AVM 12, 150.00 - 151.00 MHz), a right-left switchbox, and paired, 4-element, Yagi antennae attached to the wing struts of a Cessna 172. A portable receiver and hand held 4 element Yagi antenna were used for ground telemetry. Ground locations were determined by triangulation and/or direct observation. Mean bearing error (i.e. difference between observed and true bearing) of ground locations, derived from 21 stationary ground locations, was 6.23^{o}. Coordinates (Universal Transverse Mercator [UTM]) were recorded on computer compatible data sheets.

Statistical Analysis

Frequency data were analysed by means of the G statistic for Goodness of Fit, and Test of Independence. The G-test was selected because of its additivity (Sokal and Rohlf 1981:692), which allowed for year by year analysis. With the exception of summed and partitioned values, all G-values were adjusted using Williams' continuity correction (Sokal and Rohlf 1981:692).

Replicated Goodness of Fit tests (G-statistic) (1982-86) were used to examine frequency distributions of overlapping print categories. The null hypothesis was that each track pattern had an equal probability of occurrence. Hence expected values for each category were calculated as 1/# categories * Total Observations.

Relationships between track patterns and trail conditions (i.e. NEW and ESTABLISHED) were evaluated (1982-86) by means of the G-Test of Independence. G-values for multiple comparisons were determined using Sidak's multiplicative inequality (Sokal and Rohlf 1981, page 731). Home ranges were calculated using the minimum area method (Mohr and Stumpf 1966, McPAAL 1986, Home Range Analysis Program, Smithsonian Inst. Washington, D.C.).

RESULTS

Snow Tracking

Overall, 535 km (5350 units) of track were surveyed and 690 trail intersections were evaluated. WO tracks (33.8%) constituted the most frequent single category of prints (Table II-1). Forty-four percent of all track segments were used by both species (COW, WOC). Within that subsample, the category COW> occurred at the highest frequency (43.3%), in each of the 4 years. The second most common classification, COW<, occurred about half as often at 22.7%.

Track patterns were independent of the estimated wolf pack size for both NEW and ESTABLISHED trails ($\underline{G} = 1.321$, df = 10, $\underline{G} = 2.134$, df = 10). Track patterns were also independent of which species established the trail ($\underline{G} = 3.12$, df = 5). Therefore, data with different pack sizes and trail origins were pooled for analysis.

There was a highly significant difference in the occurrence of track patterns recorded on NEW and ESTABLISHED trails ($\underline{G} = 34.77486$, $\underline{P} < 0.001$, df = 3). Simultaneous test procedures indicated that the overlap categories were a homogeneous subgrouping ($\underline{G} = 2.01$, df = 3), as were the single track categories WO and CO ($\underline{G} = 1.12$, df = 1). Consequently, the 2 subgroups were examined independently for both NEW and ESTABLISHED trails.

Track Overlap Analyses

Overall, the frequencies of COW and WOC tracks differed significantly from expected values (Table II-2). COW> tracks (Table II-2) occurred a disproportionate number of times on both NEW and ESTABLISHED trails (Table II-2). In general, the pattern was consistent for all 4 winters. In contrast, there was no significant difference in the frequency of WOC< and WOC> print patterns overall (Table II-2), on either NEW (Table II-2) or ESTABLISHED (Table II-2) trails.

Trail Intersection Analysis

There was a highly significant difference in the reaction of wolves and coyotes to interspecific trail junctions ($\underline{G} = 30.49$, $\underline{P} < 0.001$, df = 3). Coyote responses were influenced considerably by the presence of wolf tracks (Table II-3). For coyotes the original direction of travel was maintained in only 10.2% of the observations, and was altered in 89.8%. In contrast wolves maintained direction of travel in 68% of encounters with coyote tracks (Table II-3).

However, once on an intersecting trail, wolves and coyotes both preferred to travel the same direction as the canid that preceded them ($\underline{G} = 1.056$, $\underline{P} > 0.50$, df = 1). In contrast, the behavior of wolves and coyotes that did not use an intersecting trail was significantly different ($\underline{G} = 105.210$, $\underline{P} < 0.001$, df = 1). Wolves tended to ignore the intersecting trails, whereas coyotes avoided them.

A canid that approached a trail crossing had a choice of options. For example, a coyote could: (a) ignore a wolf trail, (b) use a wolf trail and follow wolf tracks, (c) use a wolf trail but travel in the direction opposite to wolf tracks, or (d) turn and avoid a trail. I tested the rate of observed behaviors against the expectation that each of the above options was equally probable. Choices by coyotes were non-random, differing significantly from the expected distribution ($\underline{G} = 49.841$, $\underline{P} < 0.001$, df = 3). Option 1 was selected most frequently, which suggests that coyotes usually followed wolf tracks. The decision to follow, rather than travel the opposite direction on the same trail was non-random ($\underline{G} = 15.799$, $\underline{P} < 0.001$, df = 1). Coyotes that chose not to use intersecting trails tended to avoid the trails rather than ignore them ($\underline{G} = 10.158$, $\underline{P} = 0.001$, df = 1). With the exception of winter 1984/85 this pattern of behavior was consistent for all years.

The response of wolves to coyote trails was non-random ($\underline{G} = 169.665$, $\underline{P} < 0.001$, df = 3). Wolves maintained direction of travel in the majority (68.0%) of the instances in which they intercepted coyote trails. Their reaction to coyote tracks was to ignore them, and maintain their original course ($\underline{G} = 127.390$, $\underline{P} < 0.001$, df = 1). On those occasions when wolves left their own trail and used a coyote trail (29.1%), they travelled in the direction of the coyote tracks significantly more often than in the opposite direction ($\underline{G} = 12.009$, $\underline{P} < 0.001$, df = 1).

Chapter 2

Capture and Telemetry Data

Fifteen of 23 coyotes captured near the park boundary were fitted with radio collars and the remaining ten were ear-tagged. Radio monitoring of collared animals was carried out from 1982-84 (Table II-4). Owing to the extremely low survival rate of collared animals and the consequent low numbers of relocations, the calculated areas of only 5 home ranges reached asymptotes. Although the calculated areas of 4 other coyotes failed to reach an asymptote, sufficient locations were obtained to plot areas of core activity.

All radio-monitored coyotes travelled extensively within wolf territories. The 5 defined home ranges were nested entirely within the boundaries of established wolf territories. Two coyotes were resident within the Clear Lake territory (3 wolves), and 3 in the Muskrat Lake territory (7-10 wolves).

Coyote #13 (adult female) was located 24 times in an area less than 2 km^2. She was initially captured near a domestic cow carcass, which had been investigated by the Muskrat Lake wolf pack. Her home range was wholly within the area used by that pack. Radio contact was lost in November 1983 and she was subsequently recaptured by a trapper at Ballantyne Bay, Saskatchewan in February 1984, a straight line distance of 544 km (Carbyn and Paquet 1986).

Coyote #10 (adult male) was monitored between 7 January

1983 and 24 November 1984. Transmission ceased in March 1983 but resumed in May and continued uninterrupted until the end of 1984. His home range was mostly within the park and overlapped the territories of both the Clear Lake and Muskrat Lake wolf packs, as well as the home range of Coyote #13. Coyote #10 was located 19 times on and near Clear Lake. On 3 occasions it was seen feeding on abandoned wolf kills.

Coyote #65 (adult female) was located mostly on or near Clear Lake, through August 1984. Her home range partially overlapped the Clear Lake and Muskrat Lake wolf territories.

The home range of coyote #80 (adult male) overlapped the territories of the Lake Audy and Clear Lake wolf packs. His movements appeared to be concentrated on Shoal Lake and Lake Audy. He was twice observed from the air scavenging wolf-killed elk on Lake Audy.

Coyote #30 (adult male) was active within the southern most portion of the Muskrat Lake wolf territory. He was last located on 6 January 1985. Occasional forays were made into agricultural areas adjacent to the park. He was never sighted from the air or ground but was twice radio-located within approximately 100 m of wolves resting near a kill.

Aggressive Interactions

Coyotes were observed within 150 m of wolves on several occasions (_n_ = 9) but there was no indication of aggressive behavior either by wolves or coyotes. However, agonistic encounters obviously occurred as 23 coyotes (7 females, 16 males) were discovered during the study that had been killed by wolves. None of the coyotes had been consumed by wolves. Eleven of the 23 coyotes were found within 200 m of kill sites and 14 of the 23 were discovered on snowmobile trails. No radio-collared coyotes were killed by wolves.

Miscellaneous Observations

Wolves and coyotes were often observed in close proximity to one another. For example, single coyotes were observed following wolves on 3 separate occasions, always at a distance greater than 100 m. Coyotes were also observed scavenging at or near wolf dens (n = 3) and rendezvous sites (n = 5). In 1 instance, coyotes fed on elk and beaver carrion accumulated near the den while a single adult male wolf and 4 pups rested less than 100 meters away.

Interspecific vocalizations

Vocalizations are believed to be important for territorial maintenance in wolves and coyotes (Harrington and Mech 1979). Therefore, interspecific howling may function to maintain ecological separation when the 2 species are sympatric. I did not attempt to quantify this relationship but several anecdotal observations are of interest. First, coyotes and wolves frequently vocalized simultaneously, or nearly so, in response to human imitations of wolf howls. Second, simultaneous howling of wolves and coyotes also occurred without human interference.

Third, coyote bark howls were recorded on several occasions near active wolf rendezvous sites (_n_ = 5). On 2 of the occasions wolves responded with group howls. Seven single coyote howls were recorded during a 48-hour period while a wolf den site was under close observation. None of the howls appeared to be in response to vocalizations by the wolves under observation. Although the wolves did not respond vocally, their ears were erect, and they faced in the direction of the howls. On 4 occasions tail wagging, body rubbing, and muzzle biting followed cessation of the coyote howling.

DISCUSSION

The results of this study clearly indicate that winter movements of coyotes in RMNP were not random relative to wolves. Contrary to expectation, however, coyotes did not avoid wolves, either on a gross or fine spatial scale. Coyotes may, in fact, have been attracted to areas where wolves were active.

Radio-telemetry revealed a substantial overlap of wolf territories and coyote home ranges in RMNP (also see Carbyn 1982). Because of restrictions on trapping within the park, all coyotes were captured along the park boundary, which for the most part is along the outer margins of wolf territories. No wolves reside soley in agricultural areas outside the park. Consequently, it was not possible to determine by telemetry if coyote movements were more common in core areas of wolf territories or in buffer zones between territories (Hoskinson and Mech 1976, Mech 1977).

Snow tracking, interspecific vocalizations, and direct observations revealed that coyotes were active throughout the core areas of wolf territories. Within core areas, coyotes and wolves commonly used identical travel routes, often only a few minutes apart. The movements of wolves and coyotes were not always associated, but the high frequency of overlapping tracks indicated that coyotes were not repulsed by wolves as had been postulated. Moreover, the tendency of coyotes to follow wolf tracks at interspecific trail junctions, and on NEW or ESTABLISHED paths suggests that coyotes did not attempt to avoid wolves.

Responses of wolves to an intersecting trail appeared to be unaffected by the presence of coyotes. Wolves seldom changed trails when fresh coyote tracks were encountered (Table II-3). They did, however, have a tendency to follow coyotes, rather than go in the opposite direction, once they did change trails (Table II-3). It is difficult to reconcile this finding with the analysis of track overlap which showed there was no difference in the frequency of WOC> and WOC<, and that overall wolf movements were random relative to those of coyotes. Possibly wolves were attempting to prey on coyotes. Yet, of the 23 coyotes killed by wolves during the study none were found while tracking wolves following coyotes, nor were there any indications of chases.

Analysis of the predatory behavior and dietary habits of wolves and coyotes in RMNP suggests that coyotes obtain the major portion of their food by scavenging, that they are heavily dependent on carrion provided by wolves, and that partitioning of food resources by the 2 canids allows for ecological overlap (Meleshko 1986, Chapter 5). On 36 occasions, tracks of coyotes following wolves led directly to wolf-killed ungulates. In addition all wolf kills examined in the field ($\underline{n}$ = 198) were visited by coyotes and probably scavenged by them.

The high proportion of COW> tracks suggests that following wolves to their kills could be an important foraging strategy of coyotes. The behavior could well be learned as a coyote would be reinforced positively each time a carcass was located and fed upon. Although the probability of finding a wolf kill should be similar whether coyotes follow or backtrack on wolf prints, coyotes chose the former option a significantly greater number of times. That may have been because there is: (a) likely a greater amount of consumable biomass available from new kills, (b) less handling time required because choice portions are easy to consume, (c) an increased opportunity to feed on the more nutritious portions of the carcass, and (d) a competitive advantage over other terrestrial scavengers in gaining early and possibly exclusive access to the carcass.

Although I cannot provide quantitative data on the relationship of available biomass and carcass age, observations indicated that coyotes at kills must compete with aggressive conspecifics as well as other mammalian and avian scavengers (Chapter 5). Subordinate coyotes were frequently displaced from carcasses by other coyotes, while dominant animals were required to expend energy defending carcasses. Consequently, it would be advantageous to feed in the absence of other scavengers. That could best be accomplished through optimizing the search effort by trailing wolves, and arriving first at a kill.

Chapter 2

CONCLUSIONS

The overlap of wolf and coyote movements in RMNP was substantial. Spatial segregation of the 2 species did not occur at any detectable level, and coyotes did not seem to be displaced by the activities of wolves. Wolves behaved aggressively toward coyotes but there was no evidence that they actively pursued them. Overall, the movements of wolves were neutral relative to coyotes, which suggests that wolves killed coyotes only opportunistically.

Coyotes were likely attracted to wolves because of the abundant carrion available from wolf kills. Their movements appear to be part of a foraging strategy that depends on tracking wolves to kill sites and feeding on abandoned carcasses. Because coyotes and wolves in RMNP use the same prey in a different manner they probably avoid competition and are able to coexist (Chapter 5, Meleshko 1986).

Wolves are not able to exclude coyotes from RMNP through direct aggression because of the large reserve of coyotes in surrounding agricultural areas that are available to repopulate the park quickly. Physical exclusion may be beyond the energetic capability of wolves. Therefore, the proximate reason why coyotes are excluded from some areas by wolves appears to be related to a lack of wolf-provided carrion for coyotes to scavenge, and secondarily because of direct aggression. Spatial separation is only a secondary manifestation, which occurs when the risks associated with living within active wolf areas outweigh the benefits provided by scavenging.

Table II-1. Summary of wolf/coyote track patterns recorded from 1982-1986 within the boundaries of four wolf territories. One unit of track was defined as 100 m of continuous print.

	UNITS OF TRACK		
PRINT	New	Established	Total
WOC<	143	266	409
WOC>	144	259	403
COW<	201	322	523
COW>	356	663	1019
WO	516	1292	1808
CO	338	850	1188
Total	1698	3652	5350

Table II-2. Summarized analysis of data in Table II-1, based on 4 annual replicates (Appendix A). Values marked by an asterisk are statistically significant.

		Pooled		Heterogeneity		Total	
COMPARISON	TRAIL	G	df	G	df	G	df
COW vs WOC	all	229.08*	1	11.64*	3	240.71*	4
COW> vs COW<	all	162.42*	1	16.00*	3	178.42*	4
	new	43.71*	1	14.22*	3	57.93*	4
	est.	120.53*	1	27.23*	3	147.77*	4
WOC> vs WOC<	all	0.04	1	1.50	3	1.54	4
	new	0.00	1	7.39	3	7.39	4
	est	0.09	1	4.77	3	4.87	4

Table II-3. Summary of wolf/coyote behaviors at interspecific trail junctions. Observations were recorded during periods of snow cover from 1982-1986. The chronology of events was determined by track sequences and overlapping prints. Trail junctions that could not be interpreted were not included in the analyses.

	Intersection	
Behavior	Wolf Intercepted Coyote	Coyote Intercepted Wolf
Ignored Trail	117	23
Followed Trail Same Direction	37	98
Followed Trail Opposite Direction	13	50
Avoided Trail	5	54
Total Observations	172	225

Table II-4. Capture data for coyotes trapped near the periphery of RMNP in 1982 and 1983. Trapping was within the boundaries of known wolf territories.

#	Sex	No. Fixes	Date Captured	Weight (kg)	Age	Capture Location (UTM)	Status
2	M	6	2 Dec 82	7.2	pup	MM488015	dead Feb 83
13	F	47	4 Jan 83	12.3	adult	MM386095	dead Feb 84
10	M	77	7 Jan 83	14.1	adult	MM401114	dead Jan 86
5	F	8	8 Jan 83	7.9	pup	ML450048	dead Feb 83
05	F	9	29 Sep 83	12.2	adult	MM116477	dead Nov 83
15	F	41	2 Oct 83	5.8	pup	ML566030	unknown
20	F	4	2 Oct 83	6.4	pup	MM116477	dead Nov 83
30	M	32	7 Oct 83	15.2	adult	ML530050	unknown
40	F	44	16 Oct 83	12.6	adult	MM400051	dead Jan 84
45	F	37	12 Nov 83	12.3	adult	MM386093	dead Nov 85
50	F	5	12 Nov 83	11.8	adult	MM402040	dead Nov 83
60	F	21	15 Nov 83	14.9	adult	MM400080	unknown
55	M	10	15 Nov 83	13.1	adult	MM408086	dead Dec 83
75	F	17	16 Nov 83	14.1	adult	MM403040	dead Mar 84
65	F	37	18 Nov 83	13.0	adult	MM400040	unknown
70	F	14	18 Nov 83	6.8	pup	MM403112	dead Feb 84
80	M	41	1 Dec 83	----	adult	MM181183	dead Mar 84

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CHAPTER 3

Scent Marking Behavior of Sympatric Wolves (*Canis lupus*) and Coyotes (*C. latrans*) in Riding Mountain National Park

INTRODUCTION

Olfactory communication is of considerable interest to behavioral ecologists because of its relationship to social organization, reproductive behavior, spatial distribution, movements and feeding habits (Bekoff and Wells 1986). Mammalian scent marking behavior has been reviewed by Ralls (1971), Eisenberg and Kleiman (1972) and Johnson (1973). Kleiman (1966) and Macdonald (1980) have discussed the communicative functions of odours for the Carnivora, and Kleiman (1966) and Anisko (1977) have surveyed scent marking by the Canidae. Detailed field studies of scent marking by coyotes (*Canis latrans*) (Camenzind 1978, Barrette and Messier 1980, Bowen and Cowan 1980, Wells and Bekoff 1981, review by Bekoff and Wells 1986) and wolves (*C. lupus*) (Peters and Mech 1975, Rothman and Mech 1979), are limited. I am aware of no published studies of interspecific chemical communication between sympatric canids.

Most canids deposit scents throughout their environment by means of urine, feces, and glandular secretions. In wolves and coyotes urine marks are employed as olfactory advertisements for territorial ownership (Peters and Mech

1975, Rothman and Mech 1979, Barrette and Messier 1980, Bowen and Cowan 1980), for marking empty food caches (Harrington 1982, Weaver 1979), and for achieving reproductive synchrony (Rothman and Mech 1979). Other types of marks, such as feces, anal gland secretions (Asa et al. 1985a, 1985b; Raymer et al. 1984, 1985), and scratching (Fox 1975, 1977; Sands et al. 1977) may function analogously.

Non-territorial wolves rarely deposit scent marks, although they commonly investigate the marks of other wolves. Rothman and Mech (1979) postulated that reducing the number of scent marks diminishes the probability of detection by resident packs, and that investigation of foreign marks provides information as to the proximity of other wolves. Coyotes without home ranges also mark less intensely than individuals with home ranges (Barrette and Messier 1980). Moreover, both territorial wolves and coyotes with home ranges respond strongly to scent marks of alien conspecifics by marking more frequently, and by avoiding areas containing foreign scent (Peters and Mech 1975; Bowen and Cowan 1980).

Based on the close relatedness of wolves and coyotes (Nowak 1978), the numerous similarities in scent-marking behavior (Peters and Mech 1975, Barrette and Messier 1980, Bowen and Cowan 1980, Bekoff and Wells 1986), and evidence suggesting competitive exclusion of coyotes by wolves (Mech 1966, Krefting 1969, Berg and Chesness 1978, Fuller and

Keith 1981, Carbyn 1982), there is reason to believe that marking could serve as a medium for interspecific communication, and thereby influence the spatial distribution of coyotes and wolves. The objective of this study was to determine whether marking has an interspecific behavioral significance for wolves and coyotes, and, if so, whether it is involved in maintaining ecological separation of the two species. The general hypothesis tested was that coyotes living or travelling within active wolf areas would mimic the behavior of allopatric non-territorial wolves and coyotes; i.e. they would exhibit a reduced frequency of marking and avoid scent marks deposited by resident wolves, thus reducing probability of detection. A corollary hypothesis was that wolves would react to sympatric coyotes as transgressing conspecifics, and respond by increasing their scent marking activity.

This paper describes and compares intra- and interspecific urine and scratch marking behavior of sympatric wolves and coyotes. The study was carried out in Riding Mountain National Park (RMNP), an area with moderate densities of both species. Field work was conducted during the months of October through March from 1982-1986.

Chapter 3

STUDY AREA

The park is a 2974 km^2 insular wilderness located in the forest-agricultural transition zone of southwestern Manitoba (Hill 1979), 177 km north of the international boundary between Manitoba, Canada and North Dakota, U.S.A. Vegetation is dominated by mixed coniferous and deciduous forest, interspersed by lakes, grasslands, and bogs. Elevations range from 319 m to 756 m. The climate is dry continental. July is the warmest month and January the coldest with mean daily temperatures of approximately 20° C and -20° C, respectively (Environment Canada, Atmospheric Environment Service). Snow thickness is moderate with maximum thickness usually not exceeding 50 cm.

Elk (*Cervus elaphus*) and moose (*Alces alces*) are abundant throughout the study area, and deer (*Odocoileus virginianus*) are locally common (Trottier et al. 1983). Carnivores other than wolves and coyotes include the black bear (*Ursus americanus*), lynx (*Lynx lynx*), and several mustelids. Red foxes (*Vulpes vulpes*) are also present, but extremely rare.

Chapter 3

METHODS

Wolves and coyotes were tracked during periods of snow cover by snowmobile, cross-country skis, snowshoes, and travel by foot. Distances were recorded by odometer (snowmobile) and pedometer, and rounded to the nearest kilometre. Encoded data were recorded in field notebooks and subsequently transferred to computer diskette for summary and statistical analysis. Marking rates were calculated by dividing the number of marks recorded by the total distance travelled.

Designation of Travel Routes

Urine and scratch marks from wolves and coyotes were recorded along the following 4 designated travel routes:

1. Wolf only trails (WO), defined as paths used exclusively by wolves,
2. Coyote only trails (CO), defined as paths used exclusively by coyotes,
3. Wolf/coyote trails (COW), defined as paths established by wolves and subsequently travelled by coyotes,
4. Coyote/wolf trails (WOC), defined as paths established by coyotes and subsequently travelled by wolves.

Travel routes were further subdivided into a) permanent roads and trails, b) bush, and c) frozen waterways (cf. Peters and Mech 1975).

Trails were haphazardly selected on an opportunistic basis (Lehner 1979). Whenever feasible, snow tracking was supplemented by locating radio-collared coyotes via aerial and ground telemetry. When fresh wolf or coyote tracks (0-2 days after snowfall) were encountered, the travel route was classified by distinguishing visible tracks and paw-print overlap. To account for possible biases due to variable wolf numbers, tracking was carried out within the territories of two wolf packs, which differed substantially in size. As a minimum one pack was twice the size of the other pack. Because pack composition and size changed unpredictably from year to year, new packs that matched the criteria were selected annually.

In 1984 and 1985 single 10 km trail sections located on established park trails were monitored from early January through mid March to determine interspecific use of scent mounds. Following the first new January snowfall visible urine marks were flagged using coloured nylon tape, and it was noted from the presence of tracks whether the marks were deposited by wolves or coyotes. Urine marks with tracks of both species present were unclassified. Subsequently, the trails were monitored after each new snowfall of sufficient depth to cover the previous tracks. Old scent mounds that had been newly marked were identified as having been over-marked by a wolf or coyote, and new mounds were tagged with a flag of a different colour. Consequently, it was possible to determine whether wolves and coyotes used the same scent mounds, to what extent this occurred and the rate of reuse by either species.

Classification of Mark Types

Deposition of 3 discrete wolf/coyote marks, Directed Urination (DU), Non-Directed Urination (NDU), and Scratches (SCR) were recorded. Because their role in scent marking remains somewhat ambiguous, feces (scats) were ignored unless accompanied by urine or scratch marks. DUs were identified by the orientation of urine toward previously deposited urine or objects in the environment (Kleiman 1966). The target objects were as diverse as soft drink cans and mounds of wind-blown snow.

Urine deposits without obvious orientation were classified as NDUs. No attempt was made to discriminate between eliminations and scent marks.

Multiple urine deposits were often impossible to count accurately, owing to the difficulty in discriminating overlapping marks. Consequently, no more than 3 marks were recorded at a single location.

Scratches (SCRs) were defined as extended parallel tracks produced by the claws with alternating movements of stiffened fore and hind legs (Kleiman 1966). SCRs that occurred in combination with urinations and defecations were noted, as was the orientation of the scratch relative to the deposit. The urination posture was also noted whenever it could be determined from the tracks present. Data collected from within 25 m of an ungulate killed by wolves or coyotes were discarded.

Urination postures used in marking were detectable when foot placement near a urine stain could be discerned by track impressions. Postures were categorized as Raised Leg Urination (RLU) or Squat Urination (SQU) (Peters and Mech 1975) in the winters of 1983-84 and 1984-85.

Comparison of Deposition Frequency by Wolves and Coyotes

To determine whether wolves or coyotes respond to the urine and scratch marks of the opposite species, I compared marking frequencies on wolf only trails (WO), coyote only trails (CO), coyotes on wolf trails (COW), and wolves on coyote trails (WOC). I also compared the marking frequencies of small wolf packs with those of large wolf packs, and of single coyotes with those of groups of coyotes. I hypothesized that: 1) the number of scent marks on trails established by coyotes and subsequently travelled by wolves would be greater than on wolf only trails, 2) the rate of scent marking on trails established by wolves and subsequently used by coyotes would be similar to that on wolf only trails, and 3) large wolf packs and groups of coyotes would mark more frequently than small wolf packs or single animals.

Spatial Distribution of Wolf Marks

From 1982 through 1986 winter wolf territories were delineated by extensive ground monitoring of tracks, supplemented by visual observations of wolves from the air and on the ground. Monitoring was initiated following the first permanent snowfall and continued through the end of March. Over time, consistency in track numbers and repetition of wolf movements provided reliable territorial profiles. By mid-December individual packs were easily recognized by the number of tracks and the area of activity. In the absence of convincing evidence to the contrary, tracks found within a known territory were assumed to have resulted from resident wolves. Movements of adjacent packs were also monitored, which helped to clarify the origin of ambiguous tracks when, for example, a pack temporarily divided into subunits.

All winter movements were plotted on 1:50,000 topographic maps (Department of Energy, Mines and Resources 1975) and recorded as Universal Transverse Mercator (UTM) grid coordinates. The outermost points were considered territorial limits only if visited two or more times. Consequently, bias due to outlying and extra-territorial movements was minimized. In a manner analogous to the minimum convex polygon method (Mohr and Stumpf 1966), non-contiguous boundary tracks were connected to form a closed outside perimeter. That was unnecessary for 3 of the 4 territories delineated where boundaries were formed by continuous track.

Data Analysis

Where information was sufficient, sample frequency data were assigned to the following categories for analysis:

A. Deposition frequency for coyote only trails (CO)
  1. by single coyotes
  2. by two or more coyotes
B. Deposition frequency for wolf only trails (WO)
  1. by small pack
  2. by large pack
C. Deposition frequency for wolf/coyote trails (COW)
  1. within small wolf pack territory
  2. within large wolf pack territory
D. Deposition rate for coyote/wolf trails (WOC)
  1. within small wolf pack territory
  2. within large wolf pack territory

For each trail category (WO, CO, COW, WOC), I tested whether the deposition frequency of mark types (DUs, NDUs, SCRs) was independent of the trail environments in which they occurred. Yearly and pooled data were evaluated using the R X C G-Test of Independence (Sokal and Rohlf 1981:733, Rohlf 1985). Values were adjusted using Williams' continuity correction.

The relative frequency of individual and summed mark types within each trail category was examined annually for deviation from expected values using the G-test for Goodness of Fit (Sokal and Rohlf 1981:692). The null hypothesis stated that there was an equal probability of marks occurring within different categories. For each comparison, expected frequencies were calculated as the product of the total number of marks, and the proportion of the total tracking distance sampled in each mark class tested (Lehner 1979). When possible, the values were summed for the 4 winter study periods and tested for heterogeneity (Sokal and Rohlf 1981:721). Non-summed and non-partitioned _G_ values were adjusted using Williams' continuity correction.

The results of all statistical tests were considered significant at an α level ≤ 0.05.

Chapter 3

RESULTS

From 1 January 1983 to 30 March 1986, 3,606 wolf and coyote marks were recorded over a tracking distance of 1,720 km (Table III-1). Overall, trails used by both wolves and coyotes were marked more frequently than single species trails (Fig. III-1).

Marks included 2,383 DUs, 774 NDUs and 449 SCRs (Table III-2). Sixty-two percent (278) of the SCRs occurred with DUs, 27% (121) with scats, 8.5% (38) with NDUs, and 2% (9) were independent. In 12 cases the urine mark was broken apart and dispersed by scratching, and therefore could not be categorized. Thirty-three percent (148) of the SCRs were oriented directly toward the urine mark and 12% (54) partially or entirely covered the marks with displaced snow.

Scent Marking In Relation to Trail Types

Wolf only (WO) trails . - - There was a significant difference in the frequency of marking within different travel environments (Table III-3). Roads and trails were marked more often (2.64 marks/km) than bush environments (1.88 marks/km) or frozen waterways (0.73 marks/km) (G = 215.550, $P < 0.001$).

The types of marks deposited also varied significantly (G = 558.948, $P < 0.001$). DUs (1.21 DU/km) exceeded both NDUs (0.57 NDU/km) and SCRs (0.23 scr/km), with the highest relative frequency recorded along roads and trails (1.73 DU/km) (Table III-3). In 3 of the 4 study years there were significant associations between the frequencies of mark types recorded and the environments in which they were deposited. Analysis of the pooled data clearly showed that the type of mark produced by wolves was dependent on the environment in which they were travelling (G-pooled = 46.95, $P < 0.001$) (Table B-1).

Compared to bush and waterways, the number of DUs along roads and trails was disproportionately high in all 4 winters. Although the pattern was consistent (G-total = 235.43, $P < 0.001$, df = 8, G-pooled = 216.01, $P = 0.001$, df = 2), it was not uniform in magnitude (G-heterogeneity = 19.42, $P < 0.001$, df = 6) (Table B-2).

The proportions of NDUs recorded in different travel environments were in agreement with expected frequencies in all study years but 1985-86. However, overall NDUs consistently occurred at a rate lower than expected along roads and trails and higher than expected along frozen waterways (G-pooled = 12.15, $P < 0.001$, df = 2, G-heterogeneity = 0.83, $P > 0.995$, df = 6) (Table B-2).

The frequency of SCRs along frozen waterways was also lower than expected. Although insufficient data precluded replication in all 4 study years, G-values for 1983-84 (G = 14.25, $P < 0.001$, df = 2), and 1984-85 (G = 7.40, $P < .025$, df = 2) were significant, as was G-pooled (G = 33.09, $P < 0.001$, df = 2) (Table B-2).

The distribution of DUs within different travel environments varied with pack size. Large packs deposited a significantly higher percentage of DUs along roads and trails (75%) than small packs (50%), and fewer in bush environments (21% and 45% respectively) ($\underline{G} = 61.13$, $\underline{P} < 0.001$). The distribution of NDUs was also related to pack size ($\underline{G} = 20.38$, $\underline{P} < 0.001$). Larger packs produced a lower relative proportion of NDUs (30%) than smaller packs (40%).

Coyote only (CO) trails . - - On CO trails the distribution of marks among different travel environments was uneven ($\underline{G} = 119.023$, $\underline{P} < 0.001$). The overall deposition frequency was higher on roads and trails (1.71 marks/km) than in bush environments (0.86 marks/km) or frozen waterways (0.37 marks/km), particularly for DUs (1.10 DU/km) (Table III-4). In all habitats combined, DUs (0.78 DU/km) occurred most frequently followed by NDUs (0.27 NDU/km) and SCRs (0.22 scr/km) ($\underline{G} = 186.460$, $\underline{P} < 0.001$). With the exception of winter 1985 ($\underline{G} = 16.17$, $\underline{P} < 0.005$, df = 4) mark types were independent of the trail environments travelled (Table B-3).

DUs along roads and trails exceeded expected frequencies in all 4 study years. Total ($\underline{G} = 105.37$, $\underline{P} < 0.001$, df = 8) and pooled ($\underline{G} = 97.38$, $\underline{P} < 0.001$, df = 2) $\underline{G}$-tests for Goodness of Fit were both highly significant. Deviations from predicted values varied non-significantly from year to year (Table B-4).

With the exception of 1985-86 ($\underline{G} = 12.16$, $\underline{P} < 0.005$, df

= 2), NDUs appeared to be consistent with expected deposition frequencies (Table B-4). The pooled data, however, revealed a significantly lower rate of NDUs deposited along frozen waterways ($\underline{G}$-pooled = 12.04, $\underline{P} <$ 0.005, df = 2), with only minimal variability occurring in the annual replicates (Table B-4). $\underline{G}$-pooled for SCRs also indicated that an unusually low rate of SCRs occurred along frozen waterways ($\underline{G}$ = 19.72, $\underline{P} < 0.001$, df = 2) (Table B-4). Insufficient data precluded a complete year by year analysis.

The distribution of DUs, NDUs and SCRs within different travel environments was the same for single coyotes and coyote groups.

Coyotes on wolf (COW) trails . - - On COW trails the distribution of marks within different travel environments was disproportionate ($\underline{G}$ = 89.599, $\underline{P} < 0.001$). The highest overall marking frequency occurred along roads and trails (3.86 marks/km), followed by bush (2.79 marks/km) and frozen waterways (1.59 marks km) (Table III-5). As with the previous categories, DUs were deposited at the highest rate for all habitats combined (2.26 marks/km). With the exception of 1982-83 ($\underline{G}$ = 15.23, $\underline{P} < .005$, df = 4) (Table B-5), there were no associations between mark types recorded and trail environments travelled.

DUs occurred at a frequency higher than expected along roads and trails in 3 of the 4 study years. In 1985-86 DUs were consistent with expected deposition rates. Highly significant total ($\underline{G} = 129.54$, $\underline{P} < 0.001$, df = 8), pooled ($\underline{G} = 74.34$, $\underline{P} < 0.001$, df = 2), and heterogeneity ($\underline{G} = 55.20$, $\underline{P} < 0.001$, df = 6) $\underline{G}$-values reflected the the year to year variability of observations (Table B-6).

Although not evident in 3 of the 4 yearly replicates, NDUs occurred at a significantly lower than expected rate along frozen waterways ($\underline{G}$-pooled = 12.70, $\underline{P} < 0.005$, df = 2) (Table B-6). SCRs were evenly distributed among travel environments in all study years for which sufficient data were collected for analyses. $\underline{G}$-pooled for all 4 study years was also non-significant (Table B-6).

Distribution of DUs was related to the size of the wolf pack that coyotes followed ($\underline{G} = 13.198$, $\underline{P} < 0.025$). Paths established by large packs showed a higher percentage of DUs (75% vs. 57%) on roads and trails and a lower percentage in bush habitats (22% vs. 39%), than paths established by small packs. The distribution of NDUs and SCRs was independent of pack size.

Wolves on coyote (WOC) trails . - - The frequency of marking along roads and trails (3.45 marks/km) exceeded that in bush areas (2.40 marks/km) and on frozen waterways (0.53 marks/km) ($\underline{G} = 111.200$, $\underline{P} < 0.001$). DUs (1.86 marks/km) were the largest contributor, followed by SCRs (0.36 marks/km) and NDUs (0.31 marks/km) ($\underline{G} = 325.574$, $\underline{P} < 0.001$) (Table III-6). Mark types were not influenced by trail environments for either yearly or pooled data (Table B-7).

The frequency distribution of DUs among travel environments diverged significantly from the expected rates in winters 1982-83, 1983-84, and 1984-85 (Table B-8). Insufficient data were collected for analysis in 1985-86. Pooled $\underline{G}$ for all 4 years was highly significant ($\underline{G} = 88.99$, $\underline{P} < 0.001$, df = 2), and examination of the data suggested that DUs were disproportionately high along roads and trails in all annual replicates (Table B-8).

Sample sizes were insufficient to evaluate the distribution of NDUs and SCRs from year to year (Table B-8). However, $\underline{G}$-pooled was significant for both mark types ($\underline{G} = 6.94$, $\underline{P} < 0.05$, df = 2; $\underline{G} = 21.96$, $\underline{P} < 0.001$, df = 2), and in both instances was attributable to low deposition rates along frozen waterways (Table B-8).

The proportion of DUs observed in different trail environments was strongly associated with the number of wolves using the trail ($\underline{G} = 37.41$, $\underline{P} < 0.001$). For example, in the large wolf pack category 71% of the observed DUs occurred on roads and trails, compared to 49% for the small wolf pack category. NDUs and SCRs were distributed as expected.

Use of Scent Mounds by Coyotes and Wolves

In winter 1983-84, 68.4% of the coyote urine marks initially flagged ($\underline{n} = 38$) were over-marked by coyotes and 81.6% by wolves. Sixty percent of the original wolf urine marks ($\underline{n}$ = 30) were over-marked by wolves, and 83.3% by coyotes (Table III-7). An additional 31 new urine marks were recorded subsequent to the first observations, 7 by wolves, 13 by coyotes and 11 indeterminate. All of the identified marks were secondarily marked by the other species.

Seventy-three percent of the coyote scent mounds originally flagged in 1985 ($\underline{n}$ = 41) were over-marked by coyotes and 66% by wolves. Fifty-three percent of the initial wolf urine marks (62) were over-marked by coyotes and 30.6% by wolves (Table III-7). Of 41 new marks added over the winter period, 29 were deposited by wolves, 4 by coyotes and 8 could not be distinguished. All of the coyote marks were secondarily marked by wolves and 58.6% of the wolf marks were over-marked by coyotes.

Comparisons of Coyote and Wolf Marking Rates

Large wolf packs and small wolf packs. - - Annually replicated goodness of fit tests were significant for 3 of the 4 winter tracking periods, confirming a strong relationship between pack size and marking frequency. Without exception, large packs marked at a greater frequency than smaller packs. This is reflected in highly significant Total ($\underline{G}$ = 48.45, $\underline{P}$ < 0.001, df = 4) and Pooled ($\underline{G}$ = 44.18, $\underline{P}$ < 0.001, df = 1) $\underline{G}$-values. $\underline{G}$-heterogeneity was non-significant, indicating that variation among years was minor (Fig. III-2, Table B-9).

Single coyotes and coyote groups . - - Single coyotes marked at a significantly lower frequency than coyotes travelling in groups in all 4 winter study periods (G-pooled = 115.667, P < 0.001, df = 1) (Fig. III-3, Table B-10). However, a significant G heterogeneity (G = 13.625, P < 0.005, df = 3) affirmed that the magnitude of deviation from predicted rates was not uniform from winter to winter.

Large wolf pack and coyotes on large pack trails . - - Two of the 4 annual replicates showed a significantly higher number of marks along COW trails than on WO trails (Fig. III-4). One replicate (1982-83) provided the opposite result and another (1985-86) was non-significant, although a higher number of marks was recorded on COW trails (Fig. III-4, Table B-11). The G-total (G = 92.141, P < 0.001, df = 4) was highly significant, as was G-pooled (G = 19.681, P < 0.001, df = 1). Apparently, the higher number of marks recorded along WO trails in 1982-83 was compensated for by the more substantial and opposite differences recorded the following 3 winters. Overall, mixed use trails were marked more frequently than WO trails. Owing to the extreme annual variability in marking, G-heterogeneity was also highly significant (G = 72.460, P < 0.001, df = 3).

Large wolf pack (LWP) and LWP on coyote trails . - - Although a greater number of marks was recorded along mixed-use trails in 3 of 4 winters, only 1 of those 3 replicates departed significantly from expectation. Conversely, in

1982-83 the frequency of marks on mixed-use trails was significantly less than on wolf only trails. Pooled G, however, was not significant, indicating no difference between wolf only trails and interspecific trails (Fig. III-5, Table B-12).

Small wolf pack (SWP) and coyotes on SWP trails. - - The number of marks observed on mixed-use trails exceeded the number along wolf only trails in 3 of 4 winters (Fig. III-6). Pooled G ($G = 74.235$, $P < 0.001$, df = 1) was highly significant, as was G-heterogeneity ($G = 24.119$, df = 3) (Table B-13). The results strongly support the conclusion that coyotes were not inhibited from marking by the presence of wolf sign.

Small wolf pack (SWP) and SWP on coyote trails. - - Overall, a significantly higher frequency of marks was recorded on interspecific trails than wolf only trails (G-pooled = 34.828, $P < 0.001$, df = 1, Table B-14). With the exception of 1982-83 the direction of deviation was consistent, although a highly significant G-heterogeneity ($G = 99.424$, $P < 0.001$, df = 3) indicated that the magnitude varied annually (Fig. III-7, Table B-14). The marking frequency on SWP trails remained relatively constant from year to year. In contrast, an annually increasing rate of marking was evident along WOC trails (Fig. III-7).

The highest frequency of marking on COW trails occurred in winter 1985-86. That was in response to an extraterritorial foray by the Baldy Lake wolf pack into the L. Audy territory. Marking rates by coyotes following the trail used by the Baldy Lake wolves were over 4 times those observed during the rest of the study.

Marking Profiles of Intra- and Inter-Specific Travel Routes

In comparison with WO roads and trails, a greater proportion of DUs were deposited along CO roads and trails, but fewer in bush environments ($\underline{G} = 18.3722$, $\underline{P} < 0.001$, df = 2). The distribution of mark types among travel environments was similar on WO and WOC trails, but differed between CO and COW trails. The difference in the latter comparison was primarily attributable to a substantial decrease in DUs on interspecific roads and trails, and concomitant increase in bush areas ($\underline{G} = 12.2734$, $\underline{P} < 0.005$, df = 2). I suspect the reduction reflects a change in the behavior of coyotes rather than wolves, because the marking pattern on COW trails was similar to that on WO trails ($\underline{G} = 0.9285$, $\underline{P} > 0.5$, df = 2).

Temporal Distribution of Marks

The deposition frequency on WO, CO, WOC, and COW trails was summed for each mark type at weekly intervals and tested for departure from expected values. The null hypothesis stated that marking rates would remain constant from week to week. With the exception of COW trails ($\underline{G}$-pooled = 87.60, $\underline{P} < 0.001$), no significant changes were detected within any of the tracking categories (Fig. III-8). Notably, the frequency of DUs on COW trails was elevated in the latter part of January and beginning of February in each of the 4 winters.

Postures Associated with Marks

By examining the position of paw prints, I associated 43% (1,025) of all recorded urine marks with a specific marking posture. Seventy-two percent (739) of the identified marks were categorized as having been deposited from a raised leg position (RLU) and 28% (286) from a squatting position (SQU). Sixty-seven percent (687) of the identified marks were deposited on or near an object, or previous urine mark. Urine was directed at a target from a squat posture in 3.2% of the marks and from a raised leg position in 97.2%. Thus 90.3% of RLUs and 7.6% of SQUs were target directed.

General Observations

Observations of wolf/coyote interactions were infrequent. However two sightings were significant because they confirmed that coyotes used the same scent mounds as wolves. On 11 February 1984, a single coyote was observed following two wolves at a distance of approximately 100 metres. A female wolf marked (RLU) a snow mound after emerging from a lake to a nearby road. The trailing male coyote approached the spot, marked the mound (RLU) and scratched vigorously before proceeding. Examination of the marks revealed blood in the urine from one of the animals, possibly the female, which may have been in estrus.

On 18 January 1986, 6 wolves were observed travelling on a trail where a pair of coyotes had deposited 3 scent marks 45 minutes earlier. All 3 marks were double-marked by the wolves. In 2 cases 4 wolves scent marked at each site, but I was unable to determine whether they were the same 4 animals in each case. A single female wolf (determined by marking posture) marked the third urine deposit. No scratches were recorded. Thirty-three minutes later the same trail segment was used by a single male coyote, and all 3 of the original sites were investigated and marked. Examination of the marks revealed blood at 2 of the 3 locations. However, it was unclear which of the animals deposited the blood. It was also unknown if the original 2 coyotes marked previously scented sites.

Chapter 3

DISCUSSION

Previous studies of wolf and coyote scent marking have been exclusively monospecific (Peters and Mech 1975, Camenzind 1978, Rothman and Mech 1979, Barrette and Messier 1980, Bowen and Cowan 1980, Wells and Bekoff 1981). Consequently, the behavioral significance of interspecific scent marking has not been addressed. Notably, many of the findings of this study are consistent with descriptions of scent marking behavior from areas where wolves and coyotes are allopatric (Peters and Mech 1975, Rothman and Mech 1979, Barrette and Messier 1980); or, in the case of Bowen and Cowan (1980), where the two species coexist but interactions have not been described. The information presented here confirms that scent marking is an important interspecific behavioral characteristic of sympatric wolves and coyotes.

Deposition rates (marks/km) of wolves and coyotes in RMNP are similar, and closely approximate those reported elsewhere (Peters and Mech 1975, Rothman and Mech 1979, Barrette and Messier 1980, Bowen and Cowan 1980). The placement of scent marks in the environment by wolves and coyotes is also similar, with both species marking preferentially along established roads and trails and reducing their marking effort along frozen waterways. Wolves in Minnesota also mark roads and trails at a higher rate than other travel routes (Peters and Mech 1975). No similar published information is available for coyotes.

DUs are the most common form of marking for both wolves and coyotes in RMNP followed by NDUs and SCRs, respectively. Coyotes, however, when travelling in the absence of wolf sign, produce substantially more DUs along roads and trails than do wolves. Assuming that DUs and RLUs are functionally equivalent (see discussion below), then the high frequency of DUs corresponds with reports from Minnesota (Peters and Mech 1975, wolves) and Wyoming (Wells and Bekoff 1981, coyotes) where the most common marks result from raised leg urinations (RLUs).

In RMNP a disproportionate number of wolf and coyote DUs are placed along roads and trails. In contrast, NDUs and SCRs are deposited at a lower than expected frequency along frozen lakes and streams. Wolves in Minnesota also leave a preponderance of RLUs along roads and trails (Peters and Mech 1975). Corresponding published data is not available for coyotes in other areas. However, differential marking by coyotes has been observed in selected habitats of the forest/agricultural zone immediately adjacent to RMNP (McKinlay pers. comm.).

Scratches persist longer and are more conspicuous on ice than on soft snow. A dense substrate also favours deposition of sweat gland secretions from foot pads (Barrette and Messier 1980). It is logical, therefore, that scratch marks be used more often on ice than snow.

However, as noted, wolves and coyotes in RMNP scratch at an unexpectedly low rate along frozen waterways. Similar behavior has not been previously reported, although Barrette and Messier (1980) found the frequency of coyote scratching in Quebec to be positively influenced by hard packed snow. Despite the lack of corresponding evidence, limited scratch marking of frozen waterways is probably not unique to RMNP. Moreover, the behavior does not appear to be related to the areal overlap of wolves and coyotes, as scratches along frozen water bodies occur at a lower than expected rate on both mixed and single-use trails.

I agree with Barrette and Messier's (1980) suggestion that scratches are an option used to enhance or alter the meaning of other marks. However, it is notable that in this study scratches were not always added immediately subsequent to the original deposition of urine or scat; nor were they added secondarily by the original depositor. On 3 occasions wolves scratched near urine marks of coyotes, without urinating. In addition, I have twice observed captive wolves double mark urine deposits of conspecifics using scratches.

Because coyote scratches in Quebec were usually observed in conditions resulting in conspicuous marks, Barrette and Messier (1980) concluded that visual display was their main value. I question whether visual display is of primary importance, not only for scratches but for any canid scent mark. Most canids are nocturnal or crepuscular, and consequently depend less on vision than on highly developed olfaction. When wolves and coyotes investigate scratches they thoroughly sniff the marks. I suspect deposition of scent is the primary function of scratching and the visual effect only secondary.

As noted, wolves and coyotes in RMNP occasionally scratch without urinating or defecating. The behavior is important as there are no other published reports of scratch marks unaccompanied by urine or feces. Rothman and Mech (1979), working with wolves, only found scratches associated with RLUs and defecations but not SQUs. In contrast, coyotes in Grand Teton National Park Wyoming scratched after RLUs, defecations, and SQUs. In addition, McKinlay (pers. comm.) has never observed coyote scratches unaccompanied by urine and/or feces while snow-tracking in agricultural areas adjacent to RMNP. Finally, Barrette and Messier (1980) failed to find scratches that were independent of coyote urine or feces.

The independent scratch marks recorded in RMNP may have resulted from my inability to detect the presence of nearby scat or urine, although others have also observed scratch marks not associated with urine or feces (D. Burles pers. comm., J. Ryon pers. comm.). Alternatively, scratch marks without urine and feces might not occur in other areas, or researchers may not have noticed scratches because they are obscure when unaccompanied by other marks. I don't believe the behavior is related to interaction between wolves and coyotes, because scratches occur on both single and mixed-use trails.

Criteria provided by Kleiman (1966) for discriminating urine marking and simple elimination have been variously employed by canid researchers (Peters and Mech 1975, Bowen and Cowan 1980, Rothman and Mech 1979). Yet, Bekoff and Wells (1985) maintain that without direct and continuous observation of individual animals it is extremely difficult, if not impossible, to reliably apply the definition in field conditions, due to problems in analyzing "yellow snow" as well as observational biases. However, Bekoff and Wells have only demonstrated inaccuracies in the identification of the postures used by coyotes to deposit urine and not the ability of investigators to discriminate scent marks from eliminations. An association between postures and scent marking has not been adequately shown.

Several important questions, therefore, need to be resolved: 1) are particular postures associated with scent marking, 2) is the orientation of urine toward conspicuous and/or novel objects related to scent marking, and 3) are particular postures associated with directional marks?

The results from this study appear to support Kleiman's contention that directed urine deposits are for the most part scent marks. Of the 3 defined mark types used in this study, the deposition rate of DUs showed the greatest variation among travel environments and trail types. This parallels Peters and Mech's (1975) observation for RLUs and can be explained by the fact that some environments provide a greater abundance of conspicuous objects for marking (e.g. roads and trails). In addition, significant rate variations were associated with interspecific trail use, and/or differences in wolf pack sizes or coyote numbers. Such changes suggest that most DUs produced by wolves and coyotes were used to convey information to a recipient, or alternatively were an autonomic response to a stimulus odour left by previous users of the same trail. Therefore, it is highly probable that most DUs were scent marks rather than simple eliminations.

The results are also in agreement with Peters and Mech's (1975) observation that RLUs provide the most unambiguous information about scent marking. Although I did not attempt to differentiate between scent marks and simple eliminations, I used Kleiman's (1966) scent mark criteria to define a DU. This differs somewhat from the definition used by Peters and Mech (1975) for an RLU, but in practice appears to be functionally comparable. For example, most (99.3%) of the RLUs recorded by Peters and Mech were directed at objects compared to less than 1% of SQUs. In this study 90.2% of the wolf RLUs, and less than 7% of SQUs were oriented toward targets. Therefore, most target-oriented urine deposits appear to be RLUs, meaning RLUs are, for the most part, synonymous with Kleiman's definition of a scent mark.

Wells and Bekoff (1981), using different criteria, concluded that 94.4% of directly observed coyote RLUs were scent marks. However, in contrast with my own results for coyotes they estimated slightly over 80% of SQUs were also scent marks. Whether this reflects methodological or environmental differences is not easily determined, as other investigators did not classify coyote postures (Bowen and Cowan 1980, Barrette and Messier 1980) and Wells and Bekoff only recorded orientation toward previous urine marks.

Other studies have noted a positive relationship between coyote group size and the frequency of marking (Barrette and Messier 1980; Bowen and Cowan 1980; Wells and Bekoff 1981) and results from this study conform with those observations. Conversely, Peters and Mech (1975) found no association between wolf pack size and the frequency of RLUs, but did find a positive linear relationship with SQUs and SCRs. They attributed this to the fact that RLUs are typically performed only by dominant animals, and consequently the number of marking wolves is independent of pack size. Observational studies of captive wolves have reported similar findings (Woolpy 1968, Paquet, unpub., Ryon pers. comm.). However, Peters and Mech (1975) also contend that only high ranking wolves scratch and that the activity is primarily autonomic rather than eliminative. Logically, therefore, the frequency distribution of SCRs should also have been independent of pack size, which was not the case. Apparently, an alternative explanation is necessary.

As noted, in this study the marking rates of large wolf packs were significantly higher than those of small wolf packs. The discrepancy was consistent for yearly and pooled data both in the presence and absence of coyote tracks and was also reflected in interspecific tracking. Importantly, the difference was attributable to a highly significant increase in the frequency of DUs ($\underline{G}$-pooled = 36.59, $\underline{P} < 0.001$), while NDUs ($\underline{P} > 0.50$) and SCRs ($\underline{P} > 0.975$) remained relatively constant. Assuming that RLUs and DUs are nearly equivalent, this appears to be exactly the opposite of what Peters and Mech (1975) reported.

Because scratches are primarily associated with dominant wolves (Peters and Mech 1975), the frequency of SCRs should be independent of pack size (the same reasoning used by Peters and Mech to explain the constant rate of RLUs). The consistency of NDUs, however, is not easily explained. It does suggest that NDUs are not strictly eliminations and concurs with Barrette and Messier's (1980) assumption that all signs are potential scent marks, regardless of the sender's intent.

I found no evidence to support the hypothesis that coyotes modify their marking behavior to minimize the probability of detection by wolves. On the contrary, the general scenting pattern resembled that observed for territorial wolves (Peters and Mech 1975) and coyotes (Barrette and Messier 1980; Bowen 1978). Notably, wolves and coyotes share many of the same deposit sites. Both canids overmark urine deposits of the other species. However, the presence of wolf urine appears to stimulate increased marking by coyotes, while the opposite is not true. Coyotes actively re-mark wolf urine deposits rather than avoiding or simply investigating them. Moreover, coyotes add additional new scent marks along trails regularly travelled by wolves and respond to the urine of estrous wolves by overmarking the original deposit and scratching. Finally, there is a seasonal increase in RLUs along COW trails, which is attributable to coyotes. Why coyotes react to wolves in this manner is fascinating. Understanding their behavior may help elucidate the functional significance of interspecific scent marking in canids.

The simplest explanation is that coyote marking is an autonomic response to environmental stimuli such as conspicuous and/or novel odour-bearing objects (Kleiman 1966), including wolf scent mounds. However, that appears to be an unsatisfactory interpretation for two reasons. First, it can be reasoned that the deposition of urine must to a large extent be voluntary because non-territorial coyotes are known to reduce scent marking when moving through areas occupied by other coyotes (Bowen and Cowan 1978, Barrette and Messier 1980). Second, observations of coyotes in captivity indicate that scent marking is under voluntary control (Mottus 1972, Harrington 1982; Ryon pers. comm.).

Although the frequent use by coyotes of wolf scent posts implies that the response is either autonomic or agonistic (Mottus 1972; Peters and Mech 1975), it is probable that there are preferred sites in the environment for locating urine marks (Peters and Mech 1975) and wolves and coyotes simply share similar preferences. Consequently, the detectable deposition rate on mixed-use trails is lower than the actual combined rate, but still higher than on single-use trails, simply as a result of more animals using the trails.

An alternative explanation is that canids scent mark to orient themselves within their territory and that the consequent familiarity with the environment is psychologically reassuring in unknown situations (Kleiman 1966, Peters and Mech 1975). This explanation accounts for the uninhibited marking by coyotes travelling trails established by wolves.

However, if the function of scent marking is essentially a navigational aid then the deposition rate of urine by coyotes should increase within environments where orientation is difficult, and be unaffected by the presence of alien conspecifics. Evidence from the present study, as well as previous investigations (Peters and Mech 1975, Bowen and Cowan 1980) does not support this contention. For example, in all circumstances the frequency of marking was significantly higher along established roads and trails than along lakes or in the bush.

Presumably, roads should be easier to navigate than other travel routes, and therefore should be marked at a lower rate. This is precisely the opposite of what occurs, which leads to the conclusion that marking is used for more than navigation. As noted, however, the high deposition frequency along roads may, in part, reflect the abundance of suitable locations for placement of odour.

Marking could also serve to deter potential intruders from entering an area or cause their withdrawal (Hediger 1950). Accordingly, Barrette and Messier (1980) postulated that a territorial mammal should be overtly conspicuous in an area by covering it with scent. Gosling (1982) hypothesized that within their own territories owners should remove or replace marks that do not match their own odour. Both predictions were generally fulfilled by observations of coyote marking on wolf trails. Although it can only be tentatively concluded that fresh wolf urine was the stimulus for coyote marking, there is little doubt that the response was a reaction to the recent "presence" of wolves. Also the full extent of the response was probably underestimated because of the inclusion of marks from all coyotes that were tracked, rather than from territorial animals only, which generally mark at a higher rate (Barrette and Messier 1980).

The above interpretation implies that coyotes recognize wolves as trespassing conspecifics and respond agonistically by overmarking their territory. It seems, however, that coyotes should quickly learn that their efforts are ineffective, either through visual or agonistic encounters with wolves or because of the continued persistence of wolf sign in the area. In addition, it would be consistent, although not necessary, to expect the marking behavior of wolves to reflect a similar conspecific recognition of coyotes (i.e. increased marking in the presence of fresh coyote sign), which was the case only for small wolf packs. Nevertheless, direct observational evidence strongly supports the idea that coyotes react to wolves as they do to intruding conspecifics. Whether the increased marking rate is an autonomic or aggressive response remains uncertain.

Chapter 3

CONCLUSIONS

With the possible exception of scratching behavior, the marking activity of wolves and coyotes in RMNP closely parallels observations from areas where the two species do not overlap. Any major inconsistencies are probably attributable to differences in study methodologies, and not a consequence of sympatry. Moreover, there are only minor differences in the marking strategies of wolves and coyotes. Both species mark established roads and trails at a greater rate than other travel routes by significantly increasing the frequency of DUs, and both increase their rate of NDUs, and decrease their rate of SCRs along frozen waterways. The most notable difference is the greater proportion of DUs by coyotes along roads and trails.

Based on differences in deposition rates attributable to changes in social and environmental contexts, DUs by both wolves and coyotes were behaviorally distinct from NDUs and SCRs. It seems likely that DUs were purposefully deposited to transmit information and were not simple eliminations, thus conforming with Kleiman's (1966) definition of a scent mark. In addition, DUs and RLUs were found to be nearly identical for both wolves and coyotes, strongly supporting Peters and Mech's (1975) contention that RLUs are primarily scent marks.

The frequency of marking was related to the number of animals that were tracked for both wolves and coyotes. This conflicts with the results of scent-marking studies of wolves from Minnesota (Peters and Mech 1975) but is consistent with previous reports of coyote marking behavior (Bowen and Cowan 1980, Barrette and Messier 1980). The discrepancy in wolf data does not appear to be the result of the presence of coyotes in the study area, but is possibly attributable to the behavioral plasticity of wolves. Further studies are necessary to confirm the relationship between marking frequency and pack size.

The rate of marking by both wolves and coyotes was affected by the presence of sign from the other species. In most cases the response to foreign urine or scratch marks was an increased frequency of marking, or change in the pattern of marking, particularly of DUs. The response was decidedly more pronounced in coyotes than wolves, and resembled agonistic behavior typically directed toward alien conspecifics by animals maintaining home ranges or territories (Peters and Mech 1974, Bowen and Cowan 1980, Barrette and Messier 1980).

Contrary to my hypothesis, coyotes do not avoid areas marked by wolves, nor do they minimize evidence of their own activity. In general the response to wolves is active, including remarking of previously deposited wolf urine. In contrast, the response of wolves to coyote sign is relatively passive, although variable with pack size. Wolves actively investigate coyote marks, and sometimes overmark them, but not with the same fervor as they react to sign from unknown wolves (Peters and Mech 1975).

My original hypothesis implied that extensive scent marking by coyotes sympatric with wolves would be maladaptive because wolves could use the marks to locate and kill coyotes. However, increased marking by coyotes did not appear to alter the probability of coyotes being killed by wolves. I found no evidence that wolves use the marks of coyotes as aids for locating coyotes. On the contrary, there is evidence that wolves in RMNP do not actively track coyotes for the purpose of hunting them (Chapter 2).

Although I found no evidence that coyotes use wolf marks to avoid areas of wolf activity, I cannot dismiss the idea that coyotes are able to garner useful information about the proximity of wolves. At the very least, a coyote should be able to determine the freshness of various sign, and consequently judge the risk associated with travelling in the area. In RMNP, coyotes benefit from the presence of wolves by scavenging on remains of kills (Chapter 5). Spatial-temporal analysis of wolf and coyote movements has shown that coyotes actively follow wolves to carcasses (Chapter 2). Perhaps, when tracking wolves, coyotes use scent marks of wolves for navigational assistance, and as a means of maintaining safe distance.

Table III-1. Summary of marks recorded along wolf only trails (WO), coyote only trails (CO), coyote on wolf trails (COW), and wolf on coyote trails (WOC), 1982/83 through 1985/86.

TRAVEL ENVIRONMENT	TRAIL TYPE				
	WO marks/km	CO marks/km	COW marks/km	WOC marks/km	Totals marks/km
Roads & Trails	900/341	447/261	645/167	304/88	2296/857
Bush	487/259	91/106	321/115	161/67	1060/547
Frozen Waterways	103/141	28/76	100/63	19/36	250/316
Totals	1490/741	566/443	1066/345	484/191	3606/1720

Table III-2. Summary of pooled coyote and wolf marking data collected over 4 winter seasons. Figures in parentheses are total kilometres tracked within each category.

		TRAIL TYPE			
	MARK TYPE	WO (341 km)	CO (261 km)	COW (167 km)	WOC (88 km)
ROADS	DU	590	286	484	232
	NDU	219	86	100	31
	SCR	91	75	61	41
	Total	900	447	645	304
		(259 km)	(106 km)	(115 km)	(67 km)
BUSH	DU	268	46	224	110
	NDU	146	26	57	25
	SCR	73	19	40	26
	Total	487	91	321	161
		(141 km)	(76 km)	(63 km)	(36 km)
WATERWAYS	DU	41	15	73	14
	NDU	55	9	16	4
	SCR	7	4	11	1
	Total	103	28	100	19

Table III-3. Summary of pooled deposition rates recorded along WO trails in winters 1982/83 through 1985/86. For definitions of mark types see the text. Combined rates were calculated by dividing the total number of marks observed by the tracking distance accumulated in all environments.

TRAVEL ENVIRONMENT	MARK TYPE DU/km	 NDU/km	 SCR/km	Total
Roads & Trails	1.73	0.64	0.27	2.64
Bush	1.03	0.56	0.28	1.88
Frozen Waterways	0.29	0.39	0.05	0.73
Combined:	1.21	0.57	0.23	2.01

Table III-4. Summary of pooled deposition rates recorded along CO trails in winters 1982/83 through 1985/86. Combined rates were calculated by dividing the total number of marks recorded by the tracking distance accumulated in all environments. For definitions of mark types see text.

TRAVEL ENVIRONMENT	MARK TYPE DU/km	NDU/km	SCR/km	Total
Roads & Trails	1.10	0.33	0.29	1.71
Bush	0.43	0.25	0.18	0.86
Frozen Waterways	0.20	0.12	0.05	0.37
Combined:	0.78	0.27	0.22	1.28

Table III-5. Summary of pooled deposition rates recorded along COW trails in winters 1982/83 through 1985/86. Combined rates were calculated by dividing the total number of marks observed by the tracking distance accumulated in all environments. For definitions of mark types see text.

TRAVEL ENVIRONMENT	MARK TYPE DU/km	NDU/km	SCR/km	Total
Roads & Trails	2.90	0.60	0.37	3.86
Bush	1.95	0.50	0.35	2.79
Frozen Waterways	1.16	0.25	0.17	1.59
Combined:	2.26	0.50	0.32	3.09

Table III-6. Summary of pooled deposition rates recorded along WOC trails in winters 1982/83 through 1985/86. Combined rates were calculated by dividing the total number of marks recorded by the tracking distance accumulated in all environments. For definitions of mark types see text.

TRAVEL ENVIRONMENT	MARK TYPE DU/km	NDU/km	SCRT/km	Total
Roads & Trails	2.64	0.35	0.47	3.45
Bush	1.64	0.37	0.39	2.40
Frozen Waterways	0.39	0.11	0.03	0.53
Combined:	1.86	0.31	0.36	2.53

Table III-7. Summary of marking responses by wolves and coyotes to urine marks produced by the other species. Scent mounds along mixed use trails were monitored in winters 1983/84 and 1984/85.

SPECIES	# INITIAL URINE MARKS	# OVERMARKED BY WOLVES	# OVERMARKED BY COYOTES
(1983/84)			
Coyote	38	31	26
Wolf	30	18	25
(1984/85)			
Coyote	41	27	30
Wolf	62	19	33

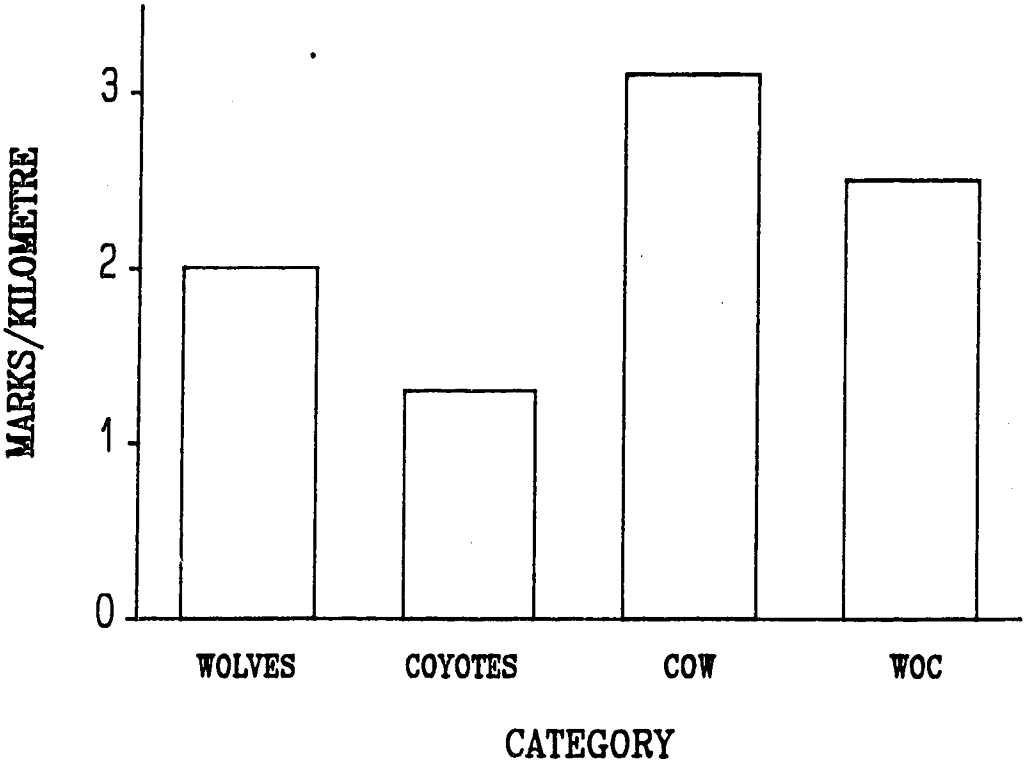

Figure III-1. Summary of pooled winter marking rates recorded along wolf trails, coyote trails, coyote on wolf trails (COW) and wolf on coyote trails (WOC), 1982/83-1985/86.

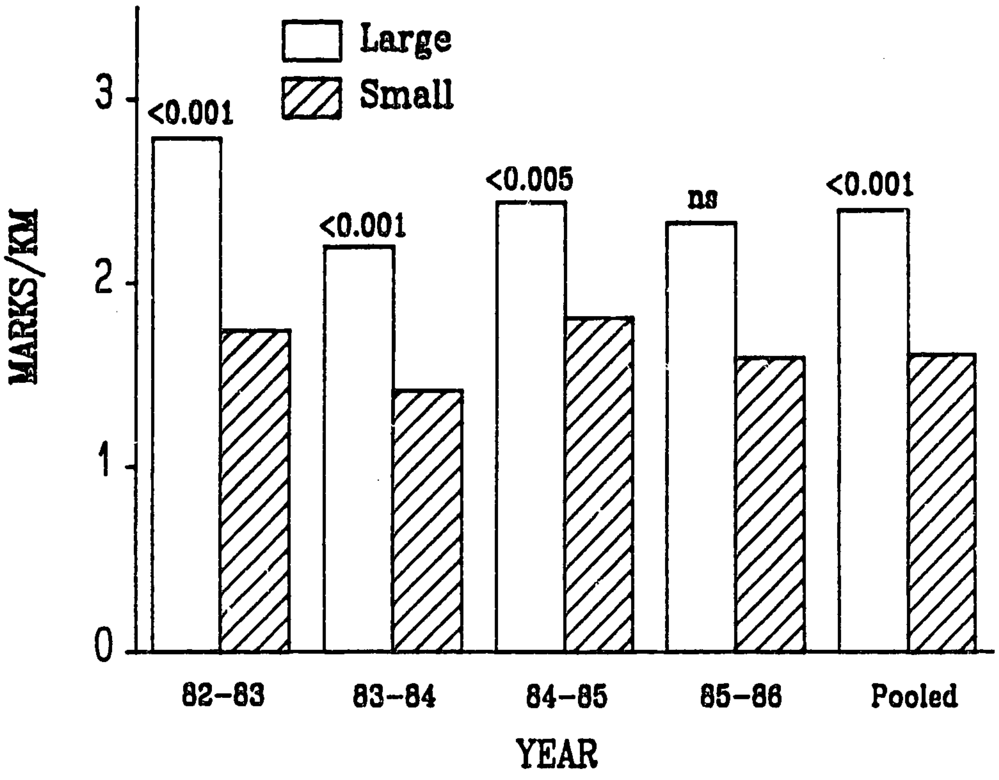

Figure III-2. Comparison of yearly and pooled marking rates recorded along trails travelled exclusively by large wolf packs and trails used exclusively by small wolf packs. Probability levels are noted above bars for rates that are significantly different.

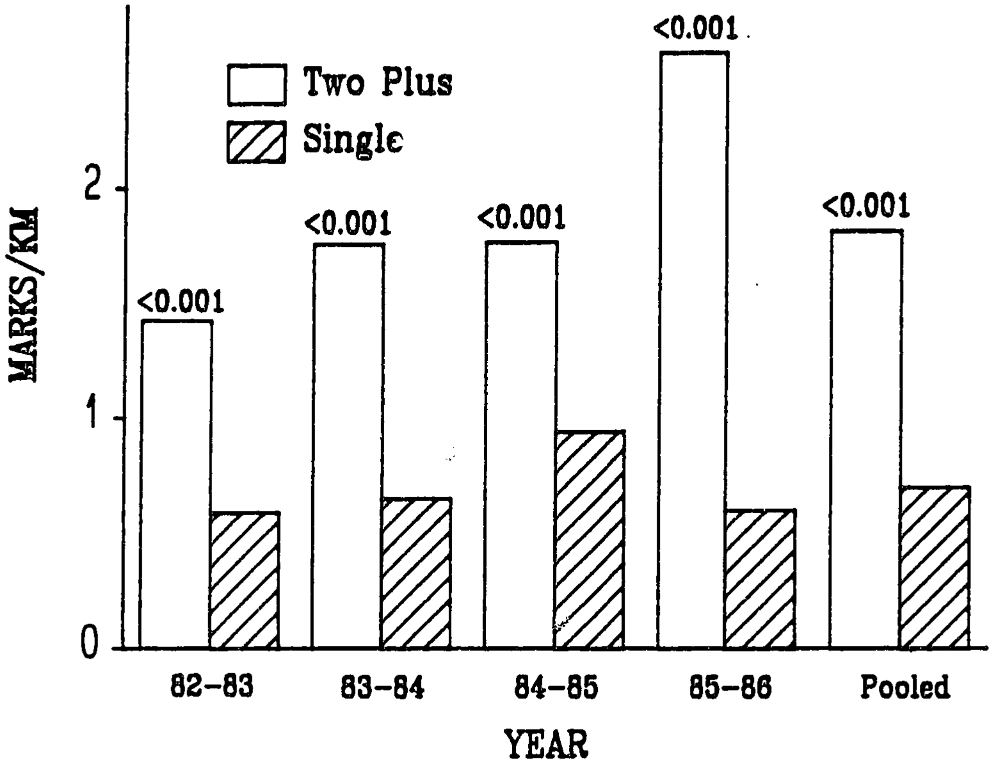

Figure III-3. Comparison of yearly and pooled marking rates recorded along trails travelled exclusively by coyote groups (>+2), and trails used exclusively by single coyotes. Probability levels are noted above paired bars for rates that are significantly different.

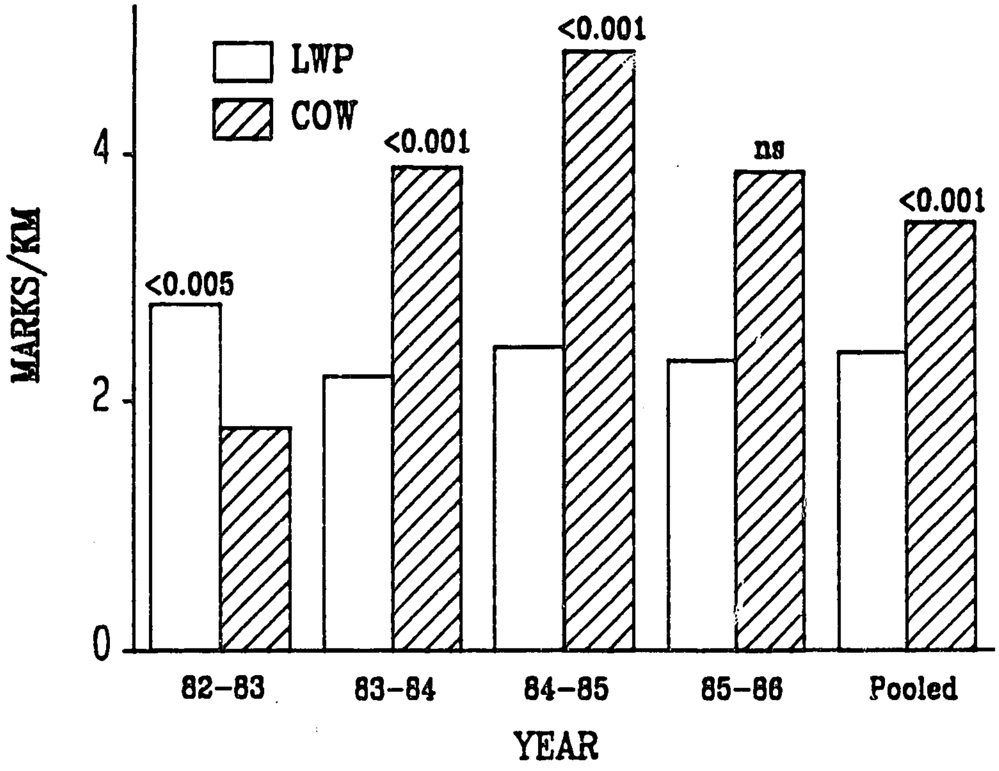

Figure III-4. Comparison of yearly and pooled marking rates recorded along trails travelled exclusively by large wolf packs (LWP), and trails established by large wolf packs and subsequently used by coyotes (COW). Probability levels are noted above paired bars for rates that are significantly different.

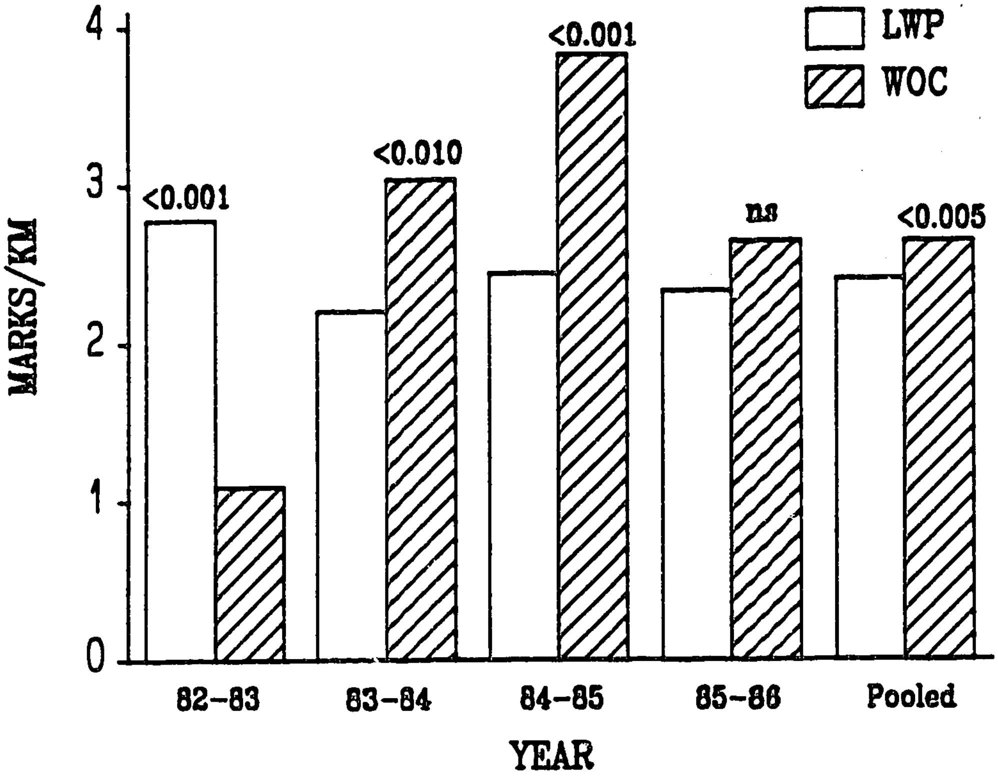

Figure III-5. Comparison of yearly and pooled marking rates recorded along trails travelled exclusively by large wolf packs (LWP), and trails established by coyotes and subsequently used by large wolf packs (WOC). Probability levels are noted above paired bars for rates that are significantly different.

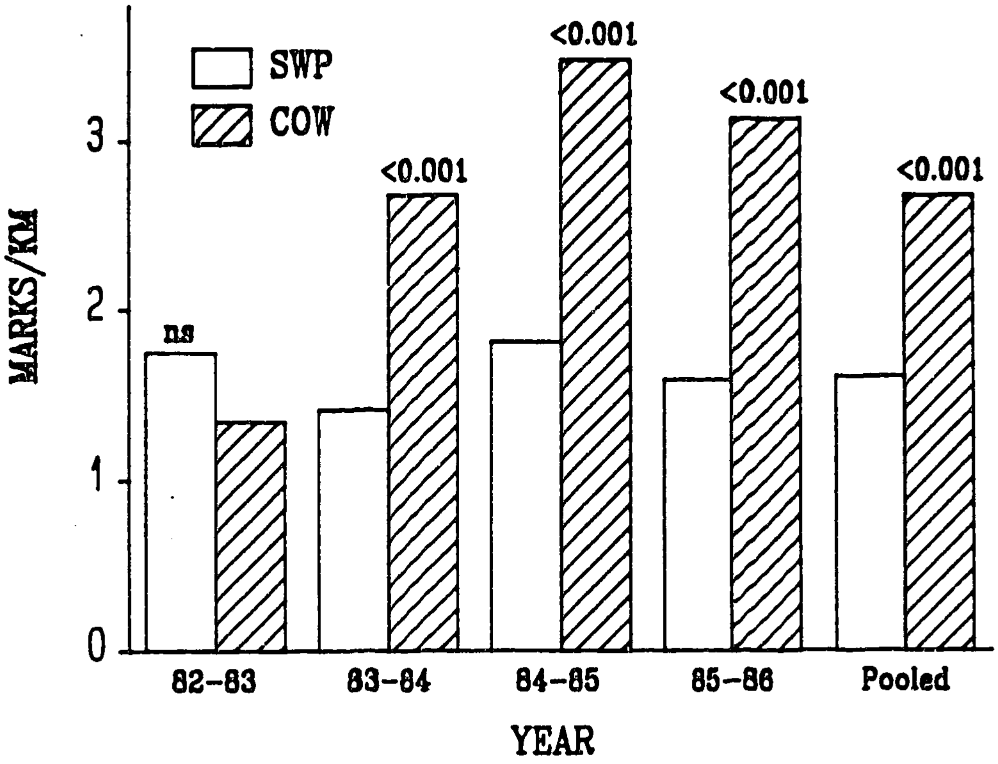

Figure III-6. Comparison of yearly and pooled marking rates recorded along trails travelled exclusively by small wolf packs (SWP), and trails established by small wolf packs and subsequently used by coyotes (COW). Probability levels are noted above paired bars for rates that are significantly different.

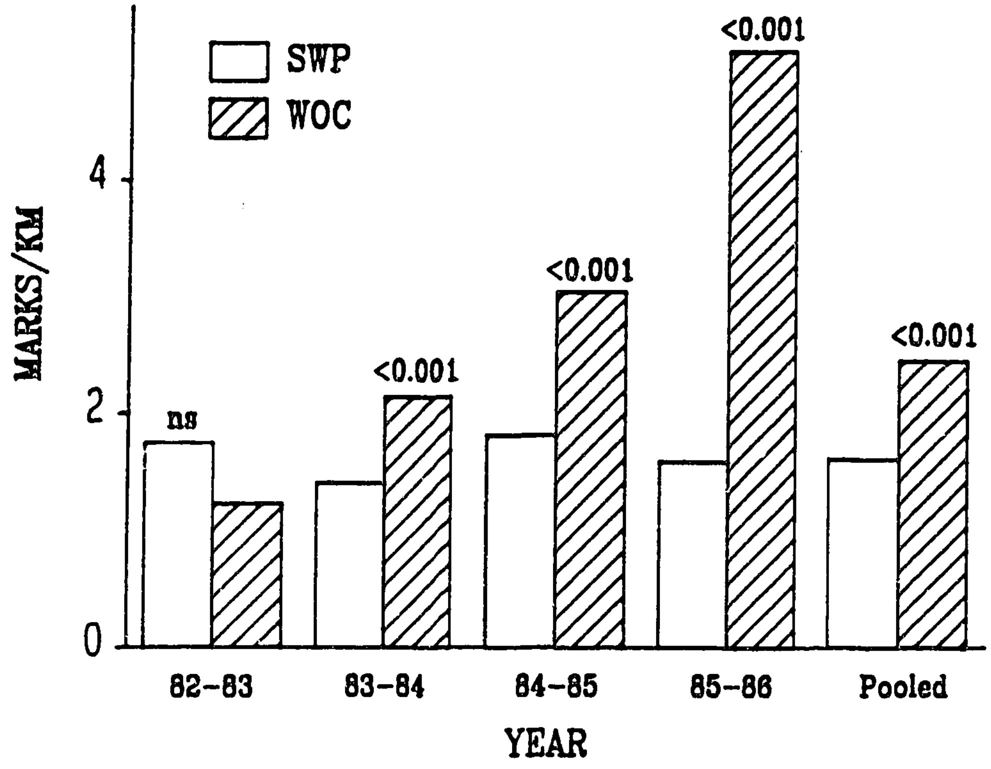

Figure III-7. Comparison of yearly and pooled marking rates recorded along trails travelled exclusively by small wolf packs (SWP), and trails established by coyotes and subsequently used by wolves (WOC). Probability levels are noted above paired bars for rates that are significantly different.

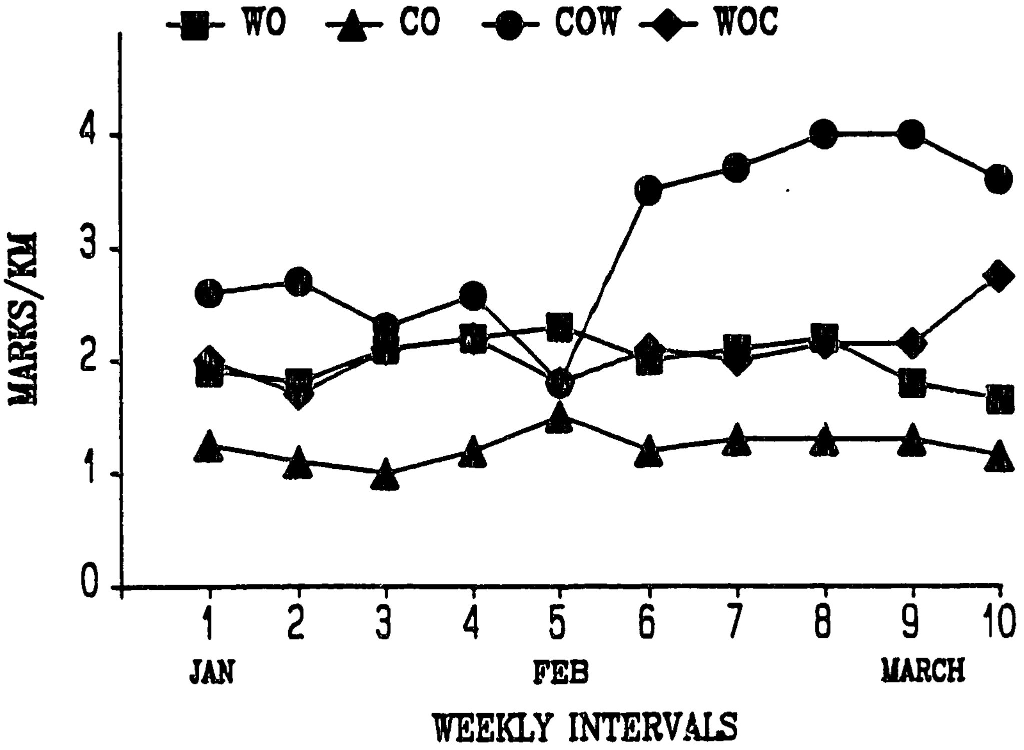

Figure III-8. Temporal distribution of marks recorded along wolf only trails, coyote only trails, coyote on wolf trails (COW), and wolf on coyote trails (WOC), during winter periods 1 January - 14 March in all study years. A significant change in marking frequency occurred only on COW trails, where marking increased in late February and early March.

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CHAPTER 4

SCENT MARKING AND TERRITORIALITY OF WOLVES (*Canis lupus*) IN RIDING MOUNTAIN NATIONAL PARK

INTRODUCTION

Scent marking as a means of defending an area should be most frequent at the periphery of a territory (Johnson 1973). Intruders could then recognize the edge of a territory by the rate at which they encounter scent marks or by a changing odour gradient (Bowen and McTaggart Cowan 1980). Peters and Mech (1975), using combined data from several packs, reported an increased rate of marking by wolves (*Canis lupus)* near territory boundaries, and concluded that the distribution of scent marks was related to territory advertisement and enforcement. Conversely, Carbyn (1980), found no difference between peripheral and interior marking rates for a wolf pack in Riding Mountain National Park, Manitoba, Canada.

Bowen and McTaggart Cowan (1980) found the density of coyote (*C. latrans*) scent marks to be highest at the edge of the territory and lowest at the centre. Neighboring conspecifics, however, failed to respect territorial boundaries. Camenzind (1978) recorded 68% of all scent marks on territorial boundaries.

No assessment of the spatial distribution of scent marks within individual wolf territories has been carried out. In this paper, I tested the hypothesis that the frequency of scent marking by wolves increases from the center to the periphery of the territory, and that the change in deposition frequency is related to boundary demarcation.

STUDY AREA

The study was conducted in Riding Mountain National Park (RMNP) between 1983 and 1986. The park is located 177 km north of the international boundary between Manitoba, Canada and North Dakota, U.S.A. Dominant vegetation is aspen (*Populus tremuloides*) and white spruce (*Picea glauca*), interspersed with black spruce (*Picea mariana*) bogs, and jack pine (*Pinus banksiana*) forest. Other large predators in the area include coyotes, lynx (*Lynx lynx*) and black bears (*Ursus americanus*). Elk (*Cervus elaphus*), deer (*Odocoileus virginianus*), moose (*Alces alces*), and beaver (*Castor canadensis*) are the primary prey species for wolves (Carbyn 1980, Meleshko 1986, Chapter 5).

Chapter 4

METHODS

Urine and scratch marks were recorded in 4 wolf territories from December through March. Tracking was done by snowmobile, cross country skis, snowshoes, or travel by foot. Distances were calculated by pedometer when travelling on foot and by odometer when travelling by snow machine. All distances were rounded to the nearest kilometre. Trails were selected haphazardly (Lehner 1979) within designated territories and followed for a minimum distance of 5 km. In 1983-84, data were collected from trails used exclusively by wolves to avoid confusion with coyote urine deposits and scratches. During the winter 1984-85 marking information was collected from trails used by: a) wolves only, and b) both wolves and coyotes.

As there is disagreement as to what constitutes a scent mark, I did not attempt to discriminate between the behavioral and physiological rates of urination and defecation (Kleiman 1966, Peters and Mech 1975, Barrette and Messier 1980, Bowen and McTaggart Cowan 1980, Bekoff and Wells 1982). Urine deposits were classified as Directed (DU) and Non-Directed (NDU). DUs were defined as marks produced by urine that had been directed toward a target (Kleiman 1966), either a physical object or previous urine deposit. Deposits without obvious orientation were classified as NDUs. Scratches were defined as extended parallel tracks produced by the claws of wolves (Kleiman

1966). Data collected within 25 m of a wolf- or coyote-killed ungulate were discarded.

Territories were delineated by extensive and repeated ground tracking of selected wolf packs (Chapter 5). Observations began when a permanent winter snow cover was established. In all cases repetitive track patterns were evident by mid-December, allowing for easy recognition of individual packs. Adjacent packs were also monitored, which helped identify questionable tracks when, for example, a pack temporarily divided into subunits. Visual observations of wolves from the air and on the ground provided additional information as to location of packs and range of movements.

Maps of territories were subdivided into 1-km wide concentric zones (shells) for analysis. Shell 1 was designated the outermost shell. The contour of each shell followed the outline of the territorial boundary. Hence, the outside edge of each shell was a constant distant from the boundary.

The frequency distribution of urine and scratches within each territory was evaluated by G-test for goodness of fit (Sokal and Rohlf 1981:692). Values were adjusted by means of Williams' correction for continuity. I assumed that wolves mark at a constant rate, regardless of physiography or speed of travel. Multiple comparisons of the same data were carried out on: 1) deposition frequencies among individual shells, and 2) pooled data from the outer 2 shells (edge) and pooled data from the remaining inner shells (center) (Peters and Mech 1975). Critical P-values were adjusted by Sidak's multiplicative inequality (Sokal and Rohlf 1981:728). The null hypothesis tested is that the frequency of urine and scratch marks per unit distance of trail is constant regardless of the location within a territory.

Expected frequencies were calculated using the formula nd_i/d where:

d_i is distance travelled in ith shell, $i = 1, 2 \ldots k$;

d is total distance travelled in the territory, $= \sum d_i$;

and, n is total scent marks recorded in the territory, $= \sum n_i$.

Chapter 4

RESULTS

This analysis is based on 922 urine and scratch marks recorded in 492 km of tracking (Table IV-1). The Audy Lake Pack had the highest overall deposition rate (2.4 marks/km) and the Clear Lake Pack the lowest (1.2 marks/km) in 1983-84. Comparison of the overall marking frequencies for all individual packs showed significant differences among packs ($\underline{G} = 63.968$, $\underline{P} < 0.001$, df = 3). Pairwise unplanned tests (Sokal and Rohlf 1981, page 728) indicated that most of the variability was attributable to differences in deposition frequencies between Clear Lake (1984-85) and the other 3 packs. The remaining subsets were homogenous.

There was no significant difference in the spatial distribution of marks recorded along wolf/coyote trails and wolf only trails for either the Audy L. ($\underline{G} = 2.153$, $\underline{P} > 0.500$, df = 4) or Clear L. (1984-85) ($\underline{G} = 1.738$, $\underline{P} > 0.500$, df = 4) territories. Therefore, the data for both trail types were pooled for analyses.

Analysis by Concentric 1-km Shells

In 3 of the 4 territories, the highest frequency of marking (all marks combined) occurred in intermediate shells, i.e. shells that were neither on the periphery nor at the centre (Tables IV-1 and IV-2). Note that the Clear Lake pack (1984-85) did not travel in the central shell, although they marked with highest frequency in the innermost shell that they used (Table IV-1). The null hypothesis was rejected for all packs for DUs (Table IV-3) and NDUs (Table IV-4). The distribution of SCRs was random in the Audy L. territory and non-random in the 2 Clear L. territories (Table IV-5). Insufficient data precluded analysis for the Baldy L. territory.

Analysis by 2-km Edge and Center

For 3 of the 4 territories there was a highly significant difference in overall marking frequency between peripheral and central areas. Clear L. (1983-84) and Audy L. wolves marked most often near territorial boundaries; the Baldy L. pack left more marks in the central part of their territory; the Clear L. (1984-85) pack showed no preference for either the periphery or the centre (Table IV-6). In all cases, differences were attributable to uneven distribution of DUs (Table IV-7) and NDUs (Table IV-8). The frequency of SCRs never departed significantly from expectation (Table IV-9).

Portions of each wolf territory examined included sections of park boundary, along which there were no neighboring packs. If, as has been postulated (Peters and Mech 1975, Bowen and McTaggart Cowan 1980, Barrette and Messier 1980), the accumulation of scent marks on a territory periphery is due to the combined contributions of residents and neighboring packs, as well as an increased stimulus for marking, a reduced rate in sections without neighboring packs would be expected. The effect would be to lower the overall rate recorded in the outermost shell. Therefore, I re-evaluated the data for winter territories from 1983-84 and 1984-85. After eliminating trail sections adjacent to the park boundary, there was no change in the relative marking frequencies throughout the territories, using either the shell ($\underline{G} = 1.738$, $\underline{P} > 0.500$, df = 3) or center/edge ($\underline{G} = 0.788$, $\underline{P} > 0.500$, df = 3) method of analysis. In addition, there were no differences in marking frequencies along park boundaries, and boundaries adjacent to neighboring wolf packs ($\underline{G} = 1.341$, $\underline{P} > 0.500$, df = 1).

Chapter 4

DISCUSSION AND CONCLUSIONS

Peters and Mech (1975) concluded that wolf marking sites are more numerous along territorial peripheries, and proposed as a model an "olfactory bowl" of scent, in which the number of marks decreases from the edge to the middle of the territory. Bowen and McTaggart Cowan (1980) described a similar distribution of scent marks in coyote territories. Barrette and Messier (1980) questioned whether these models were appropriate, because both were based on marks/km rather than marks/km^2.

In this study, analysis of marking frequency in concentric, 1-km shells gave no support to the olfactory bowl model. Analysis by comparing marking frequency in a peripheral band 2-km in width with frequency in the remaining central portion of each territory gave conflicting results. For 2 of the packs, the frequency was greater at the periphery than in the centre; in 1 case, the reverse was true; and in another, the observed frequency did not differ from expectation.

Peters and Mech (1975) pooled data from 3 wolf packs, and compared overall marking rates in a 1 km wide strip along the pack territories with marking rates in interior areas. When I pooled my data I found no significant difference in overall marking frequency between the peripheral 1 km band and centre areas ($G = 2.38$, $P > 0.50$, df = 1).

The high density of coyotes in RMNP might disrupt or alter "normal" marking behaviors of wolves. Although the data used in the analysis were carefully collected from trails with visible wolf tracks only, residual or undetected coyote scent may have been present beneath the snow. However, the distribution of marks on mixed-use trails was similar to that on wolf only trails, suggesting coyotes do not affect the placement of marks within wolf territories. In addition, concurrent studies of wolf/coyote interactions showed little response by wolves to coyote urine and scratch marks (Chapter 3).

Peters and Mech (1975) noted that physiography influences the frequency of scent marking. Marking studies concurrent with this study (Chapter 3) confirm that observation. Established roads and trails exhibit the highest number of marks and frozen waterways the lowest. Therefore, territories encompassing large bodies of water and/or an unusual configuration of roads and trails would likely show an uneven distribution of scent marks. For example, a territory with the outermost boundary bordering on a lake would likely have a lower number of marks near the periphery than might otherwise be expected in a more homogenous environment. Conversely, a territory with a large lake near the centre would have a low number of marks in the central portion.

Finally, I agree with Barrette and Messier (1980) that relative amount of time spent in each part of a territory must influence marking frequency. Foraging theory predicts that predators favour areas where hunting is easiest and prey is most abundant (Stephens and Krebs 1986). Assuming that the frequency of marking is positively associated with the time spent in an area, the non-random distribution of marks observed in RMNP might reflect foraging behavior by wolves.

In Riding Mountain the predominant prey of wolves is elk (Carbyn 1983; Meleshko 1966, Chapter 5). Winter distribution of elk is clumped and uneven (Rounds 1980, Meleshko 1986), which is partially related to cover, food resources (Trottier et al. 1983) and snow thickness (Paquet et al. in prep). Consequently, marking frequency could be elevated in areas of high elk density simply as a function of the time wolves are present hunting. The shell method of analysis used in this study would not detect these areas of concentration because several concentric shells could overlap portions of the same elk range.

However, I reject the suggestion of Barrette and Messier (1980) that marking data should be expressed as marks/unit area rather than marks/unit length. Travel routes of wolves are predictable because wolves consistently use the same trails. If it is assumed that frequent marks (or the resulting high olfactory stimulus) are sufficient to discourage intruders, then wolves ought to increase the marking rate on existing trails. To increase the overall density of marks would require a much more extensive network of trails, which would be costly in both time and energy. No such system of trails exists in RMNP, nor has one been reported in the literature.

The results show clearly that wolves mark parts of their territory differentially, but, when data for each pack are analysed separately, I conclude that the olfactory bowl model does not describe the marking behavior of wolves in RMNP. Considering the influence of variable topography and the hypothesized importance of patterns of prey distribution, I suggest that it is unlikely that the model is universally applicable.

Table IV-1. Summary of the distributional pattern of urine and scratch marks for 4 wolf packs in RMNP. Shells are numbered in ascending order from the outside to the inside, so that shell number 1 is outermost.

Pack (year)	Shell number	Number of scent marks				Total distance	Marks/ km
		DU	NDU	SCR	Total		
Clear Lake 2-3 wolves (1983-84)	1	18	31	9	58	39.0	1.5
	2	51	16	9	76	31.0	2.5
	3	19	17	5	41	56.0	0.7
	4	21	0	10	31	21.0	1.5
		111	65	33	209	174.0	1.2
Clear Lake 2-3 wolves (1984-85)	1	39	45	19	103	41.0	2.5
	2	42	12	7	61	43.0	1.4
	3	12	7	2	21	27.0	0.8
	4	15	14	5	34	10.0	3.4
	5*	0	0	0	0	0.0	0.0
		108	78	33	219	121.0	1.8
Audy Lake 5 wolves (1984-85)	1	22	19	8	49	17.0	2.8
	2	51	23	9	83	23.0	3.7
	3	9	0	5	14	7.0	2.0
	4	29	13	10	52	29.0	1.8
	5	0	2	0	2	6.0	0.3
		111	57	32	200	82.0	2.4
Baldy Lake 10 wolves (1983-84)	1	0	1	0	1	16.0	0.6
	2	6	5	2	13	8.0	1.6
	3	0	0	0	0	2.0	0.0
	4	40	2	7	49	13.0	3.8
	5	56	37	3	96	31.0	3.1
	6	34	12	2	48	24.0	2.0
	7	33	5	6	44	21.0	2.1
		169	62	20	251	115.0	2.2

* Wolf tracks were never observed in shell 5. Whether the shell was ever used is unknown.

Table IV-2. Statistical comparisons of observed and expected frequencies of urine and scratch marks in 1-km wide shells of 4 wolf territories. Expected values were calculated following procedures outlined by Lehner (1979).

Pack (year)	*G*-value	df	P
Clear Lake (1983-84)	90.232	4	<0.001
Clear Lake (1984-85)	45.612	3	<0.001
Audy Lake (1984-85)	36.536	4	<0.001
Baldy Lake (1983-84)	93.541	6	<0.001

Table IV-3. Statistical comparisons of observed and expected frequencies of DUs in 1-km wide shells of 4 wolf territories. Expected values were calculated following procedures outlined by Lehner (1979).

Pack (year)	*G*-value	df	P
Clear Lake (1983-84)	81.570	4	<0.001
Clear Lake (1984-85)	11.117	3	<0.050
Audy Lake (1984-85)	29.478	4	<0.001
Baldy Lake (1983-84)	76.812	6	<0.001

Table IV-4. Statistical comparisons of observed and expected frequencies of NDUs in 1-km wide shells of 4 wolf territories. Expected values were calculated following procedures outlined by Lehner (1979).

Pack (year)	<u>G</u>-value	df	P
Clear Lake (1983-84)	53.259	4	<0.001
Clear Lake (1984-85)	39.120	3	<0.001
Audy Lake (1984-85)	19.835	4	<0.001
Baldy Lake (1983-84)	39.716	6	<0.001

Table IV-5. Statistical comparisons of observed and expected frequencies of SCRs in 1-km wide shells of 3 wolf territories. Expected values were calculated following procedures outlined by Lehner (1979).

Pack (year)	*G*-value	df	P
Clear Lake (1983-84)	21.608	4	<0.001
Clear Lake (1984-85)	12.992	3	<0.050
Audy Lake (1984-85)	5.177	4	ns

Table IV-6. Statistical comparisons of observed and expected frequencies of urine and scratch marks in center and edge areas of 4 wolf territories. Expected values were calculated following procedures outlined by Lehner (1979).

Pack (year)	_G_-value	df	P
Clear Lake (1983-84)	48.422	1	<0.001
Clear Lake (1984-85)	3.207	1	ns
Audy Lake (1984-85)	23.426	1	<0.005
Baldy Lake (1983-84)	50.449	1	<0.001

Table IV-7. Statistical comparisons of observed and expected distributions of DUs in center and edge areas of 4 wolf territories. Expected values were calculated following procedures outlined by Lehner (1979).

Pack (year)	G-value	df	P
Clear Lake (1983-84)	23.142	1	<0.001
Clear Lake (1984-85)	1.627	1	ns
Audy Lake (1984-85)	12.480	1	<0.001
Baldy Lake (1983-84)	42.578	1	<0.001

Table IV-8. Statistical comparisons of observed and expected distributions of NDUs in center and edge areas of 4 wolf territories. Expected values were calculated following procedures outlined by Lehner (1979).

Pack (year)	*G*-value	df	P
Clear Lake (1983-84)	11.801	1	<0.001
Clear Lake (1984-85)	3.262	1	ns
Audy Lake (1984-85)	13.338	1	<0.001
Baldy Lake (1983-84)	5.598	1	<0.050

Table IV-9. Statistical comparisons of observed and expected distributions of SCRs in center and edge areas of 4 wolf territories. Expected values were calculated following procedures outlined by Lehner (1979).

Pack (year)	*G*-value	df	P
Clear Lake (1983-84)	0.000	1	ns
Clear Lake (1984-85)	1.361	1	ns
Audy Lake (1984-85)	0.123	1	ns
Baldy Lake (1983-84)	1.432	1	ns

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CHAPTER 5

FORAGING BEHAVIOR OF SYMPATRIC WOLVES (*CANIS LUPUS*) AND COYOTES (*C. LATRANS*) IN RIDING MOUNTAIN NATIONAL PARK, MANITOBA

INTRODUCTION

Taxonomists have relied on habitat selection, morphology and behavioral differences to separate 3 distinct North American species within the genus Canis - the gray wolf (*Canis lupus*), the coyote (*C. latrans*) and the red wolf (*C. rufus*) (Lawrence and Bossart 1967: 224). The species overlap geographically, anatomically and behaviorally. Genetic differences are minimal (Chiarelli 1975, Seal 1975, Kennelly 1978) with all 3 species interfertile and capable of producing fertile progeny (Gipson 1978, Hall 1978, Kennelly 1978). Interaction of behavioral mechanisms and ecological preferences may have kept the groups physically isolated allowing them to function as evolutionarily distinct units (Hall 1978). Consequently there is a general perception that coyotes and wolves are allopatric, or that coyotes are greatly reduced wherever substantial populations of wolves occur.

Allopatric distribution of the 2 species has been attributed to differences in habitat preferences, direct competition for food, and interspecific agonistic conflicts.

The perception of allopatry has been reinforced by studies that suggest that coyotes occupy zones peripheral to high wolf densities (Stenlund 1955, Berg and Chesness 1978, Carbyn 1982, Fuller and Keith 1981), occur in densities inversely proportional to those of wolves (Carbyn 1982), or are altogether displaced by wolves (Munro 1947, Krefting 1969, Mech 1966, Mech 1970, Peterson 1977, Berg and Chesness 1978).

However, the evidence for allopatry is contradictory. In contrast with areas of reported exclusion wolves and coyotes are now, or were within recent history, sympatric throughout a diverse range of North American habitats, including Yellowstone National Park, Wyoming (Murie 1940), much of the Canadian Rocky Mountains (Carbyn pers. comm.), Prince Albert National Park, Saskatchewan (Burles pers. comm.), and regions of Ontario (Schmitz and Kolenosky 1984, Schmitz and Lavigne 1987).

In Riding Mountain National Park (RMNP), Manitoba, substantial populations of both species are present. Although wolves often kill coyotes (Carbyn 1982, this paper, Chapter 2), interspecific spatial and temporal separation does not occur (this paper, Chapter 2). Coyotes establish home ranges within wolf territories (Carbyn 1982, this paper, Chapter 2) and activity of the 2 species is frequently synchronous (this paper, Chapter 2). Moreover, scat analysis has verified a high degree of dietary overlap, with both species relying on large herbivores, particularly elk (<u>Cervus elaphus</u>), for food (Meleshko 1986).

That wolves and coyotes successfully coexist in some areas and not in others is an interesting phenomenon that requires explanation. The objective of this study is to isolate species-specific foraging behaviors that may permit ecological separation of wolves and coyotes in RMNP. In theory, coexistence of similar species is largely dependent on the extent to which essential shared resources (e.g. food) are limiting and the degree of resource partitioning that occurs (Schoener 1974). Therefore, I attempted to: 1) identify food habits of wolves and coyotes <u>via</u> field observation, 2) identify strategies for food procurement employed by wolves and coyotes, and 3) document interspecific differences in predatory behavior. I hypothesized that minimal competition occurs between wolves and coyotes because: a) food resources are abundant, and b) the manner in which food is exploited differs between the 2 species.

Chapter 5

STUDY AREA

Field investigations were carried out in RMNP, Manitoba from 1982-1987. The park is a 2974 km^2 highland of mixed coniferous and deciduous forest, interspersed with lakes, grasslands, and bogs. It is located approximately 225 km northwest of Winnipeg.

Flora is representative of 3 distinct vegetative zones, the Boreal Forest, Eastern Hardwood Forest, and Prairie Grasslands (Love 1959). The park is included in the Boreal Mixedwood Forest Region of Rowe (1972).

Elevations range from 319 m to 756 m. Annual precipitation is moderate with an average rainfall of 15 cm and average snowfall of 150 cm. Maximum snow thickness does not usually exceed 50 cm. January is the coldest month with a mean daily temperature of -20° C and July the warmest month with a mean daily temperature of 20° C (Environment Canada, Atmospheric Environment Service).

Carnivores other than wolves and coyotes include black bears (_Ursus americanus_), lynx (_Lynx lynx_) and several mustelids. Red foxes (_Vulpes vulpes_) are present in surrounding agricultural areas but were not directly observed inside the park. However, foxes fitted with radio-transmitters during this study were recorded on both sides of the park boundary. Elk, moose (_Alces alces_), and beaver (_Castor canadensis_) are abundant, although all 3 species declined in numbers during the study. White-tailed deer (<u>Odocoileus virginianus</u>) are seasonally common throughout the park. Snowshoe hare (<u>Lepus americanus</u>) populations peaked in 1981, and have been low since 1982.

Chapter 5

METHODS

Ungulates killed by wolves and coyotes were located by ground and aerial observation. Locations were plotted on topographic maps (1:50,000). Signs associated with predation (e.g. presence of large numbers of ravens, scattered tufts of sheared hair, heavily traveled trails, blood-covered snow) were helpful in locating kills. Additionally, park wardens, local farmers, trappers, and hunters reported sightings of dead ungulates.

Whenever possible, a femur marrow sample and mandible or dentary bone were collected. Elk and moose ages were determined from tooth replacement and wear through 2.5 years, and by sectioning of M_1 (Flook 1970) or I_1 (Sergeant and Pimlott 1959), for older animals. In 1982-83 deer were separated into adult and fawn categories using tooth replacement and wear criteria exclusively (Severinghaus 1949). In subsequent years ages were determined by sectioning of I_1. All animals of approximately 1 year were designated as adults after 15 May. Ages of elk and moose killed by hunters outside the park were obtained from the Province of Manitoba Department of Natural Resources. Bone marrow samples were analyzed for fat content following procedures described by Verme and Holland (1973).

Chase lengths were estimated by pedometer or snow machine odometer. Snow thicknesses were measured by a graduated ski pole. Five readings were taken at the kill site and thicknesses were measured at approximately 50 meter intervals over the entire distance of the chase. Measurements were summed and a mean thickness was calculated.

Snow conditions were subjectively evaluated as fluffy, lightly crusted, or heavily crusted. Coyote tracks penetrated fluffy snow, intermittently penetrated lightly crusted snow, and consistently remained on top of heavily crusted snow. Although conditions usually changed over the length of a chase, I recorded conditions only at the site of the kill.

The approximate date of death was estimated using a combination of criteria, which varied according to season, weather, habitat type and condition of the carcass. In general, carcasses located in frequently traveled areas were assumed to be new. The presence of large numbers of ravens (Corvus corax) at a carcass was considered indicative of a recent death. To some extent the degree of carcass use allowed an estimate of time of death. The presence of wolf tracks, continued use of the carcass, newly deposited scat or urine marks, and date of last snowfall provided additional evidence.

Partially used carcasses found in summer were considered less than a week old if large portions of undecomposed flesh remained. The presence of hair, rumen contents, hide, and other decomposing portions suggested death probably occurred the previous winter (Peterson 1977). Hollow carcasses that were mummified and fully articulated were not attributed to predation.

Cause of death was determined by evaluating the kill site, as well as carcass condition. The area was examined for tracks, scat, urine marks, signs of struggle (e.g. tufts of hair, blood-stained snow or earth, erratic tracks, pieces of torn flesh), and bed sites. If feasible, the carcass was examined for puncture wounds, claw marks and subcutaneous hemorrhages. Scattered remains of deer were listed as probable predator kills unless there was evidence to the contrary.

Carcasses estimated to be less than 12 hours old were revisited at intervals of 48 hours or less, or until consumption of soft tissues was complete. The degree of use was noted during the first visit and subsequent changes were recorded during each visit thereafter (Carbyn 1983). Scavengers were identified by direct observation or indirectly by the presence of tracks, scat, and urine marks.

In 1984/85, 9 carcasses were monitored by remote photography using a 35mm Nikon FE2 body, 35mm Nikkor lens (f2.0), Nikon MD12 motor drive, Telonics TIC-2 intervalometer, Metz 60 CT-2 flash, Telonics TIR-1 infra-red motion detector, and Telonics TRU-1 radar sensor. The system was powered by 6-volt rechargeable lead acid gel cells (Technacell) and 3-volt lithium sulfide batteries

(Eternacell), allowing for cold weather operation below -35° C. The components were housed together in a portable weatherproof box, with a viewing port of optical glass, and an unobstructed opening for the infra-red sensor. The system was activated when the TIR-1 sensed radiated body heat and lateral movement relative to background IR scatter. The intervalometer was programmed to trigger a single frame and remain immune to input for 3 minutes before triggering another frame. Exposure was automatically calculated by the flash.

Statistical Analysis

Bartlett's test was used to evaluate homogeneity of multiple variances (Snedecor and Cochran 1980, page 252). If within group variances were homogenous, a 1-way analysis of variance (ANOVA) was used to test whether means differed significantly (Sokal and Rohlf, 1981, pg. 215). Otherwise Kruskall-Wallis' (Sokal and Rohlf 1981, pg. 429) nonparametric 1-way ANOVA was employed.

The _t_-test was used to test for differences between means of 2 independent groups (Snedecor and Cochran 1980, page 97.). If group variances were unequal a Rank Sum test was used (Sokal and Rohlf 1981, pg. 432). Equality of variances was tested using the _F_-test (Snedecor and Cochran 1980, page 98).

Associations were tested using the _G_-test of independence (Sokal and Rohlf 1981, pg. 731). All test values were considered significant at $\alpha \leq 0.05$.

Chapter 5

RESULTS

Prey Selection

From July 1982 through March 1986, 194 wolf-killed ungulates and 59 coyote-killed ungulates were examined. Data were also collected from 39 elk, 6 deer and 3 moose that died from causes other than predation or human hunting.

Elk were the primary prey species for wolves (Fig. V-1), accounting for 57% ($\underline{n}$ = 111) of the total wolf kills, followed by deer (28%, n = 54) and moose (15%, n = 29). Comparison with the relative abundance of prey (Meleshko 1986) revealed that elk and deer were selected preferentially ($\underline{G}$ = 69.812, $\underline{P}$ < 0.001, df = 2), whereas moose were killed less often than expected. Coyotes preyed almost exclusively on deer (95%, n = 56), and only rarely killed elk (5%, n = 3) (Fig. V-1).

Immature individuals made up a disproportionately high fraction of wolf-killed elk (Table V-1, Fig. V-2) and moose (Fig. V-3). Elk older than 7 years were also well represented in the kills, whereas deer older than 7 years were totally absent (Table V-2, Fig. V-4). Elk 2 to 7 years of age were conspicuously rare (Fig. V-2), but that same bracket constituted the largest category for deer (Figs. V-3, V-4). Thirty-seven percent of coyote kills were deer fawns and yearlings; less than 2 percent were animals older than 7 years (Fig. V-4).

Thirty-six percent (40) of the elk killed by wolves were females, 40% (44) males and 23.9% (27) unknown (Table

V-1). Search effort, however, was not uniform throughout the park. Consequently, the sample may be biased owing to the clumped and regional distribution of winter aggregations of bull elk, and of cows with calves.

Immature females appeared to be more vulnerable to wolf predation than males in the same age category. Conversely, in the >7 to 12-year-old category, males were killed more frequently than females (Table V-1).

Coyotes seldom killed elk. Two subadult cows were killed in February 1985, and 1 in January 1986. All were suffering from severe malnutrition, as revealed by extremely reduced levels of bone marrow fat. Additionally, in June 1984 a single coyote was observed attacking an elk calf. Subsequent examination of the calf, after it was euthanized, revealed several puncture wounds and contusions on the ventral side of the neck. The trachea was also partially crushed.

Females made up 26% (14) of the deer killed by wolves, males 39% (21), and unknown 35% (19) (Table V-2). Twenty-one percent (12) of the deer killed by coyotes were females, 38% (21) males, and 41% (23) unknown (Table V-3).

There was no evidence of coyote predation on moose. Wolves killed moose infrequently (Table V-4), and they showed no apparent preference for either sex.

Wolves (Table V-2) killed a higher percentage of deer in the 2 to 7-year-old age category than did coyotes (Table

V-3). Coyotes killed a greater proportion of fawns. However, interspecific differences in age selection were not significant ($\underline{G}$ = 6.59, $\underline{P}$ > 0.100, df = 3).

Condition of Wolf Prey

The mean percentage of marrow fat measured in femurs was 75.0% in elk (range = 12 - 99%, n = 102), 76.5% in deer (range = 18 - 96%, n = 41), and 74.9% in moose (range = 29 - 99%, n = 26). Most readings were concentrated in the 80-100% category for all 3 ungulates. Marrow fat levels from females were significantly higher than those for males in both elk and deer ($\underline{t}$ = 5.7, $\underline{P}$ < 0.001, df = 78; $\underline{t}$ = 2.5, $\underline{P}$ < 0.02, df = 29).

No random sample of bone marrows was available for comparison with those acquired from predator kills. However, the mean percentage of marrow fat from elk (91%, n = 79) and deer (94%, n = 61) killed near the park periphery by hunters in 1983/84 and 1984/85 was significantly higher ($\underline{t}$ = 3.13, $\underline{P}$ < 0.001, df = 152; $\underline{t}$ = 4.12, $\underline{P}$ < 0.001, df = 90) than mean fat levels obtained from wolf-killed elk and deer ($\underline{n}$ = 74, $\underline{n}$ = 30). It should be noted, however, that wolf kills were collected from November through March. In contrast, samples of deer marrow provided by hunters were from November and samples of elk marrow from December and January. An insufficient number of marrow samples from moose precluded statistical analysis for that species.

In the winter of 1984/85 snow thicknesses exceeded 100 cm in many areas of the park (Environment Canada, Atmospheric Environment Service) and a number of bull elk died of starvation. The percentage of marrow fat in those animals (* = 20.3%, $n = 33$) was significantly lower than the percentage of marrow fat in predator-killed elk (* = 72.3%, $n = 41$) that were found during the same winter ($t = 9.13$, $P < 0.001$, df = 73).

Condition of Coyote Prey

The mean percentage of marrow fat measured from the femurs of deer was 74.3% (range = 28 - 99%, n = 39). There was no difference in fat content between wolf- and coyote-killed deer ($t = 0.475$, $P > 0.900$, df = 78). However, hunter-killed deer ($n = 61$) showed a significantly higher percentage of marrow fat (94%) than those killed by coyotes (t= 2.99, $P < 0.001$, df = 99).

Wolf Chase Behavior

Successful chases of deer by wolves under variable snow thickness and conditions averaged 159 m in length (range = 0 - 1700 m). Successful chases of elk averaged 115 m (range = 5 - 1000 m), and those of moose 883 m (range = 35 - 2400 m) (Table V-5). Differences in chase lengths among the 3 species were significant ($H = 23.89$, $P < 0.001$, df = 118), although deer and elk were captured by wolves after similar distances (Mann-Whitney U Test: 2 tail, $P = 0.151$). There was a significant difference in chase lengths recorded for elk and moose (Mann-Whitney U Test: 2 tail, $P < 0.0001$), and deer and moose (Mann-Whitney $\underline{U}$ Test: 2 tail, $\underline{P} < 0.0002$) (Table V-5).

On average, male deer, and male elk were captured in a shorter distance than their female counterparts, but the differences were not significant ($\underline{t} = 0.07$, $\underline{P} = 0.947$, df = 26; Mann-Whitney $\underline{U}$ Test: 2 tail, $\underline{P} = 0.515$). Deer and elk older than 1 year were taken by wolves in about the same chase length as were fawns and calves (Mann-Whitney $\underline{U}$ Test: 2 tail, $\underline{P} = 0.287$; $\underline{t} = 0.59$, $\underline{P} = 0.565$, df = 66) (Table V-6).

Coyote Chase Behavior

Deer killed by coyotes were subdued in a mean distance of 241 m (range = 0-1700 m) (Table V-7). Males and females were captured at equivalent distances ($\underline{t} = 0.406$, $\underline{P} > 0.900$, df = 17). Fawns required shorter chases than adults and yearlings (Mann-Whitney $\underline{U}$ Test: 2 tail, $\underline{P} = 0.0018$) (Table V-6). Coyote chase distances did not differ significantly from wolf chase distances (Mann-Whitney $\underline{U}$ Test: 2 tail, $\underline{P} = 0.2463$).

Snow Thickness and Predation

To examine the effect of snow thickness on pursuit distances, chases were assigned to 1 of 3 thickness categories. The classifications approximated settled snow thicknesses believed to impede mobility of deer fawns, elk calves, and moose calves (Telfer and Kelsall 1979). ANOVA indicated no significant difference in the length of chases of elk by wolves (Table V-8) relative to snow thickness ($\underline{F}$ = 0.82, $\underline{P}$ = 0.448, df = 67). Conversely, deer pursued by wolves (Table V-8) appeared to be significantly impaired at snow thickness greater than 50 cm ($\underline{H}$ = 9.241, $\underline{P}$ < 0.01, df = 38), as were deer killed by coyotes ($\underline{H}$ = 9.6637, $\underline{P}$ < 0.01, df = 26) (Table V-9). There was no interspecific difference in the length of chases of deer by wolves (Table V-8) and coyotes (Table V-9) for any of the snow thickness categories ($\underline{P}$ = 0.5546, df = 25: $\underline{P}$ = 0.6017, df = 17: $\underline{P}$ = 0.9590, df = 23).

No moose were killed in winter when snow thicknesses were less than 30 cm (Table V-8), whereas 73% of all kills occurred when snow thicknesses exceeded 50 cm. However, chase lengths in thicknesses greater than 50 cm were significantly longer for moose than for deer or elk (Mann-Whitney $\underline{U}$ Test; 2 tailed, $\underline{P}$ = 0.0002; Mann-Whitney $\underline{U}$ test; 2 tailed, $\underline{P}$ = 0.0001). Sample sizes were inadequate to compare statistically the length of chases in shallow snow.

Comparison of all chases of elk with all chases of deer revealed no significant variation in pursuit distances by wolves. However, at snow thicknesses less than 30 cm (Table V-8), differences in chase distances were significant (Mann-Whitney $\underline{U}$ Test; 2 tailed, $\underline{P}$ = 0.0166), which suggests elk (mean distance = 91 m) were subdued with less effort than deer (mean distance = 219 m). In settled snow between 30 cm and 50 cm thick, chase lengths for deer and elk were comparable ($\underline{t} = 0.31$, $\underline{P} = 0.900$, df = 28), as was true for chase distances in snow depths greater than 50 cm (Mann-Whitney $\underline{U}$ Test: 2 tail, $\underline{P} = 0.081$).

In winter 1984-85, severely malnourished elk were ignored by wolves and many eventually died of starvation ($\underline{n} = 33$). In addition, coyotes did not feed on the carcasses of starved elk until late spring. Many starved animals were bulls ($\underline{n} = 27$) located in Birdtail Valley where snow thickness exceeded 100 cm, and where signs of wolf activity were absent. That was unusual because under "normal" winter conditions wolf kills are common in Birdtail Valley. I suspect that malnourished elk were not readily available because deep snow impeded wolf movements. Energetically, it was probably more profitable for wolves to hunt in areas where travel was easier and prey was equally abundant. Coyotes also avoided using the area, probably for similar reasons.

Snow Condition and Chase Length

There was no relationship between chase length and snow condition for either wolves (Table V-11) or coyotes (Table V-12) preying on deer ($\underline{H} = 3.335$, $\underline{P} = 0.1887$, df = 37; $\underline{H} = 0.4289$, $\underline{P} = 0.8070$, df = 28). Wolves, however, killed deer more frequently on light crusts than did coyotes ($\underline{G} = 10.8942$, $\underline{P} < 0.005$, df = 2). Snow conditions did not affect chase distances for wolf predation on elk ($\underline{F} = 0.09$, $\underline{P} = 0.910$, df 56) (Table V-11). It should be noted that snow categories were assigned according to conditions at the kill sites, and that it was possible, over the course of a chase, to encounter variable snow conditions.

Physical Condition of Prey and Chase Length

Assuming that the percentage of marrow fat found in the femur at the time of death is a measure of physical condition (see Mech 1985), then chase lengths should be shortest for animals with reduced fat levels. Accordingly, chase lengths for wolf-killed elk (Table V-10) differed significantly among 5 fat categories ($\underline{H} = 48.9402$, $\underline{P} < 0.0001$, df = 87). In general, the higher the fat content, the longer the chase. Small sample size did not allow for similar analysis of wolf-killed deer and moose (Table V-10), or coyote-killed deer.

Relationship of Habitat to Kills

Overall, there was a significant difference in the habitats where wolf- and coyote-killed deer were found ($\underline{G} = 15.625$, $\underline{P} < 0.025$, df = 6). Coyotes (Table V-13) killed deer more often on waterbodies and in deciduous areas than did wolves (Table V-14). For kills where habitat was recorded, 50% (36) of wolf-killed elk and 43% (16) of coyote-killed deer were found on or adjacent to frozen waterbodies. In contrast, only 14% (6) of deer killed by wolves and 8% (2) of moose killed by wolves were located in a similar habitat.

In the winters of 1982/83 and 1983/84 there was heavy predation by the Whitewater and Clear Lake wolf packs on elk cows, yearlings and calves along the shorelines of frozen lakes. In 1982/83, 4 cows and 3 calves killed by wolves were located on Whitewater Lake. No kills were found on that lake the following winter. On Clear Lake 14 kills were examined in 1983/84 and none the previous year.

Thirteen dead bull elk, presumed to have been killed by wolves, were found in lakes or small waterbodies during June, July and August. Nine were dragged onto the shore and consumed, 3 were fed upon in the water and 1 was abandoned. There were 3 observations of wolves chasing elk into water, one of which resulted in a kill.

Consumption Rates by Wolves

The percentage of carcass consumed was estimated for 96 wolf-killed elk, 51 deer, and 26 moose (Table V-15). Ninety-one percent (87) of the elk kills were abandoned before all edible portions were consumed. Seventy-two percent (63) of that number included animals in classes 1, 2, and 3. In contrast, only 20% of wolf-killed deer were left partially uneaten prior to desertion. Eighty-six percent (22) of wolf-killed moose remained partially unused. A substantial portion of them were in class 4.

Large wolf packs consumed a higher proportion of elk carcasses than small wolf packs before abandoning kills (Table V-16). There were only minor differences in consumption rates between large and small wolf packs for deer (Table V-17). Coyotes fed at all wolf kills and were therefore partially responsible for the rate at which carcasses were consumed.

Consumption Rates by Coyotes

Carcass consumption was estimated for 49 deer killed by coyotes (Table V-18). Seventy-eight percent (38) of the kills were fully consumed within 48 hours.

I was not usually able to confirm whether coyotes responsible for a kill were the same individuals that fed on the carcass. However, observations of what appeared to be peripheral coyotes using kills suggested that scavenging was common. The number of coyotes estimated to have fed at a kill ranged from 1 to 7. The greatest number directly observed feeding together was 5, on a wolf-killed elk. The number of coyotes involved in a kill appeared to have only minimal affect on the rate of consumption.

Seasonal Trends

Because of a reduced field effort in the summer and the difficulties associated with summer tracking, remains of animals were more frequently located during periods of snow cover. Therefore, the effect of season on selection of prey could not be determined. However, several trends were evident. First, coyote predation on deer increased during late February and most of the month of March. The declining condition of prey animals may have been a factor. Second, between May and August adult bull elk (n = 15) were killed more frequently than adult cows (n = 2). Finally, there was evidence that yearling moose were susceptible to predation during late spring and early summer. Fifty-three percent (n = 15) of the wolf-killed moose were located between 1 May and 31 July, and 93% (n = 14) of the kills were yearlings (previous year's calves).

Miscellaneous Observations

All wolf-killed ungulates were visited by coyotes. Coyote tracks led directly to wolf kills on 36 different occasions. Evidence of feeding, such as newly disarticulated bones, parts and hide, strongly suggested scavenging. Moreover, coyotes were directly observed feeding on 39 wolf kills. Remote surveillance photography recorded coyotes scavenging on all carcasses monitored (n = 9).

On 2 occasions, I observed 3 coyotes stationed within 100 m of a carcass on which wolves were feeding. The wolves appeared to ignore the coyotes, but were obviously aware of their presence. As soon as the wolves left, the coyotes commenced feeding. Although I never observed feeding wolves behave aggressively toward waiting coyotes, 11 of the 23 wolf-killed coyotes located during the study were found within 200 m of ungulates that had been preyed upon by wolves.

Extensive tracking was conducted within the Clear Lake wolf pack territory in winter 1984-85. A small pack of

3 wolves, as well as 3 solitary coyotes and a single pair, were resident in the area. Two of the 3 solitary individuals were radio-collared. The coyotes occupied widely overlapping home ranges nested mostly within the territory of the Clear Lake wolf pack (Chapter 2).

I observed numerous agonistic encounters among the five resident coyotes (_n_ = 48). All of the interactions were associated with defense of carrion (wolf kills). The three individual coyotes and the male-female pair frequently attempted to secure carcasses in possession of the others. A feeding hierarchy was evident with the pair always successful in the defense or displacement of the solitary individuals (Table V-19).

Coyotes were also observed scavenging at or near wolf dens (_n_ = 3) and rendezvous sites (_n_ = 6), usually following abandonment by wolves (_n_ = 6). On one occasion, coyotes were seen scavenging on elk and beaver carrion that had been carried to the den by wolves, while a single adult male wolf and 4 pups rested less than 100 m away.

Chapter 5

DISCUSSION

Ecological separation within carnivore guilds is effected through differences in diet, habitat selection, and escape behavior (Stanley et al. 1983). [A guild is defined as a group of species that exploit the same class of resources in a similar way (Root 1967)]. Although escape behavior is usually of minor importance to predators, aggressive interactions do occur, and survival can depend on successful avoidance of potential attackers (Van Valkenburgh 1982). Habitat differences are primarily temporal-spatial and often reflect methods of hunting (Kleiman and Eisenberg 1973). In the Kalahari, for example, leopards (*Panthera pardus*) and cheetahs (*Acinonyx jubatus*) both feed predominantly on springbok (*Antidorcas marsupialis*), but the diet of the leopard is more diverse (Mills 1984). For the most part, species similar in habitat preference and escape behavior, such as lynx (*Lynx lynx*) and coyote, or lion (*Felis leo*) and cheetah, differ in diet (Stanley et al. 1983). Where there are exceptions to this pattern, as with the 2 species of African jackals (*Canis aureus*, *C. mesomelas*) (Moehlman pers. comm.), or Kalahari lions and spotted hyaenas (*Crocuta crocuta*) (Mills 1984), competition is often reduced through slight differences in niche choice.

In RMNP wolves and coyotes actively forage in the same areas (Carbyn 1982, Chapter 2). There is no indication that coyotes adjust their movements to avoid the activities of wolves (Chapter 2). On occasion wolves kill coyotes, but do not appear to search for them actively (Chapter 2). Food habit studies, conducted concurrently with this inquiry, confirmed extensive dietary overlap between wolves and coyotes, particularly in use of ungulates (Meleshko 1986). For both species, elk was the most important food item, both in frequency of occurrence and biomass consumed. Seasonal variations in the percentage use of moose and deer were also closely associated. Although coyotes consumed more snowshoe hares (Lepus americanus) and cricetid rodents, those species did not represent a significant proportion of either canid's diet, and were therefore considered improbable sources for competition (Meleshko 1986).

The ratio of elk, deer and moose killed by wolves and examined in the field (Carbyn 1982, this study) corresponds closely with the proportional distribution of prey identified through scat analysis (Carbyn 1980, Meleshko 1986). As there is no evidence that wolves in RMNP scavenge, it is probable that material contained in wolf scat results primarily from predation. In contrast, coyote predation on ungulates is limited to deer and an occasional elk. Moreover, indirect evidence and observations of coyotes feeding on known wolf kills suggests that scavenging is important for coyotes.

Several observations help to clarify the foraging relationships of wolves and coyotes. First, wolves seldom use all of an elk or moose carcass; therefore something usually remains for scavengers, including coyotes. Second, large wolf packs consume kills faster and more thoroughly than small wolf packs; thus they leave considerably less for scavenging coyotes. Third, all wolf-killed ungulates are visited, and probably scavenged, by coyotes. Finally, coyotes appear to intentionally follow wolves to kills (Chapters 2 and 3).

Although coyotes may scavenge black bear kills, winter kills, and hunter kills, most ungulate carrion ingested by coyotes probably comes from wolf-killed elk and moose. All other sources are periodic or irregular. For example, black bear predation on ungulates is uncommon, and appears to be concentrated on newborn fawns and calves (pers. obs.). Furthermore, such small prey tends to be totally consumed by bears, which would leave little or no carrion available for scavenging. Large winter kills are uncommon and thus unreliable. Human hunters remove most edible portions of their kills, which limits the amount available to scavengers. Finally, wolf-killed deer provide only a minimal quantity of carrion as consumption by wolves is typically complete, or nearly so (Carbyn 1982, this study).

Two aspects of foraging behavior, therefore, help explain the successful coexistence of wolves and coyotes in RMNP; 1) with the possible exception of deer and beaver, the 2 canids do not compete for the prey which constitutes the major portion of their diet, and 2) the benefits that accrue to coyotes from feeding on carrion made available by wolves far outweigh the risks associated with being in close proximity to wolves. Although wolves and coyotes share the same food resource and depend upon large herbivores to a similar extent, interspecific competition is reduced by resource partitioning.

There is circumstantial evidence that coyotes from areas other than RMNP also scavenge wolf kills. For example, in Jasper National Park, elk and mule deer (*Odocoileus hemionus*) are an important year-round food for both wolves (Cowan 1947, Carbyn 1975) and coyotes (Bowen 1981). Presumably, coyotes scavenge wolf kills rather than kill elk.

Prior to their extirpation from Yellowstone National Park, wolves relied heavily on elk (Weaver 1979a), and coyotes scavenged wolf kills when the species were sympatric (Arnold 1937, Weaver pers. comm.). Elk carrion, provided by natural winter mortality (e.g. malnutrition) and grizzly bear (*Ursus arctos*) predation (Murie 1940, Houston 1978) remains an important winter food for coyotes (Weaver pers. comm.). Elk carrion is also a significant winter food for coyotes in Jackson Hole, Wyoming (Murie 1935, Weaver 1979b, Bekoff and Wells 1980).

Riding Mountain differs from many areas where wolves and coyotes are allopatric in that it is highly productive and supports moderate numbers of several large ungulates as well as a dense population of beaver. Sympatry could therefore be related to: 1) the diversity of prey in a particular area, 2) the abundance of prey, 3) the preference of wolves for particular prey species, 4) the rate of carcass consumption by wolves following a kill, 5) the completeness of consumption by wolves, and 6) the way food is acquired by coyotes.

In Minnesota, wolves and coyotes are parapatric (Berg and Chesness 1978). The predominant prey of wolves are white-tailed deer, although substantial numbers of moose are present within wolf occupied areas (Mech pers. comm.). Deer killed by wolves are usually completely consumed, which leaves few remains for scavengers (Mech pers. comm.). Coyotes, therefore, are deprived of a major potential food source, and interspecific competition with wolves is probably severe. In areas where wolves are absent, coyotes have the opportunity to prey on deer without competition, and are able to scavenge deer that die from other causes. Thus, for coyotes in Minnesota, the risks associated with coexistence likely outweigh the potential benefits.

In contrast to Minnesota, coyotes in southeastern Ontario are sympatric with wolves. Food habits of the 2 canids are similar (Schmitz and Lavigne 1987). Although deer is the only available ungulate (Richens and Hugie 1974, Hilton 1978, Schmitz and Kolenosky 1985, Schmitz and Lavigne

1987) coyotes have not been excluded by wolves. In theory, ecologically similar species should show a more pronounced size difference in habitats where they are sympatric than in non-overlapping parts of their ranges (Brown and Wilson 1956). Yet wolves and coyotes in southeastern Ontario appear to be converging on an intermediate size (Schmitz and Lavigne 1987).

It is difficult to explain why this is occurring, as important ecological details are missing from the literature. For example, it is unclear what degree of areal or ecological overlap actually exists, or what the density of each species is in zones of overlap. The association is further confounded because the "coyotes" in the area are possible wolf X coyote hybrids, descended from coyotes that invaded southeastern Ontario following the near extirpation of wolves (Schmitz and Kolenosky 1985). The wolves that inhabit the area are among the smallest of North American subspecies (Nowak 1983, Kolenosky 1983).

There is no information on coyote foraging behavior. Hence, it is not known whether coyotes prey on deer, or scavenge on deer that die from other causes. However, if coyotes are largely scavengers of sizable food items, then morphological convergence cannot be explained as a functional response to prey size, as suggested by Schmitz and Lavigne (1987). I hypothesize that the absence of character displacement is indicative of weak interspecific competition, which results either from spatial separation or some form of resource partitioning.

The extirpation of coyotes from Isle Royale has been attributed to colonization of the island by wolves (Mech 1966, Krefting 1969, Peterson 1977, Allen 1979). It is noteworthy, however, that the appearance of wolves coincided with a period of low beaver and moose populations and a trough in the snowshoe hare cycle (Krefting 1969). It is probable that prior to colonization, moose carrion, along with snowshoe hare and beaver, composed a substantial portion of the coyote's diet. Because wolves appeared at a time when food resources were limited, competition between wolves and coyotes may have been intense, which may have led to extirpation of coyotes. Because Isle Royale is an island, and access from the mainland is limited, coyotes never successfully recolonized when prey populations recovered.

Carbyn (1980) proposed that agricultural areas surrounding RMNP provide a refugium where coyotes are immune from predation by wolves. He also suggested that losses due to wolf predation on coyotes in the park are replaced by dispersers immigrating from this peripheral reservoir. Therefore, even if coyote mortality is high, immigrants can quickly repopulate the area. The hypothesis implies that although direct aggression is severe and constant, sympatry occurs because wolves are simply overwhelmed by a persistent and dependable immigration of coyotes. However, Carbyn's hypothesis does not explain why coyotes in other areas remain parapatric with wolves (e.g. Minnesota), and do not disperse into adjacent wolf-occupied areas.

I propose an alternative hypothesis, which assumes: (a) coyote mortality outside the park is higher than mortality inside the park, and (b) coyotes in the park benefit, through scavenging, from the presence of wolves. I suggest, therefore, that the proximate factor influencing wolf and coyote distribution is food supply. Direct aggression by wolves is probably a secondary influence that becomes increasingly important when scavengable remains from wolf kills are reduced or unavailable.

Currently, mortality on adjacent agricultural lands resulting from human exploitation greatly exceeds mortality from wolf predation inside the park. Trappers, hunters, and predator control activities remove an estimated 200-300 coyotes annually from a zone 5 km wide adjacent to the park boundary, an area of 1606 km^2 (Coulson pers. comm.). Comparable mortality within the park (2974 km^2) would require 370-556 coyotes to be killed annually, or the equivalent of 31-36 coyotes for each wolf pack per year. It is improbable that such a high rate of wolf predation occurs. Consequently, the risks associated with living in agricultural areas are higher than living in the park.

I would predict that under current conditions coyote territories in the agricultural areas surrounding the park are unstable relative to the park territories, owing to a high rate of human induced mortality. As a result, there is probably a seasonal influx of immature dispersers from adjacent areas. Consequently, in comparison with coyote demographics in the park, the agricultural population is likely composed of younger animals.

It is probable that vacuums created in agricultural areas as the result of coyote removal, encourage dispersers to move from inside to outside the park, rather than from outside to inside as suggested by Carbyn. Accordingly, I suggest that the park coyote population is composed primarily of residents and their offspring, and only secondarily of newly established "immigrants" from surrounding agricultural habitats.

The results of this study concur with Carbyn's (1980, 1983) conclusion that wolves prey preferentially on elk. However, since 1980 the importance of deer as a prey species appears to have increased substantially. When considered in terms of relative availability, wolves now show a preference for both deer and elk over moose. Moreover, comparison of the number of elk, deer, and moose that Carbyn (1980) reported killed by wolves with observations from this study, suggests that a significant change in prey selection has occurred ($\underline{G} = 10.723$, $\underline{P} < 0.005$, df = 2), and that it is attributable to a shift from elk to deer ($\underline{G} = 9.163$, $\underline{P} <$

0.01, df = 1). Between 1975 and 1979 deer constituted only 15% (16) of the wolf-kills examined in the field. In contrast, 28% (54) of all kills examined between 1982 and 1986 were deer. A disproportionately high number of those animals were killed in the last 2 years of the study.

Although wolves prey preferentially on both deer and elk, the latter is still the most important prey species, especially when assessed as a percentage of the total biomass consumed by wolves (Meleshko 1986). The simplest explanation for this preference is that elk are easier to procure and provide a larger caloric reward than either moose or deer. That is in accord with optimal foraging theory, which suggests that a predator should select the largest available prey that can be captured with the minimum expenditure of energy (Stephens & Krebs 1986). In RMNP elk are more abundant than either moose or deer. As well, elk approach moose in weight, are substantially larger than deer and, unlike deer, are available throughout the year. Moreover, on average, elk and deer are subdued in about one-sixth the chase distance required for moose. Circumstantial evidence from kill sites also indicates that moose are more difficult to kill once apprehended.

The ability of wolves to kill elk "easily" may be a behavioral specialization that developed for historical reasons. When wolves recolonized RMNP in the early 1940s, elk were the only large herbivores available in substantial numbers (Carbyn 1980). Consequently, wolves in RMNP may have become proficient at killing elk by necessity.

Wolf predation on elk is concentrated on calves, yearlings and animals older than 7 years. This contrasts sharply with the animals killed by hunters, which are predominantly in the 2- to 7-year age classes.

Predation on elk by coyotes was recorded in 2 of 4 years but the number of animals killed was small ($\underline{n}$ = 3). All of the animals were young and I considered them to be in very poor condition judging from low fat levels. Coyote predation on elk occurs infrequently and does not contribute significantly to the coyotes' diet.

Wolf predation on moose was relatively minor and may have been partially buffered by deer and elk. However, wolves killed many yearling moose in late spring and early summer. I suspect that yearlings, recently abandoned by their mothers, are susceptible to attack by wolves because they are inexperienced in defending themselves. Conceivably, predation patterns could shift if moose demographics change, or if density-dependent factors, such as parasites and nutrition, begin to affect the health of the moose population. There was no evidence of coyotes preying on moose.

In contrast to previous reports (Carbyn 1980, Carbyn 1982, Carbyn 1983), deer killed by both wolves and coyotes were found during this study. However, I suspect that coyote predation on deer is not a recent phenomenon. Earlier studies stressed aerial radio-telemetry, rather than ground tracking, and may have overlooked coyote-kills.

Bone marrow analyses indicated equivalent fat levels for deer killed by both wolves and coyotes. Contrary to what would be expected, chase distances were also similar, which indicates that wolves and coyotes are equally effective at capturing deer. One notable contrast in predatory behavior was the apparent preference of coyotes for fawns, and wolves for 2 to 7-year-old animals. This suggests that although deer are commonly exploited by both canids, interspecific competition is partially diminished by concentration on different age classes. It may also explain the similarity in chase distances - the size and strength of the prey would be matched with the size and strength of the predator.

Chapter 5

CONCLUSIONS

Although wolves and coyotes in RMNP are dependent on the same food resources, coexistence most likely occurs because competition is reduced by resource partitioning. Wolves kill nearly all of what they consume, including elk, moose, deer and smaller mammals. Elk and deer are the preferred prey species, but elk contributes substantially more biomass to the diet than deer, as verified by field observation and scat analysis (Carbyn 1983, Meleshko 1986, this study).

Coyotes, in contrast, acquire most of their food by scavenging abandoned wolf-killed elk. Because predation on ungulates involves considerable risk of injury and is likely energetically expensive owing to a low rate of success, there is no apparent advantage in killing prey if good quality food can be scavenged. Coyotes supplement their diet by preying on deer and smaller mammals. Potential interspecific competition over deer is diminished by age-class partitioning, choice of habitats for hunting, and the relative unimportance of deer as a dietary item.

Relationships could be altered if elk populations decline to levels that force wolves to become dependent on deer as a primary prey or increase the thoroughness with which they consume elk carcasses. In such a situation coyotes would be deprived of an essential food source and would be compelled to compete with wolves for prey such as deer. The outcome would be a substantial decline in coyote numbers or, possibly, complete exclusion of coyotes from the Riding Mountains.

Ignoring human-caused extirpation, the current North American distribution of wolves and coyotes likely reflects the distribution, abundance, and diversity of prey species available, modified by preferential selection of prey by wolves. Sympatric populations are most likely to occur in areas where moose, bison (Bison bison) and elk are numerous and preyed on by wolves. If deer are the preferred prey, the probability of successful coexistence is low even if alternative species are available because: a) the likelihood of ecological overlap is almost certain when both species are dependent on a single prey species, and b) coyotes lose the opportunity to scavenge on wolf kills because wolves preying on deer leave few remains.

Table V-1. Summary of wolf-killed elk by sex and age categories, 1982-86. Twenty-three additional elk were examined but were not aged. Numbers in parentheses are percent of total kill.

	PREY SEX			
AGE	Female	Male	Unknown	All
<1	15 (13.5)	4 (3.6)	19 (17.1)	38 (34.2)
1 - 2	4 (3.6)	7 (6.3)	0 (0.0)	11 (9.9)
>2 - 7	2 (1.8)	4 (3.6)	1 (0.9)	7 (6.3)
>7 - 12	3 (2.7)	17 (15.3)	1 (0.9)	21 (18.9)
>12	4 (3.6)	7 (6.3)	0 (0.0)	11 (9.9)
Unknown	2 (1.8)	5 (4.5)	6 (5.4)	23 (20.7)
Total	40 (36.0)	44 (40.3)	27 (23.9)	111 (100.0)

Table V-2. Summary of wolf-killed white-tailed deer by sex and age categories, 1982-86. Thirteen additional deer were examined but were not aged. Wolves selected a high proportion of prime animals. Numbers in parentheses are percent of total kill.

	PREY SEX			
AGE	Female	Male	Unknown	All
<1	0 (0.0)	1 (1.8)	10 (18.5)	11 (20.4)
1 - 2	3 (5.5)	3 (5.5)	0 (0.0)	6 (11.1)
>2 - 7	9 (16.6)	12 (22.2)	2 (3.7)	23 (42.6)
>7 - 12	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
>12	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Unknown	2 (3.7)	5 (9.2)	7 (13.0)	14 (25.9)
Total	14 (25.9)	21 (38.9)	19 (35.2)	54 (100.0)

Table V-3. Summary of coyote-killed white-tailed deer by sex and age categories, 1982-86. Twenty-one additional deer were examined but not aged. In comparison with wolves, coyotes killed a higher percentage of fawns. Numbers in parentheses are percent of total kill.

	PREY SEX			
AGE	Female	Male	Unknown	All
0 - 1	4 (7.1)	3 (5.4)	11 (19.6)	18 (32.1)
1 - 2	0 (0.0)	2 (36)	1 (1.8)	3 (5.4)
2 - 7	3 (5.4)	10 (17.9)	0 (0.0)	13 (23.2)
7 - 12	0 (0.0)	1 (1.8)	0 (0.0)	1 (1.8)
Unknown	5 (8.9)	5 (8.9)	11 (19.6)	21 (37.5)
Total	12 (21.4)	21 (37.5)	23 (41.1)	56 (100.0)

Table V-4. Summary of wolf-killed moose by sex and age categories. Seven additional moose were examined but not aged. Numbers in parentheses are percentages of total kill. Yearling moose were susceptible to predation in early spring.

	PREY SEX			
AGE	Female	Male	Unknown	All
0 - 1	4 (13.7)	0 (0.0)	1 (3.4)	5 (17.2)
1 - 2	3 (10.3)	7 (24.1)	4 (13.8)	14 (48.3)
2 - 7	2 (6.9)	1 (3.4)	0 (0.0)	3 (10.3)
7 - 12	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
> 12	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Unknown	3 (10.3)	4 (13.8)	0 (0.0)	7 (24.1)
Total	12 (41.4)	12 (41.4)	5 (17.2)	29 (100.0)

Table V-5. Mean pursuit distances recorded for successful wolf chases in snow. Distances were determined by pedometer or snow machine odometer.

	CHASE DISTANCE (metres)								
	Deer			Elk			Moose		
SEX	x̄ ±	SE	(n)	x̄ ±	SE	(n)	x̄ ±	SE	(n)
F	180.7	78.3	(12)	132.1	33.2	(29)	1047.0	449.3	(4)
M	173.5	72.0	(16)	92.5	19.1	(31)	801.0	422.0	(5)
Unk	118.2	28.9	(12)	137.9	69.1	(10)	760.0	540.1	(2)
Mean	159.1	37.5	(40)	115.4	18.6	(70)	883.0	266.2	(11)

Table V-6. Comparison of mean chase distances for adult deer and elk, with deer and elk less than 1 year old.

	WOLF KILLS						COYOTE KILLS		
	Deer			Elk			Deer		
AGE	$\bar{x}$	± SE	(n)	$\bar{x}$	± SE	(n)	$\bar{x}$	± SE	(n)
Adult	166.2	49.1	(30)	124.1	25.2	(48)	350.4	94.9	(12)
Calf/Fawn	149.0	38.5	(8)	99.1	25.3	(20)	97.0	24.7	(15)

Table V-7. Mean pursuit distance for successful coyote chases of white-tailed deer in snow. Distances were determined by pedometer or snow machine odometer.

	CHASE DISTANCE (metres)		
SEX	x̄	± SE	(n)
F	140.6	42.1	(8)
M	162.7	42.7	(11)
Unk	380.4	159.3	(12)
Mean Length	241.3	65.8	(31)

Table V-8. Summary of mean wolf chase distances recorded for different prey species in varying snow thicknesses. Thickness categories approximate settled snow levels believed to impede mobility of fawns and calves (Telfer and Kelsall 1979).

SNOW THICKNESS (cm)	CHASE DISTANCE (metres)								
	Deer			Elk			Moose		
	$\bar{x}$	± SE	(n)	$\bar{x}$	± SE	(n)	$\bar{x}$	± SE	(n)
<30	219.2	75.2	(12)	90.5	27.4	(24)			(0)
>30 - 50	200.0	95.9	(12)	165.8	62.4	(18)	1090.0	168.9	(3)
>50	40.5	12.1	(15)	116.8	33.1	(27)	805.6	312.2	(8)
Mean Length	144.6	39.1	(39)	120.4	22.7	(69)	883.2	266.2	(11)

Table V-9. Mean coyote chase distances of white-tailed deer in varying snow thicknesses.

SNOW THICKNESS (cm)	CHASE DISTANCE (metres) $\bar{x}$	± SE	(n)
<30	284.0	79.7	(15)
>30 - 50	315.7	236.2	(7)
>50	42.0	12.7	(5)
Mean Length	247.4	75.0	(27)

Table V-10. Mean wolf chase distances recorded for varying percentages of femur marrow fat. Includes data collected by RMNP warden service.

	CHASE DISTANCE (metres)								
	Deer			Elk			Moose		
PERCENT FEMUR FAT	$\bar{x}$	± SE	(n)	$\bar{x}$	± SE	(n)	$\bar{x}$	± SE	(n)
0 - 20	0.0		(4)	11.8	6.5	(30)	2.9		(3)
>20 - 40	6.7		(3)	40.0	14.0	(3)	1285.0		(2)
>40 - 60	120.0		(2)	106.4	33.3	(8)	204.9		(4)
>60 - 80	258.0	36.4	(13)	88.9	27.1	(17)	951.7	231.6	(9)
>80 - 100	160.6	19.1	(22)	138.3	40.7	(30)	700.0	156.9	(11)

Table V-11. Mean wolf chase distances recorded for different snow densities. Snow conditions were evaluated subjectively for each kill.

SNOW CONDITION	Deer $\bar{x}$	± SE	(n)	Elk $\bar{x}$	± SE	(n)	Moose $\bar{x}$	± SE	(n)
Fluffy	159.7	38.9	(14)	117.9	38.8	(26)	205.0		(2)
Light Crust	152.5	64.6	(20)	94.0	45.1	(21)	1580.0	315.3	(5)
Heavy Crust	38.5	15.9	(4)	111.5	34.4	(10)	170.0		(1)

CHASE DISTANCE (metres)

Table V-12. Summary of mean coyote chase distances of white-tailed deer recorded for different snow densities. Snow conditions were subjectively evaluated for each kill.

SNOW CONDITION	CHASE DISTANCE $\bar{x}$	± SE	(n)
Fluffy	177.8	40.5	(16)
Light Crust	107.0	35.6	(5)
Heavy Crust	137.5	46.8	(8)

Table V-13. Percentage of coyote kills found in different habitat types.

HABITAT TYPE	White-tailed Deer (n=37)
Waterbody	43
Open grassland	11
Shrub	3
Open-forest	14
Mixedwood	14
Coniferous	5
Deciduous	11

Table V-14. Percentage of wolf kills found in different habitat types. Sample sizes are in parentheses.

HABITAT TYPE	SPECIES		
	Deer (n = 42)	Elk (n = 72)	Moose (n = 24)
Waterbody	14	50	8
Open grassland	17	3	8
Shrub	12	1	0
Open-forest	21	31	38
Mixedwood	22	3	8
Coniferous	14	10	25
Deciduous	0	0	0

Table V-15. Degree of carcass use recorded for wolves feeding at new kills. Classes are modified from Carbyn (1983), and correspond to recognizable stages of carcass use. Carcasses were classified immediately following abandonment of site. Values represent the percentage of individual ungulate kill samples assigned to each class. Typically, white-tailed deer were completely consumed, leaving little for scavenging coyotes.

		PREY SPECIES		
USE CLASS	% USE	Deer (n = 51)	Elk (n = 96)	Moose (n = 26)
1	0 - 2%	0.0	1.0	7.6
2	3 - 30%	7.8	45.8	11.5
3	31 - 70%	5.9	18.8	3.8
4	71 - 99%	5.9	25.0	61.5
5	100%	80.3	9.4	15.4

Table V-16. The relationship of pack size to the degree of carcass consumption recorded for wolves feeding at new elk kills. Classes are modified from Carbyn (1983), and correspond to recognizable stages of carcass use. Carcasses were classified following abandonment of site by wolves. Values represent percentage of kill sample for each class. In general, large wolf packs consumed more than small wolf packs, leaving less for scavengers such as coyotes.

		USE CLASS			
Number Wolves	Number Kills	1 (0-2%)	2 (3-30%)	3 (31-70%)	4 (71-100%)
1-3	25	4.0	80.0	8.0	8.0
4-6	10	70.0	20.0	20.0	10.0
7-9	42	0.0	40.5	31.8	26.2
10-12	19	0.0	0.0	0.0	100.0

Table V-17. The relationship of pack size to the degree of carcass consumption recorded for wolves feeding at new deer kills. Classes are modified from Carbyn (1983), and correspond to recognizable stages of carcass use. Carcasses were classified following abandonment of site by wolves. Values represent percentage of kill sample for each class.

		USE CLASS			
Number Wolves	Number Kills	1 (0-2%)	2 (3-30%)	3 (31-70%)	4 (71-100%)
1-3	9	0.0	11.1	11.1	66.6
4-6	14	0.0	14.3	0.0	85.7
7-9	7	0.0	0.0	0.0	100.0
10-12	10	0.0	0.0	0.0	100.0

Table V-18. Use of white-tailed deer carcasses prior to abandonment. All animals were killed by coyotes. Classification categories are modified from Carbyn (1983), and correspond to recognizable stages of consumption. Values represent percentage of total kill sample assigned to each class.

Use Class	% Use	Deer (n = 49)
1	0 - 2%	0.0
2	3 - 30%	18.4
3	31 - 70%	2.0
4	71 - 99%	2.0
5	100%	77.6

Table V-19. Coyote interactions observed near wolf-killed elk carcasses on Clear L. in winter 1984-85. Five resident coyotes regularly fed on wolf kills. All 5 coyotes attempted to defend carcasses. A defensive behavior was defined as an attempt to maintain possession of a carcass when challenged by 1 or more coyotes. A displacement action was defined as an attempt to acquire possession of a carcass from 1 or more coyotes.

	DEFENSES		DISPLACEMENTS		TOTAL	
Coyote(s)	Wins	Losses	Wins	Losses	Wins	Losses
Juvenile male*	0	4	0	1	0	5
Adult male**	0	7	0	5	0	12
Adult male**	3	5	6	3	9	8
Pair* (male & female)	6	0	10	0	14	0

* sex determined by observation and ground tracking
** radio-collared

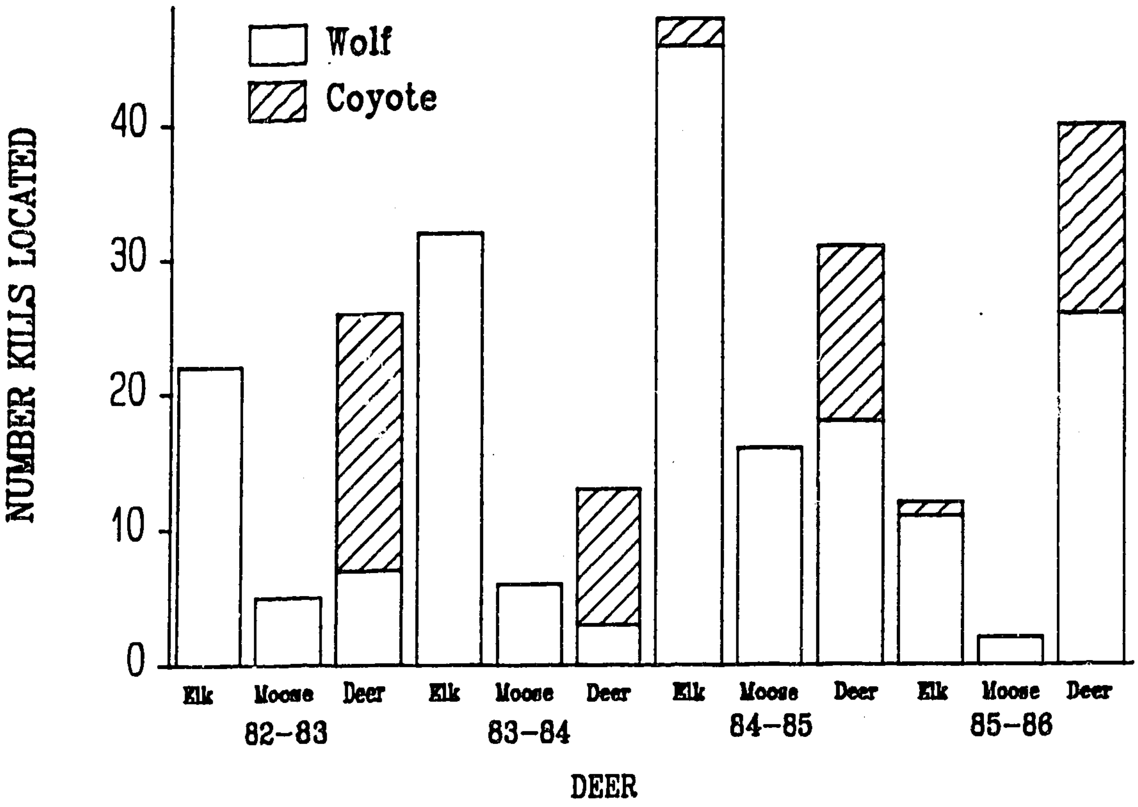

Figure V-1. Yearly comparison of wolf and coyote kills, 1982-86. With the exception of winter 1985-86 wolves preyed primarily on elk and secondarily on white-tailed deer. Coyotes preyed on white-tailed deer and on rare occasions elk.

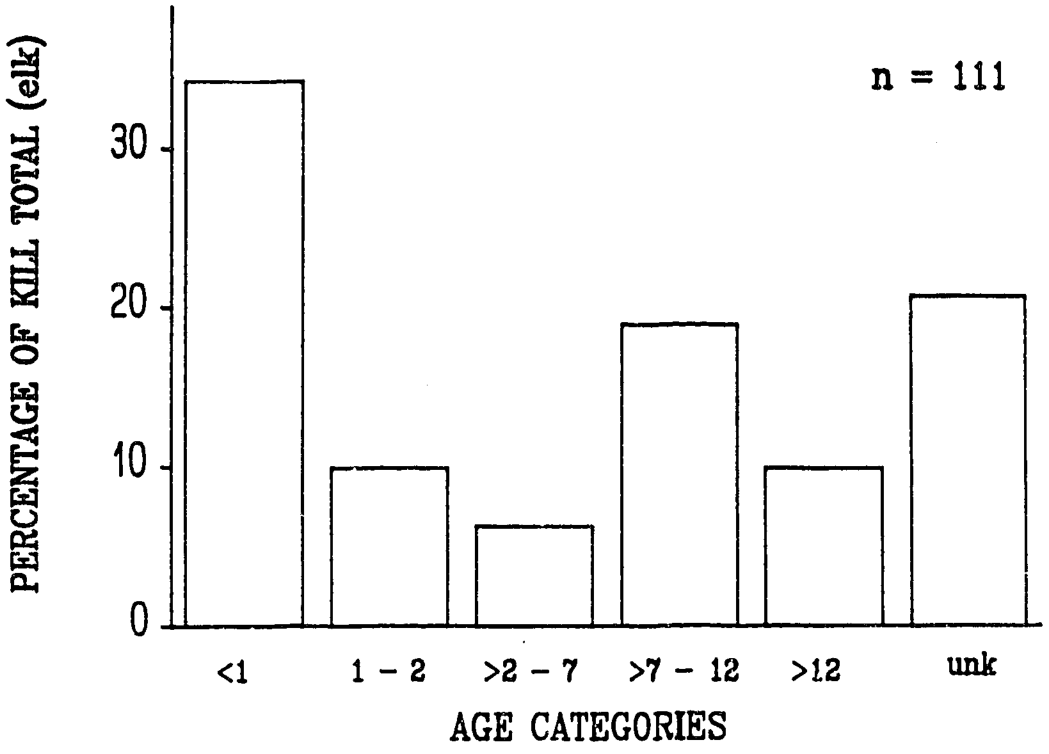

Figure V-2. Age distribution of wolf-killed elk, 1982-86. Immature animals and animals older than 7 years constituted the largest categories.

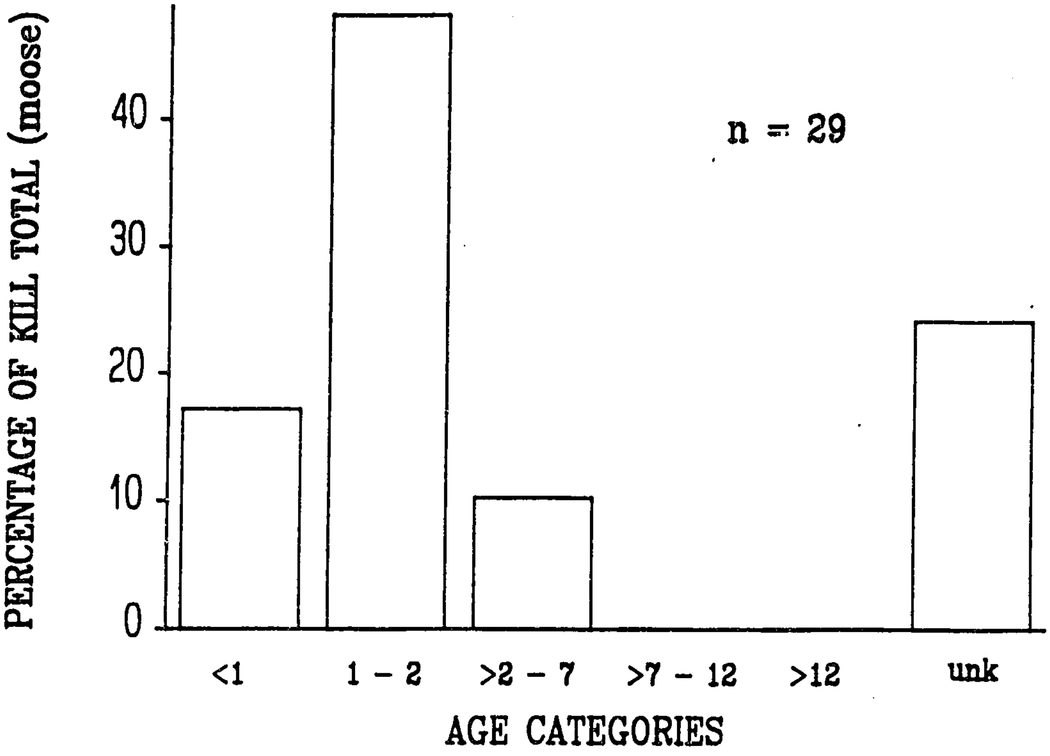

Figure V-3. Age distribution of wolf-killed moose, 1982-86. Young moose comprised the most frequent age grouping. Notably, the majority of immature moose were killed in May and June following abandonment by their mothers.

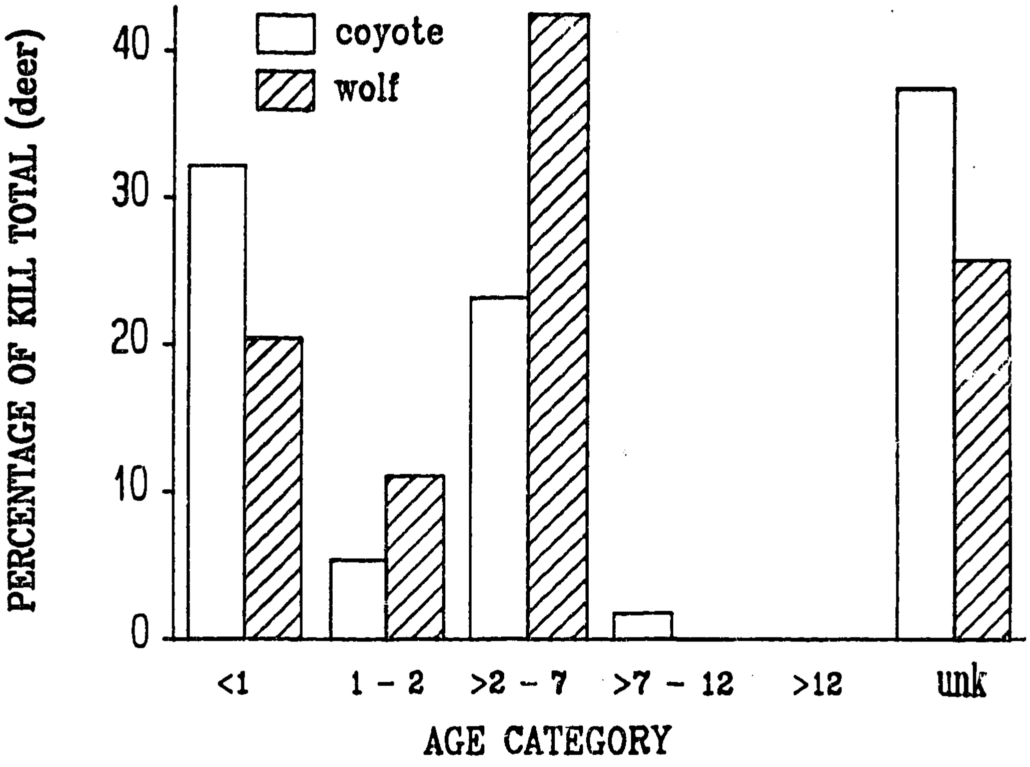

Figure V-4. Age distribution of predator-killed white-tailed deer. Coyotes killed primarily fawns. Wolves killed deer in the 2-7 cohort. Differences in selection, however, were not significant.

Chapter 5

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CHAPTER 6

GENERAL CONCLUSIONS

Complete exclusion of coyotes by wolves occurs in some areas of North America. However, the extent of ecological overlap is probably variable, as the two species are also sympatric throughout a diverse range of habitats. Elucidating the mechanisms that permit co-existence of substantial numbers of wolves and coyotes in Riding Mountain National Park helps in understanding the role of the two canids in community ecology, as well as the reasons for the current geographic distribution of the coyote.

The areal overlap of wolves and coyotes in RMNP is considerable, with no evidence that spatial segregation occurs at any level. Temporal overlap also appears to be minimal, although conclusive documentation is lacking. Despite aggression by wolves toward coyotes, coyotes are not deterred from using areas inhabited by wolves. Moreover, coyotes do little to conceal their presence from wolves, as evidenced by their spontaneous howling in active wolf areas, responsive howling to wolf vocalizations, overmarking of wolf scent-marks, and apparent lack of concern about being seen by wolves.

With the exception of the spatial distribution of marks within wolf territories, the marking behavior of wolves and coyotes is similar to that observed in areas where the two species do not coexist. The difference does not appear to be a consequence of sympatry. The marking strategies of the two species are similar. The response of both wolves and coyotes to the urine or scratch marks of the other species resembles agonistic behavior directed toward alien conspecifics by animals occupying home ranges or territories (Peters and Mech 1974, Bowen and Cowan 1980, Barrette and Messier 1980). However, the response is more pronounced in coyotes than wolves.

Rather than avoiding areas previously marked by wolves, coyotes that are travelling in wolf territories add new marks and overmark previously deposited wolf urine. There is no evidence that wolves use coyote marks as aids for tracking or preying on coyotes, so the activity does not appear to be maladaptive. Moreover, coyotes may be able to determine the freshness of various sign, and consequently judge the risk associated with travelling in the area. Wolves investigate coyote marks, and often overmark them, but not with the same intensity that they react to sign of from unknown wolves (Peters and Mech 1974, pers. obs.).

Wolves and coyotes in RMNP use the same food resources (Meleshko 1986, this study). Competition, however, is diminished by resource partitioning. Elk and deer are the preferred prey species for wolves, but elk contribute substantially more biomass to the diet than the deer. Coyotes kill large numbers of deer and the occasional elk, but acquire most of their food by scavenging wolf-killed elk (Meleshko 1986, this study). Potential competition over deer is negligible because of the relative unimportance of deer as a dietary item for wolves, as well as interspecific differences in age-class selection, and choice of hunting habitat.

Coyotes in RMNP are attracted to wolves because of the abundant carrion available from wolf kills. Their foraging strategy is to track wolves to kill sites and feed on abandoned carcasses. Relationships could be altered if elk populations decline, and wolves are forced either to rely on deer as their primary prey, or increase the thoroughness with which they consume elk or both. In such circumstances coyotes would have to compete with wolves for deer, which may result in the reduction or complete elimination of coyotes.

With the exception of human-caused extirpation, the current North American distribution of wolves and coyotes reflects the distribution, abundance, and diversity of prey species available to wolves, modified by preferential selection of prey by wolves. The proximate reason why coyotes are excluded from some areas occupied by wolves appears to be related to the absence of critical food resources, and secondarily because of direct aggression. Spatial separation is a secondary manifestation that occurs when the risks associated with living within active wolf areas outweigh the benefits provided by scavenging.

Sympatric populations of wolves and coyotes are most likely to occur in areas where moose, bison, and elk are numerous and preyed upon by wolves. If deer are the preferred prey, the probability of successful coexistence is remote because ecological overlap is almost certain. More importantly, coyotes lose the opportunity to scavenge wolf kills because wolves preying on deer leave few remains.

In summary, coyotes coexist with wolves in RMNP because the benefits of scavenging outweigh the risks of predation by wolves. This could change if the nature of the food supply is altered. The relationship suggests that the distribution of wolves and coyotes is influenced by availability and degree of use of large ungulates by wolves. Exclusive or extensive use of white-tailed deer by wolves likely diminishes the probability of coyotes and wolves coexisting.

Chapter 6

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APPENDIX A

Table A-1. Statistical analyses of the distribution of overlapping wolf and coyote prints (WOC, COW) recorded in snow tracking sessions from 1982-1986. COW prints occurred at a significantly higher rate than WOC prints. Values marked by an asterisk are significantly different.

Tests	df	_G_
Pooled	1	229.08*
Heterogeneity	3	11.64*
Total	4	240.71*

Year	df	_G_
1982/83	1	51.94*
1983/84	1	111.88*
1984/85	1	71.91*
1985/86	1	4.98*
Total	4	240.71*

Appendix A

Table A-2. Statistical analyses of the distribution of coyote on wolf (COW>, COW<) prints recorded in snow tracking sessions from 1982-1986. Coyote tracks were not independent of the direction of wolf travel. Coyotes followed wolves a disproportionate number of times. Values marked by an asterisk are significantly different.

Tests	df	_G_
Pooled	1	162.42*
Heterogeneity	3	16.00*
Total	4	178.42*

Year	df	_G_
1982/83	1	16.72*
1983/84	1	58.97*
1984/85	1	100.92*
1985/86	1	1.81
Total	4	178.42*

Appendix A

Table A-3. Statistical analyses of the distribution of coyote on wolf (COW>, COW<) prints recorded on *new* trails during snow tracking sessions from 1982-1986. Coyotes followed wolves a disproportionate number of times. Values marked by an asterisk are significantly different.

Tests	df	*G*
Pooled	1	43.71*
Heterogeneity	3	14.22*
Total	4	57.93*

Year	df	*G*
1982/83	1	20.92*
1983/84	1	27.29*
1984/85	1	9.28*
1985/86	1	0.44
Total	4	57.93*

Appendix A

Table A-4. Statistical analyses of the distribution of coyote on wolf (COW>, COW<) prints recorded on established trails during snow tracking sessions from 1982-1986. Coyotes followed wolves a disproportionate number of times. Values marked by an asterisk are significantly different.

Tests	df	G
Pooled	1	120.53*
Heterogeneity	3	27.23*
Total	4	147.77*

Year	df	G
1982/83	1	3.28
1983/84	1	31.56*
1984/85	1	107.68*
1985/86	1	5.24*
Total	4	147.77

Appendix A

Table A-5. Statistical analyses of the distribution of wolf on coyote (WOC>, WOC<) prints recorded in snow tracking sessions from 1982-1986. Wolf tracks were randomly distributed relative to the direction of coyote travel. Values marked by an asterisk are significantly different.

Tests	df	*G*
Pooled	1	0.04
Heterogeneity	3	1.50
Total	4	1.54

Year	df	*G*
1982/83	1	0.59
1983/84	1	0.28
1984/85	1	0.63
1985/86	1	0.04
Total	4	1.54

Appendix A

Table A-6. Statistical analyses of the distribution of wolf on coyote (WOC>, WOC<) prints on _new_ trails recorded in snow tracking sessions from 1982-1986. Wolf tracks were random relative to movements of coyotes. Values marked by an asterisk are significantly different.

Tests	df	_G_
Pooled	1	0.00
Heterogeneity	3	7.39
Total	4	7.39

Year	df	_G_
1982/83	1	4.94
1983/84	1	0.58
1984/85	1	0.08
1985/86	1	1.79
Total	4	7.39

Appendix A

Table A-7. Statistical analyses of the distribution of wolf on coyote (WOC>, WOC<) prints recorded on established trails in snow tracking sessions from 1982-1986. Wolf tracks were random relative to movements of coyotes. Values marked by an asterisk are significantly different.

Tests	df	G
Pooled	1	0.09
Heterogeneity	3	4.77
Total	4	4.87

Year	df	G
1982/83	1	0.47
1983/84	1	1.32
1984/85	1	1.64
1985/86	1	1.43
Total	4	4.87

APPENDIX B

Table B-1. Summary of statistical associations (G-test of independence) between mark types recorded on WO trails and the environments in which they were deposited. The null hypothesis stated that marks are deposited randomly, independent of location.

Year	G-value	df	P
1982-83	14.55*	4	< 0.010
1983-84	28.71*	4	< 0.001
1984-85	16.85*	4	< 0.005
1985-86	2.45	4	> 0.500
Pooled	46.95*	4	< 0.001

* significant

Appendix B

Table B-2. Statistical summary of observed versus expected values for mark types recorded in all travel environments on all wolf (WO) trails. For definition of mark types see text. Expected values were generated using procedures outlined by Lehner (1979). _G_-tests of goodness of fit were used to assess the relationships of frequency distributions (Sokal and Rohlf 1981).

	Wolf Only Trails			
Year	DU G-value	NDU G-value	SCR G-value	df
1982-83	57.84*	1.96	5.76	2
1983-84	105.50*	2.89	14.25*	2
1984-85	42.00*	1.00	7.40*	2
1985-86	30.09*	7.13*	-----	2
Total	235.43*	12.97	-----	8
Pooled	216.01*	12.15*	33.09*	2
Hetero.	19.42*	0.83	-----	6

* significant

Appendix B

Table B-3. Summary of statistical associations (G-test of independence) between mark types recorded on CO trails and the environments in which they were deposited. The null hypothesis stated that marks are deposited randomly, independent of location.

Year	G-value	df	P
1982-83	1.45	4	> 0.995
1983-84	3.75	4	> 0.900
1984-85	16.17*	4	> 0.025
1985-86	6.36	4	> 0.500
Pooled	7.78	4	> 0.500

* significant

Appendix B

Table B-4. Statistical summary of observed versus expected values for scent mark types recorded in all travel environments on all CO trails. For definitions of mark types see text. Expected values were generated using procedures outlined by Lehner (1979). _G_-tests of goodness of fit were used to examine frequency distributions (Sokal and Rohlf 1981).

	Coyote Only Trails			
Year	DU G-value	NDU G-value	SCR G-value	df
1982-83	8.65*	3.16	-----	2
1983-84	29.30*	0.67	-----	2
1984-85	53.26*	2.03	5.97*	2
1985-86	14.17*	12.16*	-----	2
Total	105.37*	18.02*	-----	8
Pooled	97.38*	12.04*	19.72*	2
Hetero.	7.99	5.98	-----	6

* significant

Appendix B

Table B-5. Summary of statistical associations (G-test of independence) between mark types recorded on COW trails and the environments in which they were deposited. The null hypothesis stated that marks are deposited randomly, independent of location.

Year	G-value	df	P
1982-83	15.23*	4	> 0.050
1983-84	3.15	4	> 0.900
1984-85	5.56	4	> 0.900
1985-86	4.45	4	> 0.900
Pooled	3.30	4	> 0.900

* significant

Table B-6. Statistical summary of observed versus expected values for scent mark types recorded in all travel environments on all COW trails. For definitions of mark types see text. Expected values were generated using procedures outlined by Lehner (1979). G-tests of goodness of fit were used to assess the relationships of frequency distributions (Sokal and Rohlf 1981).

	Coyote On Wolf			
Year	DU G-value	NDU G-value	SCR G-value	df
1982-83	62.00*	-----	-----	2
1983-84	20.14*	1.77	2.65	2
1984-85	46.62*	6.85*	4.40	2
1985-86	0.78	3.45	1.66	2
Total	129.54*	-----	-----	8
Pooled	74.34*	12.70*	5.82	2
Hetero.	55.20*	-----	-----	6

* significant

Appendix B

Table B-7. Summary of statistical associations (_G_-test of independence) between mark types recorded on WOC trails and the environments in which they were deposited. The null hypothesis stated that marks are deposited randomly, independent of location (Sokal and Rohlf 1981).

Year	G-Value	df	P
1982-83	2.36	4	> 0.975
1983-84	4.23	4	> 0.900
1984-85	3.10	4	> 0.900
1985-86	6.27	4	> 0.900
Pooled	6.24	4	> 0.900

Table B-8. Statistical summary of observed versus expected values for scent mark types recorded in all travel environments on all WOC trails. For definitions of mark types see text. Expected values were generated using procedures outlined by Lehner (1979). _G_-tests of goodness of fit were used to assess the relationships of frequency distributions.

	Wolf On Coyote			
Year	DU G-value	NDU G-value	SCR G-value	df
1982-83	26.99*	------	------	2
1983-84	46.78*	1.07	9.93*	2
1984-85	6.05*	------	------	2
1985-86	------	------	------	2
Total	------	------	------	8
Pooled	88.99*	6.94*	21.96*	2
Hetero.	------	------	------	6

* significant

Table B-9. Summary of *G*-tests for goodness of fit of the observed frequencies of winter marking by large wolf packs (LWP) and small wolf packs (SWP). Expected values were generated using procedures outlined by Lehner (1979).

	OBSERVED		EXPECTED				
Year	LWP	SWP	LWP	SWP	G-value	df	P
1982-83	206	94	173	127	15.361*	1	< 0.001
1983-84	253	209	202	260	22.642*	1	< 0.001
1984-85	200	219	169	250	9.381*	1	< 0.005
1985-86	212	89	186	115	9.855*	1	< 0.005
G-Total					57.239*	4	< 0.001
G-Pooled	871	611	730	752	53.897*	1	< 0.001
G-Hetero.					3.342	3	> 0.500

* significant

Appendix B

Table B-10. Summary of G-tests for goodness of fit of the observed frequencies of winter marking by single coyotes (SIN) and coyotes travelling in groups (GRP) of two or more. Expected values were generated using procedures outlined by Lehner (1979).

Year	OBSERVED		EXPECTED		G-value	df	P
	SIN	GRP	SIN	GRP			
1982-83	23	78	42	59	15.851*	1	< 0.001
1983-84	47	95	81	61	33.006*	1	< 0.001
1984-85	44	140	69	115	15.486*	1	< 0.001
1985-86	34	106	81	59	64.949*	1	< 0.001
G-Total					129.292*	4	< 0.001
G-Pooled	148	419	273	294	115.667*	1	< 0.001
G-Hetero.					13.625*	3	< 0.005

* significant

Table B-11. Summary of *G*-tests for goodness of fit of the observed frequencies of winter marking by large wolf packs (LWP) and coyotes using trails established by large wolf packs (COW). Expected values were generated using procedures outlined by Lehner (1979).

	OBSERVED		EXPECTED				
Year	LWP	COW	LWP	COW	G-value	df	P
1982-83	206	82	178	110	12.013*	1	< 0.001
1983-84	253	237	320	170	38.617*	1	< 0.001
1984-85	200	145	253	92	37.905*	1	< 0.001
1985-86	212	112	246	78	17.945*	1	> 0.001
G-Total					106.480*	4	< 0.001
G-Pooled	871	576	997	450	49.023*	1	< 0.001
G-Hetero.					57.457*	3	< 0.001

* significant

Table B-12. Summary of G-tests for goodness of fit of the observed frequencies of winter marking by large wolf packs (LWP) and large packs using trails established by coyotes (WOC). Expected values were generated using procedures outlined by Lehner (1979).

	OBSERVED		EXPECTED				
Year	LWP	WOC	LWP	WOC	G-value	df	P
1982-83	206	24	177	53	24.484*	1	< 0.001
1983-84	253	103	275	81	7.306*	1	< 0.010
1984-85	200	65	219	46	8.645*	1	< 0.005
1985-86	212	37	216	33	0.541	1	> 0.500
G-Total					40.976*	4	< 0.001
G-Pooled	871	229	887	213	1.463	1	> 0.900
G-Hetero.					39.513*	3	< 0.001

* significant

Appendix B

Table B-13. Summary of G-tests for goodness of fit of the observed frequencies of winter marking by small wolf packs (SWP) and coyotes using trails established by small wolf packs (COW). Expected values were generated using procedures outlined by Lehner (1979).

Year	OBSERVED SWP	OBSERVED COW	EXPECTED SWP	EXPECTED COW	G-value	df	P
1982-83	94	47	86	55	1.947	1	> 0.500
1983-84	209	190	270	129	40.096*	1	< 0.001
1984-85	219	146	271	94	35.256*	1	< 0.001
1985-86	89	97	120	66	21.505*	1	< 0.001
G-Total					98.354*	4	< 0.001
G-Pooled	611	480	747	344	74.235*	1	< 0.001
G-Hetero.					24.119*	3	< 0.001

Table B-14. Summary of _G_-tests for goodness of fit of the observed frequencies of winter marking by small wolf packs (SWP) and small wolf packs using trails established by coyotes (WOC). Expected values were generated using procedures outlined by Lehner (1979).

	OBSERVED		EXPECTED				
Year	SWP	WOC	SWP	WOC	G-value	df	P
1982-83	94	16	86	24	3.747	1	> 0.100
1983-84	209	122	239	92	12.799*	1	< 0.001
1984-85	219	73	244	48	13.865*	1	< 0.001
1985-86	89	46	116	19	34.185*	1	< 0.001
_G_-Total					64.596*	4	< 0.001
_G_-Pooled	611	257	685	183	34.828*	1	< 0.001
_G_-Hetero.					99.424*	3	< 0.001

APPENDIX C

Table C-1. Summary of scent-marking rates recorded for the Whitewater wolf pack (9 animals) in winter 1982-83.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	38	(106) 2.79	(27) 0.71	(16) 0.42	(149) 3.92
Bush	26	(18) 0.69	(19) 0.73	(10) 0.38	(47) 1.81
Frozen waterways	10	(4) 0.40	(5) 0.50	(1) 0.10	(10) 0.41
Comb. rate:		1.49	0.69	0.36	2.78
Total dist:	74				

Table C-2. Summary of scent-marking rates recorded for the Pacey Lake wolf pack (4 animals) in winter 1982-83.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	15	(19) 1.27	(10) 0.67	(3) 0.20	(32) 2.13
Bush	31	(31) 1.00	(18) 0.58	(6) 0.19	(55) 2.52
Frozen waterways	8	(5) 0.63	(2) 0.25	(0) 0.00	(7) 0.88
Comb. rate:		1.02	0.56	0.17	1.74
Total dist:	54				

Table C-3. Summary of combined scent-marking rates recorded for wolf packs in winter 1982-83.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	53	(126) 2.38	(37) 0.70	(19) 0.36	(182) 3.43
Bush	57	(49) 0.86	(37) 0.65	(16) 0.28	(102) 1.79
Frozen waterways	18	(9) 0.50	(7) 0.39	(1) 0.06	(17) 0.94
Comb. rate:		1.44	0.63	0.28	2.35
Total dist:	128				

Table C-4. Summary of scent-marking rates recorded for the Baldy Lake wolf pack (10 animals) in winter 1983-84.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	62	(118) 1.90	(36) 0.58	(11) 0.18	(165) 2.66
Bush	39	(47) 1.21	(22) 0.56	(8) 0.21	(77) 1.97
Frozen waterways	14	(5) 0.36	(6) 0.43	0.00	(11) 0.79
Comb. rate:		1.48	0.56	0.17	2.20
Total dist:	115				

Table C-5. Summary of scent-marking rates recorded for the Clear Lake wolf pack (3 animals) in winter 1983-84.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	35	(45) 1.29	(16) 0.46	(10) 0.29	(71) 2.03
Bush	60	(60) 1.00	(29) 0.48	(20) 0.33	(109) 1.82
Frozen waterways	53	(7) 0.13	(19) 0.36	(3) 0.06	(29) 0.55
Comb. rate:		0.76	0.43	0.22	1.41
Total dist:	148				

Table C-6. Summary of combined scent-marking rates recorded for wolf packs in winter 1983-84.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	97	(163) 1.68	(52) 0.54	(21) 0.22	(236) 2.43
Bush	99	(107) 1.08	(51) 0.52	(28) 0.28	(186) 1.88
Frozen waterways	67	(12) 0.18	(24) 0.36	(3) 0.04	(39) 0.58
Comb. rate:		1.07	0.48	0.20	1.75
Total dist:	263				

Table C-7. Summary of scent-marking rates recorded for the Audy Lake wolf pack (5 animals) in winter 1984-85.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	51	(87) 1.71	(37) 0.73	(15) 0.29	(139) 2.73
Bush	24	(24) 1.00	(19) 0.79	(10) 0.42	(53) 2.21
Frozen waterways	7	(4) 0.57	(3) 0.43	(1) 0.14	(8) 1.14
Comb. rate:		1.40	0.72	0.32	2.44
Total dist:	82				

Table C-8. Summary of scent-marking rates recorded for the Clear Lake wolf pack (2 animals) in winter 1984-85.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	63	(76) 1.21	(43) 0.68	(20) 0.32	(139) 2.21
Bush	36	(29) 0.81	(22) 0.61	(12) 0.33	(63) 1.75
Frozen waterways	22	(3) 0.14	(13) 0.59	(1) 0.05	(17) 0.77
Comb. rate:		0.89	0.64	0.27	1.81
Total dist:	121				

Table C-9. Summary of combined scent-marking rates recorded for wolf packs in winter 1984-85.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	114	(163) 1.45	(80) 0.70	(35) 0.31	(278) 2.44
Bush	60	(53) 0.90	(41) 0.68	(22) 0.37	(116) 1.93
Frozen waterways	29	(7) 0.38	(16) 0.55	(2) 0.07	(25) 0.86
Comb. rate:		1.10	0.67	0.29	2.06
Total dist:	203				

Table C-10. Summary of scent-marking rates recorded for the Pacey Lake wolf pack (10 animals) in winter 1985-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	56	(111) 1.98	(39) 0.70	(10) 0.23	(163) 2.91
Bush	19	(28) 1.47	(8) 0.42	(4) 0.21	(40) 2.11
Frozen waterways	16	(11) 0.69	(5) 0.31	(3) 0.00	(9) 0.56
Comb. rate:		1.65	0.57	0.19	2.32
Total dist:	91				

Table C-11. Summary of scent-marking rates recorded for the Clear Lake wolf pack (3 animals) in winter 1985-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	21	(27) 1.29	(11) 0.52	(3) 0.14	(41) 1.95
Bush	24	(31) 1.29	(9) 0.38	(1) 0.04	(41) 1.71
Frozen waterways	11	(2) 0.18	(3) 0.27	(1) 0.09	(7) 0.64
Comb. rate:		1.07	0.41	0.09	1.43
Total dist:	56				

Table C-12. Summary of combined scent-marking rates recorded for wolf packs in winter 1985-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	77	(138) 1.79	(50) 0.65	(16) 0.21	(204) 2.65
Bush	43	(59) 1.37	(17) 0.36	(7) 0.01	(81) 1.88
Frozen waterways	27	(13) 2.08	(8) 0.30	(1) 0.04	(16) 0.59
Comb. rate:					2.05
Total dist:	147				

Table C-13. Summary of scent-marking rates recorded for two or more coyotes in winter 1982-83.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	32	(26) 0.81	(16) 0.50	(13) 0.41	(55) 1.72
Bush	17	(6) 0.35	(7) 0.41	(6) 0.35	(19) 1.12
Frozen waterways	6	(1) 0.17	(2) 0.33	(1) 0.17	(4) 0.67
Comb. rate:		0.60	0.45	0.36	1.42
Total dist:	55				

Table C-14. Summary of scent-marking rates recorded for one coyote in winter 1982-83.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	22	(9) 0.41	(9) 0.41	0.00	(18) 0.86
Bush	9	(2) 0.22	(2) 0.22	0.00	(4) 0.44
Frozen waterways	7	(1) 0.14	0.00	0.00	(1) 0.14
Comb. rate:		0.31	0.28	0.00	0.59
Total dist:	39				

Table C-15. Summary of combined scent-marking rates recorded for coyotes in winter 1982-83.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	54	(35) 0.65	(25) 0.46	(13) 0.24	(73) 1.35
Bush	26	(8) 0.31	(9) 0.35	(6) 0.23	(23) 0.88
Frozen waterways	13	(2) 0.15	(2) 0.15	(1) 0.08	(5) 0.38
Comb. rate:		0.48	0.30	0.22	1.09
Total dist:	93				

Table C-16. Summary of scent-marking rates recorded for two or more coyotes in winter 1983-84.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	29	(42) 1.45	(9) 0.31	(20) 0.69	(71) 2.45
Bush	16	(13) 0.81	(5) 0.31	(4) 0.25	(22) 1.38
Frozen waterways	9	(1) 0.11	(1) 0.11	0.00	(2) 0.22
Comb. rate:		0.79	0.24	0.31	1.76
Total dist:	54				

Table C-17. Summary of scent-marking rates recorded for one coyote in winter 1983-84.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	39	(32) 0.82	(4) 0.10	(1) 0.03	(37) 0.95
Bush	22	(7) 0.32	(1) 0.05	0.00	(8) 0.36
Frozen waterways	11	(1) 0.09	(1) 0.09	0.00	(2) 0.18
Comb. rate:		0.56	0.08	0.01	0.65
Total dist:	72				

Table C-18. Summary of combined scent-marking rates recorded for coyotes in winter 1983-84.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	68	(74) 1.09	(13) 0.19	(21) 0.31	(108) 1.69
Bush	38	(20) 0.53	(6) 0.16	(4) 0.11	(30) 0.79
Frozen waterways	20	(2) 0.10	(2) 0.10	(1) 0.05	(4) 0.20
Comb. rate:		0.76	0.17	0.20	1.13
Total dist:	126				

Table C-19. Summary of scent-marking rates recorded for two or?more coyotes in winter 1984-85.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	47	(71) 1.51	(18) 0.38	(24) 0.51	(113) 2.40
Bush	19	(6) 0.32	(8) 0.42	(7) 0.37	(21) 1.11
Frozen waterways	13	(1) 0.08	(3) 0.23	(2) 0.15	(6) 0.46
Comb. rate:		0.99	0.37	0.42	1.77
Total dist:	79				

Table C-20. Summary of scent-marking rates recorded for one coyote in winter 1984-85.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	29	(25) 0.86	(6) 0.21	(5) 0.17	(36) 1.24
Bush	9	(2) 0.22	(2) 0.23	(2) 0.22	(6) 0.67
Frozen waterways	9	(1) 0.11	(1) 0.11	0.00	(2) 0.22
Comb. rate:		0.60	0.19	0.15	0.94
Total dist:	47				

Table C-21. Summary of combined scent-marking rates recorded for coyotes in winter 1984-85.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	76	(96) 1.18	(24) 0.32	(29) 0.38	(149) 1.96
Bush	28	(8) 0.25	(10) 0.36	(9) 0.32	(27) 0.96
Frozen waterways	22	(2) 0.10	(4) 0.18	(2) 0.09	(8) 0.36
Comb. rate:		0.84	0.30	0.32	1.46
Total dist:	126				

Table C-22. Summary of scent-marking rates recorded for two or more coyotes in winter 1985-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	29	(61) 2.10	(18) 0.62	(11) 0.38	(90) 3.10
Bush	8	(7) 0.88	(1) 0.13	(0) 0.00	(10) 1.25
Frozen waterways	4	(6) 1.50	(0) 0	(0) 0	(6) 1.50
Comb. rate:		1.80	0.46	0.27	2.59
Total dist:	41				

Table C-23. Summary of scent-marking rates recorded for one coyote in winter 1984-85.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	34	(20) 0.59	(6) 0.30	(1) 0.03	(27) 0.79
Bush	6	(3) 0.50	(0) 0	(0) 0	(3) 0.50
Frozen waterways	17	(3) 0.18	(1) 0.06	(0) 0	(4) 0.24
Comb. rate:		0.46	0.12	0.02	0.60
Total dist:	37				

Table C-24. Summary of combined scent-marking rates recorded for coyotes in winter 1985-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	63	(81) 1.29	(24) 0.38	(12) 0.19	(117) 1.86
Bush	14	(10) 0.71	(1) 0.07	(0) 0	(13) 0.93
Frozen waterways	21	(9) 0.43	(1) 0.05	(0) 0	(10) 0.48
Comb. rate:					1.43
Total dist:	98				

Table C-25. Summary of scent-marking rates recorded for coyotes using trails established by the Whitewater wolf pack (9 animals) in winter 1982-83.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	24	(53) 2.29	(5) 0.21	(6) 0.25	(66) 2.75
Bush	12	(5) 0.42	(3) 0.25	(4) 0.33	(12) 1.00
Frozen waterways	10	(1) 0.10	(2) 0.20	(1) 0.10	(4) 0.40
Comb. rate:		0.94	0.22	0.23	1.78
Total dist:	46				

Table C-26. Summary of scent-marking rates recorded for coyotes using trails established by the Pacey Lake wolf pack (4 animals) in winter 1982-83.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	15	(28) 1.87	(3) 0.20	(4) 0.27	(35) 2.33
Bush	12	(6) 0.50	(2) 0.17	(2) 0.17	(10) 0.83
Frozen waterways	8	(1) 0.13	(1) 0.13	0.00	(2) 0.25
Comb. rate:		0.83	0.17	0.22	1.34
Total dist:	35				

Table C-27. Summary of combined scent-marking rates recorded for coyotes using trails established by wolf packs in winter 1982-83.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	39	(83) 2.13	(8) 0.21	(10) 0.26	(101) 2.59
Bush	24	(11) 0.46	(5) 0.21	(6) 0.25	(22) 0.92
Frozen waterways	18	(2) 0.17	(3) 0.17	(1) 0.06	(6) 0.33
Comb. rate:		1.19	0.20	0.21	1.59
Total dist:	81				

Table C-28. Summary of scent-marking rates recorded for coyotes using trails established by the Baldy Lake wolf pack (10 animals) in winter 1983-84.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	35	(126) 3.60	(13) 0.37	(9) 0.26	(148) 4.23
Bush	21	(58) 2.76	(10) 0.48	(7) 0.33	(75) 3.57
Frozen waterways	5	(12) 2.40	(2) 0.40	0.00	(14) 2.80
Comb. rate:		3.21	0.41	0.26	3.89
Total dist:	61				

Table C-29. Summary of scent-marking rates recorded for coyotes using trails established by the Clear Lake wolf pack (3 animals) in winter 1983-84.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	15	(44) 2.93	(5) 0.33	(5) 0.33	(54) 3.60
Bush	41	(86) 2.10	(13) 0.32	(11) 0.27	(110) 2.68
Frozen waterways	15	(22) 1.47	(2) 0.13	(2) 0.13	(26) 1.73
Comb. rate:		2.14	0.28	0.24	2.68
Total dist:	71				

Table C-30. Summary of combined scent-marking rates recorded for coyotes using trails established by wolf packs in winter 1983-84.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	50	(170) 3.40	(18) 0.36	(14) 0.28	(202) 4.04
Bush	62	(144) 2.32	(23) 0.37	(18) 0.29	(185) 2.98
Frozen waterways	20	(34) 1.70	(4) 0.20	(2) 0.10	(40) 2.00
Comb. rate:		2.64	0.34	0.26	3.23
Total dist:	132				

Table C-31. Summary of scent-marking rates recorded for coyotes using trails established by the Audy Lake wolf pack (5 animals) in winter 1984-85.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	21	(80) 3.81	(21) 1.00	(15) 0.71	(116) 5.52
Bush	6	(13) 2.17	(8) 1.33	(3) 0.50	(24) 4.00
Frozen waterways	3	(2) 0.67	(2) 0.67	(1) 0.33	(5) 1.67
Comb. rate:		3.17	1.03	0.63	4.83
Total dist:	30				

Table C-32. Summary of scent-marking rates recorded for coyotes using trails established by the Clear Lake wolf pack (2 animals) in winter 1984-85.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	19	(55) 2.89	(27) 1.42	(9) 0.47	(91) 4.79
Bush	13	(26) 2.00	(14) 1.08	(7) 0.54	(47) 3.62
Frozen waterways	10	(3) 0.30	(4) 0.40	(1) 0.10	(8) 0.80
Comb. rate:		2.00	1.07	0.40	3.48
Total dist:	42				

Table C-33. Summary of combined scent-marking rates recorded for coyotes using trails established by wolves in winter 1984-85.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	40	(135) 3.38	(48) 1.20	(24) 0.60	(207) 5.18
Bush	19	(39) 2.05	(22) 1.16	(10) 0.53	(71) 3.74
Frozen waterways	13	(5) 0.38	(6) 0.54	(2) 0.15	(13) 1.00
Comb. rate:		2.49	1.06	0.50	4.04
Total dist:	72				

Table C-34. Summary of scent-marking rates recorded for coyotes using trails established by the Pacey L. wolf pack (10 animals) in winter 1985-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	18	(41) 2.28	(16) 0.89	(10) 0.56	(67) 3.72
Bush	4	(17) 4.25	(2) 0.50	(5) 1.25	(24) 6.00
Frozen waterways	7	(14) 2.00	(3) 0.43	(4) 0.57	(21) 3.00
Comb. rate:		2.48	0.72	0.66	3.86
Total dist:	29				

Table C-35. Summary of scent-marking rates recorded for coyotes using trails established bye the Clear Lake wolf pack (3 animals) in winter 1985-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	20	(45) 2.25	(10) 0.50	(3) 0.15	(58) 2.90
Bush	6	(13) 2.17	(5) 0.83	(1) 0.17	(19) 3.17
Frozen waterways	5	(18) 3.60	(0) 0	(2) 0.40	(20) 4.00
Comb. rate:		1.97	0.48	0.19	3.13
Total dist:	31				

Table C-36. Summary of combined scent-marking rates recorded for coyotes using trails established by wolves in winter 1985-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	38	(96) 2.5	(26) 0.68	(13) 0.34	(125) 3.29
Bush	10	(30) 3.00	(7) 0.70	(6) 0.06	(43) 4.30
Frozen waterways	12	(32) 2.67	(3) 0.25	(6) 0.50	(41) 3.42
Comb. rate:					3.48
Total dist:	60				

Table C-37. Summary of scent-marking rates recorded for Whitewater wolves using trails established by coyotes in winter 1982-83.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	6	(12) 2.00	(1) 0.17	(2) 0.33	(15) 2.50
Bush	8	(3) 0.38	(2) 0.25	(1) 0.13	(8) 0.75
Frozen waterways	7	(1) 0.14	0.00	0.00	(1) 0.14
Comb. rate:		0.68	0.14	0.14	1.09
Total dist:	22				

Table C-38. Summary of scent-marking rates recorded for Pacey Lake wolves using trails established by coyotes in winter 1982-83.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	7	(11) 1.57	(1) 0.14	(2) 0.29	(14) 2.00
Bush	5	(2) 0.40	0.00	0.00	(2) 0.40
Frozen waterways	3	0.00	0.00	0.00	0.00
Comb. rate:		0.87	0.07	0.13	1.23
Total dist:	15				

Table C-39. Summary of combined scent-marking rates recorded for wolves using trails established by coyotes in winter 1982-83.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	13	(23) 1.77	(2) 0.15	(4) 0.31	(29) 1.23
Bush	13	(5) 0.39	(2) 0.15	(1) 0.08	(8) 0.62
Frozen waterways	10	(1) 0.10	0.00	0.00	(1) 0.10
Comb. rate:		0.78	0.11	0.14	1.03
Total dist:	37				

Table C-40. Summary of scent-marking rates recorded for Baldy Lake wolves using trails established by coyotes in winter 1983-84.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	20	(62) 3.10	(8) 0.40	(8) 0.40	(78) 3.90
Bush	8	(15) 1.88	(4) 0.50	(2) 0.25	(21) 2.63
Frozen waterways	6	(2) 0.33	(2) 0.33	0.00	(4) 0.67
Comb. rate:		2.32	0.41	0.29	3.03
Total dist:	34				

Table C-41. Summary of scent-marking rates recorded for Clear Lake wolves using trails established by coyotes in winter 1983-84.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	22	(53) 2.41	(6) 0.27	(10) 0.45	(69) 3.14
Bush	20	(30) 1.50	(4) 0.20	(8) 0.40	(42) 2.10
Frozen waterways	15	(8) 0.53	(2) 0.13	(1) 0.07	(11) 0.73
Comb. rate:		1.60	0.21	0.33	2.14
Total dist:	57				

Table C-42. Summary of combined scent-marking rates recorded for wolves using trails established by coyotes in winter 1983-84.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	42	(115) 2.74	(14) 0.33	(18) 0.43	(147) 3.50
Bush	28	(45) 1.61	(8) 0.29	(10) 0.36	(63) 2.25
Frozen waterways	21	(10) 0.48	(4) 0.19	(1) 0.05	(15) 0.71
Comb. rate:		1.87	0.29	0.32	2.47
Total dist:	91				

Table C-43. Summary of scent-marking rates recorded for Audy Lake wolves using trails established by coyotes in winter 1984-85.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	10	(27) 2.70	(6) 0.60	(9) 0.90	(42) 4.20
Bush	5	(14) 2.80	(4) 0.80	(3) 0.60	(21) 4.20
Frozen waterways	2	(2) 1.00	0.00	0.00	(2) 1.00
Comb. rate:		2.53	0.59	0.71	3.82
Total dist:	17				

Table C-44. Summary of scent-marking rates recorded for Clear Lake wolves using trails established by coyotes in winter 1984-85.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	8	(17) 2.13	(4) 0.50	(4) 0.50	(25) 3.13
Bush	14	(28) 2.00	(9) 0.64	(10) 0.71	(47) 3.36
Frozen waterways	2	(1) 0.50	0.00	0.00	(1) 0.50
Comb. rate:		1.92	0.54	0.58	3.04
Total dist:	24				

Table C-45. Summary of combined scent-marking rates recorded for wolves using trails established by coyotes in winter 1984-85.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	18	(44) 2.44	(10) 0.56	(13) 0.72	(67) 3.72
Bush	19	(42) 2.21	(13) 0.68	(13) 0.68	(68) 3.58
Frozen waterways	4	(3) 0.75	0.00	0.00	(3) 0.75
Comb. rate:		2.17	0.56	0.63	3.37
Total dist:	41				

Table C-46. Summary of scent-marking rates recorded for Pacey Lake wolves using trails established by coyotes in winter 1985-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	10	(24) 2.40	(5) 0.50	(2) 0.20	(31) 3.10
Bush	3	(5) 1.67	(0) 0	(1) 0.33	(6) 2.00
Frozen waterways	1	(0) 0	(0) 0	(0) 0	(0) 0
Comb. rate:		2.07	0.36	0.21	2.64
Total dist:	14				

Table C-47. Summary of scent-marking rates recorded for Clear Lake wolves using trails established by coyotes in winter 1985-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	5	(26) 5.20	(0) 0	(4) 0.80	(30) 6.00
Bush	4	(13) 3.25	(2) 0.50	(1) 0.25	(16) 4.00
Frozen waterways	0	(0) 0	(0) 0	(0) 0	(0) 0
Comb. rate:					5.11
Total dist:	9				

Table C-48. Summary of combined scent-marking rates recorded for wolves using trails established by coyotes in winter 1985-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	15	(50) 3.33	(5) 0.33	(5) 0.33	(61) 4.07
Bush	7	(18) 0.38	(2) 0.29	(2) 0.29	(22) 3.14
Frozen waterways	1	(0) 0	(0) 0	(0) 0	(0) 0
Comb. rate:					
Total dist:	23				

Table C-49. Summary of large wolf pack scent-marking rates, 1982-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	207	(422) 2.04	(139) 0.67	(45) 0.22	(606) 2.93
Bush	108	(117) 1.08	(68) 0.63	(32) 0.30	(217) 2.01
Frozen waterways	47	(24) 0.51	(19) 0.40	(2) 0.04	(45) 0.96
Comb. rate:					2.40
Total dist:	362				

Table C-50. Summary of small wolf pack scent-marking rates, 1982-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	134	(167) 1.25	(80) 0.60	(36) 0.27	(283) 2.11
Bush	151	(151) 1.00	(78) 0.52	(39) 0.26	(268) 1.77
Frozen waterways	94	(17) 0.18	(37) 0.39	(5) 0.05	(59) 0.99
Comb. rate:					1.61
Total dist:	379				

Table C-51. Summary of combined small wolf pack and large wolf pack scent-marking rates, 1982-1986.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	341	(590) 1.70	(219) 0.64	(91) 0.27	(900) 2.64
Bush	259	(268) 1.03	(146) 0.57	(73) 0.28	(487) 1.88
Frozen waterways	141	(41) 0.29	(55) 0.39	(7) 0.05	(103) 0.73
Comb. rate:					2.01
Total dist:	741				

Table C-52. Summary of scent-marking rates for two or more coyotes, 1982-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	137	(200) 1.46	(61) 0.45	(68) 0.50	(329) 2.40
Bush	60	(32) 0.53	(21) 0.35	(17) 0.28	(70) 1.17
Frozen waterways	32	(9) 0.28	(6) 1.88	(3) 0.09	(18) 1.78
Comb. rate:					
Total dist:	229				

Table C-53. Summary of single coyote marking rates, 1982-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	124	(86) 0.69	(25) 0.20	(7) 0.06	(118) 0.95
Bush	46	(14) 0.30	(5) 0.11	(2) 0.04	(21) 0.46
Frozen waterways	44	(6) 0.14	(3) 0.07	(0) 0	(9) 0.20
Comb. rate:					
Total dist:	214				

Table C-54. Summary of combined coyote marking rates, 1982-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	261	(286) 1.10	(86) 0.33	(75) 0.29	(447) 1.71
Bush	106	(46) 0.43	(26) 0.25	(19) 0.18	(91) 0.86
Frozen waterways	76	(15) 0.20	(9) 0.12	(4) 0.05	(28) 0.37
Comb. rate:					1.28
Total dist:	443				

Table C-55. Summary of scent-marking rates for coyotes following large wolf packs, 1982-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	98	(300) 3.06	(55) 0.56	(40) 0.41	(395) 4.03
Bush	43	(93) 1.19	(23) 0.53	(19) 0.45	(135) 3.14
Frozen waterways	25	(29) 1.16	(9) 0.36	(6) 0.24	(44) 1.76
Comb. rate:					3.46
Total dist:	166				

Table C-56. Summary of scent-marking rates for coyotes following small wolf packs, 1982-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	69	(172) 2.49	(45) 0.65	(21) 0.30	(283) 3.45
Bush	72	(131) 1.82	(34) 0.47	(21) 0.29	(186) 2.58
Frozen waterways	38	(44) 1.16	(7) 0.18	(5) 0.13	(56) 1.47
Comb. rate:					2.93
Total dist:	179				

Table C-57. Summary of combined scent-marking rates for coyotes following wolf packs, 1982-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	167	(484) 2.90	(100) 0.60	(61) 0.37	(645) 3.86
Bush	115	(224) 1.95	(57) 0.50	(40) 0.35	(321) 2.79
Frozen waterways	63	(73) 1.16	(16) 0.25	(11) 0.17	(100) 1.59
Comb. rate:					1.61
Total dist:	379				

Table C-58. Summary of scent-marking rates for large wolf packs following coyotes, 1982-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	46	(125) 2.7	(20) 0.43	(21) 0.46	(166) 3.40
Bush	24	(37) 1.54	(10) 0.42	(7) 0.29	(54) 2.25
Frozen waterways	16	(5) 0.31	(2) 0.13	(0) 0	(7) 0.44
Comb. rate:					2.64
Total dist:	86				

Table C-59. Summary of scent-marking rates for small wolf packs following coyotes, 1982-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	42	(107) 2.55	(11) 0.26	(20) 0.48	(138) 3.29
Bush	43	(73) 1.70	(15) 0.35	(19) 0.44	(107) 2.49
Frozen waterways	20	(9) 0.45	(2) 0.10	(1) 0.05	(12) 0.60
Comb. rate:					2.45
Total dist:	105				

Table C-60. Summary of combined scent-marking rates for wolves following coyotes, 1982-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	88	(232) 2.64	(31) 0.32	(41) 0.47	(304) 3.45
Bush	67	(110) 1.64	(25) 0.37	(26) 0.39	(161) 2.40
Frozen waterways	36	(14) 0.39	(4) 0.11	(1) 0.03	(19) 0.53
Comb. rate:					2.53
Total dist:	191				

Chapter 5

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CHAPTER 6

GENERAL CONCLUSIONS

Complete exclusion of coyotes by wolves occurs in some areas of North America. However, the extent of ecological overlap is probably variable, as the two species are also sympatric throughout a diverse range of habitats. Elucidating the mechanisms that permit co-existence of substantial numbers of wolves and coyotes in Riding Mountain National Park helps in understanding the role of the two canids in community ecology, as well as the reasons for the current geographic distribution of the coyote.

The areal overlap of wolves and coyotes in RMNP is considerable, with no evidence that spatial segregation occurs at any level. Temporal overlap also appears to be minimal, although conclusive documentation is lacking. Despite aggression by wolves toward coyotes, coyotes are not deterred from using areas inhabited by wolves. Moreover, coyotes do little to conceal their presence from wolves, as evidenced by their spontaneous howling in active wolf areas, responsive howling to wolf vocalizations, overmarking of wolf scent-marks, and apparent lack of concern about being seen by wolves.

With the exception of the spatial distribution of marks within wolf territories, the marking behavior of wolves and coyotes is similar to that observed in areas where the two species do not coexist. The difference does not appear to be a consequence of sympatry. The marking strategies of the two species are similar. The response of both wolves and coyotes to the urine or scratch marks of the other species resembles agonistic behavior directed toward alien conspecifics by animals occupying home ranges or territories (Peters and Mech 1974, Bowen and Cowan 1980, Barrette and Messier 1980). However, the response is more pronounced in coyotes than wolves.

Rather than avoiding areas previously marked by wolves, coyotes that are travelling in wolf territories add new marks and overmark previously deposited wolf urine. There is no evidence that wolves use coyote marks as aids for tracking or preying on coyotes, so the activity does not appear to be maladaptive. Moreover, coyotes may be able to determine the freshness of various sign, and consequently judge the risk associated with travelling in the area. Wolves investigate coyote marks, and often overmark them, but not with the same intensity that they react to sign of from unknown wolves (Peters and Mech 1974, pers. obs.).

Wolves and coyotes in RMNP use the same food resources (Meleshko 1986, this study). Competition, however, is diminished by resource partitioning. Elk and deer are the preferred prey species for wolves, but elk contribute substantially more biomass to the diet than the deer. Coyotes kill large numbers of deer and the occasional elk, but acquire most of their food by scavenging wolf-killed elk (Meleshko 1986, this study). Potential competition over deer is negligible because of the relative unimportance of deer as a dietary item for wolves, as well as interspecific differences in age-class selection, and choice of hunting habitat.

Coyotes in RMNP are attracted to wolves because of the abundant carrion available from wolf kills. Their foraging strategy is to track wolves to kill sites and feed on abandoned carcasses. Relationships could be altered if elk populations decline, and wolves are forced either to rely on deer as their primary prey, or increase the thoroughness with which they consume elk or both. In such circumstances coyotes would have to compete with wolves for deer, which may result in the reduction or complete elimination of coyotes.

With the exception of human-caused extirpation, the current North American distribution of wolves and coyotes reflects the distribution, abundance, and diversity of prey species available to wolves, modified by preferential selection of prey by wolves. The proximate reason why coyotes are excluded from some areas occupied by wolves appears to be related to the absence of critical food resources, and secondarily because of direct aggression. Spatial separation is a secondary manifestation that occurs when the risks associated with living within active wolf areas outweigh the benefits provided by scavenging.

Sympatric populations of wolves and coyotes are most likely to occur in areas where moose, bison, and elk are numerous and preyed upon by wolves. If deer are the preferred prey, the probability of successful coexistence is remote because ecological overlap is almost certain. More importantly, coyotes lose the opportunity to scavenge wolf kills because wolves preying on deer leave few remains.

In summary, coyotes coexist with wolves in RMNP because the benefits of scavenging outweigh the risks of predation by wolves. This could change if the nature of the food supply is altered. The relationship suggests that the distribution of wolves and coyotes is influenced by availability and degree of use of large ungulates by wolves. Exclusive or extensive use of white-tailed deer by wolves likely diminishes the probability of coyotes and wolves coexisting.

Chapter 6

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APPENDIX A

Table A-1. Statistical analyses of the distribution of overlapping wolf and coyote prints (WOC, COW) recorded in snow tracking sessions from 1982-1986. COW prints occurred at a significantly higher rate than WOC prints. Values marked by an asterisk are significantly different.

Tests	df	G
Pooled	1	229.08*
Heterogeneity	3	11.64*
Total	4	240.71*

Year	df	G
1982/83	1	51.94*
1983/84	1	111.88*
1984/85	1	71.91*
1985/86	1	4.98*
Total	4	240.71*

Appendix A

Table A-2. Statistical analyses of the distribution of coyote on wolf (COW>, COW<) prints recorded in snow tracking sessions from 1982-1986. Coyote tracks were not independent of the direction of wolf travel. Coyotes followed wolves a disproportionate number of times. Values marked by an asterisk are significantly different.

Tests	df	G
Pooled	1	162.42*
Heterogeneity	3	16.00*
Total	4	178.42*

Year	df	G
1982/83	1	16.72*
1983/84	1	58.97*
1984/85	1	100.92*
1985/86	1	1.81
Total	4	178.42*

Table A-3. Statistical analyses of the distribution of coyote on wolf (COW>, COW<) prints recorded on <u>new</u> trails during snow tracking sessions from 1982-1986. Coyotes followed wolves a disproportionate number of times. Values marked by an asterisk are significantly different.

Tests	df	<u>G</u>
Pooled	1	43.71*
Heterogeneity	3	14.22*
Total	4	57.93*

Year	df	<u>G</u>
1982/83	1	20.92*
1983/84	1	27.29*
1984/85	1	9.28*
1985/86	1	0.44
Total	4	57.93*

Appendix A

Table A-4. Statistical analyses of the distribution of coyote on wolf (COW>, COW<) prints recorded on established trails during snow tracking sessions from 1982-1986. Coyotes followed wolves a disproportionate number of times. Values marked by an asterisk are significantly different.

Tests	df	G
Pooled	1	120.53*
Heterogeneity	3	27.23*
Total	4	147.77*

Year	df	G
1982/83	1	3.28
1983/84	1	31.56*
1984/85	1	107.68*
1985/86	1	5.24*
Total	4	147.77

Appendix A

Table A-5. Statistical analyses of the distribution of wolf on coyote (WOC>, WOC<) prints recorded in snow tracking sessions from 1982-1986. Wolf tracks were randomly distributed relative to the direction of coyote travel. Values marked by an asterisk are significantly different.

Tests	df	G
Pooled	1	0.04
Heterogeneity	3	1.50
Total	4	1.54

Year	df	G
1982/83	1	0.59
1983/84	1	0.28
1984/85	1	0.63
1985/86	1	0.04
Total	4	1.54

Appendix A

Table A-6. Statistical analyses of the distribution of wolf on coyote (WOC>, WOC<) prints on new trails recorded in snow tracking sessions from 1982-1986. Wolf tracks were random relative to movements of coyotes. Values marked by an asterisk are significantly different.

Tests	df	G
Pooled	1	0.00
Heterogeneity	3	7.39
Total	4	7.39

Year	df	G
1982/83	1	4.94
1983/84	1	0.58
1984/85	1	0.08
1985/86	1	1.79
Total	4	7.39

Appendix A

Table A-7. Statistical analyses of the distribution of wolf on coyote (WOC>, WOC<) prints recorded on established trails in snow tracking sessions from 1982-1986. Wolf tracks were random relative to movements of coyotes. Values marked by an asterisk are significantly different.

Tests	df	G
Pooled	1	0.09
Heterogeneity	3	4.77
Total	4	4.87

Year	df	G
1982/83	1	0.47
1983/84	1	1.32
1984/85	1	1.64
1985/86	1	1.43
Total	4	4.87

APPENDIX B

Table B-1. Summary of statistical associations (_G_-test of independence) between mark types recorded on WO trails and the environments in which they were deposited. The null hypothesis stated that marks are deposited randomly, independent of location.

Year	G-value	df	P
1982-83	14.55*	4	< 0.010
1983-84	28.71*	4	< 0.001
1984-85	16.85*	4	< 0.005
1985-86	2.45	4	> 0.500
Pooled	46.95*	4	< 0.001

* significant

Appendix B

Table B-2. Statistical summary of observed versus expected values for mark types recorded in all travel environments on all wolf (WO) trails. For definition of mark types see text. Expected values were generated using procedures outlined by Lehner (1979). G-tests of goodness of fit were used to assess the relationships of frequency distributions (Sokal and Rohlf 1981).

	Wolf Only Trails			
Year	DU G-value	NDU G-value	SCR G-value	df
1982-83	57.84*	1.96	5.76	2
1983-84	105.50*	2.89	14.25*	2
1984-85	42.00*	1.00	7.40*	2
1985-86	30.09*	7.13*	-----	2
Total	235.43*	12.97	-----	8
Pooled	216.01*	12.15*	33.09*	2
Hetero.	19.42*	0.83	-----	6

* significant

Appendix B

Table B-3. Summary of statistical associations (*G*-test of independence) between mark types recorded on CO trails and the environments in which they were deposited. The null hypothesis stated that marks are deposited randomly, independent of location.

Year	G-value	df	P
1982-83	1.45	4	> 0.995
1983-84	3.75	4	> 0.900
1984-85	16.17*	4	> 0.025
1985-86	6.36	4	> 0.500
Pooled	7.78	4	> 0.500

* significant

Table B-4. Statistical summary of observed versus expected values for scent mark types recorded in all travel environments on all CO trails. For definitions of mark types see text. Expected values were generated using procedures outlined by Lehner (1979). G-tests of goodness of fit were used to examine frequency distributions (Sokal and Rohlf 1981).

	Coyote Only Trails			
Year	DU G-value	NDU G-value	SCR G-value	df
1982-83	8.65*	3.16	-----	2
1983-84	29.30*	0.67	-----	2
1984-85	53.26*	2.03	5.97*	2
1985-86	14.17*	12.16*	-----	2
Total	105.37*	18.02*	-----	8
Pooled	97.38*	12.04*	19.72*	2
Hetero.	7.99	5.98	-----	6

* significant

Appendix B

Table B-5. Summary of statistical associations (*G*-test of independence) between mark types recorded on COW trails and the environments in which they were deposited. The null hypothesis stated that marks are deposited randomly, independent of location.

Year	G-value	df	P
1982-83	15.23*	4	> 0.050
1983-84	3.15	4	> 0.900
1984-85	5.56	4	> 0.900
1985-86	4.45	4	> 0.900
Pooled	3.30	4	> 0.900

* significant

Appendix B

Table B-6. Statistical summary of observed versus expected values for scent mark types recorded in all travel environments on all COW trails. For definitions of mark types see text. Expected values were generated using procedures outlined by Lehner (1979). _G_-tests of goodness of fit were used to assess the relationships of frequency distributions (Sokal and Rohlf 1981).

	Coyote On Wolf			
Year	DU G-value	NDU G-value	SCR G-value	df
1982-83	62.00*	-----	-----	2
1983-84	20.14*	1.77	2.65	2
1984-85	46.62*	6.85*	4.40	2
1985-86	0.78	3.45	1.66	2
Total	129.54*	-----	-----	8
Pooled	74.34*	12.70*	5.82	2
Hetero.	55.20*	-----	-----	6

* significant

Appendix B

Table B-7. Summary of statistical associations (*G*-test of independence) between mark types recorded on WOC trails and the environments in which they were deposited. The null hypothesis stated that marks are deposited randomly, independent of location (Sokal and Rohlf 1981).

Year	G-Value	df	P
1982-83	2.36	4	> 0.975
1983-84	4.23	4	> 0.900
1984-85	3.10	4	> 0.900
1985-86	6.27	4	> 0.900
Pooled	6.24	4	> 0.900

Table B-8. Statistical summary of observed versus expected values for scent mark types recorded in all travel environments on all WOC trails. For definitions of mark types see text. Expected values were generated using procedures outlined by Lehner (1979). _G_-tests of goodness of fit were used to assess the relationships of frequency distributions.

	Wolf On Coyote			
Year	DU G-value	NDU G-value	SCR G-value	df
1982-83	26.99*	------	------	2
1983-84	46.78*	1.07	9.93*	2
1984-85	6.05*	------	------	2
1985-86	------	------	------	2
Total	------	------	------	8
Pooled	88.99*	6.94*	21.96*	2
Hetero.	------	------	------	6

* significant

Appendix B

Table B-9. Summary of _G_-tests for goodness of fit of the observed frequencies of winter marking by large wolf packs (LWP) and small wolf packs (SWP). Expected values were generated using procedures outlined by Lehner (1979).

	OBSERVED		EXPECTED				
Year	LWP	SWP	LWP	SWP	G-value	df	P
1982-83	206	94	173	127	15.361*	1	< 0.001
1983-84	253	209	202	260	22.642*	1	< 0.001
1984-85	200	219	169	250	9.381*	1	< 0.005
1985-86	212	89	186	115	9.855*	1	< 0.005
_G_-Total					57.239*	4	< 0.001
_G_-Pooled	871	611	730	752	53.897*	1	< 0.001
_G_-Hetero.					3.342	3	> 0.500

* significant

Table B-10. Summary of G-tests for goodness of fit of the observed frequencies of winter marking by single coyotes (SIN) and coyotes travelling in groups (GRP) of two or more. Expected values were generated using procedures outlined by Lehner (1979).

	OBSERVED		EXPECTED				
Year	SIN	GRP	SIN	GRP	G-value	df	P
1982-83	23	78	42	59	15.851*	1	< 0.001
1983-84	47	95	81	61	33.006*	1	< 0.001
1984-85	44	140	69	115	15.486*	1	< 0.001
1985-86	34	106	81	59	64.949*	1	< 0.001
G-Total					129.292*	4	< 0.001
G-Pooled	148	419	273	294	115.667*	1	< 0.001
G-Hetero.					13.625*	3	< 0.005

* significant

Appendix B

Table B-11. Summary of *G*-tests for goodness of fit of the observed frequencies of winter marking by large wolf packs (LWP) and coyotes using trails established by large wolf packs (COW). Expected values were generated using procedures outlined by Lehner (1979).

	OBSERVED		EXPECTED				
Year	LWP	COW	LWP	COW	G-value	df	P
1982-83	206	82	178	110	12.013*	1	< 0.001
1983-84	253	237	320	170	38.617*	1	< 0.001
1984-85	200	145	253	92	37.905*	1	< 0.001
1985-86	212	112	246	78	17.945*	1	> 0.001
G-Total					106.480*	4	< 0.001
G-Pooled	871	576	997	450	49.023*	1	< 0.001
G-Hetero.					57.457*	3	< 0.001

* significant

Appendix B

Table B-12. Summary of G-tests for goodness of fit of the observed frequencies of winter marking by large wolf packs (LWP) and large packs using trails established by coyotes (WOC). Expected values were generated using procedures outlined by Lehner (1979).

	OBSERVED		EXPECTED				
Year	LWP	WOC	LWP	WOC	G-value	df	P
1982-83	206	24	177	53	24.484*	1	< 0.001
1983-84	253	103	275	81	7.306*	1	< 0.010
1984-85	200	65	219	46	8.645*	1	< 0.005
1985-86	212	37	216	33	0.541	1	> 0.500
G-Total					40.976*	4	< 0.001
G-Pooled	871	229	887	213	1.463	1	> 0.900
G-Hetero.					39.513*	3	< 0.001

* significant

Appendix B

Table B-13. Summary of *G*-tests for goodness of fit of the observed frequencies of winter marking by small wolf packs (SWP) and coyotes using trails established by small wolf packs (COW). Expected values were generated using procedures outlined by Lehner (1979).

	OBSERVED		EXPECTED				
Year	SWP	COW	SWP	COW	G-value	df	P
1982-83	94	47	86	55	1.947	1	> 0.500
1983-84	209	190	270	129	40.096*	1	< 0.001
1984-85	219	146	271	94	35.256*	1	< 0.001
1985-86	89	97	120	66	21.505*	1	< 0.001
G-Total					98.354*	4	< 0.001
G-Pooled	611	480	747	344	74.235*	1	< 0.001
G-Hetero.					24.119*	3	< 0.001

Table B-14. Summary of _G_-tests for goodness of fit of the observed frequencies of winter marking by small wolf packs (SWP) and small wolf packs using trails established by coyotes (WOC). Expected values were generated using procedures outlined by Lehner (1979).

	OBSERVED		EXPECTED				
Year	SWP	WOC	SWP	WOC	G-value	df	P
1982-83	94	16	86	24	3.747	1	> 0.100
1983-84	209	122	239	92	12.799*	1	< 0.001
1984-85	219	73	244	48	13.865*	1	< 0.001
1985-86	89	46	116	19	34.185*	1	< 0.001
_G_-Total					64.596*	4	< 0.001
_G_-Pooled	611	257	685	183	34.828*	1	< 0.001
_G_-Hetero.					99.424*	3	< 0.001

APPENDIX C

Table C-1. Summary of scent-marking rates recorded for the Whitewater wolf pack (9 animals) in winter 1982-83.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	38	(106) 2.79	(27) 0.71	(16) 0.42	(149) 3.92
Bush	26	(18) 0.69	(19) 0.73	(10) 0.38	(47) 1.81
Frozen waterways	10	(4) 0.40	(5) 0.50	(1) 0.10	(10) 0.41
Comb. rate:		1.49	0.69	0.36	2.78
Total dist:	74				

Table C-2. Summary of scent-marking rates recorded for the Pacey Lake wolf pack (4 animals) in winter 1982-83.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	15	(19) 1.27	(10) 0.67	(3) 0.20	(32) 2.13
Bush	31	(31) 1.00	(18) 0.58	(6) 0.19	(55) 2.52
Frozen waterways	8	(5) 0.63	(2) 0.25	(0) 0.00	(7) 0.88
Comb. rate:		1.02	0.56	0.17	1.74
Total dist:	54				

Table C-3. Summary of combined scent-marking rates recorded for wolf packs in winter 1982-83.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	53	(126) 2.38	(37) 0.70	(19) 0.36	(182) 3.43
Bush	57	(49) 0.86	(37) 0.65	(16) 0.28	(102) 1.79
Frozen waterways	18	(9) 0.50	(7) 0.39	(1) 0.06	(17) 0.94
Comb. rate:		1.44	0.63	0.28	2.35
Total dist:	128				

Table C-4. Summary of scent-marking rates recorded for the Baldy Lake wolf pack (10 animals) in winter 1983-84.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	62	(118) 1.90	(36) 0.58	(11) 0.18	(165) 2.66
Bush	39	(47) 1.21	(22) 0.56	(8) 0.21	(77) 1.97
Frozen waterways	14	(5) 0.36	(6) 0.43	0.00	(11) 0.79
Comb. rate:		1.48	0.56	0.17	2.20
Total dist:	115				

Table C-5. Summary of scent-marking rates recorded for the Clear Lake wolf pack (3 animals) in winter 1983-84.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	35	(45) 1.29	(16) 0.46	(10) 0.29	(71) 2.03
Bush	60	(60) 1.00	(29) 0.48	(20) 0.33	(109) 1.82
Frozen waterways	53	(7) 0.13	(19) 0.36	(3) 0.06	(29) 0.55
Comb. rate:		0.76	0.43	0.22	1.41
Total dist:	148				

Table C-6. Summary of combined scent-marking rates recorded for wolf packs in winter 1983-84.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	97	(163) 1.68	(52) 0.54	(21) 0.22	(236) 2.43
Bush	99	(107) 1.08	(51) 0.52	(28) 0.28	(186) 1.88
Frozen waterways	67	(12) 0.18	(24) 0.36	(3) 0.04	(39) 0.58
Comb. rate:		1.07	0.48	0.20	1.75
Total dist:	263				

Table C-7. Summary of scent-marking rates recorded for the Audy Lake wolf pack (5 animals) in winter 1984-85.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	51	(87) 1.71	(37) 0.73	(15) 0.29	(139) 2.73
Bush	24	(24) 1.00	(19) 0.79	(10) 0.42	(53) 2.21
Frozen waterways	7	(4) 0.57	(3) 0.43	(1) 0.14	(8) 1.14
Comb. rate:		1.40	0.72	0.32	2.44
Total dist:	82				

Table C-8. Summary of scent-marking rates recorded for the Clear Lake wolf pack (2 animals) in winter 1984-85.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	63	(76) 1.21	(43) 0.68	(20) 0.32	(139) 2.21
Bush	36	(29) 0.81	(22) 0.61	(12) 0.33	(63) 1.75
Frozen waterways	22	(3) 0.14	(13) 0.59	(1) 0.05	(17) 0.77
Comb. rate:		0.89	0.64	0.27	1.81
Total dist:	121				

Table C-9. Summary of combined scent-marking rates recorded for wolf packs in winter 1984-85.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	114	(163) 1.45	(80) 0.70	(35) 0.31	(278) 2.44
Bush	60	(53) 0.90	(41) 0.68	(22) 0.37	(116) 1.93
Frozen waterways	29	(7) 0.38	(16) 0.55	(2) 0.07	(25) 0.86
Comb. rate:		1.10	0.67	0.29	2.06
Total dist:	203				

Table C-10. Summary of scent-marking rates recorded for the Pacey Lake wolf pack (10 animals) in winter 1985-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	56	(111) 1.98	(39) 0.70	(10) 0.23	(163) 2.91
Bush	19	(28) 1.47	(8) 0.42	(4) 0.21	(40) 2.11
Frozen waterways	16	(11) 0.69	(5) 0.31	(3) 0.00	(9) 0.56
Comb. rate:		1.65	0.57	0.19	2.32
Total dist:	91				

Table C-11. Summary of scent-marking rates recorded for the Clear Lake wolf pack (3 animals) in winter 1985-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	21	(27) 1.29	(11) 0.52	(3) 0.14	(41) 1.95
Bush	24	(31) 1.29	(9) 0.38	(1) 0.04	(41) 1.71
Frozen waterways	11	(2) 0.18	(3) 0.27	(1) 0.09	(7) 0.64
Comb. rate:		1.07	0.41	0.09	1.43
Total dist:	56				

Table C-12. Summary of combined scent-marking rates recorded for wolf packs in winter 1985-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	77	(138) 1.79	(50) 0.65	(16) 0.21	(204) 2.65
Bush	43	(59) 1.37	(17) 0.36	(7) 0.01	(81) 1.88
Frozen waterways	27	(13) 2.08	(8) 0.30	(1) 0.04	(16) 0.59
Comb. rate:					2.05
Total dist:	147				

Table C-13. Summary of scent-marking rates recorded for two or more coyotes in winter 1982-83.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	32	(26) 0.81	(16) 0.50	(13) 0.41	(55) 1.72
Bush	17	(6) 0.35	(7) 0.41	(6) 0.35	(19) 1.12
Frozen waterways	6	(1) 0.17	(2) 0.33	(1) 0.17	(4) 0.67
Comb. rate:		0.60	0.45	0.36	1.42
Total dist:	55				

Table C-14. Summary of scent-marking rates recorded for one coyote in winter 1982-83.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	22	(9) 0.41	(9) 0.41	0.00	(18) 0.86
Bush	9	(2) 0.22	(2) 0.22	0.00	(4) 0.44
Frozen waterways	7	(1) 0.14	0.00	0.00	(1) 0.14
Comb. rate:		0.31	0.28	0.00	0.59
Total dist:	39				

Table C-15. Summary of combined scent-marking rates recorded for coyotes in winter 1982-83.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	54	(35) 0.65	(25) 0.46	(13) 0.24	(73) 1.35
Bush	26	(8) 0.31	(9) 0.35	(6) 0.23	(23) 0.88
Frozen waterways	13	(2) 0.15	(2) 0.15	(1) 0.08	(5) 0.38
Comb. rate:		0.48	0.30	0.22	1.09
Total dist:	93				

Table C-16. Summary of scent-marking rates recorded for two or more coyotes in winter 1983-84.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	29	(42) 1.45	(9) 0.31	(20) 0.69	(71) 2.45
Bush	16	(13) 0.81	(5) 0.31	(4) 0.25	(22) 1.38
Frozen waterways	9	(1) 0.11	(1) 0.11	0.00	(2) 0.22
Comb. rate:		0.79	0.24	0.31	1.76
Total dist:	54				

Table C-17. Summary of scent-marking rates recorded for one coyote in winter 1983-84.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	39	(32) 0.82	(4) 0.10	(1) 0.03	(37) 0.95
Bush	22	(7) 0.32	(1) 0.05	0.00	(8) 0.36
Frozen waterways	11	(1) 0.09	(1) 0.09	0.00	(2) 0.18
Comb. rate:		0.56	0.08	0.01	0.65
Total dist:	72				

Table C-18. Summary of combined scent-marking rates recorded for coyotes in winter 1983-84.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	68	(74) 1.09	(13) 0.19	(21) 0.31	(108) 1.69
Bush	38	(20) 0.53	(6) 0.16	(4) 0.11	(30) 0.79
Frozen waterways	20	(2) 0.10	(2) 0.10	(1) 0.05	(4) 0.20
Comb. rate:		0.76	0.17	0.20	1.13
Total dist:	126				

Table C-19. Summary of scent-marking rates recorded for two or?more coyotes in winter 1984-85.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	47	(71) 1.51	(18) 0.38	(24) 0.51	(113) 2.40
Bush	19	(6) 0.32	(8) 0.42	(7) 0.37	(21) 1.11
Frozen waterways	13	(1) 0.08	(3) 0.23	(2) 0.15	(6) 0.46
Comb. rate:		0.99	0.37	0.42	1.77
Total dist:	79				

Table C-20. Summary of scent-marking rates recorded for one coyote in winter 1984-85.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	29	(25) 0.86	(6) 0.21	(5) 0.17	(36) 1.24
Bush	9	(2) 0.22	(2) 0.23	(2) 0.22	(6) 0.67
Frozen waterways	9	(1) 0.11	(1) 0.11	0.00	(2) 0.22
Comb. rate:		0.60	0.19	0.15	0.94
Total dist:	47				

Table C-21. Summary of combined scent-marking rates recorded for coyotes in winter 1984-85.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	76	(96) 1.18	(24) 0.32	(29) 0.38	(149) 1.96
Bush	28	(8) 0.25	(10) 0.36	(9) 0.32	(27) 0.96
Frozen waterways	22	(2) 0.10	(4) 0.18	(2) 0.09	(8) 0.36
Comb. rate:		0.84	0.30	0.32	1.46
Total dist:	126				

Table C-22. Summary of scent-marking rates recorded for two or more coyotes in winter 1985-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	29	(61) 2.10	(18) 0.62	(11) 0.38	(90) 3.10
Bush	8	(7) 0.88	(1) 0.13	(0) 0.00	(10) 1.25
Frozen waterways	4	(6) 1.50	(0) 0	(0) 0	(6) 1.50
Comb. rate:		1.80	0.46	0.27	2.59
Total dist:	41				

Table C-23. Summary of scent-marking rates recorded for one coyote in winter 1984-85.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	34	(20) 0.59	(6) 0.30	(1) 0.03	(27) 0.79
Bush	6	(3) 0.50	(0) 0	(0) 0	(3) 0.50
Frozen waterways	17	(3) 0.18	(1) 0.06	(0) 0	(4) 0.24
Comb. rate:		0.46	0.12	0.02	0.60
Total dist:	37				

Table C-24. Summary of combined scent-marking rates recorded for coyotes in winter 1985-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	63	(81) 1.29	(24) 0.38	(12) 0.19	(117) 1.86
Bush	14	(10) 0.71	(1) 0.07	(0) 0	(13) 0.93
Frozen waterways	21	(9) 0.43	(1) 0.05	(0) 0	(10) 0.48
Comb. rate:					1.43
Total dist:	98				

Table C-25. Summary of scent-marking rates recorded for coyotes using trails established by the Whitewater wolf pack (9 animals) in winter 1982-83.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	24	(53) 2.29	(5) 0.21	(6) 0.25	(66) 2.75
Bush	12	(5) 0.42	(3) 0.25	(4) 0.33	(12) 1.00
Frozen waterways	10	(1) 0.10	(2) 0.20	(1) 0.10	(4) 0.40
Comb. rate:		0.94	0.22	0.23	1.78
Total dist:	46				

Table C-26. Summary of scent-marking rates recorded for coyotes using trails established by the Pacey Lake wolf pack (4 animals) in winter 1982-83.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	15	(28) 1.87	(3) 0.20	(4) 0.27	(35) 2.33
Bush	12	(6) 0.50	(2) 0.17	(2) 0.17	(10) 0.83
Frozen waterways	8	(1) 0.13	(1) 0.13	0.00	(2) 0.25
Comb. rate:		0.83	0.17	0.22	1.34
Total dist:	35				

Table C-27. Summary of combined scent-marking rates recorded for coyotes using trails established by wolf packs in winter 1982-83.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	39	(83) 2.13	(8) 0.21	(10) 0.26	(101) 2.59
Bush	24	(11) 0.46	(5) 0.21	(6) 0.25	(22) 0.92
Frozen waterways	18	(2) 0.17	(3) 0.17	(1) 0.06	(6) 0.33
Comb. rate:		1.19	0.20	0.21	1.59
Total dist:	81				

Table C-28. Summary of scent-marking rates recorded for coyotes using trails established by the Baldy Lake wolf pack (10 animals) in winter 1983-84.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	35	(126) 3.60	(13) 0.37	(9) 0.26	(148) 4.23
Bush	21	(58) 2.76	(10) 0.48	(7) 0.33	(75) 3.57
Frozen waterways	5	(12) 2.40	(2) 0.40	0.00	(14) 2.80
Comb. rate:		3.21	0.41	0.26	3.89
Total dist:	61				

Table C-29. Summary of scent-marking rates recorded for coyotes using trails established by the Clear Lake wolf pack (3 animals) in winter 1983-84.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	15	(44) 2.93	(5) 0.33	(5) 0.33	(54) 3.60
Bush	41	(86) 2.10	(13) 0.32	(11) 0.27	(110) 2.68
Frozen waterways	15	(22) 1.47	(2) 0.13	(2) 0.13	(26) 1.73
Comb. rate:		2.14	0.28	0.24	2.68
Total dist:	71				

Table C-30. Summary of combined scent-marking rates recorded for coyotes using trails established by wolf packs in winter 1983-84.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	50	(170) 3.40	(18) 0.36	(14) 0.28	(202) 4.04
Bush	62	(144) 2.32	(23) 0.37	(18) 0.29	(185) 2.98
Frozen waterways	20	(34) 1.70	(4) 0.20	(2) 0.10	(40) 2.00
Comb. rate:		2.64	0.34	0.26	3.23
Total dist:	132				

Table C-31. Summary of scent-marking rates recorded for coyotes using trails established by the Audy Lake wolf pack (5 animals) in winter 1984-85.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	21	(80) 3.81	(21) 1.00	(15) 0.71	(116) 5.52
Bush	6	(13) 2.17	(8) 1.33	(3) 0.50	(24) 4.00
Frozen waterways	3	(2) 0.67	(2) 0.67	(1) 0.33	(5) 1.67
Comb. rate:		3.17	1.03	0.63	4.83
Total dist:	30				

Table C-32. Summary of scent-marking rates recorded for coyotes using trails established by the Clear Lake wolf pack (2 animals) in winter 1984-85.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	19	(55) 2.89	(27) 1.42	(9) 0.47	(91) 4.79
Bush	13	(26) 2.00	(14) 1.08	(7) 0.54	(47) 3.62
Frozen waterways	10	(3) 0.30	(4) 0.40	(1) 0.10	(8) 0.80
Comb. rate:		2.00	1.07	0.40	3.48
Total dist:	42				

Table C-33. Summary of combined scent-marking rates recorded for coyotes using trails established by wolves in winter 1984-85.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	40	(135) 3.38	(48) 1.20	(24) 0.60	(207) 5.18
Bush	19	(39) 2.05	(22) 1.16	(10) 0.53	(71) 3.74
Frozen waterways	13	(5) 0.38	(6) 0.54	(2) 0.15	(13) 1.00
Comb. rate:		2.49	1.06	0.50	4.04
Total dist:	72				

Table C-34. Summary of scent-marking rates recorded for coyotes using trails established by the Pacey L. wolf pack (10 animals) in winter 1985-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	18	(41) 2.28	(16) 0.89	(10) 0.56	(67) 3.72
Bush	4	(17) 4.25	(2) 0.50	(5) 1.25	(24) 6.00
Frozen waterways	7	(14) 2.00	(3) 0.43	(4) 0.57	(21) 3.00
Comb. rate:		2.48	0.72	0.66	3.86
Total dist:	29				

Table C-35. Summary of scent-marking rates recorded for coyotes using trails established bye the Clear Lake wolf pack (3 animals) in winter 1985-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	20	(45) 2.25	(10) 0.50	(3) 0.15	(58) 2.90
Bush	6	(13) 2.17	(5) 0.83	(1) 0.17	(19) 3.17
Frozen waterways	5	(18) 3.60	(0) 0	(2) 0.40	(20) 4.00
Comb. rate:		1.97	0.48	0.19	3.13
Total dist:	31				

Table C-36. Summary of combined scent-marking rates recorded for coyotes using trails established by wolves in winter 1985-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	38	(96) 2.5	(26) 0.68	(13) 0.34	(125) 3.29
Bush	10	(30) 3.00	(7) 0.70	(6) 0.06	(43) 4.30
Frozen waterways	12	(32) 2.67	(3) 0.25	(6) 0.50	(41) 3.42
Comb. rate:					3.48
Total dist:	60				

Table C-37. Summary of scent-marking rates recorded for Whitewater wolves using trails established by coyotes in winter 1982-83.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	6	(12) 2.00	(1) 0.17	(2) 0.33	(15) 2.50
Bush	8	(3) 0.38	(2) 0.25	(1) 0.13	(8) 0.75
Frozen waterways	7	(1) 0.14	0.00	0.00	(1) 0.14
Comb. rate:		0.68	0.14	0.14	1.09
Total dist:	22				

Table C-38. Summary of scent-marking rates recorded for Pacey Lake wolves using trails established by coyotes in winter 1982-83.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	7	(11) 1.57	(1) 0.14	(2) 0.29	(14) 2.00
Bush	5	(2) 0.40	0.00	0.00	(2) 0.40
Frozen waterways	3	0.00	0.00	0.00	0.00
Comb. rate:		0.87	0.07	0.13	1.23
Total dist:	15				

Table C-39. Summary of combined scent-marking rates recorded for wolves using trails established by coyotes in winter 1982-83.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	13	(23) 1.77	(2) 0.15	(4) 0.31	(29) 1.23
Bush	13	(5) 0.39	(2) 0.15	(1) 0.08	(8) 0.62
Frozen waterways	10	(1) 0.10	0.00	0.00	(1) 0.10
Comb. rate:		0.78	0.11	0.14	1.03
Total dist:	37				

Table C-40. Summary of scent-marking rates recorded for Baldy Lake wolves using trails established by coyotes in winter 1983-84.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	20	(62) 3.10	(8) 0.40	(8) 0.40	(78) 3.90
Bush	8	(15) 1.88	(4) 0.50	(2) 0.25	(21) 2.63
Frozen waterways	6	(2) 0.33	(2) 0.33	0.00	(4) 0.67
Comb. rate:		2.32	0.41	0.29	3.03
Total dist:	34				

Table C-41. Summary of scent-marking rates recorded for Clear Lake wolves using trails established by coyotes in winter 1983-84.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	22	(53) 2.41	(6) 0.27	(10) 0.45	(69) 3.14
Bush	20	(30) 1.50	(4) 0.20	(8) 0.40	(42) 2.10
Frozen waterways	15	(8) 0.53	(2) 0.13	(1) 0.07	(11) 0.73
Comb. rate:		1.60	0.21	0.33	2.14
Total dist:	57				

Table C-42. Summary of combined scent-marking rates recorded for wolves using trails established by coyotes in winter 1983-84.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	42	(115) 2.74	(14) 0.33	(18) 0.43	(147) 3.50
Bush	28	(45) 1.61	(8) 0.29	(10) 0.36	(63) 2.25
Frozen waterways	21	(10) 0.48	(4) 0.19	(1) 0.05	(15) 0.71
Comb. rate:		1.87	0.29	0.32	2.47
Total dist:	91				

Table C-43. Summary of scent-marking rates recorded for Audy Lake wolves using trails established by coyotes in winter 1984-85.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	10	(27) 2.70	(6) 0.60	(9) 0.90	(42) 4.20
Bush	5	(14) 2.80	(4) 0.80	(3) 0.60	(21) 4.20
Frozen waterways	2	(2) 1.00	0.00	0.00	(2) 1.00
Comb. rate:		2.53	0.59	0.71	3.82
Total dist:	17				

Table C-44. Summary of scent-marking rates recorded for Clear Lake wolves using trails established by coyotes in winter 1984-85.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	8	(17) 2.13	(4) 0.50	(4) 0.50	(25) 3.13
Bush	14	(28) 2.00	(9) 0.64	(10) 0.71	(47) 3.36
Frozen waterways	2	(1) 0.50	0.00	0.00	(1) 0.50
Comb. rate:		1.92	0.54	0.58	3.04
Total dist:	24				

Table C-45. Summary of combined scent-marking rates recorded for wolves using trails established by coyotes in winter 1984-85.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	18	(44) 2.44	(10) 0.56	(13) 0.72	(67) 3.72
Bush	19	(42) 2.21	(13) 0.68	(13) 0.68	(68) 3.58
Frozen waterways	4	(3) 0.75	0.00	0.00	(3) 0.75
Comb. rate:		2.17	0.56	0.63	3.37
Total dist:	41				

Table C-46. Summary of scent-marking rates recorded for Pacey Lake wolves using trails established by coyotes in winter 1985-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	10	(24) 2.40	(5) 0.50	(2) 0.20	(31) 3.10
Bush	3	(5) 1.67	(0) 0	(1) 0.33	(6) 2.00
Frozen waterways	1	(0) 0	(0) 0	(0) 0	(0) 0
Comb. rate:		2.07	0.36	0.21	2.64
Total dist:	14				

Table C-47. Summary of scent-marking rates recorded for Clear Lake wolves using trails established by coyotes in winter 1985-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	5	(26) 5.20	(0) 0	(4) 0.80	(30) 6.00
Bush	4	(13) 3.25	(2) 0.50	(1) 0.25	(16) 4.00
Frozen waterways	0	(0) 0	(0) 0	(0) 0	(0) 0
Comb. rate:					5.11
Total dist:	9				

Table C-48. Summary of combined scent-marking rates recorded for wolves using trails established by coyotes in winter 1985-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	15	(50) 3.33	(5) 0.33	(5) 0.33	(61) 4.07
Bush	7	(18) 0.38	(2) 0.29	(2) 0.29	(22) 3.14
Frozen waterways	1	(0) 0	(0) 0	(0) 0	(0) 0
Comb. rate:					
Total dist:	23				

Table C-49. Summary of large wolf pack scent-marking rates, 1982-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	207	(422) 2.04	(139) 0.67	(45) 0.22	(606) 2.93
Bush	108	(117) 1.08	(68) 0.63	(32) 0.30	(217) 2.01
Frozen waterways	47	(24) 0.51	(19) 0.40	(2) 0.04	(45) 0.96
Comb. rate:					2.40
Total dist:	362				

Table C-50. Summary of small wolf pack scent-marking rates, 1982-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	134	(167) 1.25	(80) 0.60	(36) 0.27	(283) 2.11
Bush	151	(151) 1.00	(78) 0.52	(39) 0.26	(268) 1.77
Frozen waterways	94	(17) 0.18	(37) 0.39	(5) 0.05	(59) 0.99
Comb. rate:					1.61
Total dist:	379				

Table C-51. Summary of combined small wolf pack and large wolf pack scent-marking rates, 1982-1986.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	341	(590) 1.70	(219) 0.64	(91) 0.27	(900) 2.64
Bush	259	(268) 1.03	(146) 0.57	(73) 0.28	(487) 1.88
Frozen waterways	141	(41) 0.29	(55) 0.39	(7) 0.05	(103) 0.73
Comb. rate:					2.01
Total dist:	741				

Table C-52. Summary of scent-marking rates for two or more coyotes, 1982-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	137	(200) 1.46	(61) 0.45	(68) 0.50	(329) 2.40
Bush	60	(32) 0.53	(21) 0.35	(17) 0.28	(70) 1.17
Frozen waterways	32	(9) 0.28	(6) 1.88	(3) 0.09	(18) 1.78
Comb. rate: Total dist:	229				

Table C-53. Summary of single coyote marking rates, 1982-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	124	(86) 0.69	(25) 0.20	(7) 0.06	(118) 0.95
Bush	46	(14) 0.30	(5) 0.11	(2) 0.04	(21) 0.46
Frozen waterways	44	(6) 0.14	(3) 0.07	(0) 0	(9) 0.20
Comb. rate: Total dist:	214				

Table C-54. Summary of combined coyote marking rates, 1982-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	261	(286) 1.10	(86) 0.33	(75) 0.29	(447) 1.71
Bush	106	(46) 0.43	(26) 0.25	(19) 0.18	(91) 0.86
Frozen waterways	76	(15) 0.20	(9) 0.12	(4) 0.05	(28) 0.37
Comb. rate: Total dist:	443				1.28

Table C-55. Summary of scent-marking rates for coyotes following large wolf packs, 1982-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	98	(300) 3.06	(55) 0.56	(40) 0.41	(395) 4.03
Bush	43	(93) 1.19	(23) 0.53	(19) 0.45	(135) 3.14
Frozen waterways	25	(29) 1.16	(9) 0.36	(6) 0.24	(44) 1.76
Comb. rate:					3.46
Total dist:	166				

Table C-56. Summary of scent-marking rates for coyotes following small wolf packs, 1982-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	69	(172) 2.49	(45) 0.65	(21) 0.30	(283) 3.45
Bush	72	(131) 1.82	(34) 0.47	(21) 0.29	(186) 2.58
Frozen waterways	38	(44) 1.16	(7) 0.18	(5) 0.13	(56) 1.47
Comb. rate:					2.93
Total dist:	179				

Table C-57. Summary of combined scent-marking rates for coyotes following wolf packs, 1982-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	167	(484) 2.90	(100) 0.60	(61) 0.37	(645) 3.86
Bush	115	(224) 1.95	(57) 0.50	(40) 0.35	(321) 2.79
Frozen waterways	63	(73) 1.16	(16) 0.25	(11) 0.17	(100) 1.59
Comb. rate:					1.61
Total dist:	379				

Table C-58. Summary of scent-marking rates for large wolf packs following coyotes, 1982-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	46	(125) 2.7	(20) 0.43	(21) 0.46	(166) 3.40
Bush	24	(37) 1.54	(10) 0.42	(7) 0.29	(54) 2.25
Frozen waterways	16	(5) 0.31	(2) 0.13	(0) 0	(7) 0.44
Comb. rate:					2.64
Total dist:	86				

Table C-59. Summary of scent-marking rates for small wolf packs following coyotes, 1982-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	42	(107) 2.55	(11) 0.26	(20) 0.48	(138) 3.29
Bush	43	(73) 1.70	(15) 0.35	(19) 0.44	(107) 2.49
Frozen waterways	20	(9) 0.45	(2) 0.10	(1) 0.05	(12) 0.60
Comb. rate:					2.45
Total dist:	105				

Table C-60. Summary of combined scent-marking rates for wolves following coyotes, 1982-86.

	Distance	DU/km	NDU/km	Scratches/km	Rate
Roads & trails	88	(232) 2.64	(31) 0.32	(41) 0.47	(304) 3.45
Bush	67	(110) 1.64	(25) 0.37	(26) 0.39	(161) 2.40
Frozen waterways	36	(14) 0.39	(4) 0.11	(1) 0.03	(19) 0.53
Comb. rate:					2.53
Total dist:	191				