

WINTER SPATIAL RELATIONSHIPS OF WOLVES AND COYOTES IN RIDING MOUNTAIN NATIONAL PARK, MANITOBA

PAUL C. PAQUET

Department of Zoology, University of Alberta, Edmonton, Alberta, Canada T6G 2N1
Present address: Box 1443, Canmore, Alberta, Canada T0L 0M0

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

Investigators of parapatric or sympatric populations of wolves (*Canis lupus*) and coyotes (*C. latrans*) have shown that coyotes tend to be situated outside areas of intense wolf activity, implying avoidance of wolves by coyotes (Berg and Chesness, 1978; Carbyn, 1982; Fuller and Keith, 1981; Hoskinson and Mech, 1976). However, distribution of the two species might simply reflect differences in habitat selection and use of prey (Todd et al., 1985). Alternatively, coyotes and wolves may favor similar environments. Spatial segregation could result from predation or harassment of coyotes by wolves. In such circumstances, survival of coyotes probably would be higher in zones peripheral to areas of high wolf density. Over time, coyotes might learn to recognize the risks of living close to wolves (Carbyn, 1982). Allopatric distribution then would be attributable to avoidance.

In Riding Mountain National Park, Manitoba, coyotes occupy home ranges entirely within the boundaries of wolf territories, and do not appear to avoid wolves (Carbyn, 1982; Paquet, 1989). Moreover, coyotes in Riding Mountain National Park and elsewhere often track wolves through snow. The possible spatial relationships between sympatric wolves and coyotes in Riding Mountain National Park are: coyote movements are random relative to wolves; coyotes are attracted to wolf areas; or coyotes avoid wolf areas. The objective of this study was to assess winter movements of both canids to determine which interspecific relationship prevails. I hypothesized that coyotes would avoid active wolf areas and that mutual use of trails would occur randomly.

STUDY AREA

Riding Mountain National Park is a 2,974-km² nature reserve (51°N, 100°W) in southwestern Manitoba with an elevational range of 319–756 m. The park occupies a transition zone between prairie grasslands to the south and boreal forests to the north. Dominant cover is aspen-poplar forest (*Populus tremuloides*, *P. balsamifera*), interspersed with sedge (*Carex* sp.)-willow (*Salix* sp.) wetlands, upland fescue (*Festuca* sp.) prairie, and mixed-coniferous forest. Agriculture has modified drastically the surrounding landscape so that the park is now an isolated segment of the once expansive aspen-parkland region.

The weather is dry continental (Carbyn, 1982). July is the warmest month with a mean daily temperature of 16.2°C and January the coldest with a mean daily temperature of -20.7°C (Environment Canada, Atmospheric Environment Service, 1988). Snow accumulation is moderate with maximum depth usually ≤50 cm.

Moose (*Alces alces*) and elk (*Cervus elaphus*) are common throughout the park. White-tailed deer (*Odocoileus virginianus*) are seasonally abundant. Mammalian carnivores include black bears (*Ursus americanus*), lynx (*Felis lynx*), and several mustelids. Red foxes (*Vulpes vulpes*) are rare within the park interior, but common in adjacent agricultural areas. Snowshoe hare (*Lepus americanus*) populations peaked in 1982 and remained low throughout the study.

METHODS

Information about wolf and coyote travel was collected by means of snow tracking from 1982 to 1986. In 1982–1984, snow tracking was supplemented, for coyotes only, by aerial and ground radiotelemetry.

Canid trails were selected haphazardly (Lehner, 1979). Five successive kilometers of tracking constituted

TABLE 1.—Summary of wolf and coyote track patterns on new and established trails recorded from 1982 to 1986 within the boundaries of four wolf territories in Riding Mountain National Park, Manitoba. One unit of track was defined as 100 m of continuous print.

Print	Units of tracks		
	New	Established	Total
Wolf backtracks coyote	143	266	409
Wolf follows coyote	144	259	403
Coyote backtracks wolf	201	322	523
Coyote follows wolf	356	663	1,019
Wolf only	516	1,292	1,808
Coyote only	338	850	1,188
Totals	1,698	3,652	5,350

a "tracking session," and each tracking session was divided into 100-m units. Distances were measured by pedometer or odometer. Fresh canid tracks (0–2 days after snowfall) were classified as wolf only, coyote only, wolf on coyote, or coyote on wolf. When tracks of both species were evident, overlapping prints were examined to determine which species used the trail first, and the direction of travel. The categories wolf on coyote, and coyote on wolf, were subdivided according to whether both species were traveling in the same or opposite directions.

To avoid biases from the influence of snow conditions, data were collected from routes on which >20 cm of snow had accumulated (new trails), and routes on which there was evidence of a definite path and <20 cm of accumulated snow (established trails).

The following tracking data were recorded: estimated number of both species; units of wolf-only and coyote-only tracks; units of wolf on coyote and coyote on wolf; direction of tracks; and number of times two trails approached, joined, or crossed. The following possibilities were recognized: both trails had been used by the same species or each trail had been used by a different species; junctions, at which a canid intercepted a trail and followed it toward the preceding user by one or more units; junctions, at which a canid intercepted a trail and followed it away from the preceding user by one or more units; approaches, at which a canid avoided an intercepted trail by not crossing it and not moving parallel to it for one or more units; crossings, at which a second traveler crossed the first trail and continued on the same course for one or more units—ignored the trail.

Frequency data were analyzed 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), which allowed for year-by-year analysis. Except for summed and partitioned values, all *G*-values were adjusted using Williams' continuity correction (Sokal and Rohlf, 1981).

Replicated goodness-of-fit tests (*G*-statistic; 1982–1986) 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/number of categories × total observations.

Relationships between track patterns and trail conditions were evaluated by means of the *G*-test of independence. *G*-values for multiple comparisons were determined by use of Sidak's multiplicative inequality (Sokal and Rohlf, 1981).

RESULTS

Overall, 535 km (5,350 units) of tracks were surveyed and 690 trail intersections were evaluated. Wolf-only tracks (34%) constituted the most frequent category of prints (Table 1). Of all track segments, 44% were used by both species. Within that subsample, coyotes following wolves occurred at the highest frequency (43%) in each of the 4 years. The second most common classification, coyotes backtracking wolves, occurred about one-half as often (23%).

Track patterns were independent of the estimated size of the wolf pack for both new and established trails ($G = 1.321$, *d.f.* = 10; $G = 2.134$, *d.f.* = 10, respectively). Track patterns also were independent of which species established the trail ($G = 3.12$, *d.f.* = 5). Therefore, data for different pack sizes and trail origins were pooled for analysis.

TABLE 2.—Summary of wolf and coyote behaviors at interspecific trail junctions. Observations were recorded during periods of snow cover from 1982 to 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.

Behavior	Intersection	
	Wolf intercepted coyote trail	Coyote intercepted wolf trail
Ignored trail	117	23
Followed trail same direction	37	98
Followed trail opposite direction	13	50
Avoided trail	5	54
Total observations	172	225

There was a highly significant difference in the occurrence of track patterns recorded on new and established trails ($G = 34.77$, $d.f. = 3$, $P < 0.001$). Simultaneous test procedures indicated that the overlap categories were a homogeneous subgrouping ($G = 2.01$, $d.f. = 3$), as were the single-track categories, wolf only, and coyote only ($G = 1.12$, $d.f. = 1$). Consequently, the two subgroups were examined independently for all snow conditions.

The frequencies of coyote on wolf tracks, and wolf on coyote tracks, differed significantly from expected values ($G = 11.64$, $d.f. = 3$, $P < 0.01$). Coyotes following wolves occurred a disproportionate number of times ($G = 16.00$, $d.f. = 3$, $P < 0.01$). In general, the pattern was consistent for all four winters. In contrast, there was no significant difference in the frequency of wolves following or backtracking coyotes ($G = 1.50$, $d.f. = 3$). There was a highly significant difference in the reaction of wolves and coyotes to interspecific trail junctions ($G = 30.49$, $d.f. = 3$, $P < 0.001$). For coyotes, the original direction of travel was maintained in only 10%, and was altered in 90% of the observations. In contrast, wolves maintained direction of travel in 68% of encounters with coyote trails (Table 2). However, once on an intersecting trail, wolves and coyotes tended to travel the same direction as the canid that preceded ($G = 1.06$, $d.f. = 1$, $P > 0.50$). In contrast, the behavior of wolves and coyotes that did not use an intersecting trail was significantly different ($G = 105.21$, $d.f. = 1$, $P < 0.001$). Wolves tended to ignore the intersecting trails, whereas coyotes avoided them.

A canid that approached a trail crossing had several options. For example, a coyote could ignore a wolf trail, follow wolf tracks, backtrack wolves, or turn and avoid a trail. I tested the rate of observed behaviors against the expectation that each of these options was equally probable. Choices by coyotes differed significantly from the expected distribution ($G = 49.84$, $d.f. = 3$, $P < 0.001$). Coyotes usually followed wolf tracks. The decision to follow, rather than backtrack was nonrandom ($G = 15.80$, $d.f. = 1$, $P < 0.001$). Coyotes that did not use intersecting trails tended to avoid the trails rather than ignore them ($G = 10.16$, $d.f. = 1$, $P = 0.001$).

The response of wolves to coyote trails was nonrandom ($G = 169.67$, $d.f. = 3$, $P < 0.001$). Their reaction was to ignore them (68%) and maintain their original course ($G = 127.39$, $d.f. = 1$, $P < 0.001$). When wolves left their own trail and used a coyote trail (29%), they tended to follow coyotes ($G = 12.01$, $d.f. = 1$, $P < 0.001$).

Resting coyotes were observed within 150 m of wolves on nine occasions. Single coyotes were observed following wolves seven times, always at a distance > 100 m. Coyotes also were observed scavenging at or near wolf dens ($n = 3$) and rendezvous sites ($n = 5$). In one instance, two coyotes fed on elk and beaver (*Castor canadensis*) carrion accumulated near the den while an adult male wolf and four pups rested < 100 m away.

There was no indication of aggressive behavior either by wolves or coyotes. However, agonistic encounters obviously occurred as 23 coyotes (seven females, 16 males) killed by wolves were discovered. No coyote was consumed by wolves. Eleven of 23 coyotes were found within 200 m of kills, and 14 of the 23 were discovered on snowmobile trails. Twenty of the coyotes were

<1 year in age. None was found while tracking wolves following coyotes. Pursuit distances averaged <5 m ($n = 17$), and tracking evidence suggested that most coyotes were taken by surprise.

DISCUSSION

This study clearly indicates that winter movements of coyotes in Riding Mountain National Park were not random relative to wolves. Coyotes were active throughout wolf territories, and both species 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. Moreover, the tendency of coyotes to follow wolf tracks suggests that coyotes did not attempt to avoid wolves, and may have been attracted to areas where wolves were active. Movements of wolves appeared to be unaffected by the presence of coyotes.

Coyotes at Riding Mountain National Park obtain most of their food by scavenging large ungulates killed by wolves (Meleshko, 1986; Paquet, 1989). Cyclical changes in snowshoe hare populations do not affect this behavior (Meleshko, 1986). Partitioning of food resources by the two canids allows for ecological overlap (Meleshko, 1986; Paquet, 1989). On 36 occasions, coyotes followed wolves directly to wolf-killed ungulates. In addition, all wolf kills examined in the field ($n = 198$) were scavenged by coyotes within 24 h of abandonment by wolves.

The high proportion of coyotes following wolves suggests that following wolves to their kills is a useful foraging strategy. The behavior could 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 tracks, coyotes chose the former option significantly more often. That may have been because there is likely more consumable biomass available from new kills, less handling time required because choice portions are easy to consume, a greater opportunity to feed on the more nutritious portions of the carcass, and a competitive advantage over other terrestrial scavengers in gaining early and possibly exclusive access to the carcass.

Coyotes at kills must compete with aggressive conspecifics and other scavengers (Paquet, 1989), so it would be advantageous to feed in the absence of other secondary users. That could best be accomplished through optimizing the search effort by trailing wolves, and arriving first at a kill.

The overlap of wolf and coyote movements in Riding Mountain National Park was substantial. Spatial segregation of the two species did not occur at any detectable level, and coyotes did not appear to be displaced by the activities of wolves. Wolves occasionally killed coyotes, but there was no evidence that they actively hunted them. Overall, the movements of wolves were neutral relative to coyotes; I suggest that wolves killed coyotes only opportunistically.

ACKNOWLEDGMENTS

Financial support was provided by The World Wildlife Fund (Canada and USA); The Department of Zoology, University of Alberta; The Canadian Wildlife Service, Environment Canada; Manitoba Department of Natural Resources; Canadian Wolf Defenders, Calgary, Alberta; Wildlife Defense Northwest, Portland, Oregon; and J. F. Paquet. The Canadian Park Service and the staff of Riding Mountain National Park assisted in numerous ways. W. A. Fuller, R. O. Peterson, and J. A. Murie provided helpful editorial suggestions. I am especially thankful to L. N. Carbyn of the Canadian Wildlife Service, without whom this study would not have been possible.

LITERATURE CITED

- BERG, W. E., AND R. A. CHESNESS. 1978. Ecology of coyotes in northern Minnesota. Pp. 229–246, *in* Coyotes: biology, behavior, and management (M. Bekoff, ed.). Academic Press, New York, 384 pp.
- CARBYN, L. N. 1982. Coyote population fluctuations and spatial distribution in relation to wolf territories in Riding Mountain National Park, Manitoba. *The Canadian Field-Naturalist*, 96:176–183.
- FULLER, T., AND L. B. KEITH. 1981. Non-overlapping ranges of coyotes and wolves in northeastern Alberta. *Journal of Mammalogy*, 62:403–405.
- HOSKINSON, R. L., AND L. D. MECH. 1976. White-

- tailed deer migration and its role in wolf predation. *The Journal of Wildlife Management*, 40:429–441.
- LEHNER, P. N. 1979. *Handbook of ethological methods*. Garland STPM Press, New York, 403 pp.
- MELESHKO, D. W. 1986. Feeding habits of sympatric canids in an area of moderate ungulate density. M.S. thesis, University of Alberta, Edmonton, 89 pp.
- PAQUET, P. C. 1989. Behavioral ecology of sympatric wolves (*Canis lupus*) and coyotes (*C. latrans*) in Riding Mountain National Park, Manitoba. Ph.D. dissert., University of Alberta, Edmonton, 227 pp.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry: the principles and practice of statistics in biological research*. Second ed. W. H. Freeman and Company, San Francisco, 859 pp.
- TODD, A. W., KEITH, L. B., AND C. A. FISCHER. 1985. Population ecology of coyotes during a fluctuation of snowshoe hares. *The Journal of Wildlife Management*, 45:629–640.

Submitted 16 January 1990. Accepted 19 June 1990.