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RELATIONSHIP BETWEEN COYOTE GROUP SIZE AND DIET IN SOUTHEASTERN COLORADO

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Abstract: We investigated the diet of coyotes (*Canis latrans*) on the Piñon Canyon Maneuver Site (PCMS) in southeastern Colorado from February 1983 to June 1986. Based on regression analysis, 71% of the variation in the volume of large prey (e.g., adult ungulates) in coyote scats could be explained by coyote group size; 77% of this variation could be explained by coyote group size and snow depth. Snow depth alone explained 28% of the variation in the volume of large prey in the scats. Coyote group size explained 19% of the variation in the volume of medium size prey (e.g., lagomorphs and ungulate fawns) and 38% of the variation in the volume of small prey (e.g., rodents). Coyote groups were largest in winter and smallest in summer. Most juveniles dispersed before the largest group sizes were observed. Group foraging and snow depth may influence prey selection by coyotes in southeastern Colorado.

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Diets of coyotes have been examined (Fichter et al. 1955, Gipson 1974, MacCracken 1981) but few studies have examined the relationship of prey selection and coyote social organization. In Jasper National Park, Alberta, during summer, when rodents were the major food, mean coyote group size was 1.4 (Bowen 1978, 1981). In winter, when ungulates were the major food, group size averaged 2.0. Mean group size in Wyoming was 1.3 coyotes in summer, when rodents were the major resource consumed; in winter, when ungulate carrion dominated the diet, coyote group size was 1.8 (Bekoff and Wells 1980). Bekoff and Wells (1980) noted that during 3 successive winters in Rocky Mountain National Park, Colorado, when no ungulate carrion was available, coyotes preyed on small mammals throughout the year. Mean group size for coyotes was 1.1 in summer and winter. Bowen (1978, 1981) and Bekoff and Wells (1980) concluded that when coyotes were feeding on large prey, group sizes were correspondingly larger, which increased foraging efficiency. They further observed that delayed dispersal of pups resulted in the formation of larger packs; however, seasonal variation in the diet still accounted for much of the variation in the number of pack members observed together. Messier and Barrette (1982) found no relationship between prey size and coyote group size in Quebec; they concluded that larger coyote groups could be explained by delayed dispersal of juveniles. The

objective of our study was to document the diet of coyotes in southeastern Colorado and examine the relationship between prey size, pack sociality, time of juvenile dispersal, and group size.

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STUDY AREA

The 1,040-km² study area is located along the west rim of the Purgatoire River in Las Animas County, Colorado. The climate is semiarid with a mean annual precipitation of 26–38 cm. Mean monthly temperatures range from –1 C in January to 23 C in July. Elevations range from 1,310 to 1,740 m.

There were 3 distinct habitats on the study area: shortgrass prairie, limestone breaks, and canyons. The central and western portion was shortgrass prairie. Blue grama (*Bouteloua gracilis*), western wheatgrass (*Agropyron smithii*),

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and galleta (*Hilaria jamesii*) dominated the prairie vegetation. In the north, the Black, Big Arroyo, and the Bear Spring hills were limestone breaks dominated by pinyon pine (*Pinus edulis*) and one-seed juniper (*Juniperus monosperma*). The Purgatoire River Canyon system consisted of pinyon-juniper woodlands on sandstone.

The PCMS had large-scale cattle ranching since the late 1800's. Cattle grazing and coyote control were practiced until the U.S. Army acquired the PCMS for military training in 1982. Trapping and hunting coyotes and cattle grazing occurred on ranches surrounding the PCMS during our study.

METHODS

We collected coyote scats every 2 weeks along regular, designated routes in all 3 habitats. Each scat was placed in a paper bag and labeled with the date and location. Scats were air-dried for >1 month, crumbled by hand, and analyzed. Skeletal and hair reference collections and hair keys (Adorjan and Kolenosky 1969, Moore et al. 1974) were used to identify food items. Volume was visually estimated to the nearest 20% for each food item identified. Only prey items >20% of volume were included in data analysis (modified from Knowlton 1964, Bowen 1981, Andelt et al. 1987) because small prey are often overestimated in diets when frequency of occurrence techniques are used (Martin et al. 1946, Weaver and Hoffman 1979). Volumes of prey in the diet were relative amounts consumed, not measures of absolute quantities consumed, and were constrained to total 100%.

Prey items were divided into 3 classes according to weight and the cooperative foraging needed to capture, defend, and share the prey (modified from Bowen 1981). Small prey weighed <0.5 kg and included vegetation, insects, reptiles, birds, and rodents. Cooperation among coyotes was not necessary to capture small prey, and the food was not shared. Medium prey weighed 0.5–10 kg and included lagomorphs and ungulate fawns. Coyotes may cooperate to capture medium size prey and the prey item may be shared. Large prey weighed >10 kg and consisted of adult ungulates and calves of domestic cattle. Cooperation among coyotes was generally needed to capture or defend the large prey, and the food was regularly shared (Bowen 1981). Prey weights are from Armstrong (1972), and Burt and Grossenheider (1976).

We calculated a mean coyote group size for

each month by recording group size observations on the study area. We defined group size as the number of coyotes seen together at 1 time. Researchers observed coyotes during diurnal hours while traveling about the study area and included marked and unmarked animals. Sightings were made from vehicles, helicopters, or on foot. The sampling effort (70 hr/week) and area was consistent and constant among seasons. A group was not the number of coyotes occupying 1 territory, but the number of coyotes observed interacting together. The estimate of group size did not include groups of coyotes observed at or near carcasses, as these could be temporary aggregations (Camenzind 1978).

To investigate the diet of groups of different sizes, we analyzed the stomach contents of coyotes removed during an aerial gunning operation in winter–spring 1987. All coyotes that were alone, in pairs, or in a group, were shot from a helicopter. The carcass was recovered and the stomach contents analyzed. Food items were identified and visually estimated to the nearest 10% of total volume of the stomach. Food items were then categorized into the 3 prey classes used in scat analysis. Empty stomachs were given a value of 100% empty for comparison to other classes. The relative amount of empty, small, medium, and large classes was compared for different group sizes by Chi-square analysis.

We documented sociality of pack members by observing radio-collared coyotes sharing the same territory. We captured all members of a pack with a hand-held net gun fired from a helicopter (Barrett et al. 1982), or by manual capture following aerial pursuit (Gese et al. 1987). Social cohesion was measured by the number of times a pack member was located alone, with its mate, or with ≥ 2 associates. Coyotes were assumed to be interacting if they were seen together or were ≤ 100 m from each other as determined by radio telemetry. At least 2 compass bearings with an intersecting angle >20 and <160° were used to triangulate an animal's position. If the location of the 2 animals was ≤ 100 m apart, the animals were recorded as being together. We examined the number of times the radio-collared coyotes were together in winter (Nov–Apr) versus summer (May–Oct).

We documented the time of dispersal of juveniles by observing radio-collared coyote pups captured in their natal home range when 3–4 months old. We defined dispersal as the movement an animal makes from its point of origin

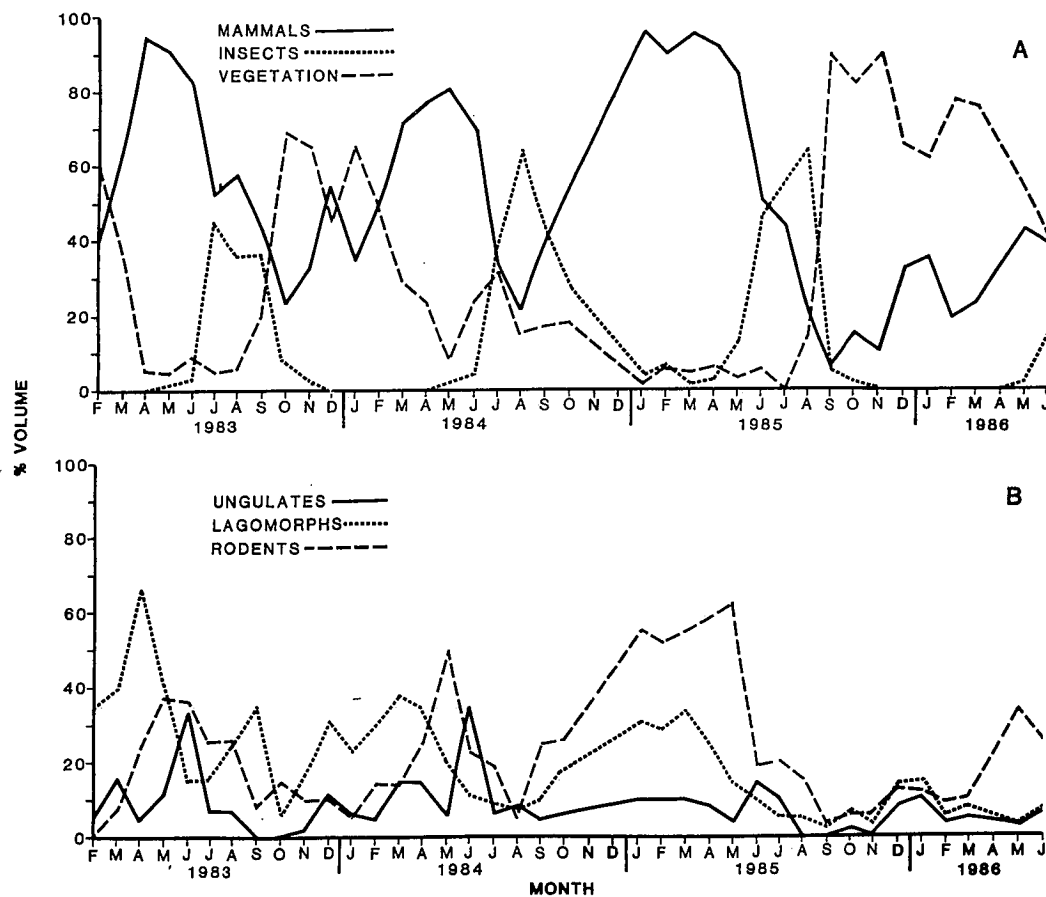


Fig. 1. Monthly percent volume of (A) major food items and (B) mammalian food items in coyote scats collected on the Piñon Canyon Maneuver Site, Colorado, 1983-86.

to the place where it reproduces or would have reproduced if it had survived and found a mate (Howard 1960).

We used linear regression of the mean coyote group size observed for each month versus the corresponding monthly relative volume of prey in each prey class. We used multiple linear regression on the mean group size versus the volume of large prey and the sum of weekly snow depths/month. Snow depth records were compiled by the Federal Aviation Administration at the Las Animas County Airport located approximately 24 km southwest of the study area.

RESULTS

We collected and analyzed 3,270 coyote scats. Thirty-seven food items were consumed, including mammals, birds, reptiles, insects, and

vegetation. Peak volumes of mammals, insects (mainly Orthoptera), and vegetation (primarily juniper berries) showed seasonal trends (Fig. 1A). Volumes of different sized mammals also showed seasonal trends in the coyote scats (Fig. 1B).

During the study we made 846 observations of coyote group size. Large groups were more frequent in winter than in summer ($\chi^2 = 56.2$, 3 df, $P < 0.005$). Of 422 observations during winter, 43% ($n = 181$) were singles, 31% ($n = 131$) were pairs, 19% ($n = 81$) were trios, and 7% ($n = 29$) were ≥ 4 coyotes together. Of 424 sightings during summer, 58% ($n = 245$) were singles, 34% ($n = 147$) were pairs, 7% ($n = 29$) were trios, and 1% ($n = 3$) was ≥ 4 coyotes in a group.

There was a negative correlation between coyote group size and volume of small prey consumed; 38% of the variation of small prey in the coyote scats was explained by coyote group

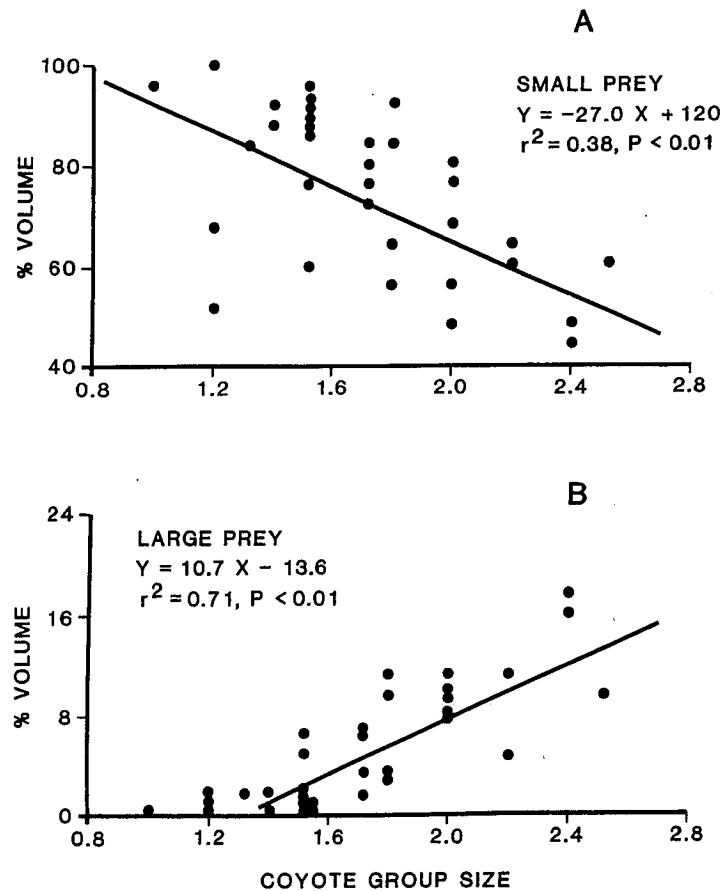


Fig. 2. Regressions of monthly group sizes of coyotes versus monthly percent volume of (A) small prey items and (B) large prey items in coyote scats over 33 months on the Piñon Canyon Maneuver Site, Colorado, 1983–86.

size ($F = 20.91$; 1, 31 df; $P < 0.005$) (Fig. 2A). There was a positive relationship between coyote group size and percent volume of medium size prey where 19% of the variation in the volume of medium size prey (Y) was explained by coyote group size (X) ($Y = 15.6X - 6.05$; $F = 8.71$; 1, 31 df; $P < 0.01$).

Seventy-one percent of the variation of large prey in scats was explained by coyote group size ($F = 79.50$; 1, 31 df; $P = 0.005$) (Figs. 2B and 3). Seventy-seven percent of the variation in the volume of large prey in scats was explained by coyote group size and the sum of weekly snow depths/month. Snow depth alone explained only 28% of the variation in the volume of large prey in the scats ($F = 13.58$; 1, 31 df; $P < 0.005$).

There was a difference in prey selection between group sizes ($\chi^2 = 102.77$, 6 df, $P < 0.005$) of 25 coyotes (7 singles, 6 pairs, and 2 groups of 3) killed during winter–spring 1987. Single

coyotes had relative volumes of 43, 27, 30, and 0% for empty, small, medium, and large prey classes, respectively. Pairs had relative volumes of 17, 25, 36, and 22% for these classes. Groups had relative volumes of 0, 28, 22, and 50% for these classes. As group size increased, amount of large prey increased. Also, many single coyotes had empty stomachs, whereas no member of a group had an empty stomach.

To test the hypothesis that coyote sociality among pack members was different throughout the year, we observed 7 different coyote groups in which all members were radiocollared. Four mated pairs of adults, 2 groups of 3 coyotes (ad mated pairs with 1 ad M, or 1 yearling M), and 1 group of 4 coyotes (1 ad F, 3 ad M) were observed. The groups were more cohesive during winter than summer ($\chi^2 = 57.3$, 3 df, $P < 0.005$). The breeding pair in each group was located together a mean of 38% of the time in

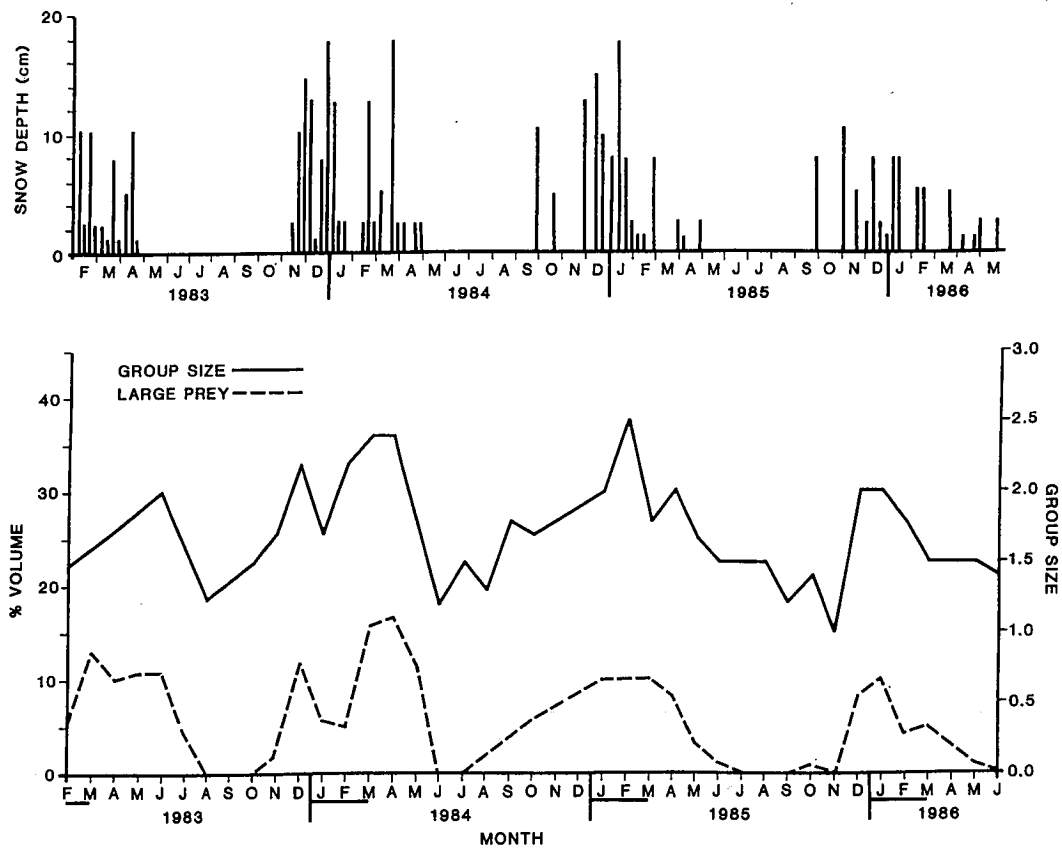


Fig. 3. Temporal changes in weekly snow depth, coyote group size, and volume of large prey in scats of coyotes on the Piñon Canyon Maneuver Site, Colorado, 1983–86. The solid lines under months indicate breeding seasons.

winter and 15% in summer. The breeding pair was accompanied by another pack member 23% of the time in winter and 7% in summer. The pack of 4 was together 17% of the time in winter and 3% in summer.

We documented the time of dispersal of 11 radio-collared pups. Seven (64%) dispersed by January, 2 pups (18%) delayed dispersal until spring, and 2 remained in their natal home range. The largest groups we observed were during February–April, after the majority of juvenile dispersal.

DISCUSSION

Seasonal availability of foods is a major influence on coyote diet (Clark 1972, MacCracken and Hansen 1982, Andelt et al. 1987). On PCMS, coyotes changed foods seasonally. Juniper berries, available in winter, were a major component of the winter diet. The volume of rodents in the diet showed peaks in spring of each year. Jackson (1985), working in southcentral Colo-

rado on an area with similar habitats, found the highest relative abundances of rodents in spring. Grasshoppers were eaten in summer, when they were available.

Coyotes changed their diets when prey species became vulnerable to predation. Pronghorn (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*) fawns are most vulnerable when ≤ 1 month old (Steigers and Flinders 1980, Barrett 1984, Firchow 1986). Coyotes took advantage of this vulnerability, as reflected in the large volume of ungulate remains in the scats in June of each year. On our study area, pronghorn fawn mortality was 89 and 80% for 1983 and 1984, respectively, and coyote predation was responsible for 71% of the mortality (Firchow 1986). Mortality of mule deer fawns was 71% in 1983 and 78% in 1984, and coyote predation accounted for 76% of the mortalities (Gerlach 1987).

On our study area, changes in coyote group size appeared to affect the relative amount of

small prey in the diet. When coyotes were feeding mostly on small prey, group size was smallest. Coyotes do not need to hunt together when preying on rodents, fruits, reptiles, or insects, and 1 coyote does not benefit from the small prey that another has caught.

During winter, coyotes were in larger groups. As group size increased, the amount of large prey in coyote scats and stomachs increased. Bowen (1981) found that 84% of the variation in the amount of mule deer in the diet of coyotes was explained by pack size. On our study area, it appears that increased group size, and to a lesser extent snow depth, allowed coyotes to forage more successfully for adult ungulates during winter. The addition of snow seemed an important influence on prey selection. On our study area, most coyote predation on adult pronghorns occurred after heavy snowfall (Firchow 1986). During the rest of the year, adult ungulates were present, but preyed upon less because of smaller coyote group size, lack of snow cover, reduced vulnerability, availability of alternate prey (Hamlin et al. 1984), lack of ungulate carcasses, or unknown factors.

Possible mechanisms driving the increase in coyote group size and subsequent change in foraging ecology may be increased sociality among pack members during the breeding season and delayed juvenile dispersal (Alexander 1974; Bekoff and Wells 1980, 1981, 1986; Messier and Barrette 1982; Bekoff et al. 1984). Social cohesion of the resident groups was highest during winter in our study area. The frequency of large groups was also higher during winter. Camenzind (1978) found pack cohesiveness was greatest during winter, and lowest in summer in Wyoming, and reported that these changes appeared to be related to changing feeding patterns. Huegel and Rongstad (1985) observed that 83% of the winter diet of an adult male coyote in northern Wisconsin prior to 15 February was snowshoe hare (*Lepus americanus*). After 15 February, 84% of the coyote's diet consisted of white-tailed deer (*O. virginianus*) that he killed. Prior to 15 February, the coyote traveled alone 76% of the time. He traveled with other coyotes on 67% of the days after 15 February. Huegel and Rongstad (1985) concluded that snow conditions and increased coyote sociality may have influenced predation of deer. Hilton (1978) reported that in December all coyote tracks in northwestern Maine were single and these single animals rarely pursued deer and made no kills.

However, from January to late February, >80% of the track sets were of 2 coyotes, and they pursued deer more often and were successful 79% of the time (Hilton 1978).

Delayed juvenile dispersal may explain the increase in group size. Nondispersing pups have been found to assist in the formation of packs (Bekoff 1977, Camenzind 1978, Messier and Barrette 1982); however, most pups we monitored dispersed 2 months prior to the time we observed the largest groups. Other studies found similar timing of juvenile dispersal. Dispersal in south Texas occurred mainly in the fall and winter as litters broke up (Knowlton 1972). Young coyotes in Alberta started to disperse in October (Nellis and Keith 1976). Five of 8 radio-tagged subadults in Alberta dispersed during their first winter (Bowen 1982). More than 70% of the juveniles dispersed from their parental home range in October and November in Minnesota (Berg and Chesness 1978).

The formation of coyote packs appears to be advantageous for finding, acquiring, and defending food, and the care and survival of pups (Bowen 1978; Camenzind 1978; Bekoff and Wells 1980, 1981, 1986; Messier and Barrette 1982). Although most pups we monitored left in fall, the nondispersing pups could account for some of the increase in group size; however, we believe that the increase in group size was caused mostly by increased sociality among adult pack members during the breeding season. The traditional view that the formation of groups increases foraging of large prey appears to have been supported. We believe that group size influenced prey selection, but prey size did not influence group size, as hypothesized by Bowen (1978, 1981). We conclude that an increase in coyote group size allowed the groups to forage for large prey and that the increase in group size was caused by increased sociality among pack members during the breeding season.

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