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Yellow-bellied Marmots as Prey of Coyotes

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ABSTRACT.—Analysis of contents of 395 coyote (Canis latrans) scats collected for 6 yr at a subalpine locality in Colorado showed that yellow-bellied marmots (Marmota flaviventris) were a regular and frequent prey of coyotes during summer. There was no evidence that marmots were especially vulnerable to predation by coyotes during the mating season or during the time of dispersal. Marmots were most vulnerable to predation during July, for unknown reasons. Marmots apparently served as alternate prey of coyotes; marmot occurrence in scats was greatest during years when gophers, probably a preferred prey of coyotes, were infrequent in scats.

Introduction

The risk of predation may influence many aspects of mammalian behavior, including sociality (Alexander, 1974), foraging (Holmes, 1984), mating system (Armitage, 1986) and habitat selection (Andersen and Johns, 1977). Predation risk, however, usually is assumed rather than demonstrated; quantitative evaluation, even on a relative basis, is seldom reported.

The behavior of the yellow-bellied marmot (Marmota flaviventris), a large, hibernating, ground-dwelling squirrel, has been studied intensively since 1962 near Rocky Mountain Biological Laboratory (RMBL), Gunnison Co., Colorado (Armitage, 1986, and references cited therein). Several species of potential predators of marmots are resident near RMBL, and coyotes (Canis latrans) in particular are common (Van Vuren, 1990). Predation, however, is not considered a major source of mortality for marmots near RMBL (Armitage and Downhower, 1974), for several reasons. During more than 5000 h of observation over 20 yr, only two instances of predation on marmots were witnessed, both involving coyotes (Armitage, 1982). Marmots were observed to chase off small carnivores such as weasels (Mustela frenata) and martens (Martes americana) (Travis and Armitage, 1972). Further, in other areas where coyotes and marmots coexist, marmots comprise less than 7% of seasonal diets of coyotes (Murie, 1940; Ferrel et al., 1953; Hawthorne, 1972; MacCracken and Hansen, 1982; Van Vuren and Thompson, 1982).

During the summer of 1972, however, remains of yellow-bellied marmots were identified in 25% of 106 fresh coyote scats collected near RMBL (Powell, 1972). This discovery suggested that the risk of predation, particularly by coyotes, may be more important to yellow-bellied marmots than previously thought.

I describe coyote diets near RMBL to determine: (1) if the results of Powell (1972) are representative of the long-term importance of marmots as prey of coyotes; (2) if marmots are more vulnerable to predation during the mating season (Armitage, 1986) or during dispersal (Svendsen, 1974), and (3) if marmots are a focus of coyote foraging efforts or are alternate prey actively sought only when other prey are scarce.

MATERIALS AND METHODS

Diets were evaluated by identifying the contents of 395 coyote scats collected from 1984 through 1989 near RMBL, elevation 2900 m. Vegetation in the area was a mosaic of aspen

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(Populus tremuloides) woodlands, spruce (Picea spp.) and fir (Abies spp.) groves, and subalpine meadows rich in forbs. Scats were collected May through September, the active season of marmots, by searching all roads and trails within 3 km of RMBL at intervals of 1 mo or less. Scats found at the beginning of May were assigned to the period October-April. Scats found thereafter were assigned to the month in which they were collected. Scats collected away from roads or trails were included only if they could be assigned reliably to a given month based on freshness of appearance and odor. Scats collected from May through September, but for which the month was uncertain, were excluded from monthly analyses but were included in seasonal and annual analyses. Summer was defined as May through September.

Scats were enclosed in fine-mesh nylon bags, soaked at least 24 h in mild detergent, then rinsed thoroughly in warm water. Residual material was air-dried, separated by hand, and identified by comparison with specimens collected from the vicinity and housed at RMBL or the Mammal Collection of the University of Kansas Museum of Natural History. Coyote diets were calculated as percent frequency of occurrence of prey items among scats during a given time. All percentages were arcsine-transformed for statistical analysis.

Marmot remains recovered from scats were assigned to age class (young, yearling or adult; Armitage and Downhower, 1974) whenever possible, according to characters such as degree of epiphysial fusion, size of the sagittal crest, size of the scapula, claw shape and dentition. Annual variation in marmot numbers in the study area was estimated by totaling the number of individual yearling and adult marmots identified during intensive trapping at 16 localities near RMBL during each of the 6 yr of the study.

RESULTS

Prey items identified in scats fell into three groups based on overall frequency of occurrence. Voles (chiefly Microtus montanus) and gophers (Thomomys talpoides), which occurred in 43–45% of all scats, were the most prominent prey items in coyote scats during all months from May through September, as well as October-April (Table 1). Snowshoe hares (Lepus americanus), yellow-bellied marmots, birds, jumping mice (Zapus princeps), mule deer (Odocoileus hemionus) and elk (Cervus elaphus), and porcupines (Erethizon dorsatum) were seasonally important and occurred in 7–15% of scats overall (Table 1). Chipmunks (Eutamias spp.), golden-mantled ground squirrels (Spermophilus lateralis), deer mice (Peromyscus maniculatus), muskrats (Ondatra zibethicus) and garter snakes (Thamnophis sirtalis) were eaten irregularly and infrequently and occurred in 2% or less of all scats.

Yellow-bellied marmots occurred in 17% of all scats collected during summer (range among years, 10–38%); only voles and gophers were more frequent in scats during summer. Marmot occurrence in scats was greatest during July and least during May (Table 1).

Although marmots trapped in the study area varied annually from 61 to 92 individuals, numbers were relatively stable the last 4 yr of the study when 88–92 individuals per year were identified. Summer percentages among years of marmots in scats were not significantly positively correlated (one-tailed test) with marmot numbers in the study area (r=-0.65, P>0.50), nor were they significantly negatively correlated (one-tailed test) with summer percentages of voles (r=0.32, P>0.50), snowshoe hares (r=-0.68, P>0.05), birds (r=0.22, P>0.50) or jumping mice (r=-0.30, P>0.20), but they were significantly negatively correlated (one-tailed test) with summer percentages of gophers (r=-0.83, P<0.025).

Remains of 32 marmots recovered from scats could be aged; they included 17 adults, 13 yearlings and two young. The ratio of adults to yearlings identified in scats did not differ

	May	June	July	August	Sept	Oct-April	Overall
n	116	78	20	31	15	121	395
Vole	55	42	35	35	60	37	45
Gopher	53	49	45	52	60	23	43
Snowshoe hare	11	17	5	29	13	18	15
Marmot	11	19	35	16	13		12
Bird	8	15	35	29		7	12
Jumping mouse	3	27	20	13	13	1	10
Deer and elk	3	3	15	10	13	17	9
Porcupine	9	1	5		7	11	7

TABLE 1.—Percent frequency of occurrence of prey items identified in coyote scats collected near RMBL, Colorado, 1984 through 1989. Prey that occurred in 2% or less of scats overall are not shown

from the mean ratio of adult to yearling marmots (1.55:1) trapped in the study area (G-test for goodness of fit, G = 0.199, P > 0.50).

DISCUSSION

The high frequency of voles in coyote scats is consistent with other studies of coyote diets (Murie, 1940; Gier, 1957; Hawthorne, 1972; Todd et al., 1981), but the high frequency of gophers is not. The year-round percentage of gophers in scats near RMBL (43%) is the highest yet reported. Andersen and MacMahon (1981) suggested that inadequate food was the primary cause of death in subalpine populations of gophers; my results, apparently the first on diets of coyotes in subalpine habitats, indicate that mortality from predation should not be discounted. Further, the high frequency of gophers in coyote scats throughout the year indicates that gopher vulnerability was not restricted to seasonally dispersing juveniles.

Snowshoe hares appeared to be common near RMBL during most years of the study; hence, a 15% occurrence in coyote scats seems low considering the primacy of lagomorphs in coyote diets reported for other localities (Gier, 1957; MacCracken and Hansen, 1982; Pederson and Tuckfield, 1983). Habitat use by coyotes elsewhere corresponds to availability of major prey (Litvaitis and Shaw, 1980; Todd et al., 1981); coyotes near RMBL may have foraged mostly in subalpine meadows where voles and gophers were abundant, but where snowshoe hares were scarce. Birds were particularly frequent in scats during July and August, probably as a result of vulnerability of newly fledged young (Van Vuren and Thompson, 1982). Deer and elk occurred most frequently in scats during winter (October-April), possibly as carrion; another peak in occurrence, during July, probably derived from vulnerability of neonates (Salwasser, 1974; Van Vuren and Thompson, 1982).

Summer occurrences of marmots in scats 1984–1989 (10–38%) are consistent with Powell's 1972 results (25%). Taken together, these findings indicate that marmots are a regular and frequent prey of coyotes during summer.

Marmots mate during the first half of May. Males in particular are active aboveground at this time, and snow cover often is extensive (Van Vuren, 1990), leading to the expectation that predation risk would be relatively high because of increased exposure to predators (Armitage, 1986). This expectation was not supported; frequency of marmots in coyote scats was lowest during May (Table 1). Perhaps coyotes in May focused on other prey that were easier to catch. The ground surface in meadows was exposed for several days after snow melted but before appreciable growth of herbaceous vegetation, probably increasing the

vulnerability of species such as gophers and voles. Also, snowmelt saturated the soil with water and may have forced gophers to disperse over the surface to drier soil (Ingles, 1949; Hansen and Ward, 1966). Gophers and especially voles occurred most frequently in scats during May (Table 1).

Most dispersing marmots are yearlings and emigrate May through July (Van Vuren, 1990). If dispersers are particularly vulnerable to predation (Svendsen, 1974), there should be a relatively high frequency of occurrence of marmots in scats from May through July and a yearling bias among marmot remains recovered from scats. These predictions were not realized. Marmots were relatively frequent in scats only in July (Table 1), and there was no bias toward yearlings among ageable marmot remains. Coyotes were not preying predominantly on dispersers.

Vulnerability of newly emerged young (Hawthorne, 1972), which first appear above-ground near RMBL during July, might account for the July peak in occurrence of marmots in scats. However, the scarcity of ageable remains of young marmots in scats (2 of 32 overall, 1 of 5 in July) suggests that young were not highly vulnerable to predation. Young marmots near RMBL typically remain close to the safety of their natal burrows for some time after emergence, probably reducing susceptibility to predation. The relatively high rate of predation on marmots in July remains unexplained; perhaps the cause lies not in marmot vulnerability but in an unidentified functional response by coyotes to changing prey availability.

Snowshoe hares in Alberta, unlike near RMBL, are a major prey of coyotes (Todd et al., 1981). In Alberta, hare occurrence in coyote diets was positively correlated with hare density and negatively correlated with occurrence of several other prey in diets (Todd et al., 1981; Todd and Keith, 1983), leading to the conclusion that coyotes shifted to alternate prey when hares were scarce (Todd and Keith, 1983).

I propose a similar relationship between gophers and marmots near RMBL. Marmot occurrence in coyote diets was not positively correlated with marmot numbers in the study area but was negatively correlated with occurrence of gophers in coyote diets. Gophers, because of their larger size (ca. 150 g) in comparison with voles (ca. 50 g), could be the single most important prey of coyotes near RMBL. Estimates of gopher abundance were not available, but subalpine populations of Thomomys talpoides elsewhere vary markedly in density among years (Hansen and Ward, 1966; Andersen and MacMahon, 1981). If annual variation in summer occurrence of gophers in coyote diets (23-65%) resulted from variation in gopher abundance, then the inverse relationship between marmots and gophers in scats suggests that marmots were alternate prey, subject to increased predation pressure when gophers were scarce. Marmots probably are difficult for coyotes to capture, but their proposed importance as alternate prey may derive from relative stability of numbers (Armitage and Downhower, 1974; this study) and predictability of location. Marmots are common near RMBL and usually live in colonies; those colonies under study have been occupied continuously since at least 1962. Thus, a hungry coyote during summer always knows where to find marmots to stalk.

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