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Predation on Yellow-bellied Marmots (*Marmota flaviventris*)

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ABSTRACT.—I determined cause-specific mortality of yellow-bellied marmots (*Marmota flaviventris*) to assess the importance of predation as a mortality factor. Contrary to earlier findings based on visual observation, almost all (98%) mortality during the summer active season was caused by predation. Coyotes (*Canis latrans*) were the most important predators, followed by badgers (*Taxidea taxus*), American martens (*Martes americana*), black bears (*Ursus americanus*) and raptors, probably golden eagles (*Aguila chrysaetos*). Predation on marmots is cryptic; none of the predation events were observed and, in most cases, the marmot was consumed or removed so quickly and completely that searching for carcass remains would have been fruitless.

INTRODUCTION

Predation has important behavioral, ecological and evolutionary effects on prey species. The risk of predation may influence foraging behavior (Kotler *et al.*, 1991), social behavior (Fitzgibbon, 1990) and habitat selection (Berger, 1991). Further, removal of individuals by predators may have consequences for population dynamics (Reid *et al.*, 1995) and biogeography (Sievert and Keith, 1985), as well as the evolution of antipredator defenses (Lima and Dill, 1990).

Predation on some large vertebrates can be evaluated through observation (*e.g.*, Fitzgibbon, 1990), but for medium and small species the act of predation is seldom witnessed and the animal may be entirely consumed, leaving no evidence. Disappearance of a marked individual is an unreliable indicator of predation because animals may disappear for other reasons (Murie, 1992; Waser *et al.*, 1994). Moreover, even when predation is established, identification of the predator, an important factor in understanding the effects of predation on the prey, may be difficult (Major, 1991).

The yellow-bellied marmot (*Marmota flaviventris*) is a large (2–4 kg), ground-dwelling squirrel that is widely distributed in western North America. Anecdotal accounts show that several mammalian and avian predators prey upon yellow-bellied marmots (Frase and Hoffmann, 1980), with potential effects on marmot foraging behavior (Armitage, 1982; Carey and Moore, 1986), habitat selection (Andersen and Johns, 1977), social behavior (Armitage and Johns, 1982) and mating system (Armitage, 1986). However, because predation on marmots is rarely observed (Frase and Hoffmann, 1980), the magnitude of predation and the identity of the predators responsible is rarely, if ever, known. Such is the case for a population of yellow-bellied marmots in the East River Valley in Colorado that has been studied intensively since 1962 (Armitage, 1991). Although coyotes (*Canis latrans*) and golden eagles (*Aguila chrysaetos*) were known to prey on these marmots (Armitage and Downhower, 1974; Armitage, 1982), observations of predation were rare (Armitage, 1982), suggesting that it was not a major cause of mortality (Armitage and Downhower, 1974). Radiotelemetry, however, can circumvent biases that affect visual observation as a means of detecting predation. My objective was to use radiotelemetry to assess the importance of predation on yellow-bellied marmots by determining cause-specific mortality during the summer active season.

METHODS

The study was conducted from 1984 through 1995 in the East River Valley near Rocky Mountain Biological Laboratory (RMBL), Gunnison County, Colorado. Topography was typical of a glaciated, high-altitude valley; slopes were gentle on the valley floor, elevation 2850–2930 m, but rose abruptly to ca. 3900 m elevation on surrounding peaks. Vegetation was an interspersion of subalpine meadows rich in forbs, aspen (*Populus tremuloides*) woodlands and spruce (*Picea* spp.) forests, with dense patches of willows (*Salix* spp.) along streams. Areas above timberline supported alpine meadows and shrubs, or were largely devoid of vegetation.

Yellow-bellied marmots were common in the valley and lived in discrete habitat patches, typically open meadows relatively free of trees and shrubs that contained rocks (boulders, outcrops or talus) under which burrows were excavated (Svendsen, 1974). Larger patches were inhabited by colonies that supported as many as 12 adult (≥2-y old) females and usually one adult male, and smaller noncolonial patches were inhabited by one adult female and sometimes an adult male (Van Vuren and Armitage, 1994). About 60 to 100 adult and yearling marmots lived in the study area. Marmots hibernated from September until early May.

Each summer from 1984 through 1993 I instrumented 13 to 51 marmots with radiotransmitters for a total of 295 marmots. All marmots were ear-tagged for identification and dye-marked for visual recognition. Transmitters were surgically implanted into the peritoneal cavity; surgery and the implanted transmitter had no effect on subsequent growth, survival or reproduction (Van Vuren, 1989). Transmitters were constructed as sealed cylinders 21 mm in diameter and 90 mm long, with a mass of 35 g (≤4% of body mass). Each transmitter was coated with a layer of surgical-grade beeswax 2 mm thick; the beeswax rendered the transmitter physiologically inert and also retained tooth impressions when bitten by a predator. Most marmots were yearlings (ca. 1–2 kg) when first instrumented (Van Vuren, 1990). Transmitters had an expected life of 2 y, but some expired prematurely; transmitters were replaced in some marmots. Thus, the time a given marmot carried a transmitter varied from a few weeks to 5 y, but was usually 1–2 y.

Resident mammalian predators that might prey upon marmots included coyotes, black bears (*Ursus americanus*), badgers (*Taxidea taxus*), American martens (*Martes americana*) and long-tailed weasels (*Mustela frenata*). Red foxes (*Vulpes vulpes*) and mountain lions (*Puma concolor*) were potential predators, but were rarely recorded in the vicinity. Resident avian predators included golden eagles, red-tailed hawks (*Buteo jamaicensis*), Swainson's hawks (*B. swainsoni*) and goshawks (*Accipiter gentilis*). Great horned owls (*Bubo virginianus*) were common, but owls are nocturnal whereas marmots are diurnal.

I radiolocated marmots every 1–3 d throughout the active season (May–September). Mortality was suggested by a constant signal that did not vary in location or intensity, then was confirmed by recovery of the transmitter. Cause of death was determined based on evidence found at the site. I assigned predation as the cause if the carcass had been bitten or eaten. In most cases I identified the predator based on tooth impressions in the beeswax coating of the transmitter, which I compared with the dentition of museum specimens of mammalian predators collected from the area.

For transmitters found on the ground surface, I identified mammalian predators, except badgers, on the basis of tooth impressions. I assigned badgers as the predator when I found the transmitter within a marmot burrow that had been recently excavated by a badger; such excavations are unmistakable in appearance. Raptors typically pluck the fur from larger mammalian prey before eating; thus, I assigned raptors as the predator when the transmitter

TABLE 1.—Cause-specific mortality of yellow-bellied marmots (n = 97) near Rocky Mountain Biological Laboratory, Colorado, 1984–1995

Cause of mortality	n	%
Human activities	2	2
Died underground, cause unknown	2	2
Predator	93	96
Coyote	46	47
Badger	10	10
American marten	7	7
Black bear	7	7
Raptor	6	6
Unidentified predator	17	18

was recovered on the surface of the ground, had no tooth impressions and was accompanied by large quantities of marmot fur.

My analysis was based on three assumptions. First, a recovered transmitter meant the marmot was dead. Although channel catfish (*Ictalurus punctatus*) can expel an implanted transmitter from the peritoneal cavity (Summerfelt and Mosier, 1984), marmots apparently cannot. No instrumented marmot was recaptured without its transmitter, nor was any marmot recaptured or observed after its transmitter had been recovered.

Second, I assumed that a transmitter recovered from a carcass that had been bitten or eaten meant the marmot had died from predation. The alternative, that some marmots died aboveground of other causes and subsequently were scavenged, is possible but unlikely. Because marmots seek refuge in their burrows, mortality unrelated to predation would have to be sudden. Since 1962 sick or dead marmots ≥1-y old have been observed aboveground only twice (Armitage and Downhower, 1974; K. B. Armitage, pers. comm.).

Third, I assumed that tooth impressions in the transmitter identified the predator responsible rather than a subsequent scavenger. Because beeswax is soft at body temperature but hardens as it cools, I could distinguish tooth impressions made at the time of death from those made after the transmitter had cooled.

RESULTS

Ninety-seven instrumented marmots died during the active season (Table 1). Two died because of human activities, one from being struck by a vehicle and the other from a gunshot wound. Two more died underground in burrows that showed no sign of disturbance by badgers; cause of death was unknown but was attributed to natural factors.

The remaining 93 marmots were killed by predators. Of these, 46 were killed by coyotes. Coyote tooth impressions in transmitters included canines, incisors, premolars and molars. In two cases tooth impressions matched those of both red foxes and coyotes, but I ruled out foxes because of their rarity in the study area. Coyote fur was sometimes found entangled on shrubs beside the transmitter. In all cases, remains of the marmot were limited to a few tufts of fur, often including the tip of the tail and sometimes portions of the digestive tract. Transmitters were found in every habitat in the study area and at elevations ranging from the valley floor to 3840 m, well above timberline. I never found a transmitter in or near a coyote den or in a coyote scat.

Ten marmots were killed by badgers. None of the transmitters had tooth impressions, but all were found buried with part or all of the marmot carcass under ≥10 cm of loose

soil inside the burrow. In two cases I found the entire carcass of the marmot, still buried and uneaten 7–10 d after death. Five badger-caused mortalities occurred when the marmot was killed in a "flight" burrow, a shallow burrow occupied temporarily when marmots are threatened (Armitage, 1988).

Seven marmots were killed by martens. Marten tooth impressions in transmitters were limited to canines. In five of these cases I found no remains of the marmot and in the other two I found portions of the digestive tract. All seven transmitters were found in conifer forests, the preferred habitat of martens (Hargis and McCullough, 1984). The largest marmot killed by a marten was a 4-y-old male that weighed ca. 4 kg at the time of death in late August.

Seven marmots were killed by black bears. Most tooth impressions were made by canines but a few were by incisors and molars. I found no marmot remains except a few hairs and, in one case, the tip of the tail. Transmitters were found in a variety of habitats but were never found in or near a bear den or in a bear scat.

Six marmots were killed by raptors. All six transmitters were found on open steep slopes above 3100 m with little vegetation; in addition to large quantities of fur, I found some pieces of everted skin and a few bones, but no flesh. I found golden eagle feathers beside two of the transmitters.

Seventeen marmots were killed by predators that could not be identified. All 17 transmitters were found on the ground surface, none had any tooth impressions, none were accompanied by marmot remains other than a few hairs and occasionally a portion of the digestive tract and none were associated with evidence of badger activity. These circumstances suggest coyotes, bears or martens. I suspect that most were killed by coyotes; indeed, I later recovered the eartags of 1 of the 17 marmots from a coyote scat.

The locations of transmitters of predator-killed marmots showed a clumped distribution (Fig. 1). One cluster of locations encompassed three adjacent marmot colonies at the north end of the study area, 500–1000 m northwest of the confluence of the East River and Rock Creek. Another cluster was along the East River, beginning about 1 km below the confluence with Copper Creek. The river here enters a narrow, steep-walled canyon; some marmots, mostly noncolonial, lived in burrows in the canyon wall and foraged on the rim above. A third cluster was on the east slope of Gothic Mountain, an area of dense willows that supported few marmots.

DISCUSSION

Coyotes and bears left little, if any, of the marmot carcass. I suspect that these predators began feeding on the marmot immediately after killing it, eventually biting into the transmitter which was then discarded as inedible, often along with gut contents or the tail tip. The marmot was consumed entirely on the spot, or perhaps the remainder of the carcass was carried off. Martens left similar evidence but were too small (ca. 1 kg) to have consumed the entire carcass, so after feeding they evidently dragged the remainder of the carcass away.

In contrast, badgers left much of the carcass, ranging from a large portion of the skin to the entire carcass, and buried it under loose soil. Badgers apparently had cached the uneaten portion, a behavior reported for badgers and other carnivores (Macdonald, 1976). Half of the marmots killed by badgers were dug out of flight burrows whose entrances lacked the encirclement of rocks thought to resist enlargement by badgers (Andersen and Johns, 1977). The other half, however, were excavated from burrows that were at least partially protected by rocks, indicating that the close association between marmot burrows and rocks (Svendsen, 1974) does not always provide protection from badger predation.

Raptors also left substantial remains, especially plucked fur and everted skin, presumably

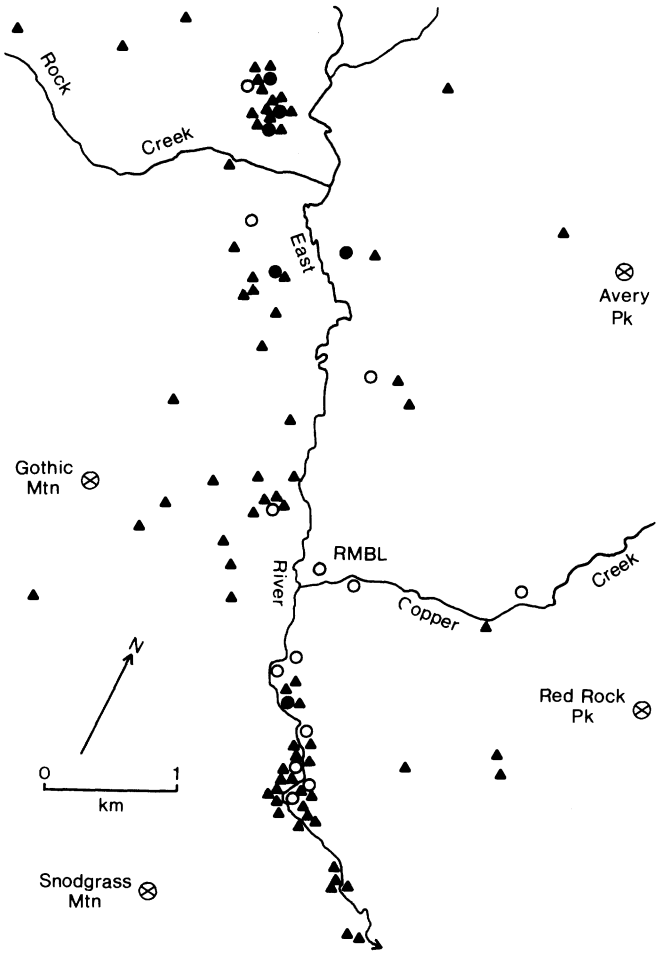

FIG. 1.—Locations of 73 yellow-bellied marmots killed by predators (solid triangles) near Rocky Mountain Biological Laboratory (RMBL), Colorado, 1984–1995. Localities known to be inhabited by marmots are indicated as colonies (solid circles) or noncolonial sites (open circles). An additional 20 marmots were killed at locations outside the area covered by the map. Mortalities appear clustered in three areas: one encompasses three marmot colonies located 500–1000 m northwest of the confluence of the East River and Rock Creek; another is along the East River, beginning about 1 km below the confluence with Copper Creek; and the third is on the east slope of Gothic Mountain

to facilitate digestion. Surprisingly, however, I found no flesh and few bones, indicating the raptor consumed part of the carcass and carried off the rest. Only golden eagles seem large enough to consume and carry so much, so I conclude that they were most likely the raptor responsible, a conclusion that is supported by discovery of golden eagle feathers at two locations. Yellow-bellied marmots were the most important prey of golden eagles in eastern Washington (Marr and Knight, 1983).

The risk of predation was not uniformly distributed throughout the study area. One cluster, which occurred on a slope that supported three of the six marmot colonies in the

study area, may have resulted from a greater availability of marmots rather than predation risk *per se*. However, the other two clusters appear to be "population sinks," areas that attract marmots (similar to "dispersal sinks"; Lidicker, 1975), but which have an unusually high risk of mortality (Knight *et al.*, 1988). One such sink was located in a narrow canyon where many marmots, both residents and dispersers, were killed. Dispersers often moved down the canyon. Further, several sites there had suitable burrows and foraging areas that attracted resident marmots, mostly noncolonial. However, patches of willows and groves of spruce or aspen provided concealment for predators; marmots usually avoid high vegetation that can hide predators (Armitage, 1982). Also, predators approaching along the canyon rim may have been visually screened from marmots moving between burrows in the canyon wall and foraging areas behind the rim. The other sink was on the east slope of Gothic Mountain, which also had extensive patches of willows and groves of spruce and aspen. Although few marmots resided there, most that did were killed. Further, some dispersers were killed there when following a discontinuous scarp that extended across the east slope of Gothic Mountain, parallel to the East River. Apparently these two areas contained habitat features that were attractive to marmots, but which also made them especially vulnerable to predation; marmots may face such trade-offs in habitat selection (Armitage, 1982).

Predation on yellow-bellied marmots is cryptic. None of the predation events documented in my study were observed, despite the fact that several marmots were killed in areas where behavioral observations were conducted frequently. Indeed, only two predation events on marmots were observed in the same study area in >5000 h of behavioral observations over 20 y (Armitage, 1982); in contrast, I documented 93 deaths due to predators in 12 y. Further, in most cases predator-killed marmots were consumed or removed so quickly and completely that intensive systematic searches to locate remains of carcasses would have been fruitless; I often had difficulty doing so even with the assistance of a radiotransmitter.

My study demonstrates that, contrary to earlier findings based on visual observation (Armitage and Downhower, 1974), predation is the dominant cause of mortality among these marmots during the active season, accounting for 98% of natural mortalities. Thus, predation is an important factor in the behavior, ecology and evolution of yellow-bellied marmots.

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