MOUNTAIN SHEEP AND COYOTES: PATTERNS OF PREDATOR EVASION IN A MOUNTAIN UNGULATE

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I used retrospective analyses to investigate relationships among terrain type, reactions of prey, and age and sex of prey and outcomes of encounters between mountain sheep (*Ovis canadensis*) and coyotes (*Canis latrans*). Adult females fled from coyotes more often when in open terrain and young always fled regardless of type of terrain. Young were less likely to survive encounters with coyotes than were adults, and no adult females were killed by coyotes. When types of terrain were pooled, females were more apt to flee than were males, but no difference existed in proportion of females and young that fled. When terrain type and sex of adults were pooled, no difference in survival existed between adults that fled and those that did not. When coyotes were encountered in open terrain, female mountain sheep fled more frequently than did female mule deer (*Odocoileus hemionus*). Ungulates less dependent on terrain for predator evasion than are mountain sheep may employ a more plastic strategy than artiodactyls inhabiting precipitous terrain.

Key words: *Canis latrans*, coyote, *Odocoileus hemionus*, mule deer, *Ovis canadensis*, mountain sheep, behavior, predation, habitat use

Coyotes (*Canis latrans*) are medium-sized, typically solitary, coursing carnivores; these canids are the most common predators sympatric with mountain sheep (*Ovis canadensis*—Kelly, 1980). Despite their abundance, there is conflicting evidence that predation by coyotes is an important influence on populations of mountain sheep (Hass, 1989; Mills, 1937). Nevertheless, predation influences behavior and use of habitats by male and female mountain sheep differently (Berger 1991, Bleich et al., 1997; Festa-Bianchet, 1988).

A preponderance of evidence supports the notion that differential habitat use by females and males of sexually dimorphic ungulates is adaptive (Main et al., 1996). For example, during periods of sexual segregation male mountain sheep occupy areas in which they are more likely to encounter predators, and are less likely to evade them, than do females; simultaneously, these males obtain nutrients not available to females (Bleich et al., 1997). Conversely, females and their offspring maximize the probability of survival by occupying areas that have lower densities of predators and in which the opportunities to detect and evade predators are greater than in areas used by males (Bleich et al., 1997). Additionally, females and their offspring generally occur in larger social groups than do males (Bleich et al., 1997). As a result of these differences, the responses of males and females to predators would be expected to differ, and these responses may vary among habitats. Behavioral responses to the threat of predation also may vary with age, and differential survival would be expected between young and adult mountain sheep.

Predation may elicit overt behavioral changes by ungulates, such as modification of vigilance behavior and foraging efficiency (Berger, 1978*a*; Berger et al., 1983; Frid, 1997; Molvar and Bowyer, 1994), abandonment of formerly used habitats (Wehausen, 1996), or differential use of habitats by parturient and nonparturient females (Kohl-

mann et al., 1996). Among prey, reactions to predators may vary from retreat to overt aggression (Berger, 1979; Bowyer, 1987) and, within species, individuals may respond along a continuum from charging the predator to rapid retreat (Berger, 1991). Moreover, body condition of adults or offspring can influence the reaction of maternal females when confronted by a predator (Smith, 1987).

Antipredator mechanisms (Kruuk, 1964) can be either direct (flight or aggression) or indirect (vigilance, social behavior, or use of specific habitats). Both have implications for survival of individuals, although direct responses are more likely to be reported in the literature (Berger, 1991). Nevertheless, observations of interactions between large mammalian predators and their prey are difficult to obtain and frequently are anecdotal because such encounters are observed infrequently and have not been a primary focus of researchers.

I investigated the ways that habitat may have affected direct antipredator strategies of mountain sheep, the manner in which those strategies influenced outcomes of their encounters with coyotes, and compared responses of female mountain sheep and female mule deer (*Odocoileus hemionus*) to coyotes encountered in non-mountainous terrain. I hypothesized that 1) responses of mountain sheep to coyotes would differ as a function of habitat type, and the sex and age of the sheep involved, 2) outcomes of encounters with coyotes would be influenced by the direct response of the prey to the predator, and 3) responses of mountain sheep to coyotes would differ from responses of mule deer.

Materials and Methods

I relied on observations (n = 42) of direct interactions between coyotes and mountain sheep compiled by Berger (1991:67, table 1). I classified mountain sheep as males or females (≥1-year-old), and young (<1-year-old). I used the terms open terrain and escape terrain to describe flat or rolling non-rocky areas and rocky or steep mountainous areas, respectively. I based my analyses on the habitat in which interactions occurred and, with one exception, on the age and sex of mountain sheep reported by Berger (1991); I treated one yearling male as an adult because it occupied habitat typically used by adult males during the encounter. Group sizes of mountain sheep or coyotes were not available and, thus, could not be considered in this paper.

I used data from Bowyer (1987:521, fig. 3) on responses of mule deer to elucidate potential differences in responses of these ungulates and mountain sheep to the threat of predation by coyotes. Mule deer are well-adapted to flee and make use of vegetation to hide from predators. In contrast, mountain sheep largely are dependent on terrain features to evade predators. For interspecific analyses, I considered only female sheep, because available data were nearly all for female deer (R. T. Bowyer, pers. comm.); hence, results would not be confounded by intersexual differences in strategies of predator evasion.

The number of observations of coyotes interacting with mountain sheep males (n = 9), females (n = 23), and young (n = 10) reported by Berger (1991) and the observations of mule deer and coyotes (n = 16) reported by Bowyer (1987) indicated that univariate statistical tests were most appropriate. I used categorical analyses (G-test, Fisher exact test—Zar, 1984) to test for associations ($P \leq 0.10$) between habitat type and age and sex of mountain sheep and responses to coyotes, as well as the outcomes of such encounters, and to test for effects of behavior of mountain sheep on outcomes of encounters. Similarly, I used a G-test to compare responses of female mountain sheep and mule deer to coyotes encountered in open terrain. I tested for differences in responses of mule deer to coyotes with a binomial test (Zar, 1984). Where appropriate for contingency tables, I applied the sequential Bonferroni technique to decrease the probability of Type I error (Rice, 1989). I estimated statistical power ($1 - \beta$) according to Cohen (1969:209–265). Where sample size was small, or $\beta > 0.70$, I presented data without statistical analyses, thereby providing the reader an opportunity to consider the potential importance of the observations. When I failed to reject a null hypothesis, I included the effect size (Δ) with the test statistics (Steidl et al., 1997).

RESULTS

Effect of terrain on behavior and survival.—When mountain sheep (all categories of age and sex combined) encountered coyotes, they fled more often ($G = 6.693$, $d.f. = 1$, $P = 0.010$) when in open (20 of 25) than when in escape terrain (7 of 17). When young were excluded from this analysis, adults still fled more often ($P < 0.001$) when in open terrain (17 of 22) than when in escape terrain (0 of 10). Likewise, adult females fled more often ($P = 0.001$) when in open terrain (15 of 16) than when in escape terrain (0 of 7). Sample size was inadequate to allow a meaningful comparison of males that fled when in open terrain (2 of 6) and escape terrain (0 of 3). All 10 young that encountered coyotes fled, regardless of terrain type.

No adult females were killed in either open ($n = 7$) or escape ($n = 16$) terrain. Sample sizes were inadequate to allow meaningful comparisons of the proportions of males killed in either open (2 of 6) or escape (0 of 3) terrain, or of young killed in open (2 of 3) or escape (2 of 7) terrain. Mortality of young in open terrain (67%) was, however, 2.4 times that in steep terrain (28%).

Effects of age and sex on behavior and survival.—When type of terrain was pooled, there was a significant difference ($G = 15.493$, $d.f. = 2$, $P < 0.001$) in the proportion of individual young (10 of 10), females (15 of 23), and males (2 of 9) that fled when they encountered coyotes. Pairwise comparisons indicated that young ($P = 0.001$) and females ($P = 0.049$) fled more often than males, and that young fled more often than females ($P = 0.071$).

A significant difference ($G = 11.455$, $d.f. = 2$, $P = 0.003$) also occurred among the proportion of young (3 of 10), females (0 of 23), and males (2 of 9) that died during encounters with coyotes. Pairwise comparisons indicated that proportionately fewer young survived encounters than did females, or adults in general ($P = 0.005$ and $P = 0.021$, respectively), and that proportionately more males than females died ($P = 0.073$). Sample sizes were inadequate to allow a meaningful comparison between young and males.

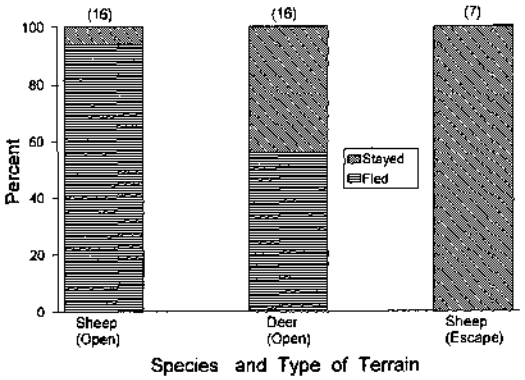

FIG. 1.—Proportions of female mountain sheep and female mule deer that fled or did not flee when coyotes were encountered. Data are from Berger (1991:67, table 1) and Bowyer (1987:521, fig. 3).

Effect of behavior on survival.—When sexes of adults were combined and type of terrain was pooled, none of the 15 adults that did not flee were killed, and only 2 of the 12 that fled died ($P = 0.188$, $\Delta \approx 0.06$). All young that encountered coyotes fled, and they were killed more often (4 of 10) than were adults (2 of 27) that fled ($P = 0.014$).

Responses of mountain sheep and mule deer to coyotes.—No difference existed in the proportion of mule deer that fled (9 of 16) or stayed (7 of 16) when they encountered coyotes in open terrain ($P > 0.50$). When I compared responses of female mountain sheep and female mule deer (Fig. 1), mountain sheep fled more often ($G = 6.578$, $d.f. = 1$, $P = 0.010$) than mule deer. In contrast, deer fled more often ($G = 8.859$, $d.f. = 1$, $P < 0.003$) than sheep when the latter encountered coyotes in escape terrain. Proportions of deer (1 of 16) and mountain sheep (0 of 23) killed by coyotes essentially were identical.

Discussion

Consistent with hypothesis 1, responses to coyotes varied with terrain, sex, and age of mountain sheep. Adults fled more frequently when encounters occurred in open terrain that facilitated pursuit by these coursing predators. Young mountain sheep always fled when they encountered coyotes and did so more often than adults. Moreover, young were killed proportionately more often than adults. Young are substantially smaller than adults (Bleich et al., 1997) and likely are more vulnerable to predation by medium sized predators (Berger, 1991; Curio, 1976).

Regardless of the response to coyotes, higher proportions of young and male mountain sheep were killed than were females. In the eastern Mojave Desert, males occupied areas with more coyotes in which they were especially vulnerable to predators during periods of sexual segregation (Bleich et al., 1997). Because of their small size and inexperience, juveniles may be less adept than adults at escaping from coyotes. For example, Shank (1977) reported that two fleeing young were killed when they were herded away from escape terrain by coyotes but adults apparently learn to not be herded.

No difference existed in the proportion of adults that were killed, whether or not they attempted to escape, leading me to reject hypothesis 2. Nevertheless, young fled in all instances, and were more apt to be killed by coyotes than were adults. The lack of a relationship between the behavior of adults and being killed by coyotes was surprising; among domestic sheep and mule deer, those that fled were attacked or pursued more often than those that did not (Bowyer, 1987; Connolly et al., 1976).

When predators are encountered, responses by ungulates may be influenced by presence of offspring and this, in turn, may influence habitat use or responses by prey (Kohlmann et al., 1996). Young frequently have been present when female mountain sheep initiated aggressive behavior toward coyotes (Ashcroft, 1986; Berger, 1978*b*; Bleich, 1996; Goodson and Stevens, 1994; Hornocker, 1969; Woolf and O'Shea, 1968). Female mountain sheep are philopatric (Luikart and Allendorf, 1996; Ramey, 1995) and seldom disperse from home ranges of their mothers (Bleich et al., 1996; Geist, 1971); hence, females and young occupying the same ranges have a very high probability of being closely related. Whether or not juveniles that are defended are the offspring of the adults involved is not always certain, but females in matriarchal societies that defend young are likely to enhance their inclusive fitness (Berger, 1978*b*; Bleich, 1996; Griffith, 1988; Hamilton, 1964).

Circumstances under which defense of young and predator harassment (Berger, 1979) are probable may vary with adult body condition, or age and condition of the offspring (Hass, 1990; Smith, 1987), and likely are a function of potential benefits to the adult(s) involved (Robertson and Biermann, 1979). For example, during years when females are in good physical condition, they should be more likely to defend their young because the average probability of offspring survival is greater than when females are in poor condition. Similarly, females should be less inclined to defend offspring that are in poor, rather than in good, condition (Smith, 1987). Prior to an extended period of depressed recruitment (Wehausen et al., 1987), Berger (1978*b*) and Bleich (1996) reported that female mountain sheep actively defended young against predators. Despite several years of intensive field work in the same geographic area, however, DeForge and Scott (1982) observed no defense of offspring during a period when young were compromised by disease.

Models of habitat suitability developed for mountain sheep (Bleich and Holl, 1982; Bleich et al., 1992; Cunningham, 1989; Hansen, 1980) have emphasized the importance of escape terrain as a habitat feature, and Holl (1982) demonstrated a strong re-

lationship between density of females and available escape terrain. Data summarized herein suggest that the terrain in which encounters initially occurred did not affect the probability of adult females being killed by coyotes. Young, however, may be especially vulnerable to predation, and females may enhance their fitness by selecting habitats in which offspring are less apt to encounter and more likely to evade predators (Bleich et al., 1997).

Mountain ungulates are especially dependent on steep and rugged terrain to avoid predation (Schaller, 1977). The strategy of reducing risk may differ for ungulates adapted to less precipitous terrain where the ability to escape predators is more limited, but hiding (Geist, 1981:171), increasing group size (sensu Hamilton, 1971), or confronting predators (Griffith, 1988) are successful strategies. Mule deer in open terrain demonstrated no propensity to flee (Bowyer, 1987:521, fig. 3), but mountain sheep almost always fled when they encountered coyotes away from escape terrain. In contrast, female mountain sheep never fled when they encountered coyotes in escape terrain—a situation in which they are adept at evading predation. Rachlow and Bowyer (1991) reported low neonatal mortality among Dall's sheep (*Ovis dalli*), even in a predator-rich environment. Likewise, mortality due to predation by coyotes was not detected among female mountain sheep occupying steep terrain in a desert environment (Bleich et al., 1997). Female mountain sheep employ a general strategy of flight when in open terrain and stand their ground or act aggressively when they encounter coyotes in escape terrain. In contrast, mule deer, and perhaps other cervids occupying less precipitous terrain, employ a more plastic predator evasion strategy that may be affected by the proximity of vegetative cover. As with mountain sheep, female mule deer exhibit active defense of young under certain circumstances (Bowyer, 1987; Griffith, 1988).

There is a strong effect of habitat, age, and sex on behavioral responses of mountain sheep to predators and the subsequent outcome of such encounters. Additionally, ungulates well-adapted to mountainous terrain respond differently to the threat of predation than those occupying less precipitous terrain. Several aspects of risk, however, are the subject of much uncertainty (Lima and Dill, 1990), and rigorous analyses of antipredator behaviors frequently are confounded by differences among species (Kohlmann et al., 1996).

An integrative approach (Frid, 1997) that simultaneously considers effects of visibility (Risenhoover and Bailey, 1985), availability of escape terrain (Bleich et al., 1997), group size of predators and prey (Bowyer, 1987; Elgar, 1989; Fitzgibbon and Lazarus, 1995), and effects of age and sex will likely be productive in understanding differences in predator-evasion strategies of ungulates occupying mountainous and nonmountainous terrain. Moreover, stalking and coursing predators may elicit differing responses by prey. As a consequence, hunting strategies of different predators also should be considered by researchers studying responses of large mammals to the threat of predation.

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