

## SELECTION OF MULE DEER BY MOUNTAIN LIONS AND COYOTES: EFFECTS OF HUNTING STYLE, BODY SIZE, AND REPRODUCTIVE STATUS

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Predation on mule deer (*Odocoileus hemionus*) by mountain lions (*Puma concolor*) and coyotes (*Canis latrans*) was examined to test effects of hunting style and body size, and for mountain lions reproductive status, on selection of prey. Mountain lions, which hunt by stalking, selected  $\leq 1$ -year-old mule deer as prey. Body condition of mule deer did not affect prey selection by coyotes or mountain lions, and both predators preyed upon females and older adult deer more often than expected based on the percentage of these groups in the population. Female mountain lions selected female deer, but male mountain lions did not. Female mountain lions without offspring, however, did not differ from male mountain lions in prey selection. Coyotes did not select for young deer. Female mountain lions with kittens were selective for young deer in late summer.

Key words: California, *Canis latrans*, coyote, mountain lion, mule deer, *Odocoileus hemionus*, predation, prey, *Puma concolor*

Differences in age, sex, and physical condition may predispose parts of an ungulate population to predation and cause important changes in the demography and dynamics of prey (Curio 1976; Taylor 1984). For example, selection by wolves (*Canis lupus*) for older age classes of moose (*Alces alces*) on Isle Royale led to a younger population of moose but also contributed to population fluctuations of both species (Mclaren and Peterson 1994). Susceptibility to predation may vary with size of predator (Bekoff et al. 1984; Huggard 1993; Ross and Jalkotzy 1996) or method of hunting (stalking versus coursing—Kruuk 1972; Kunkel et al. 1999). Ungulate populations are subject to predation by both canids and felids, and these predators often vary in body size and style of hunting (Mech 1970; Packer et al. 1990; Schaller 1972). Physical condition of prey can affect

their ability to escape predation (Huggard 1993; Peterson 1977), and predators may kill animals in poor condition preferentially (Ackerman et al. 1984; Mech 1970) because selection for more vulnerable prey requires less energy and poses less risk to the predator. Further, antipredator strategies of prey may vary with group size, age, sex, and habitat use by prey (Bleich 1999; Bowyer 1987; Karanth and Sunquist 1995).

Large mammalian carnivores exhibit different styles of hunting. Some species use coursing tactics; others use stealth to stalk and ambush prey (Kleiman and Eisenberg 1973). Coursing predators, such as wolves, may pursue moose for long distances (Mech 1970), apparently assessing moose condition and the likelihood of a successful kill (Peterson 1977). Wild dogs (*Lycaon pictus*) also pursue prey over great distances (Estes and Goddard 1967), and Kruuk (1972) noted that spotted hyenas (*Crocuta*

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*crocuta*) were more successful at killing prey if the chase was >300 m. Coyotes (*Canis latrans*) exhibit variability in their social behavior (Bowen 1981; Harrison 1992; Messier and Barrette 1982) and have been reported to stalk or lie in wait when hunting small mammals (Bowyer 1987; Wells and Bekoff 1982). Hunting of ungulates by coyotes, however, typically involves coursing tactics in which prey are approached, tested, and sometimes pursued over long distances (Bleich 1999; Bowyer 1987; Gese and Grothe 1995).

Most felids are stalking predators (Ewer 1973; Leyhausen 1979) that rely on cover and stealth (Seidensticker 1976; Sunquist 1981) to approach prey closely and then rush and pursue an individual over a relatively short distance (Bank and Franklin 1998; Elliott et al. 1977; Van Orsdol 1984). This form of ambush hunting has been reported for mountain lions (*Puma concolor*—Bank and Franklin 1998; Beier et al. 1995). When prey occur in groups (e.g., mule deer, *Odocoileus hemionus*—Bowyer 1984), the stalking technique of felids could limit their ability to select for young, old, or weakened animals (Schaller 1972).

Body size of prey also may influence selection by carnivores (Bekoff et al. 1984; Kunkel et al. 1999). Most ungulates are sexually dimorphic, with males substantially larger than females (Ralls 1977; Weckerly 1998). Additionally, males often possess horns or antlers that can increase the risk of injury to a predator (Hornocker 1970). Most felids are solitary hunters and tend to kill species weighing more than half their own body weight (Gittleman 1985; Packer 1986). Because male mountain lions can be >50% larger in body size than females (Dixon 1982), sexual dimorphism may lead to differences between males and females in ability to kill prey and risk associated with doing so. Furthermore, mountain lions are substantially larger than coyotes; in California, these canids weigh about 9.8–11.2 kg (Hawthorne 1971). Although coyotes can hunt in packs (Bowen

1981; Bowyer 1987), thereby increasing size of prey they kill, body size still may play a role in selection of prey.

Prey selection also may vary among social categories within a predator species as a result of differences in behavior or energetic needs. Male and female mountain lions may encounter different sex and age classes of deer at varying frequencies because of differences in habitat selection, timing and amount of movement, or home-range size of these large predators. Energetic needs of male and female mountain lions likely vary because of differences in body size or demands of rearing young, but data on this topic are few.

We compared mortality caused by mountain lions and coyotes versus that caused by automobiles for a single population of mule deer to examine selection of ungulate prey by predators that differ substantially in body size, hunting style, and reproductive status. We predicted that coyotes, a small coursing predator, would be more likely than mountain lions, a large stalking hunter, to select mule deer that were younger or in poor physical condition. We also predicted that male and female mountain lions would not differ in their selection of prey unless other factors besides hunting style (e.g., body size or reproductive state) were important determinants of prey selection. We predicted that female mountain lions would kill a greater proportion of young deer than would males and that female mountain lions also would kill a greater proportion of adult female deer than would male mountain lions. If body size affected prey selection by coyotes and mountain lions, we also predicted that such marked differences in body size would lead to a preponderance of small prey items in the diet of coyotes, even though these canids often hunt in packs. We also predicted that mountain lions with different reproductive demands would kill mule deer differentially with respect to sex and age classes of deer.

## MATERIALS AND METHODS

*Study area.*—Round Valley is located on the east side of the Sierra Nevada in eastern California (37°24'N, 118°34'W). Deer inhabit about 90 km<sup>2</sup> during November–April, but the area of use varies with snow depth (Kucera 1988). Most mule deer that overwinter in Round Valley migrate in spring to high-elevation ranges in summer (Kucera 1992; Pierce et al. 1999). A small proportion of the herd, however, remains on the eastern side of the mountains and is prey for resident mountain lions and coyotes throughout the year.

Dominant vegetation is characteristic of the Great Basin (Storer and Usinger 1968) and includes a mosaic of bitterbrush (*Purshia tridentata*), sagebrush (*Artemisia tridentata*), and rabbitbrush (*Chrysothamnus nauseosum*). Patches of blackbrush (*Coleogyne ramosissima*) and mormon tea (*Ephedra nevadensis*) also are interspersed. *Salix*, *Rosa*, and *Betula occidentalis* occur in riparian areas. Detailed descriptions of the study area were provided by Kucera (1992) and Pierce et al. (1999).

Our study began in November 1991 at the end of a prolonged drought. Annual precipitation during the study was highly variable: the coefficient of variation of annual precipitation was 51% during 1983–1998, and annual precipitation ranged from 5.3 to 25.2 cm, with 72% occurring between November and March. Mean monthly temperatures on the winter range (November–March) varied from 0°C to 16°C. Estimated numbers of deer on the winter range increased gradually over the period of the study from 939 (10 deer/km<sup>2</sup>) in 1991 to 1,913 (21 deer/km<sup>2</sup>) in 1997, whereas mean number of mountain lions decreased from 6.1 in winter 1992–1993 to 3.0 in 1996–1997 (Pierce et al., in press).

*Sampling prey and predators.*—Three hundred ten mule deer (217 females, 93 males) were captured and fitted with radiocollars during winter or spring 1993–1997. Deer were captured using Clover traps ( $n = 9$ —Clover 1956), drop nets ( $n = 2$ —Conner et al. 1987), and a net gun fired from a helicopter ( $n = 299$ —Krausman et al. 1985). Deer were captured on their winter range, and individuals from groups that already included an animal with a collar were intentionally avoided. Collars were distributed among adult males and females in the approximate proportion of their occurrence in the population (1:3). Deer <1 year old ( $n = 113$ ) were fitted with expand-

able collars (Bleich and Pierce 1999); their sex ratio was close to 1:1. Twenty-one adult mountain lions (12 females, 9 males) and 21 offspring (<1 year old; 14 male, 7 female) were captured with the aid of hounds (adults and kittens;  $n = 38$ —Davis et al. 1996) or foot snares ( $n = 4$ ) during November 1991–May 1996. We weighed mountain lions to the nearest 2.5 kg using a spring scale, and mean weight of adult mountain lions was determined using the 1st recorded weight for each individual. All adults were fitted with radiocollars. Nine kittens ( $\leq 6$  months old) from 3 litters were captured in natal dens (Bleich et al. 1996). Age of young mountain lions was estimated with weight, pelage characteristics, and patterns of tooth eruption (Anderson 1983; D. Ashman et al., in litt.). All methods used in this research were approved by an Institutional Animal Care and Use Committee at the University of Alaska–Fairbanks.

Helicopter surveys were conducted annually in January to determine number of deer in the study area and proportions of adult males, adult females, and young. Transects were flown with 3 observers and extended across the entire study area at an elevation where deer tracks in snow could no longer be seen.

*Deer mortality and predation.*—We located mule deer killed by mountain lions and coyotes during 1991–1998 by back-tracking lions from daytime positions, investigating mortality signals from transmitter-equipped deer, locating mountain lions at night via telemetry, and investigating locations of scavenging birds. All marked deer were monitored daily for mortality signals, and causes of mortality were determined by examining wounds, tracks, and feces in the vicinity of carcasses. Additionally, remote photography (Pierce et al. 1998) facilitated determination of the predator responsible for a kill. Lower incisors and femurs were collected from all carcasses of mule deer for age analysis with cementum annuli (Low and Cowan 1963) and for analysis of fat with ether extraction of marrow in long bones (Neiland 1970).

We collected feces of carnivores opportunistically for analysis of diets. Although many feces for both predators were gathered near locations of kills, coyote feces were located throughout the study area, especially along roads. Feces of mountain lions were numerous at latrines (locations used repeatedly for scent marking) and near resting areas. Feces of mountain lions also

were located by hounds while trailing mountain lions. Identification of food in fecal samples was determined from remains of bone, teeth, and claws and from hair samples examined for color, length, thickness, and medullary characteristics (Big Sky Laboratory, Florence, Montana). Remains identified from carnivore feces were categorized as mule deer, small animals (<15 kg), or other and were summarized as percentage occurrence in feces.

We used data from deer killed by automobiles during 1991–1998 to estimate sex, age class, and physical condition of prey available to predators. Use of such animals as a random sample of a population has been questioned (O’Gara and Harris 1988) because deer in poor condition may be more likely to use roadways for paths of travel through deep snow. This potential problem, however, was not a consideration for our study area. Most deer (55% of 191 deer) killed by automobiles were collected from Highway 395, and snow depth rarely was greater than a few centimeters in the vicinity of that roadway; deer killed along the roadway were not there to avoid deep snow. To ensure our sample of deer killed by automobiles was not biased, we tested for differences in age composition of those deer killed during winter (October–April) against data obtained from aerial surveys conducted in January of each year.

In addition to using deer killed by automobiles as a sample of the deer population, we estimated proportion of postnatal deer (<4 months old) in the population during late summer (July–September) by fetal rates. Adult females were shot at random annually in March following the methods of Kucera (1997). The mean number of fetuses per adult female ( $n = 86$ ) in 1992–1996 was used to estimate the proportion of postnatal deer in the population in late summer. Use of fetal rates to estimate the available proportion of postnatal deer during late summer did not account for mortality and therefore was an overestimate. Thus, our estimate of selection for postnatal deer by predators was conservative.

*Data analysis.*—We used chi-square analysis (Zar 1984) to compare the proportion of <1-year-old deer killed by automobiles in late summer (July–September) with the proportion of postnatal deer (<4 months old) expected, based on fetal rates of adult females collected in March. Consequently, we used only data from October–June to test for prey selection by moun-

tain lions and coyotes. For comparisons made within the adult age category (e.g., sex and age of adults), data from throughout the year were used because they were not biased by the birthing season of mule deer.

Analysis of variance (Neter et al. 1990) was used to test for differences in age of adult deer killed by automobiles, mountain lions, and coyotes. Differences in the percentage of fat in the marrow of adult females killed by vehicles in March 1993 and 1994 and adult females collected in March of the same years also were evaluated with analyses of variance. We used multidimensional chi-square analysis (Zar 1984) to determine if there were differences in categories of age and condition and in sex of mule deer killed by automobiles, mountain lions, and coyotes in October–June. Mule deer were categorized as young (<1 year) or adult and good condition (>50% fat in bone marrow) or poor condition to meet assumptions of chi-square analysis (Zar 1984). Use of bone-marrow fat to index condition may be problematic because these fat deposits are the last to be used by ungulates (Mech and DelGiudice 1985); therefore, an animal that has used most of its body-fat reserves and is in poor condition may still have some fat in the marrow of their long bones. Measures of body condition based on kidney fat and heart fat rarely were available for deer killed by mountain lions and coyotes because those organs often were consumed. When bone-marrow fat in red deer (*Cervus elaphus*) reached about 50%, kidney fat approached about 25% (Riney 1955). Low kidney fat coincides with other indices of malnutrition; therefore, our results assumed that deer with  $\leq 50\%$  bone-marrow fat were in poorer condition than those deer with  $> 50\%$  bone-marrow fat. We used multidimensional chi-square analysis to test for differences in age, condition, and sex of mule deer (from all months) killed by automobiles and in social categories of mountain lions. Social categories of mountain lions included solitary adult males, solitary adult females, adult females with juveniles (>6 months old but not independent), and adult females with kittens ( $\leq 6$  months old—Pierce et al. 1998).

Because female mountain lions gave birth to litters in late summer (Bleich et al. 1996), females with young consistently had a higher proportion of young deer available as prey relative to other social categories. Therefore, we parti-

TABLE 1.—Proportion of adult ( $\geq 1$  year old) and young ( $< 1$  year old) mule deer in poor ( $\leq 50\%$  bone-marrow fat) and good ( $> 50\%$  bone-marrow fat) condition killed by automobiles and predators in the eastern Sierra Nevada, California (1991–1998). Proportions were not different among sources of mortality for young deer or adults ( $P > 0.05$ ).

| Source of mortality | Deer age and physical condition |          |          |          |          |          |
|---------------------|---------------------------------|----------|----------|----------|----------|----------|
|                     | Adult                           |          |          | Young    |          |          |
|                     | Good (%)                        | Poor (%) | <i>n</i> | Good (%) | Poor (%) | <i>n</i> |
| Automobiles         | 80                              | 20       | 106      | 50       | 50       | 24       |
| Mountain lions      | 80                              | 20       | 99       | 69       | 31       | 74       |
| Coyotes             | 74                              | 26       | 27       | 62       | 38       | 13       |

tioned our data to test for prey selection by female mountain lions with kittens. Using a chi-square test, we compared the proportion of postnatal deer killed by female mountain lions with kittens with the proportion of postnatal deer in the population during late summer as estimated from fetal rates.

#### RESULTS

Analysis of prey remains in carnivore feces indicated that mule deer were the primary food of mountain lions, occurring in 73% of feces, whereas remains of mule deer occurred in 17% of coyote feces ( $\chi^2 = 65.21$ , *d.f.* = 1,  $P < 0.001$ ). Desert cottontails (*Sylvilagus audubonii*) and black-tailed jack rabbits (*Lepus californicus*) were the primary species of small animals in the diet of mountain lions and coyotes.

The proportion of young in the population as determined by aerial surveys ( $26\% \pm 4.4$  *SD*) did not differ from that estimated from deer killed by automobiles ( $25\% \pm 8.4\%$ ) during all years pooled ( $\chi^2 = 0.16$ , *d.f.* = 1,  $P = 0.69$ ) or during any year ( $P \geq 0.19$ ). Additionally, percentage of fat in the bone marrow of mule deer collected in March ( $78\% \pm 20\%$ , *n* = 31) did not differ from the percentage observed for adult females killed by vehicles in March ( $64\% \pm 19\%$ , *n* = 6;  $F = 2.70$ , *d.f.* = 1, 36,  $P = 0.10$ ). For deer killed during all months, more young deer than adults in the population were in poor condition ( $\chi^2 = 5.6$ , *d.f.* = 1,  $P < 0.05$ ; Table 1); however, no selection occurred with respect to physical condition for deer killed by predators or by

automobiles among young deer or adults (Table 1). Additionally, mule deer in poor condition comprised a small proportion of the deer killed by all sources (Table 1).

Analysis of age, sex, and condition of mule deer killed by automobiles, mountain lions, and coyotes from October to June indicated no difference in the sex or condition of mule deer for all ages combined (Table 2). Mountain lions, however, killed a greater proportion of young deer than did automobiles ( $P < 0.01$ ; Fig. 1). Coyotes did not select more young (26%) than expected based on the proportion killed by automobiles (21%;  $P = 0.42$ ; Fig. 1). When comparing sex and age of adult mule deer among sources of mortality, mountain lions and coyotes killed more females than did automobiles ( $P < 0.05$ ; Fig. 1), and the mean age of adult deer killed by predators was greater than that of adult deer killed by automobiles ( $P < 0.001$ ; Fig. 2).

Mean weight of 8 adult male mountain lions ( $55$  kg  $\pm 7.7$  *SD*) was  $> 25\%$  the mean weight of 11 adult females ( $40 \pm 5.1$  kg). Social categories of mountain lions did not differ when contrasted with sex or condition of deer preyed upon by these animals and of deer killed by automobiles, when age categories of deer were combined (Table 3). When only adult deer were considered, however, a higher percentage of female deer were killed by female mountain lions (79%) than were killed by automobiles (63%;  $\chi^2 = 6.02$ , *d.f.* = 1,  $P < 0.05$ ), but female and male (81%;  $\chi^2 = 2.70$ , *d.f.*

TABLE 2.—Proportion of male and female mule deer in poor ( $\leq 50\%$  bone-marrow fat) or good ( $> 50\%$  bone-marrow fat) condition killed by automobiles or predators in the eastern Sierra Nevada, California, October–June (1991–1998). Data collected from July through September were excluded because of a high proportion of postnatal deer ( $< 4$  months old) in the populations that were under-represented in mortality data. Proportions were not different among sources of mortality for condition or sex ( $P > 0.05$ ).

| Source of mortality | Deer physical condition and sex |          |          |          |            |          |
|---------------------|---------------------------------|----------|----------|----------|------------|----------|
|                     | Condition                       |          |          | Sex      |            |          |
|                     | Good (%)                        | Poor (%) | <i>n</i> | Male (%) | Female (%) | <i>n</i> |
| Automobiles         | 81                              | 19       | 101      | 38       | 62         | 144      |
| Mountain lions      | 78                              | 22       | 157      | 36       | 64         | 152      |
| Coyotes             | 72                              | 28       | 43       | 24       | 76         | 46       |

= 1;  $P = 0.10$ ) mountain lions killed the same percentage of female deer. Female mountain lions killed a greater proportion of young deer than did males ( $\chi^2 = 4.81$ ,  $d.f. = 1$ ,  $P < 0.05$ ) or automobiles ( $\chi^2 = 31.01$ ,  $d.f. = 1$ ,  $P < 0.001$ ; Fig. 3). Considered separately, solitary females still selected proportionally more young deer than were killed by automobiles ( $\chi^2 = 11.12$ ,  $d.f.$

= 1,  $P < 0.001$ ); however, solitary females did not differ from male mountain lions in selection of age categories of deer ( $\chi^2 = 1.18$ ,  $d.f. = 1$ ,  $P = 0.18$ ; Fig. 3).

Despite the concordance between proportions of young deer killed by automobiles during October–April and proportions observed in annual surveys, comparison of

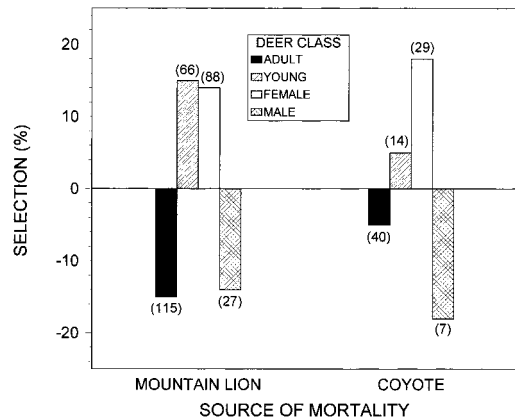


FIG. 1.—Proportion of  $< 1$ -year-old and adult mule deer killed from October to June and proportion of adult male and female deer killed annually by mountain lions and coyotes in the eastern Sierra Nevada, California, 1991–1998. Proportion of deer in different sex and age categories killed by predators was compared with the proportion available in the population as indexed by deer killed by automobiles (0 on y-axis; % selection = % use – % available). Sample sizes are given in parentheses.

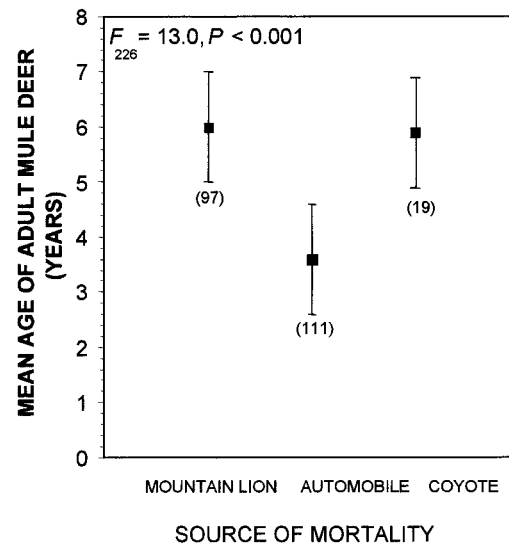


FIG. 2.—Mean ( $\pm SE$ ) age of adult mule deer killed by mountain lions, coyotes, and automobiles in the eastern Sierra Nevada, California, 1991–1998. Ages of deer were determined by analysis of cementum annuli. Adult deer killed by mountain lions and coyotes were older than those killed by automobiles. Sample sizes are shown in parentheses.

TABLE 3.—Proportion of male and female mule deer killed in poor ( $\leq 50\%$  bone-marrow fat) or good ( $> 50\%$  bone-marrow fat) condition that were killed by automobiles or various social categories of mountain lions in the eastern Sierra Nevada, California (1991–1998). There was no difference ( $P > 0.05$ ) in the condition or the sex of mule deer killed by mountain lions and those killed by automobiles when all age categories and all months were combined.

| Source of mortality                         | Deer physical condition and sex |          |          |          |            |          |
|---|---------------------------------|----------|----------|----------|------------|----------|
|   | Condition                       |          |          | Sex      |            |          |
|   | Good (%)                        | Poor (%) | <i>n</i> | Male (%) | Female (%) | <i>n</i> |
| Automobiles                                 | 78                              | 22       | 132      | 40       | 60         | 111      |
| Mountain lions                              |                                 |          |          |          |            |          |
| Solitary males                              | 77                              | 23       | 22       | 34       | 76         | 25       |
| Solitary females                            | 68                              | 32       | 47       | 38       | 72         | 57       |
| Females with juveniles                      | 86                              | 14       | 28       | 41       | 59         | 22       |
| Females with kittens ( $\leq 6$ months old) | 73                              | 27       | 37       | 47       | 53         | 32       |

the proportion of young deer killed by automobiles (15%) and the estimated proportion of young deer based on fetal rates (51%) in late summer indicated that postnatal deer were underrepresented in our sample of deer killed by automobiles ( $\chi^2 = 21.70$ ,  $d.f. = 1$ ,  $P < 0.001$ ). Mountain lions with kittens still selected postnatal deer

(92%) during late summer compared with the proportion of postnatal deer estimated by fetal rates ( $\chi^2 = 7.94$ ,  $d.f. = 1$ ,  $P < 0.01$ ).

#### DISCUSSION

Hunting style was not an important factor in prey selection of mule deer; only mountain lions selected young deer (Fig. 1), but both mountain lions and coyotes selected older deer among adults (Fig. 2). Previous researchers (Hornocker 1970; Spalding and Lesowski 1971) also reported similar results with mountain lions selecting young prey. Predation on older age classes has been reported for wolves preying on white-tailed deer (*O. virginianus*—Pimlott et al. 1969), moose (Mech 1970; Peterson et al. 1998), caribou (*Rangifer tarandus*—Kuyt 1972), and Dall's sheep (*Ovis dalli*—Murie 1944). Neither mountain lions nor coyotes selected individuals with low percentages of bone-marrow fat. That outcome indicated that predation on younger and older deer was not associated with especially poor body condition. The hypothesis that a stalking predator would not be as selective as a coursing predator was rejected because mountain lions were as selective, relative to availability of different age and condition categories of prey, as were coyotes.

The hypothesis that body size of the

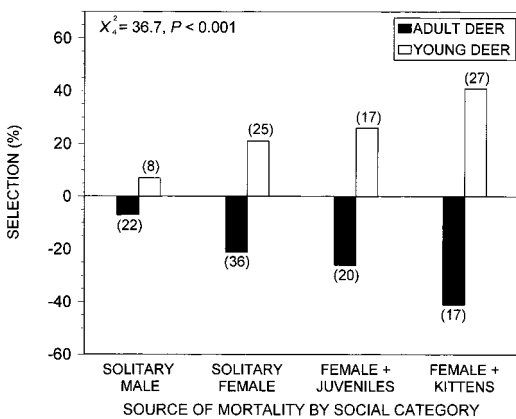


FIG. 3.—Proportion of  $< 1$ -year-old and adult mule deer killed by mountain lions of different social categories: solitary males, solitary females, females with juveniles ( $> 6$  months old but not independent), and females with kittens ( $\leq 6$  months). Proportion of young and adult deer killed by each social category of mountain lion was compared with the proportion available as indexed by deer killed by automobiles (0 on y-axis; % selection = % use - % available).

predator affects prey selection was supported for predation by mountain lions and coyotes on prey species of different sizes and for predation by mountain lions on adult mule deer. Coyotes had a higher proportion of small prey in their diets than did mountain lions, despite the ability of coyotes to hunt in packs and kill large prey (Bowen 1981; Bowyer 1987). Collection of feces throughout the 6 years of our study helped prevent biases associated with population fluctuations and prey switching in coyotes (O'Donoghue et al. 1998; Patterson et al. 1998) and biases associated with changes in density and distribution of mountain lions and their primary prey (Pierce et al. in press). Coyotes also were more omnivorous than mountain lions, which were strict carnivores, a pattern that has been observed previously for canids and felids (Bowyer et al. 1983; Litvaitis and Harrison 1989). Further, female mountain lions selected female deer, whereas male mountain lions did not. Selection of female deer by mountain lions in our study was contrary to the findings of Hornocker (1970) but was consistent with those of Bleich and Taylor (1998), who reported that female deer from populations directly north of Round Valley were killed by mountain lions in greater proportion than expected based on their frequency in the population. Hornocker (1970) reported selection for male prey and proposed that male deer and elk (*Cervus elaphus*) were weakened during the mating season and therefore more prone to predation by mountain lions. Male ungulates also spatially segregate from females seasonally (Bleich et al. 1997; Bowyer 1984; Bowyer et al. 1996) and may select habitats that place them at more risk for predation than do females (Bleich et al. 1997; Hornocker 1970). The proportion of adult male deer on the winter range in Round Valley, as indexed by aerial surveys, increased during 1992–1997 from 12% to 45% of the adult population compared with 19% for the population of ungulates in Idaho (Hornocker 1970). Such an increase in the proportion

of males in the deer population suggests a probable increase in the proportion of young animals in that segment of the population; therefore, a large proportion of the male deer available to mountain lions and coyotes in Round Valley may have been younger and not in weakened physical condition from mating activities.

Predation on both young and adult deer by both coyotes and mountain lions caused us to reject the hypothesis that body size differences between these 2 predators underlie differences in prey selection because coyotes did not select for young deer (Fig. 1). Because our results were for October–June, postnatal deer may have been underrepresented in predator kills because fewer remains of young are left and their carcasses are more difficult to locate (Johnsingh 1993; Schaller 1967). No deer killed by coyotes were located during late summer, possibly because coyotes completely consumed postnatal deer before we could locate carcasses. During other studies, coyotes have preyed heavily on young deer in late summer (Andelt 1985; Bowyer 1987; Litvaitis and Shaw 1980). Coyotes also often hunted in packs in Round Valley (B. M. Pierce, in litt.) and elsewhere (Bowen 1981; Bowyer 1987; Messier and Barrette 1982) and may benefit energetically by killing larger prey (Kruuk 1975; Peterson 1977).

Female mountain lions rearing offspring selected young deer as prey. This outcome may be the result of physiological constraints of lactation. During lactation, female mountain lions may need a more consistent intake of protein than do males. Because protein is stored as muscle, drawing upon protein reserves for too long can affect locomotion (Wannemacher and Cooper 1970). Young deer may be easier than adults to catch because young animals lack experience in escaping predators and may lack stamina (Curio 1976; Schaller 1972); therefore, young deer may provide a smaller but more consistent source of food. We hypothesize that for lactating females the risk of an unsuccessful hunt and the accom-

panying drain on protein reserves may overshadow the benefit of killing larger prey. Male mountain lions may have lower killing rates, killing larger prey less often and gorging themselves to store fat. Such a strategy would allow males to make long-range movements in search of females and in defense of their relatively large territories (Anderson et al. 1992).

Sexual segregation in both predator and prey also may have led to differences in prey selection with respect to age categories of deer. Female mountain lions with kittens were located at relatively low elevations during the late summer compared with other mountain lions (Pierce et al. 1999). Male deer segregate from females with young during spring and summer (Bowyer 1984; Bowyer et al. 1996; Main and Coblenz 1996) and consequently may have been encountered at lower frequencies by mountain lions at lower elevations.

Our study demonstrated that presence of dependent young was a critical factor affecting prey selection by mountain lions. Contrary to our prediction, differences in hunting style between mountain lions and coyotes was not important in prey selection; the stalking predator was as selective as the coursing predator. Differences in body size between coyotes and mountain lions may be important for the selection of prey species but not for the selection of deer from October to June. Body size was not an important factor for selection of deer by mountain lions because solitary male and female mountain lions both killed young and adult deer in proportion to their availability.

Other investigators (Hornocker 1970; Mech 1970; Mech and Frenzel 1971) have reported similar results for prey selection among multiple species of prey or by a single species of predator. Our results, however, emphasize the importance of considering reproductive status of the predator when attempting to predict how that species of predator may affect a prey population. Further study of the effects of the energy

demands of reproduction on prey selection by carnivores is needed to understand predator-prey relationships more completely.

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