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COUGAR PREDATION ON MOOSE IN SOUTHWESTERN ALBERTA

P. Ian Ross[1] and Martin G. Jalkotzy[1]

[1]Arc Wildlife Services Ltd., 2201 34 St. SW, Calgary AB T3E 2W2, Canada

ABSTRACT: Prey selection, and kill and consumption rates by cougars (*Puma concolor*) were studied in the Sheep River area of southwestern Alberta during winter from 1981 to 1994. We investigated 368 kills made by cougars. All 5 ungulate species available within the study area were taken by cougars. Ungulates provided >99% of the biomass consumed by both male and female cougars between November and April each year. Female cougars killed mostly mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*), but all males we studied specialized in moose (*Alces alces*). Of 54 moose fed upon by cougars, 4 were adults which had been found dead and scavenged. Forty-four calves (7-12 months) and 6 yearlings (13-20 months) were killed by cougars: 14 by females, 34 by males, and 2 by cougars of unknown sex. Moose comprised an estimated 12 % of the biomass consumed in winter by female cougars, and 92 % of that for males. A model derived from observed kill rates and the estimated cougar-population structure predicted that cougars in the 515 km^2 study area would kill 18 moose calves and 3 yearlings each winter between December and March. This represented 16-30 % of the estimated early winter calf crop.

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Moose are a holarctic species with a global distribution greater than that of any other cervid. Throughout this circumpolar range, they have evolved in the presence of predation as a major mortality factor. Wolves (*Canis lupus*) and bears (*Ursus arctos* and *U. americanus*) kill moose of all ages in most areas, and predation may strongly limit or even regulate moose populations (e.g., Gasaway *et al.* 1992). Siberian tigers (*Panthera tigris altaica*) occasionally kill moose in the Russian far east (Schaller 1967, H.B. Quigley, Hornocker Wildl. Inst., pers. commun.). Neonatal calves may be vulnerable to a number of medium-sized predators such as coyotes (*C. latrans*; Peterson 1955), but older moose are probably too large to be killed by most other predators.

The cougar also occupies a vast but very different distribution, comprising much of the Western hemisphere and spanning extremely diverse environments covering >100° of latitude. They are highly specialized predators with a very generalized diet. Many prey species have been identified, and it is likely that cougars will kill and eat most vertebrates (Anderson 1983). However, because of their size and the fact that they do not hunt cooperatively, cougars are constrained to killing prey of moderate size (Sunquist and Sunquist 1989).

The distributions of moose and cougars overlap in parts of northwestern North America. Relative to the broad distribution of each, opportunities to study interactions between the 2 species are limited. One region of sympatry is the foothills and mountains of southwestern Alberta. Here, we studied winter food habits of cougars between 1981 and 1994 to assist in the management of populations of cougars and ungulates.

STUDY AREA

The cougar study area was 780 km^2 centered on the Sheep River (50°39' N, 114°38' W) on the eastern slope of the Rocky Mountains in southwestern Alberta. Elevations ranged from 1,280 m in the rolling ranchlands in the east to 2,740 m in the front ranges of the Rocky Mountains. Most of the area was foothills below 2,000 m. Dense forest dominated by trembling aspen (*Populus *tremuloides*) and white and Engelmann spruce (*Picea glauca, P. engelmannii*) occurred in the east and south, and lodgepole pine (*Pinus contorta*) prevailed in the west and north. Understories were well-developed and included dense mountain alder (*Alnus tenufolia*), willow (*Salix* spp.), and many other shrubs.

Mean monthly temperatures varied from -9.6 C in January to 13.7 C in July (McGregor 1984), although temperature ranges of -40 C to 34 C occurred each year. Maximum snowfall occurred in November-December and March-April. Accumulations ranged from 2 m on northern and eastern slopes to none on southern and western slopes that were exposed to warm chinook winds.

In addition to moose, white-tailed deer (*O. virginianus*), mule deer, and elk were widespread throughout the study area. Bighorn sheep (*Ovis canadensis*) were also common, but restricted to small winter ranges. Potential cougar prey in the form of numerous smaller mammals and birds also occurred. Predators of moose included wolves and black and grizzly bears. Winter human population of the study area was <10, including our personnel. Moose hunting was conducted each year under limited-entry permits for both sexes.

METHODS

Winter food habits of cougars were studied between December and April from 1981-82 through 1993-94. Cougars were captured using trained hounds and immobilizing drugs, following the techniques of Hornocker (1970). Eighty-seven cougars were captured, and 60 were radiocollared. From 1981-82 to 1988-89, cougar kills (n = 117) were found by searching areas of concentrated activity of radiocollared cougars. We attempted to obtain 1 radiolocation/day for each of 5-10 cougars, depending on their accessibility and our research priorities. Any time that a cougar tightly localized its activity for a period of >1 day, that site was intensively searched following the cougar's departure. Searching was facilitated by nearly-complete snow cover during this period. This technique was biased towards finding carcasses of large (>15kg) prey, because such carcasses would take longer to consume. However, because most ungulates required several days to consume, we presume that our ability to detect different ungulate species and age classes was unbiased. The exception was deer fawns and bighorn lambs which could be consumed by a large family group in <1 day. Therefore, this cohort may be underestimated in our analyses.

From 1989-90 to 1993-94, cougar kills (n = 259) were found by intensively searching all radiolocations (≥1/day/cougar) of 3-7 adult and independent subadult cougars. Again, nearly continuous snow cover enhanced searching conditions. When conditions permitted, we continuously snow-tracked cougars between radiolocations to search for kills. These kills comprised predation sequences. A predation sequence was a period in which we documented at least 2 sequential ungulate kills for an individual cougar. Cougars were considered the cause of death based on field necropsy results or when tracks and other sign indicated cougar predation. Moose were aged as calves, yearlings, or adults according to tooth replacement and body size. We collected a sample long bone from 23 moose that were killed by cougars for later analysis of marrow-fat content, following procedures described by Neiland (1970).

The moose population was estimated by a single, habitat-stratified aerial survey flown over part (515 km^2) of the study area in February 1992 by Alberta Fish and Wildlife (AFW; now Natural Resources Service, Alberta Environmental Protection) (Jorgenson 1992). The survey area was stratified into 3 classifications of relative habitat quality for moose. A random sample of blocks from within each stratum was surveyed from a Bell 206 helicopter, and moose were counted and classified as cows, calves, and bulls.

We estimated the number of moose killed by cougars during winters 1989-90 through 1993-94 by first including only those moose known to have been killed by cougars, then, to account for kills made by unmarked or unmonitored cougars, we generated a crude model of cougar predation incorporating our estimate of marked and unmarked cougars. Predation rates were calculated from predation sequences we observed during 1989-90 to 1993-94. Size and structure of the cougar population was estimated using data from a 9-year radiotelemetry study conducted within this area (Ross and Jalkotzy 1992, AFW 1992). Unmarked cougars were documented by the presence of their tracks (Ross and Jalkotzy 1992). "Winter" was defined as the period between late November and early- to mid-April during which we systematically tracked cougars. Kills made outside this period were excluded from analyses of winter predation rates.

We estimated live weights of moose from published records. The Sheep River area lies within the transition zone between the distributions of *A. a. andersoni* and *A. a. shirasi* (Peterson 1955). Weights of Shiras moose have been reported by Doutt (1970) and Schladweiler and Stevens (1973). Lynch *et al.* (1996) weighed 151 *A. a. andersoni* carcasses from Elk Island National Park, Alberta, about 340 km north of Sheep River.

Irrespective of their subspecific status, moose from southern Alberta are believed to be lighter than those from Elk Island National Park (G. Lynch, Alta. Env. Protection, pers. commun.). In light of these data, we assigned winter live-weight estimates of 150 kg, 250 kg, and 350 kg to moose calves, yearlings, and adult cows, respectively, at Sheep River. Biomass available to cougars at each carcass was calculated as the product of the estimated live weight and a utilization factor of 0.79, determined in captive feeding trials (Ackerman 1982), minus any observed losses to scavengers.

RESULTS

Prey species selectivity

Between 1981-82 and 1993-94, we examined 368 cougar kills. Fifty moose kills (14 % frequency of occurrence) were found (Table 1). By comparison, we found 32 elk, 201 mule deer, 30 bighorn sheep, and 21 white-tailed deer which had been killed by cougars. Male cougars killed 34 moose, females killed 14, and cougars of unknown sex killed 2.

Four moose carcasses, all adult cows, were scavenged by cougars. Three were scavenged by adult females, and the fourth by an adult male. Adding these scavenged carcasses, and converting to edible biomass, moose contributed 30 % of the biomass consumed in winter by all cougars. This was second in importance only to mule deer (38%), and was followed by elk (22 %), bighorn sheep (6 %), white-tailed deer (4 %), and non-ungulate prey (<1 %).

Moose comprised 4.4 % of the kills made by female cougars, and contributed 12 % of the biomass they consumed during winter. For male cougars, moose constituted 69 % of kills, and contributed 92 % of the biomass they consumed in winter. Males also killed 2 bighorn sheep, 2 mule deer, 1 white-tailed deer, 1 elk, 3 cougars, and 6 prey of other taxa.

Because of high mortality rates among radiocollared male cougars in our study, we were able to intensively monitor a single male during 1990-1994. We did, however, document 23 kills by 8 other radiocollared males, as well as 5 kills made by unknown male cougars, between 1981 and 1994. Moose comprised 18 (64 %) of these kills (16 calves, 2 yearlings). Other ungulates totaled 3 (11 %) of the kills, and non-ungulates comprised 7 kills (25 %).

Predation on moose was not confined to adult cougars. At least 2 moose kills were made by subadult, recently-independent cougars (Table 1). One of these moose was known to be the first kill made by 1 cougar since its independence.

Moose population size and structure

A habitat-stratified aerial survey conducted in February 1992 estimated a total of 331 ± 120 (80% C.L.) moose for the 515 km^2 moose survey area (Jorgenson 1992). The observed sex/age ratio predicted the population to be composed of 198 cows, 58 bulls, and 75 calves.

Selection for classes of moose

Of the 50 moose killed by cougars, 44 (88 %) were calves and the remainder were yearlings aged 13-20 months. The sex/age ratio of moose observed during the February 1992 aerial survey was 38 calves: 29 bulls: 100 cows (Jorgenson 1992). Calves comprised 23 % of the observed population on this survey. It appears that cougars strongly selected for calf moose over other classes. Because no adult moose were found to have been killed by cougars, yet adults were the most prevalent age class, we conclude that cougars avoided predation on adult moose. The proportion of yearlings in the moose population was not estimated, so we were unable to evaluate selection for this class.

Marrow-fat content from calves and yearlings killed by cougars averaged 19.9 % (S.E. = 4.46; range 0.04-65.7; $n = 23$). Sixteen (70 %) of the 23 samples had marrow fat below 25 %, and 9 (39 %) were below 10 %.

Kill rates of moose by cougars

Between 1989-90 and 1993-94, we monitored 1 male and 12 female cougars, and recorded 31 predation sequences spanning a total of 1849 cougar-days. Mean sequence length was 59.7 days (range 6-123). Eight sequences covered essentially the entire winter period. Based on our observations of predation rates and prey species selection, we calculated a winter kill rate of 4.4 moose/100 days/male cougar (range = 2.4-6.8; $n = 3$ sequences). Moose appeared in each of the 3 sequences we monitored for the single male cougar.

Table 1. Moose killed during winter by cougars, Sheep River area, Alberta, 1981-82 to 1993-94.

	Moose Class					
	Calf			Yearling		
Cougar Class	Female	Male	Unknown	Female	Male	Total
Adult female	5	5	2	2		14
Adult male	17	7	4	1	2	31
Subadult male	1					1
Unknown male		1			1	2
Adult unknown	1					1
Subadult unknown		1				1
Total	24	14	6	3	3	50

The mean winter kill rate for females was 0.5 moose/100 days/female cougar (range = 0-4.4; $n = 28$ sequences). Moose appeared in only 5 of the 28 female predation sequences. Eight females never killed a moose during sequences that we monitored. Conversely, the 4 female cougars which did kill moose did so fairly regularly, with a mean kill rate of 2.6 moose/100 days/cougar (range 1.1-4.4; n

= 5 sequences).

Cougar density for the 515 km^2 moose survey area has been estimated at 3.5/100 km^2 (AFW 1992), so the estimated cougar population was about 18. Of this total, independent cougars numbered 3 males and 8 females (Ross and Jalkotzy 1992). We therefore estimated that over a 4-month winter period, male and female cougars would kill 16 and 5 moose, respectively, in this area. Eighteen of these moose would be calves and 3 would be yearlings.

We attempted to estimate the minimum number of calves present on 1 December 1992. Our model predicts that during December-February, cougars would kill about 12 calves, so we added 12 to the estimated number of moose calves from the February survey (75±27 @ 80% C.L.). Therefore, the modified range of estimates for calf numbers present on 1 December is 60-114. This ignores mortality from all causes aside from cougar predation that may affect the moose population between December and February. Using this rudimentary estimate, cougars killed 16-30 % of the early-winter population of calf moose between December and April.

DISCUSSION

Moose contributed substantially to the winter diet of cougars in the Sheep River area of southwestern Alberta. Male cougars appeared to select strongly for moose-calf prey, in preference to other classes or other species. Female cougars also relied heavily on moose; only mule deer and elk contributed more to their diets in winter.

Food habits of cougars, and mortality factors of moose, have been studied in many areas, but rarely where the 2 species are sympatric. Cougars, therefore, have not been previously implicated as significant predators of moose. We found a single reference to moose as a documented prey item for cougars (Spalding and Lesowski 1971). These authors found moose remains in 4 (3.0 %) of 132 cougar stomachs from southern British Columbia.

Adult cow moose are formidable defenders of their calves, particularly to predators such as wolves (Mech 1970). The cougar lacks the body size of the bear and the cooperative hunting strategy of the wolf, so it would appear to be poorly-suited to preying on dependent moose calves. We had no opportunities to witness the act of cougar predation on moose. However, snow cover occasionally permitted reconstruction of circumstances based on field sign. Most calves were attended by their mothers at the time of the attack. Commonly, the moose were bedded, or were standing and feeding. The cougar stalked the pair, or group, to within close range (<20 m), then launched a sudden rush. Sign indicated that all moose fled, with the victim being attacked and subdued relatively quickly. In at least a few cases, an adult moose, likely the victim's mother, returned to the scene and may have displaced the cougar. Presumably, by this time the victim was dead. We recorded several unsuccessful attacks on moose calves, but none that resulted from aggressive defence by the cow.

Possible explanations for the observed sexual differences in cougar predation on moose are speculative. Male home ranges overlapped those of females (Ross and Jalkotzy 1992), and access to all resident ungulates was more-or-less equivalent for all cougars. Male cougars average about 40 % heavier than females (Anderson 1983). Physically, they are probably better equipped to kill large prey than are females. However, female cougars also killed moose calves and yearlings. Additionally, all adult elk kills we found were made by females, and we presume adult elk to be more difficult to stalk and kill than calf moose.

Female cougars frequently are responsible for the energetic requirements of a dependent litter, as well as themselves. Meeting these needs may require an attempt to exploit virtually all predation opportunities they encounter. Female cougars, therefore, end up hunting more often and killing more ungulates than do males, and may become more proficient hunters. Because moose were less abundant than other ungulates (at least mule deer) and their distribution was patchy, female cougars probably encountered moose less frequently than other prey species. Male home ranges are larger and their daily movement rates are greater than females' (Ross and Jalkotzy 1992, P.I. Ross and M.G. Jalkotzy, unpubl. data), so males are more likely than females to find moose. Male cougars, with lower energetic obligations, may be able to be more selective. Moose calves may be relatively vulnerable prey for cougars because of their naiveté, and because of the relatively small groups in which they are usually found. In 1 example, during 103 km of continuous snow-tracking of 1 male cougar, we documented 5 predation attempts on mule deer and 3 on moose calves, all of which were unsuccessful. However, during this period he did kill 3 moose calves.

All moose killed by cougars had depleted fat reserves. More than one-third of the calves and yearlings killed had marrow-fat levels below 10 %, the "point of no return" described by Franzmann and Arneson (1976). Presumably, these animals would not have survived the winter. To this extent, at least, it appears that cougar predation was compensatory to other moose mortality. We were unable to ascertain whether marrow-fat levels from cougar-killed moose were representative of all moose in the population.

Nearly all moose killed by cougars in our study were calves, and no adult moose kills were found. It seems apparent both that calves were selected and adult moose avoided by cougars. However, data on relative availability of these classes within the population preclude statistical testing of these hypotheses. The only recent moose classification data for the study area were collected during February. Moose mortality that occurred between November and February could not be estimated and may have been significant to all classes, but especially to calves. Hence, the age structure of the early-winter moose population, and the degree to which cougars were actually selecting for or against particular classes of moose are unknown.

Similarly, the utility of our model in predicting overwinter moose losses to cougar predation is compromised by incomplete moose inventory data. We surmise that the moose population in November was higher than that estimated during the February survey, unless immigration offset mortality. Additionally, we had only a single census estimate, and no ability to detect trends in the moose population over the duration of our study. It took us several years to collect the data required to calculate predation rates and generate a predictive model for moose losses to the cougar population. The large mammal community in southwestern Alberta is complex. It is a multipredator/multiprey system involving cougars, wolves, black bears, grizzly bears, and 6 ungulates (including mountain goat [*Oreamnos americanus*]). We have no information on possible influences on our model of significant changes in the densities of moose, alternate prey species, other predators, or cougars.

Furthermore, our calculation of male kill rates was based on data from a single cougar; the influence of individual behavior is therefore potentially exacerbated. However, observations of other male cougars indicated that moose were the most commonly-killed prey for all males that we studied. We determined that prey-species selection at Sheep River was to some extent a function of individual cougar behavior (e.g., bighorn sheep: Ross *et al.* 1997; also female predation on moose: this study).

Nonetheless, our data identified a previously-undocumented important predator of moose. By extrapolating backwards from observed numbers of moose calves in February, adding the predicted number of calves killed by cougars, it was possible to crudely estimate the minimum number of calves available to cougars at the beginning of winter. This resulted in an estimate of overwinter losses to cougar predation of 16-30 % of the calf moose crop. Cougar predation persists until moose are at least 20 months old, and undoubtedly affects calves prior to December as well. Characteristics of cougar predation on moose during May-November are not known.

We also identified an important food source for cougars. In some areas, such as Sheep River, young moose essentially sustain male cougars. Female cougars also derive substantial energy from moose kills. The cougar's ability to consistently kill young moose may have important implications for dispersal and possible recolonization of former cougar ranges, such as much of central and eastern Canada. The cougar's supposed dependence on deer (Ackerman 1982, Anderson 1983) may be weaker than originally believed. Linkage corridors between occupied and vacant but suitable habitats that are inhabited by moose but not deer, may in fact be able to support dispersing cougars. Subadult cougars are the most frequent dispersers (Lindzey 1987), and they too are capable of killing moose.

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