

# ENCOUNTER COMPETITION BETWEEN BEARS AND COUGARS: SOME ECOLOGICAL IMPLICATIONS

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**Abstract:** Black bears (*Ursus americanus*) or grizzly bears (*Ursus arctos*) visited 8 of 55 cougar-killed (*Felis concolor*) ungulates in Glacier National Park (GNP), Montana, from 1992 to 1995, and 19 of 58 cougar kills in Yellowstone National Park (YNP), Wyoming, from 1990 to 1995. Bears displaced cougars from 4 of 8 carcasses they visited in GNP and 7 of 19 in YNP. Cougar predation provided an average of 1.9 kg/day (range = 0–6.8 kg/day) of biomass to bears that fed on cougar-killed ungulates. This biomass was an important percent (up to 113%) of the daily energy needs of bears when compared to their caloric requirements reported in the literature. We suggest that ungulate carrion resulting from cougar predation is important nutritionally to bears in some regions and seasons. Cougars that were displaced from their kills by bears lost an average of 0.64 kg/day of ungulate biomass, or 17–26% of their daily energy requirements. Biologists modelling or measuring cougar predation rates should be aware that losses to scavengers may be significant.

*Ursus* 10:55–60

**Key words:** black bear, competition, cougar, Glacier National Park, grizzly bear, predation, *Puma concolor*, scavenging, *Ursus americanus*, *Ursus arctos*, Yellowstone National Park.

Encounter competition is a form of interference competition that occurs when 1 or more mobile, nonspatially-attached individuals are harmed as they directly pursue a common resource (Schoener 1983). This harm includes injuries resulting from physical interactions, loss of time, or theft of food. For carnivores, the disputed resource may be prey that a subordinate carnivore has killed and a dominant carnivore intends to scavenge.

Interactions between cougars and scavengers that were present near cougar-killed prey have been reported (Boyd and O’Gara 1985, Spreadbury 1989, White and Boyd 1989, Harrison 1990, Green 1994). Koehler and Hornocker (1991) found 4 bobcats (*Lynx rufus*) and 2 coyotes (*Canis latrans*) killed by cougars near prey cache sites. Harrison (1990) found that a maternal female cougar residing where coyote abundance was reduced by humans killed ungulate prey less frequently than a maternal female living where coyote numbers were not manipulated. Coyotes displaced cougars from their kills less frequently where coyote numbers were controlled.

Although interactions between cougars and scavengers near cougar-killed prey have been documented, the ecological importance of encounter competition remains unclear. Our objective was to (1) document the frequency that black bears and grizzly bears used cougar-killed ungulates, (2) estimate the ungulate biomass made available to bears as a result of cougar predation, and (3)

document the frequency that cougars were displaced from ungulate prey and calculate the quantity of biomass that cougars lost to bears.

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## STUDY AREAS

### Glacier National Park

Cougar–bear interactions were documented concurrent with studies of cougar–wolf (*Canis lupus*) relationships in a 790-km<sup>2</sup> area along the North Fork of the Flathead River in Glacier National Park (GNP) in northwest Montana. Cougars preyed on elk (*Cervus elaphus*), white-tailed deer (*Odocoileus virginianus*), moose (*Alces alces*), and mule deer (*Odocoileus hemionus*). The valley was gently rolling terrain supporting a montane forest interspersed with meadows. It was bordered by steep mountains, 1700–3000 m in elevation. Snow accumulation prompted ungulates to winter at elevations <1600 m from late November to April. Thereafter, ungulates used progressively higher elevations associated with phenological changes in vegetation.

Black bears and grizzly bears were common. Some grizzlies were active outside their dens for at least part of the winter, particularly in the Kintla Lakes area of GNP, where carrion was relatively abundant.

### Yellowstone National Park

Cougars were studied in the northern portion of Yellowstone National Park (YNP), Wyoming, and the contiguous Paradise Valley of south-central Montana. The winter density of adult–subadults ranged from 2.1 to 3.5 per 100 km<sup>2</sup> on a 662-km<sup>2</sup> core area where they spent winter months on ungulate ranges between 1550–2500 m. Elk and mule deer were far more abundant than moose and white-tailed deer. Wintering elk counts ranged from 9,400 to 19,000 from 1990 to 1995 (Mack and Singer 1992; J. Mack, YNP, unpubl. data). Mule deer counts ranged from 1,600 to 2,500 between 1990 and 1994 (Lemke 1994). During late spring, summer, and autumn, cougars used elevations up to 2900 m and preyed on ungulates that were dispersed relative to their restricted distribution in winter. Ungulate ranges supported montane forest, sagebrush steppe, and grassland steppe.

A minimum of 236 grizzly bears were present in the 20,000-km<sup>2</sup> Greater Yellowstone Ecosystem in autumn 1992 (U.S. Fish and Wildl. Serv. 1993, Eberhardt et al. 1994). Black bears were commonly observed. Bears used dens from mid-November to mid-April.

## METHODS

### Documenting Cougar Predation

Responses of bears to ungulates killed by radiocollared cougars were documented during winter,

1992–95, in GNP and during spring–autumn, 1990–95, in YNP. Using methods reported by Shaw (1977), cougars were located 1–3 times daily, between 0600 and 2300 hours from the ground or from airplanes, without disturbing them. All location sites were intensively searched by walking the contours of slopes at 1–20 m intervals to locate carcasses after cougars left. Tracking hounds were used to assist searches of locations and to trail cougars between location sites. Intact ungulate carcasses were necropsied to distinguish cougar predation from that of other carnivores by looking for gross pathology or feeding behaviors described in O’Gara (1978), Wade and Bowns (1982), and Alberta Agriculture (1990). Cougars were monitored on consecutive days until at least 2, but typically 4 ungulates were killed. We attempted to document all ungulates killed by cougars during this period, called a predation sequence.

### Bear Visits to Cougar Prey

Bear visits to cougar-killed ungulates were detected by observing bears or by noting the presence of bear scats, hair, or tracks near carcasses. Hair samples of carnivores were identified to genus or species by personnel at the Wyoming Game and Fish Laboratory in Laramie, following Moore et al. (1974). We could not always discern the species of bear that used cougar prey. Displacement of cougars from cougar kills was recorded as a special case of bear visitation. To identify displacement, we compared the weight of the ungulate carcass that remained (after use by the bear) to the amount present, on average, after cougars left kills without bear displacement. When possible, we interpreted tracks of cougars and bears visible in the snow and radiotelemetry data to discern bear displacement.

### Biomass Eaten by Bears

We estimated the wet ungulate biomass eaten by bears (BEB) feeding on cougar kills only in YNP. Biomass was considered available to bears only if we detected bears at a cougar kill. BEB was the difference between the live-weight of the ungulate and the amount consumed by the cougar, multiplied by the estimated fractional consumption of carcasses by bears. To approximate the energy content of BEB, we converted BEB to its caloric equivalent by assuming dry weight was 32.4% of wet weight (Robbins et al. 1974, Robbins 1993) and multiplying dry weight by its digestible energy of 4.6 kcal/g (Mealey 1975). BEB for each cougar kill was summed to estimate total BEB and divided by the

length of the predation sequence in days to estimate daily BEB.

**Weights of Ungulate Prey.**—The weights of ungulates killed by cougars were estimated using age-specific and sex-specific growth models constructed from empirical data on live and field-dressed weights (Greer and Howe 1964; D. Pac, unpubl. data). Field-dressed weights were corrected for loss of viscera using coefficients obtained from Quimby and Johnson (1951) or calculated from Anderson et al. (1974). Birth weights and dates of parturition were estimated from Johnson (1951), Robinette et al. (1973), Pac et al. (1991), or elk calf mortality studies (J. Mack, YNP, unpubl. data). Weight maxima, minima, rates of weight loss in winter, and rates of weight gain in spring–summer were obtained from Johnson (1951), Greer (1965), Robinette et al. (1973), and Anderson et al. (1974). Ages were estimated for deer and elk using tooth replacement and wear patterns (Quimby and Gaab 1957, Robinette et al. 1957).

**Cougar Consumption.**—The ungulate biomass cougars consumed from their kills was estimated as the product of the daily cougar consumption (specific to cougar social class) and the days the cougar remained at the carcass. Daily consumption was estimated by subtracting the weight of uneaten portions of ungulates from estimated live weights and dividing by the number of days (to the nearest 0.5 day) that the cougar fed. Daily cougar consumption was independently determined from instances when scavengers did not use cougar kills.

**Portion of Ungulates Eaten by Bears.**—Bear consumption was estimated at 50% of cougar-killed elk based on 3 visual estimates made by Green (1994). Bear consumption of deer was estimated at 93%, based on a visual estimate made by Green (1994), 2 estimates in this study, and 2 estimates calculated by subtracting estimated cougar consumption and weights of carcass remains from live weights of deer fed on by bears. Our estimates of bear consumption were imprecise and probably over-estimated individual bear use because (1) they were based

on a small number of observations, (2) coyotes, avifauna, decomposers, tissue autolysis and decay, and water evaporation reduced carrion biomass, particularly if bears intermittently fed over extended periods (>3 days) on cougar kills, and (3) >1 bear may have fed from carcasses. Therefore, BEB values were crude estimates of individual bear consumption.

### Biomass that Cougars Lost

The biomass cougars lost (BCL) was estimated when bears displaced cougars from cougar kills. The fractional consumption by cougars was multiplied by estimated live weight of the ungulate to predict the biomass that would have been consumed if cougars had not been displaced. The estimated biomass the cougar consumed before it was displaced (daily consumption rate multiplied by the number days the cougar was present at the kill) was subtracted from this predicted cougar consumption to determine BCL. BCL for kills was summed for predation sequences to estimate total BCL and divided by the length of a sequence to estimate daily BCL. Total BCL for sequences was less than total BEB because bears often scavenged cougar kills that cougars had already abandoned.

## RESULTS

Fifty-five ungulates were killed by cougars in GNP and 58 in YNP (Table 1). Fifteen (27%) of 55 ungulate kills in GNP occurred in the Kintla Lakes area where bears were often active outside their dens during the winter. Of these 15 kills, 5 were visited by grizzlies (3 cases of displacement) and 2 by an unknown bear species (1 displacement). Bears visited 42% ( $n = 26$ ) of cougar kills we monitored in YNP during spring, 25% ( $n = 24$ ) in summer, and 25% in autumn ( $n = 8$ ). Visitation during spring was greater than summer and autumn combined, but not significantly so ( $\chi^2 = 1.95$ ,  $P = 0.09$ , 1-sided test).

The mean total BEB for predation sequences in YNP was 45 kg (SD = 55,  $n = 11$ ). The range was from

**Table 1. Frequencies bears visited or displaced (disp.) cougars from cougar-killed ungulates, Glacier National Park, 1992–95, and Yellowstone National Park, 1990–95.**

	Glacier National Park (winter, $n = 55$ )				Yellowstone National Park (spring–autumn, $n = 58$ )			
	No. visits <sup>a</sup> (%)		No. disp. (%)		No. visits <sup>a</sup> (%)		No. disp. (%)	
Black bear	0	(0)	0	(0)	8	(14)	4	(7)
Grizzly bear	6	(11)	3	(5)	1	(2)	1	(2)
Unknown bear	2	(4)	1	(2)	10	(17)	2	(3)

<sup>a</sup> Visits include instances when bears displaced cougars from cougar kills. Data for visitation by bears that were not associated with predation sequences were included.

zero kg during a 55-day sequence to 157 kg in 23 days. The mean daily BEB was 1.9 kg/day (SD = 2.5,  $n = 11$ , range = 0–6.8).

The mean total BCL for predation sequences was 16 kg (SD = 31,  $n = 11$ ). The range was from zero kg during a 55-day sequence to 94 kg in 20 days. The mean daily BCL was 0.64 kg/day (SD = 1.4,  $n = 11$ , range = 0–4.7).

Daily consumption rates of cougars averaged 8.5 kg/day for subadults (self-sufficient cougars <24 months) and nonmaternal females combined ( $n = 7$  cougars), 16.7 kg/day for family groups ( $n = 5$  groups), and 13.8 kg/day for an adult male. Prey consumption by cougars averaged 82% by subadults and 46% by adults ( $n = 12$  cougars). Cougar predation rates averaged 1 ungulate/8.7 days (SD = 4.1,  $n = 11$  sequences; 11 cougars).

## DISCUSSION

Bears in our study areas used cougar kills frequently. Although reports of bear–cougar interactions are nearly absent from the literature, we found about 1 in 7 cougar-killed ungulates were scavenged by bears in GNP and 1 in 3 in YNP. Bears displaced cougars from about 1 in 14 kills in GNP and 1 in 8 kills in YNP. Considering only the Kintla Lakes area of GNP, bears visited about 1 in 2 cougar kills and displaced them from 1 in 4 kills during winter months. Green (1994) documented that bears visited 3 of 14 cougar-killed ungulates (1 displacement by a grizzly bear) in northern YNP.

We assume that the frequency with which bears detect cougar-killed prey is highest where ungulates, cougars, and bears exhibit strong spatial overlap and occur at high densities. Because bears and cougars use low elevation habitats during the spring in the mountainous portions of the northwestern United States and western Canada (Seidensticker et al. 1973, Murphy 1983, Servheen 1983, Logan and Irwin 1985, Mack 1988, Raine and Kansas 1990, this study), encounter competition between bears and cougars may increase during spring in this region. Our YNP data weakly supported ( $P < 0.09$ ) that bears visited cougar kills more frequently in spring than during summer and autumn.

The absence of elaborate caching (e.g., in the trees) by cougars supports the hypothesis that frequent responses by ursids and canids to cougar-killed prey are not universal. Although large felids cache more extensively than small ones, food caching is not as common or stereotyped in felids as in canids (Kleiman and Eisenberg 1973). Frequent displacement by scavengers could provide natural selection for more elaborate caching of kills by cougars. Alternatively, it may suggest that cougars can success-

fully defend at least some of their kills from challengers or cope with encounter competitors by feeding on their prey between periods of use by dominant species.

Infrequent but windfall feeding opportunities for bears on cougar-killed ungulates were suggested by the high standard deviation (SD = 55) of the total BEB for predation sequences relative to its mean (45 kg). BEB was zero kg for 27 of 38 cougar-killed ungulates found during predation sequences. However, the ungulate biomass available to bears was potentially significant energetically to them. The mean daily BEB (1.9 kg/day) converted to about 2,830 kcal/day. This value represented 71% of the 4,000-kcal/day energy budget of a nonhibernating 103-kg captive black bear (David 1987), and equaled 113% of the 2,500-kcal/day budget of a hibernating, 204-kg captive grizzly bear (Watts and Jonkel 1988).

The daily BEB was highest when cougars killed large (>80 kg) ungulates and bears visited a high number of cougar kills during a sequence. The highest daily BEB (6.8 kg/day) occurred when a female cougar accompanied by 2 large (42 and 55 kg) kittens killed 4 elk (2 large calves and 2 cows) in 23 days. Bears visited 3 of these kills and displaced the cougars once. We estimated that bears obtained 157 kg of carrion during this sequence.

BEB values were crude estimates because we lacked adequate data concerning consumption of cougar-killed prey by bears. More than 1 bear may have fed on individual cougar kills. We also did not evaluate the direct and indirect energy costs and benefits, or the risks of injury, associated with obtaining this food relative to alternative foraging strategies available to bears. Therefore, we can only hypothesize that cougar-killed prey provided significant energy gains to bears.

Interactions between cougars and other carnivores at cougar kills may directly influence the behavior and survival of dominant competitors. Bears may develop behaviors that, over long periods (>2 weeks) increase their likelihood of detecting cougar kills. For example, the habitat selections and activity schedules of bears may be altered if they predictably and more efficiently obtain food through encounter competition than through alternative foraging strategies. Bears may also temporarily change their behavior in direct response to carrion they have discovered. Bear survival may be reduced if the prospective food rewards provide sufficient incentive for them to take risks. We found 5 coyotes that were killed by cougars near cougar-killed ungulates. Boyd and O'Gara (1985) and Koehler and Hornocker (1991) made similar observations.

Mean daily BCL (0.64 kg/day) was surprisingly high, about 26% of the 2.2–2.7 kg/day required for a single adult female cougar, or 17% of the 3.4–4.3 kg/day required for a single adult male cougar as estimated from an energetics model (Ackerman et al. 1986). The high standard deviation (SD = 31) of total BCL relative to its mean (16 kg) suggested that losses by cougars to bears were sporadic.

The cougar's solitary nature and predatory specialization on large vertebrate prey may predispose it to the adverse effects of displacement. Cougars may lose a considerable energy investment when displaced by an aggressive scavenger or may incur injuries when defending their kills. Cougar death due to interspecific fighting with scavengers at cougar kills has been documented (White and Boyd 1989). The alternative of killing additional prey to compensate for losses to scavengers, however, also carries energetic costs and risk of injury. Ross et al. (1995) noted that 3 (27%) of 11 cougar deaths in Alberta from natural causes were related to acquisition of prey. In response to scavenger pressures, cougars may restrict themselves to habitats and behavior patterns in which interference is unprofitable to dominant species (Case and Gilpin 1974).

Differences in morphology and behavior among large North American carnivores contribute to asymmetry in the effects of encounter competition. Morphological characteristics (e.g., claws, long canines) or social hunting patterns allow some carnivores to take disproportionately large prey (Bekoff et al. 1984). Large felids such as cougars singly and consistently kill prey as large or larger than themselves (Kleiman and Eisenberg 1973). Unlike many large canids, solitary felids are not normally communal feeders (Kleiman and Eisenberg 1973) and usually do not consume kills as quickly as canids. The small mass of cougars relative to North American bears and their small group size relative to wolves and coyotes may often preclude cougars from successfully defending their kills. These typical attributes of Felidae (Kleiman and Eisenberg 1973, Eisenberg 1986) contribute to agonistic interactions between cougars, ursids, and canids at cougar kills where these species are sympatric.

Asymmetry in encounter competition is also enhanced by the cougar's poor olfaction and mobility relative to other carnivores. Cougars may not discover carrion from non-cougar sources as efficiently as canids, ursids, and mustelids. Felids use their olfactory senses less than canids for foraging (Kleiman and Eisenberg 1973). Canids possess cursorial adaptations (Hildebrand 1954) that enhance travel speed and coverage of territories,

giving them a competitive edge over felids in detecting carrion.

Although it appears that encounter competition confers effects that are negative on cougars and positive on bears, some proximate and ultimate benefits to cougars may result from encounter and exploitation competition between cougars and their co-evolved competitors. For example, although spacing in cougar territories is probably driven indirectly by interspecific competition for the resources that space provides, displacement of cougars from their kills by other carnivores could further enhance spacing and decrease the likelihood that individual cougars might deplete their local food supplies.

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