

CHAPTER. 2

COUGAR-PREY RELATIONSHIPS

Although cougars prey on a wide variety of animals including rabbits (*Sylvilagus* spp), hares (*Lepus* spp), skunks (*Mephitis* spp), porcupines (*Erethizon dorsatum*), beavers (*Castor canadensis*), bobcats (*Lynx rufus*), coyotes, and rodents, ungulates provide most of the prey biomass consumed by cougars throughout their range. In North America it is unlikely that a cougar population can be sustained in the absence of ungulates. The number of prey killed per cougar varies with the number and age of dependent young (Ackerman et al. 1986), season (Ross et al. 1997, Hayes et al. 2000), nutritional condition of the prey (Logan and Sweanor 2001), competition from other predators (Kunkel et al. 1999), and usurpation of kills by scavengers (Harrison 1990). Using an energetics model, Ackerman et al. (1986) estimated that an adult male cougar kills 1 deer every 8 to 11 days, an adult female without kittens every 14 to 17 days, and a female with 3 juveniles every 3.3 days. Connolly (1949) reported that an adult cougar killed 1 deer every 9.7 days during winter. Predation rates on bighorn sheep and mule deer by females with kittens averaged 1 animal every 3-8 days (Harrison 1990). Beier et al. (1995) estimated that each cougar kills about 48 large mammals and 58 small mammals per year.



Bobcat with kill. In the ecological systems that cougars inhabitat, both exploitative and interference competition with other predators probably occurs.



Adult cougar on an elk kill.

Shaw (1980) estimated that cougars annually removed 15-20% of the mule deer population on the Kaibab Plateau in Arizona. Anderson et al. (1992) estimated that cougars annually killed 8-12% of the mule deer population on the Uncompahgre Plateau, Colorado. Cougars killed an estimated 2-3% of an elk herd and 3-5% of a deer herd annually in Yellowstone National Park in Idaho, Montana and Wyoming (Murphy 1998). In Alberta, a single cougar killed approximately 9% ($n = 11$) of the early-winter bighorn sheep population including 26% ($n = 6$) of the lambs (Ross et al. 1997).

These percentages, by themselves, do not express the impact on prey populations, because this impact depends on whether predation mortality is additive or compensatory. The impact of predation is greater when mortality due to predation is *additive* to other types of mortality, and less when deaths due to cougars are *compensated* by reductions in other types of mortality, or increases in recruitment.

We offer managers the following major principles of cougar-prey relationships (numbers 1, 3, 4, 6, 8, 10 and 11) and our main recommendations for managing these interactions (numbers 2, 5, 7, and 9).

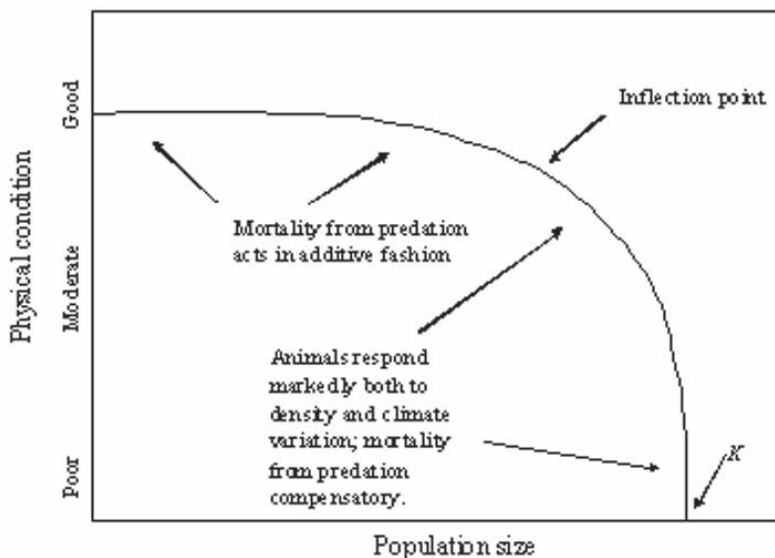


Figure 2.1. Relationship between physical condition of individuals and population density, for a typical ungulate species. There is little change in physical condition (and subsequent changes in reproduction or survival) below the inflection point. As population size approaches carrying capacity, K , physical condition declines markedly, but this can be masked by response to environmental variation (Kie et al. 2003).

1. If members of an ungulate population are in poor physical condition, cougar predation probably has little net effect on ungulate numbers. When individuals in an ungulate population are in excellent condition, cougar predation can have a large effect on recruitment, and cougar control may increase ungulate numbers.

The ungulate prey of cougars, including deer, elk, bighorn, and moose have life history characteristics affected by density dependent processes (McCullough 1979, Boyce 1989, Bowyer et al. 1999, Keech et al. 2000). As population density increases and approaches carrying capacity (K , the number of animals at or near equilibrium with their food supply – Kie et al. 2003), individuals increasingly compete for resources; fecundity, survivorship and nutritional condition decline (McCullough 1979); and incidence of disease increases (Eve and Kellogg 1977, Sams et al. 1996). These changes lead to low recruitment as N approaches K (Figures 2.1, 2.2). However, as an ungulate population approaches K , weather and other environmental factors cause increasingly large variability in the population response (Figure 2.2). This can obscure the underlying relationship between population density and recruitment. While ungulate managers seldom know where a population is in relation to K , the body condition of its members may indicate whether the population is below or above carry capacity (Figure 2.1).

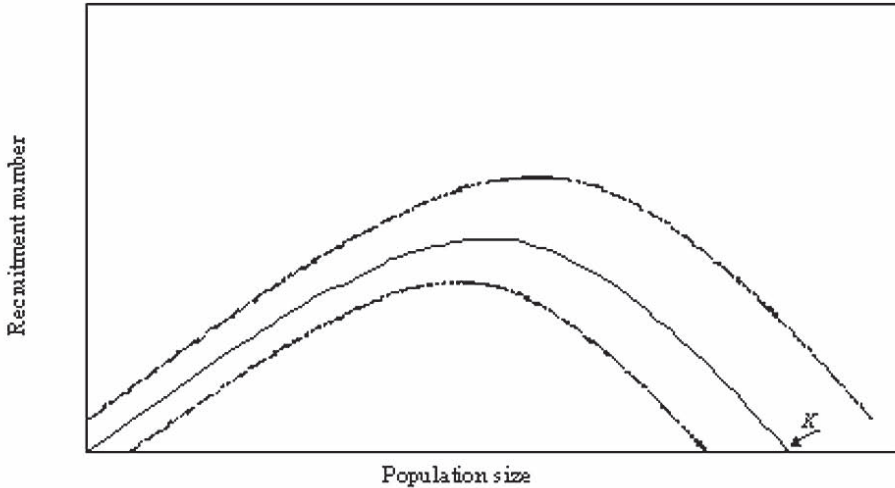


Figure 2.2. Both recruitment of young and variation in recruitment vary with population size of adult females (adapted from McCullough 1979, Bowyer et al. 2000). Variation in recruitment increases as density increases from the peak of parabola to carrying capacity (K) because environmental variation is more able to help or harm ungulates in poor physical condition (adapted from Kie et al. 2003).

Where individuals in an ungulate population are in excellent nutritional condition, predation by cougars will have a larger effect on the rate of increase than if the prey are in poor condition. Any animal removed from a population well below K probably would have survived if not preyed upon, and probably was not hindering reproduction or survival of other individuals through competition. Under these circumstances, cougar predation is largely additive mortality that slows the growth rate of the prey population. However, in a prey population in poor condition, where individuals are restricting the reproduction and survival of conspecifics through competition, cougar predation helps lower prey population density, reduces competition, and increases the likelihood of survival and reproduction for the remaining individuals in the prey population (Caughley 1979, Bartmann et al. 1992). Under those circumstances, cougar predation is compensated for by increased recruitment and survival of remaining prey (compensatory mortality). Mortality caused by predation in this scenario has little depressing effect on the prey population (Bailey 1984).

Bowyer et al. (in press) provide a conceptual model for managers to use in determining when predation might have a large impact on prey population size such that the prey population would respond to predator removal. This approach (Table 2.1) relates individual condition and reproductive characteristics of ungulates to the likelihood that the population is subject to additive mortality by predation.

If the goal of management is to maintain large ungulate populations (e.g., to support a large sport harvest), this approach suggests that reducing cougars will only help when the ungulate population is below the inflection point of Figure 2.1, and exhibits characteristics indicated in the middle column of Table 2.1. In fact, predation at high prey density can be beneficial, because it helps prevent damage to range quality, thereby increasing stability of the ungulate-vegetation system (Bowyer et al. 1997, Jordan et al. 2000), and helps maintain ungulate body and antler size (French et al.1956, Anderson 1981, Ullrey 1983, Suttie and Kay 1983).

Low-density traits will be evident in *any* population far below *K*, even if it experiences *no* predation. Therefore, even when the ungulate population is apparently well below *K*, a decision to reduce cougar numbers only makes sense when the manager has data that indicates cougar predation is the strongest limiting factor operating on the ungulate population. Furthermore, if there is no alternate prey (i.e., cougars subsist almost entirely on the ungulate of concern), cougar numbers will (after a time lag) decline even without increased cougar harvest.

Table 2.1. Life-history characteristics of ungulates that reflect the relative differences in a population regulated by predators versus food (Bowyer et al. 2005).

Life-history characteristic	Population size mainly affected by predation ^b	Population size mainly affected by food
Physical condition of adult females	better	poorer
Pregnancy rate of adult females	higher	lower
Pause in annual production by adult females	less likely	more likely
Yearlings pregnant ^a	usually	seldom
Corpora lutea counts of adult females ^a	higher	lower
Litter size ^a	higher	lower
Age at first reproduction for females	younger	older
Weight of neonates	heavier	lighter
Mortality of young	additive	compensatory
Age at extensive tooth wear	older	younger
Diet quality	higher	lower

^a Some species of ungulates may show limited variability in these characteristics.

^b These traits will be evident in *any* population far below *K*, even if it experiences *no* predation. The manager should have evidence of significant mortality due to predation before concluding that reducing predation would increase ungulate recruitment.

*Adult male cougar
stealing a kill.*



2. After a sudden decline in prey carrying capacity, an increased cougar harvest may help avoid problems caused by a time lag in the response of cougars to changes in prey.

Changes in cougar populations in response to prey densities may involve time lags that may be problematic for managers (Logan and Sweanor 2001). For instance, when the number of their primary prey declines, cougars may switch to livestock and pets (Torres et al. 1996), or other species of wildlife (Jorgenson et al. 1997, Logan and Sweanor 2001). In these circumstances, a moderate to high cougar harvest may reduce the rate of decline of the ungulate population, competition among cougars, impacts on livestock and pets, and potential risk to humans. However, it is possible that vacancies created by the loss of resident adult cougars may be filled by immigrating subadults (about 10-30 months of age), in the short-term, resulting in increased densities.

3. We suspect that cougar predation can keep a prey population at an unnaturally low density (a “predator pit”).

Holling (1959) demonstrated that additive mortality due to predation could interact with density-dependent prey dynamics (Figure 2.2) to create either 1 or 2 stable equilibrium densities for the prey population. The theoretical basis is strong, and it is plausible that such dynamics exist for some predator-prey systems. In vertebrate predator-prey systems, the higher equilibrium (near but somewhat below the carrying capacity set by food resources) is considered the natural state of affairs, but following a catastrophe (such as severe winter weather, drought, a tornado, a disease epidemic, or isolation

of a population segment by a freeway), mortality from predation can, in theory at least, keep prey at an equilibrium far below food-based K – a situation referred to as a “predator pit” (Haber 1977, Bergerud et al. 1983, Messier 1994).

Predator pits have been postulated to occur for caribou (*Rangifer tarandus*) interacting with wolves in Alaska (Ballard et al. 1997), for moose interacting with wolves (Messier 1994), for pronghorn (*Antilocapra americana*) interacting with coyotes (Dunbar et al. 1999), for wild horses (*Equus caballus*) interacting with cougars in Nevada (Turner et al. 1992), and for bighorn sheep interacting with cougars in California (Hayes et al. 2000, Schaefer et al. 2000) and Arizona (Kamler et al. 2002). In addition, cougar predation caused the near extinction of porcupines in a Nevada basin (Sweitzer et al. 1997). We believe that some of these situations probably do represent predator pits. However, we caution that the existence of a 2-equilibrium system has never been demonstrated in nature or in the laboratory. Many, perhaps all, unmanaged ungulate-predator systems could have a single equilibrium prey density (Messier 1994).

4. The presence of: a) alternative prey; b) excellent prey condition and reproduction; c) high mortality due to predation; and d) historic evidence of a much larger prey population suggest the existence of a predator pit.

A predator pit occurs only in multiple-prey systems (Gasaway et al. 1992), where alternative prey provides a subsidy that keep cougar numbers high. In a putative bighorn pit, for instance, cougar numbers would rapidly decline (via emigration, or low



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survival or reproduction) as predation reduced bighorn numbers, unless alternate prey (such as cattle or deer) sustained cougars at densities where they regularly encounter bighorn.

Because predator pits, by definition, are far below K , the prey population of concern should exhibit the characteristics of a population well below K (Table 2.1), namely excellent physical condition and high fecundity. If individuals in the prey population exhibit poor physical condition, then a predator pit does not exist.

Finally, if a predator pit exists, there must be evidence that the prey population had the potential to be several-fold larger than at present. Data on predation mortality are best obtained from radio-tagged prey.

These 4 conditions are necessary, but not sufficient, to prove the existence of a pit. Conclusive demonstration would require precise measurements of how cougar numbers and numbers of prey killed per cougar vary with prey density (Messier 1994) – measurements which can probably never be made at any reasonable cost. Nonetheless, a persuasive case exists when these 4 conditions are met.

5. Managers should use an adaptive management approach to design meaningful case studies of potential predator pits involving cougars.

When a manager finds that a predator pit is the most plausible explanation for non-recovery of a prey population, a manager may choose to propose cougar control for a number of years. Opponents will also argue that even if the management action is followed by prey recovery, the recovery may have occurred even without cougar control. The argument, in a nutshell, is that management action to control cougars to benefit one prey population is an unreplicated case study, proving nothing. However, a well-designed scientific study can provide reliable information on cougar-prey relationships. Chapter 6 offers further advice on using management actions as research efforts to reduce scientific uncertainty.

6. Cougar predation may limit some small, isolated bighorn populations.

Cougar predation has been an important factor in the decrease of bighorn sheep populations in California (Hayes et al. 2000, Schaefer et al. 2000) and Arizona (Kamler et al. 2002). Ross et al. (1997) found no relationship between the density of alternative prey and cougar predation on bighorn sheep, suggesting that the high rate of predation on bighorn was a result of encounter rate and not prey switching. Logan and Sweeney (2001) came to a similar conclusion for a bighorn sheep population in southern New Mexico. Wehausen (1996) implicated cougar predation in the decline of bighorn sheep across several subpopulations in the Sierra Nevada. However, habitat abandonment in



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response to predation risk by cougars – rather than direct predation mortality – was hypothesized to be the cause of low reproduction rates, and resultant population declines of bighorn sheep in the Sierra Nevada. Cougar predation on bighorn sheep appears to be sporadic (Sawyer and Lindzey 2002). This variability may be caused by individual cougars becoming specialists at preying on bighorn sheep (Ross et al. 1997), by changes in densities of primary prey (Schaefer et al. 2000, Logan and Sweanor 2001), by differences in the probability of cougars encountering bighorn sheep, by time lags in prey switching, or by small differences in habitat characteristics among populations (Kamler et al. 2002).

Skeptics of predator control often argue that cougars and bighorn coexisted for several thousand years in the western United States, and that it is therefore unlikely that cougar predation limits bighorn sheep populations today. However, during the past 150 years, some bighorn sheep populations have been decimated by diseases carried by domestic sheep, some residual populations have become isolated by roads and urbanization, cow-calf operation in the habitats of some populations provide an alternative prey subsidy (thus increasing the likelihood of cougar presence), and fire suppression in the habitats of some populations have decreased forage quality, increased ambush cover, and increased densities of mule deer (thus plausibly attracting cougars).

7. Targeted removal of cougars could benefit small bighorn sheep populations limited mainly by cougar predation.

For populations of bighorn sheep with more than 15 ewes, modeling of cougar predation on bighorn sheep has suggested that indiscriminant predator removal is not more effective in reducing extinction risk than would be selective removal of individuals that specialize in killing bighorn sheep (Ernest et al. 2002). Indiscriminant predator removal creates vacancies that are likely to be filled by dispersing juveniles. Indiscriminate predator control may remove individuals that did not frequently kill bighorn sheep, but will be replaced by individuals that do. Finally, if alternative food sources such as deer were readily available, a constant and extremely high level of cougar removal (i.e., more than 28%) might be necessary to prevent rapid recovery of the cougar population (Logan and Sweanor 2001). This level of predator control may not be acceptable to the interested public. For those reasons, where bighorn sheep populations are threatened, selective cougar removal is recommended.

8. Cougars select vulnerable prey, and are adaptive, opportunistic predators.

Numerous authors have described the gender, age class, and condition of prey killed by cougars. Hornocker (1970), Spalding and Lesowski (1971), Shaw (1977), Ackerman et al. (1984), and Murphy (1998) all suggested that vulnerability of individual prey may be the most important factor in their selection by cougars. Those investigations identified individuals in younger or older age classes, or in poorer condition, as being selected by cougars. Nowak (1999) found selection by cougars for younger deer and elk. Among adult deer and bighorn sheep, cougars also may prey on males selectively (Hornocker 1970, Ackerman 1982, Harrison 1990), especially when males are in a weakened condition following the rut (Robinette et al. 1959, Shaw 1977, Harrison 1990), or during drought (Logan and Sweanor 2001). Ross et al. (1997) reported selection for young bighorn sheep by cougars. Pierce et al. (2000a) reported that cougars selected deer in young and old age classes, and that females were selected among adult deer. Preference for females among adult mule deer also has been reported for other populations of cougars (Bleich and Taylor 1998). Recent investigations suggested that cougars do not select prey in poor condition (Kunkel et al. 1999, Pierce et al. 2000a); however, bone marrow fat has been the primary index used to determine prey condition by most investigators. Although the percentage of bone marrow fat was not related to prey selection by cougars (Kunkel et al. 1999, Pierce et al. 2000a), they selected for older animals. Thus, percentage of marrow fat may not adequately reflect vulnerability of an animal to predation by a cougar (Pierce et al. 2000a).

Size of prey may affect selection by cougars. Cougars in Montana selected deer over elk, and elk over moose (Kunkel et al. 1999). However, Nowak (1999) found no preference between deer and elk.

Sex and age of a cougar likely affects its diet (Murphy 1998, Anderson and Lindzey 2003). Ross and Jalkotzy (1996) reported that male cougars were more likely to kill moose than were females. Solitary cougars may be more likely to eat smaller prey than will females with kittens (Ackerman 1982). Ackerman suggested that killing large prey to provide for their offspring would be a desirable strategy for mothers, and populations of cougars could not exist in areas devoid of large ungulate prey. Pierce et al. (2000a), however, reported that female cougars with kittens (less than 6 months old) were significantly more likely to kill young deer (less than 1 year of age) than were single female or male adults. Birth pulses of cougar populations often coincide with the birth pulse of their primary prey (Logan and Sweanor 2001, Pierce et al. 2000a), suggesting that timing of reproduction in cougars may be influenced by the availability of vulnerable, young prey.

Variation in prey selection is notable for some populations of cougars as vulnerability or availability of prey changes. During the wet season in coastal California, cougars increased predation rates on feral pigs (*Sus* sp.) (Craig 1986) and, in Utah, they killed twice as many black-tailed jackrabbits (*Lepus californicus*) during winter (Ackerman et al. 1984) when compared to summer. Adult male deer may be taken at a higher rate during winter when they are in a weakened condition from the rut (Robinette et al. 1959, Shaw 1977). The vulnerability of newborn calves results in high depredation rates on cattle in Arizona (Shaw 1977, Cunningham et al. 1995).

9. Determining prey selection requires a comparison of diet with availability of prey.

Litvaitis et al. (1994) distinguish between *use* and *selection* of foods by wildlife. *Use* simply indicates the relative amount of food consumed, and can be based on proportion of prey items or prey biomass comprised of a particular item. *Selection* implies that a food item is exploited disproportionately to its availability in the animal's home range. According to these definitions, an observation by agency personnel that mule deer (or adult male mule deer) comprise 60% of cougar prey carcasses encountered probably says little about *use*, and even less about *selection*. This observation would reflect use if the prey carcasses encountered were an unbiased sample of prey taken by cougars, but would not reflect use if some prey items are easier to detect than others, or if the habitats searched by the personnel are not representative of the landscape. Documenting selection is even more difficult, as it requires measuring availability of prey, which in turn is a function of the abundance and behavior of each prey item.

10. Cougars affect, and are affected by, other carnivores in their ecological systems.

In the ecological systems that cougars inhabit, both exploitative and interference competition with other predators probably occurs. The diets of wolves (Kunkel et al. 1999), coyotes (Pierce et al. 2000a, Harrison 1990), bears (*Ursus* spp.) (Murphy 1998), bobcats (Koehler and Hornocker 1991), and jaguars (*P. onca*) (Iriarte et al. 1990) overlap extensively with that of cougars. Differential habitat and prey selection may allow for

coexistence of cougars with those other carnivores. In some instances, scavenging of their caches by other carnivores causes cougars to increase predation rates (Harrison 1990). Cougars kill smaller carnivores. Koehler and Hornocker (1991) reported cougars did not feed on bobcats they killed, and Beier and Barrett (1993) reported that cougars killed and ate bobcats and coyotes. Conversely, cougars have been killed by packs of wolves (White and Boyd 1989, Boyd and Neale 1992). Those observations suggest that competition is an important factor affecting the predator-prey dynamics of multipredator systems that include cougars.

11. Cougars affect the structure and diversity of ecological communities.

The important prey species of cougars in North America are often sympatric with each other. Limitation of population growth by predation may help to increase species richness by decreasing competition (Paine 1974) or by increasing niche partitioning (Hutchinson 1957, MacArthur 1972) within the prey community (Longland and Price 1991, Pierce et al. 1992). As the availability of one prey species increases, predation by cougars may switch to that prey species, affecting its population growth. This may reduce predation on a competing prey species and allow for both prey species to coexist. Competition from cougars also may increase species richness among smaller predators by disproportionately influencing the numbers of one species more than another (Terborgh et al. 1999). This can happen through direct and indirect competition for prey or through direct predation on smaller predators. For example, cougars compete directly with coyotes for mule deer in the eastern Sierra Nevada. As cougar populations decreased, predation on mule deer by coyotes increased (Pierce et al. 1999a). Coyotes probably compete more directly with foxes and bobcats than with cougars; therefore, the presence of cougars may benefit those other smaller species. Because cougars kill and cache large prey, other carnivores and bird species benefit by scavenging (Hornocker 1970, Pierce et al. 1998, Beier 1995).

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