Prey Specialization by Individual Cougars in Multiprey Systems

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Introduction

The cougar (*Puma concolor*) has made a remarkable recovery in North America over the last half century. This can be attributed primarily to the termination of predator-bounty programs and to a change in management status for cougar from vermin to big-game species. Most western states and provinces now boast healthy, harvestable populations of the big cats (Beausoleil and Martorello 2005), and the animals are even reoccupying parts of their historic range east of the Rocky Mountains (Neilsen et al. 2005). This is a rare success story in a world where most of our large carnivores are threatened, and many are even critically endangered through habitat loss and overharvest. A plethora of recent scientific work on predators (Ray et al. 2005) suggests that recovering and maintaining large carnivores in ecosystems can have benefits that go beyond their intrinsic value as wilderness icons, their recreational and economic value as big-game species and furbearers, or the inherent fascination that they hold for most people. Growing populations of wolves in North America, for example, have been shown to decrease populations of ungulate prey and, through what is known as a trophic cascade, to increase the biomass of plants that benefit numerous other species, from songbirds to beaver (Hebblewhite et al. 2005). Predators also may influence population dynamics and community structure by changing the behavior of their ungulate prey (Brown et al. 1999). Predation risk imposed by healthy populations of predators can cause ungulates to avoid certain areas, resulting in an alteration of ecosystem structure and increased biodiversity (Ripple and Beschta 2004). The predatory behavior of cougars, therefore, can have a substantial influence on ecosystems.

This same predatory behavior, however, can result in unwanted declines in populations of prey that are locally or regionally endangered or that have recreational and economic importance for hunters and other wildlife enthusiasts. While cougar predation may have compensatory effects on ungulate populations in some cases (Hornocker 1970, Laundre 2005), although detailed experimental evidence is often required to clearly implicate predation as a major limiting or regulatory factor for prey (Boutin 1992), there have been several documented cases where cougar predation is the primary cause of population decline (Wehausen 1996, Festa-Bianchet et al. 2006). Indeed in some cases, cougars have taken prey to the brink of local extinction (Sweitzer et al. 1997, Logan and Sweanor 2001), leaving little doubt about the potential for predation by cougars to negatively affect the population viability of prey.

Cougar predation, therefore, can be considered to have both positive and negative effects, depending on perspective and context. To optimize these effects through management, a firm understanding of cougar predatory behavior is required. This paper examines one important aspect of this behavior—prey specialization by individuals—which can have important implications for the extent that cougars influence populations of their prey. We begin by discussing cougar predation in multiprey systems because it is in these systems that the effects of cougar predation are most pronounced and because this is where strong individual preferences for a particular species of prey (specialization) is possible. Next, we review the literature as it pertains to cougar prey specialization and also provide some new data from the first year of an ongoing study of cougar predatory behavior along the eastern slopes of Alberta's Rocky Mountains. Finally, we discuss the management implications of prey specialization by cougars and the gaps in our knowledge that still need to be addressed by future research to improve the performance of management actions.

Cougar Impacts on Prey and the Importance of Multiprey Systems

The effect that large carnivores have on populations of their ungulate prey has been studied and hotly debated in North American wildlife management circles for decades. It is a topic that has predominantly centered on wolf-ungulate systems and has focused chiefly on interactions between wolves and their primary prey (Bergerud et al. 1983, Boutin 1992, Messier 1994, White and Garrott 2005). Until recently, other predators and types of systems had not received the same attention. In the case of cougars, this was no doubt due to preliminary data suggesting that their predatory behavior did not restrict the growth of prey populations (Hornocker 1970), perhaps because cougar populations were constrained by social factors to a level below that set by food supply (Seidensticker et al. 1973). In the 1990s, however, reports of cougars depressing populations of their prey began to emerge (Turner et al. 1992, Wehausen 1996, Ross et al. 1997, Sweitzer et al. 1997). These case studies, combined with research dispelling the idea that social factors kept cougar populations below what food availability would predict (Pierce et al. 2000, Logan and Sweanor 2001), catapulted cougars to the foreground of predator-prey debates.

In direct opposition to Hornocker's (1970) early belief, with respect to bighorn sheep (*Ovis canadensis*), that, "the numbers taken by lions are insignificant," (23), several of the reported examples of cougars depressing populations of prey involve bighorn. For small populations of these sheep, even a single cougar is capable of causing substantial mortality. In Alberta, for example, a lone female cougar was responsible for killing 9 percent of a sheep population, including 26 percent of the lambs, over the course of a few months during winter (Ross et al. 1997). In the peninsular ranges of California, cougars reportedly killed 26 percent of the sheep in one population and are thought to be capable of impeding the recovery of endangered populations. In the Sierra Nevada, cougar predation has been identified as the single most important factor in the precipitous decline of what had previously been a successful reintroduction of bighorn (Wehausen 1996), and cougar predation has recently been identified as a primary cause of four major declines in three populations of sheep in Alberta and Montana (Festa-Bianchet et al. 2006). Bighorn are not the only species to be affected, however. Populations of mule deer (*Odocoileus hemionus*), feral horses (*Equus caballus*), mountain caribou (*Rangifer tarandus*) and even porcupines (*Erethizon dorsatum*) have suffered declines as a direct result of cougar predation (Turner et al. 1992, Sweitzer et al. 1997, Kinley and Apps 2001, Robinson et al. 2002).

In nearly every case of prey depression reported for cougars, the species suffering a decline is a secondary prey item in a multiprey system. The critical feature of multiprey systems that exacerbates the ability of cougars to negatively affect prey is the ability of the cougar population to sustain itself on alternate prey. The impact this has on ungulate prey can take two forms. The first is known as apparent competition, which occurs when two or more prey species collectively contribute to the maintenance of a larger predator population than could be sustained on any one prey type alone, to the detriment of all types of prey (Holt 1977). The second is known as indirect amensalism, which occurs when the presence of one prey species negatively affects a second prey species, but the presence of the second has little or no effect on the first. Asymmetrical apparent competition (i.e., approaching indirect amensalism) may be common in vertebrate predator-prey systems (Chaneton and Bonsall 2000), and, if the smaller population of alternate prey is the more negatively affected, predation may rapidly become depensatory. This is especially true if the predator numerical response to population reductions of alternate prey is delayed or nonexistent because of a strong association of predator populations to those of their primary prey.

In many predator-prey systems, predation on small populations of alternate prey is rare and may be incidental to the search for primary prey (Schmidt et al. 2001). In such cases, small populations are less likely to be adversely affected by predation, especially if they are able to occupy habitats that are rarely frequented by the predator in its search for primary prey species (Schmidt 2004). In systems where selection of prey by predators occurs, however, the negative effects of asymmetrical apparent competition on populations of secondary prey are greatly exaggerated if the secondary prey species also happens to be the preferred prey (i.e., taken at a rate greater than available). Cougars often exhibit prey selection in multiprey systems (Hornocker 1970, Kunkel et al. 1999) and, thus, are capable of such exaggerated impacts. For example, in a cougar, white-tailed deer (*Odocoileus virginianus*) and mule deer system in southern British Columbia, white-tailed deer were the primary prey of cougars and, consequently, a primary determinant of cougar carrying capacity (Robinson et al. 2002). Cougars in this system, however, selected heavily for mule deer, which suffered a predation rate of nearly double that of white-tailed deer. White-tailed deer populations are stable and continue to support a relatively large cougar population that is capable of exerting sustained pressure on the dwindling population of preferred mule deer prey (Robinson et al. 2002). This has resulted in a steady predator-caused decline in mule deer numbers, which is ultimately a result of asymmetrical apparent competition with white-tailed deer. Similar situations have been suggested for cougar-caused declines in mountain caribou (Kinley and Apps 2001) and bighorn sheep (Rominger et al. 2005). Multiprey systems where cougar populations can be supported by large populations of one or more species of primary prey and where cougars demonstrate a preference for killing individuals from a smaller population of secondary prey, therefore, are the most highly prone to experiencing the negative effects of cougar predation.

Prey Specialization in Cougars

Cougars are normally considered to be a generalist predator. As a description of the species, this is certainly true. Cougars live in a broad variety of habitats and kill a full spectrum of prey. Cougars in North America kill primarily deer (*Odocoileus* spp.) but also prey upon elk (*Cervus elaphus*), moose (*Alces alces*), pronghorn (*Antilocapra americana*), bighorn sheep, mountain goats (*Oreamnos americanus*), caribou, coyotes (*Canis latrans*), black bear (*Ursus americanus*), porcupine, beaver (*Castor canadensis*), small rodents, fish, various birds and other cougars, to name a few (Ross et al. 1997, Murphy 1998, Kinley and Apps 2001, Logan and Sweanor 2001, Sunquist and Sunquist 2002). In Central and South America, they have been known to eat brocket deer (*Mazama* sp.), armadillos (*Dasypus* spp.), hare (*Lepus* spp.), guanacos (*Lama guanicoe*), white-tailed deer, mule deer, desert bighorn sheep, peccaries (*Tayassuidae* sp.), capybaras (*Hydrochoerus hydrochaeris*), rhea (*Rhea* sp.), vizcacha (*Lagostomus maximus*) and caiman (*Caiman* sp.) (Sunquist and Sunquist 2002, Rosas-Rosas et al. 2003). Indeed, cougars are the epitome of a generalist predator.

However, there is growing speculation and some evidence that, while the species is capable of preying on almost anything, an individual cougar may focus its predatory efforts and can even specialize on a particular type of prey. Specialization by individual cougars is simply an extreme form of the selection discussed in the previous section, but it takes place at the level of the individual instead of the level of the population. In the purest sense, an individual specialist would consume only a single type of prey. Cougar in single-prey systems are *de facto* specialists, but cougars in multiprey systems are extremely unlikely to ever meet this definition of specialization. How, then, can we define individual specialization for cougar in multiprey systems? We set forward three criteria that should be met if individual specialization exists. First, the species of prey being specialized on should comprise the primary component of the individual cougar's diet. Second, the species being specialized upon should be selected such that the focal species is consumed more often than would be expected on the basis of availability. Third, if specialization is an individual characteristic, then individuals should differ in their preference patterns, and some individuals might not specialize at all (i.e., individual-level specialization and population-level specialization are different things).

If cougars exhibit individual specialization in this way, it could have important implications for predator-prey dynamics and management. In a multiprey system, individual specialization focused on a smaller population of secondary prey can have effects similar to those produced when the population of predators selects for the secondary prey. These effects are likely to be more erratic than those caused by population-level preferences for prey, and they also may be more severe. When specialists are not present, the population of secondary prey does not suffer more than incidental predation and may do well even when there are large numbers of predators. When specialists are in the system, on the other hand, a small and isolated population of prey could be drastically reduced or even eliminated by the specialist over a short period of time, with no subsequent effect on the predator population.

Predation by individual cougar specialists has recently been suggested as a primary determinant of the population dynamics of bighorn sheep in three separate locations in western North America (Festa-Bianchet et al. 2006). Bighorn were monitored for over 80 population years and 4 separate declines driven by cougar predation occurred. In each case, the cougar predation episode had a clear and abrupt beginning and end. The authors point out that this pattern is consistent with predation by a specialist predator because the predation periods are sharply defined, which one would expect if it is caused by an individual specialist that enters and leaves the system. Unfortunately, they have only limited data to support this. Indeed, while information on cougar dietary habits is reasonably common (Ross et al. 1997, Murphy 1998, Logan and Sweanor 2001, Rosas-Rosas et al. 2003), detailed information on the killing rates and predatory patterns of individual cougars is scarce in the published literature.

The most comprehensive data currently available on individual prey specialization come from a study of cougar predation conducted at Sheep River in southwestern Alberta. Individual radio-collared females in this study varied greatly in their predation patterns. Of five females that had home ranges overlapping with bighorn range, three rarely or never killed sheep, one occasionally killed sheep and another focused almost exclusively on sheep during some years (Ross et al. 1997). The fact that mule deer were much more abundant than bighorn and that individual cougars differed so drastically in their predation patterns is strong evidence that the sheep-killing cougar exhibited specialization. Males at Sheep River killed moose almost exclusively despite much higher availability of deer in the study area (Ross and Jalkotzy 1996), but it is difficult to say if this was a result of population-level selection by males or because the single intensively monitored male in the study was an individual moose specialist.

Individual Cougar Predation Patterns in Westcentral Alberta

We have recently completed the first year of a study of cougar ecology in a multiprey ecosystem situated along the central eastern slopes of Alberta's Rocky Mountains. Our 5,791.-square-mile (15,000-km^2) study site (approximately centered at 52°16'0"N, -115°38'0"W) contains a wide variety of wild ungulate prey, including white-tailed deer, mule deer, elk, moose, bighorn sheep, feral horses, and very small numbers of mountain caribou and mountain goats. Our initial data on the predatory behavior of cougars in this environment helps to shed more light on individual-prey specialization. From December 2005 to March 2006 we deployed global positioning system (GPS) radio collars on 15 independent adult and subadult cougars. We monitored each cougar intensively by downloading GPS data from the collar monthly, or in some cases biweekly, for as long as the collar continued to collect data. We entered the data into a GIS program (ArcGIS 9.0), identified clusters of GPS locations and visited these locations to find kills. This technique was pioneered for cougars (Anderson and Lindzey 2003) and has since become a popular method for assessing prey composition and kill rate in large carnivores (e.g., Sand et al. 2005). Because we had downloadable GPS information (from Lotek model 4400S), we were able to visit location clusters soon after they were made, increasing our chance of finding kills. We visited 1,243 cluster locations, and we identified 510 cougar predation events and 24 cougar scavenging events at cluster sites.

Figures 1 and 2 represent the percentages of individual prey items and the biomass of cougar diet for our entire sample of kills. These are the kinds of population-level data that are normally presented in the literature and used by managers. Very different management strategies are required, however, for a population of cougars where all individuals tend to have similar prey composition and where a population that has a great deal of variation in predation patterns and may include specialist predators. Consequently, we use preliminary data

Figure 1. Percentage of individual prey items in the aggregate diet of all cougar monitored.

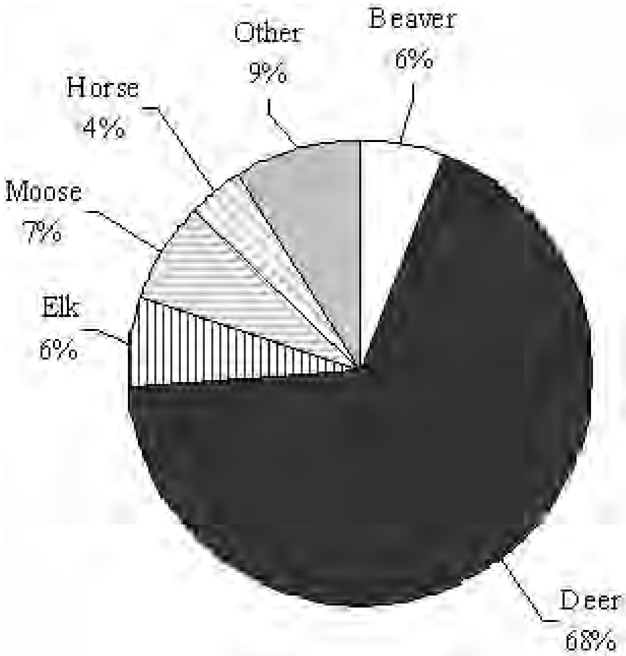
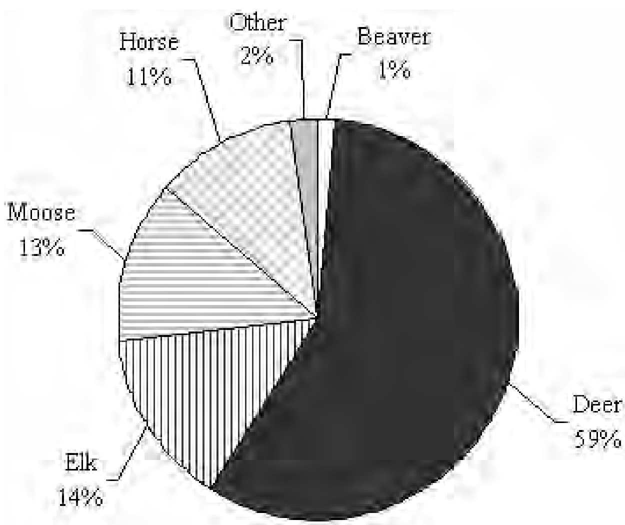


Figure 2. Percentage of prey biomass in the aggregate diet of all cougar monitored.



from 9 cougars for which we have continuous kill information for a period of at least 8 months (Tables 1 and 2) to look for evidence of individual prey preference and specialization. We examine only wild-ungulate kills when examining individual variation in predation because these are the most important component of cougar diet, making up over 85 percent of all kills and over 95 percent of the biomass consumed by cougars. We visited 375 ungulate kills for the 9 cougars over approximately 90 cougar-months of monitoring. We are fairly certain that we obtained a near census of large-ungulate kills for each cougar over the entire period it was monitored. We are somewhat concerned that our cluster visitation methods caused us to slightly underestimate neonate predation in spring, but it is unlikely that this would greatly affect our observed patterns of ungulate prey composition (Tables 1 and 2).

Table 1. Prey items killed for individual cougars monitored continuously for at least 8 months in westcentral Alberta.

Cougar ID	Number of kills	Percentage species composition				Species most commonly consumed
		Elk	Horse	Moose	Deer	
0003R	32	3.13	0.00	9.38	87.50	Deer
9823R	32	6.25	0.00	0.00	93.75	Deer
9825R	27	0.00	0.00	3.70	96.30	Deer
9827R	35	14.29	48.57	22.86	14.29	Horse
9871R	55	5.45	5.45	0.00	89.09	Deer
9873R	50	2.00	0.00	2.00	96.00	Deer
9876R	38	13.16	0.00	31.58	55.26	Deer
9878R	56	16.07	0.00	10.71	73.21	Deer
9879R	50	2.00	0.00	4.00	94.00	Deer

Table 2. Biomass of prey killed for individual cougars monitored continuously for at least 8 months in westcentral Alberta.

Cougar ID	Total biomass (kg)	Percentage species composition				Species comprising the majority of biomass
		Elk	Horse	Moose	Deer	
0003R	2015	3.97	0.00	14.89	81.14	Deer
9823R	1775	17.46	0.00	0.00	82.54	Deer
9825R	1605	0.00	0.00	21.81	78.19	Deer
9827R	5325	12.58	66.67	15.02	5.73	Horse
9871R	3635	9.90	8.25	0.00	81.84	Deer
9873R	3390	9.44	0.00	2.95	87.61	Deer
9876R	3890	25.71	0.00	41.13	33.16	Moose
9878R	3950	28.86	0.00	15.19	55.95	Deer
9879R	3195	2.50	0.00	10.95	86.54	Deer

Five species of wild ungulate (elk, mule deer, white-tailed deer, moose and feral horses) were killed by the nine cougars examined here. We did not differentiate between the two deer species in this analysis because species identification was impossible for a large number (39 percent) of the deer kills we visited. The inability to identify species was particularly common for fawns, which cougars often consume entirely. Availability of the various ungulate species differs across the study area, but deer are by far the most abundant prey in the home ranges of all of the cougars we examine here. It is, therefore, not surprising that deer were the most important prey item for most cougar (Tables 1 and 2). Cougar 9827R is the clear exception. Cougar 9827R meets all three of the criteria of an individual specialist outlined previously. Horses made up the majority of his diet (particularly in terms of biomass), and they were consumed at a rate much higher than availability would suggest. Moreover, there is substantial variation in individual predation patterns among cougars at the study site. Both 9873R and 9878R have home ranges that are subsumed within that of 9827R, for instance. And, there is a great deal of variation in prey composition in the diets of these three cats, despite similar availability of prey.

When looking at Table 1, however, it is apparent that none of the cougar we monitored were pure specialists. Each cougar exhibited at least some tendency to generalize. Some cougar may be specializing in the primary prey—deer—to the near exclusion of other ungulate prey (e.g. 9825R and 9873R). But, specialization on primary prey is more difficult to identify because we require better information on the relative abundance of each prey species in each cougar home range before it will be possible to determine whether deer are being selected. Similarly, we do not currently have sufficient details on ungulate-prey availability at the home-range scale to quantify selection for secondary prey when they do not dominate the diet. This kind of selection may be occurring, however, and also may vary greatly between individuals. Cougar 9876R, for instance, consumes substantially more moose and fewer deer than most other cougars. In terms of biomass (Table 2), 9876R might even be considered a moose specialist. In addition, 9878R and 9873R have overlapping home ranges with similar prey availability, yet 9878R consumes considerably more elk and moose than does 9873R, indicating that 9878R may be selecting for secondary elk and moose prey.

Individual cougars may also avoid certain types of prey. With the exception of 9827R, the cougars examined here do not often prey on horses, even though feral horses are available to most of them. Avoidance in the case of horses may be due to their lower vulnerability to cougar predation, but 9827R avoids deer, which are highly susceptible to cougar predation, indicating that the degree of vulnerability alone does not dictate selection. Hence, it would appear that individual identity is an important component of cougar predation patterns at our study site and that cougars may cover a gradient of preferences for species of secondary prey that ranges from specialization to avoidance.

Management Implications and Future Research

As we note above, specialization by individual cougars has the potential to produce erratic, and sometimes severe, impacts on populations of secondary ungulate prey in a multiprey system. We give examples of cougar specialization from the literature and from our recent work in westcentral Alberta. Cougar specialization may not be uncommon, and at least one of nine cougars we studied intensively meets all the criteria of an individual specialist. When cougars that specialize on small secondary prey populations that are of management concern (e.g., bighorn sheep, mountain caribou) are not present in a system, incidental predation by cougars might not be sufficient to cause population decline. When specialists are present, however, predation is focused instead of incidental and negative impacts are far more likely. In these cases, management action may be necessary to prevent unwanted population declines.

Our research shows that, while pure specialization is unlikely in cougars, individual cougars can develop tendencies to focus primarily on one or a few types of prey, sometimes selecting strongly for secondary prey even if that prey item does not dominate the diet. Such individual preference for secondary prey can result in management problems similar to those caused by specialization and can call for similar management responses.

Lethal control may be necessary to prevent the negative consequences of apparent competition and indirect amensalism on small populations of alternate prey in multiprey systems (Gibson 2006). Cougar populations are easily controlled by hunting, and increases in cougar population density have been reversed by liberal hunting regimes (Lambert et al. 2006). Where cougars are known to negatively impact ungulate population dynamics, general population reductions may be effective at curbing these impacts (Cougar Management Guidelines Working Group 2005), particularly in situations where the amount of incidental predation is directly related to predator-population size, where there is population-level selection for secondary prey or where primary-prey populations have declined, forcing cougars to switch to secondary prey (Logan and Sweanor 2001). In such situations, it can also be important to reduce populations of the primary prey that drive the cougar numerical response (Gibson 2006). However, if the negative impacts of cougar predation are driven by specialization or strong individual-level selection, general population reduction will be ineffective if the specialist is missed. And, reductions of predators through a reduction of primary prey might not translate into a reduction of the number of specialists. Identification and targeted removal of the specialist(s) may be the best management option in such cases because it can preserve the integrity of the population of secondary prey without compromising the cougar population or requiring the reduction of primary prey.

Ernest et al. (2002) found that, to preserve very small populations of bighorn sheep (less than 15 ewes) in imminent danger of extinction via cougar predation, total removal of cougars from sheep habitat would be necessary. Their models of cougar-sheep dynamics also suggest, however, that removal of only cougars that kill a sheep (putative specialists) reduces the risk of decline and extinction in larger populations of bighorn. Thus, selective removal can be an effective solution where the cougar population itself is a conservation concern or where there are political, economic or ecological reasons to avoid complete removal of cougars. Specialists must be identified before they are removed and this represents an important challenge. Cougars are secretive by nature and ubiquitously cache their kills by dragging them under trees or rocks and burying them or by otherwise concealing them from plain view. The potential to remove specialist cougar by catching them on a fresh kill of the species of interest is, therefore, limited unless the prey are wearing radio collars with mortality sensors. Even if a cougar is removed after killing a single sheep, there is no guarantee that a specialist has been removed. Our data show that small numbers of secondary species are killed by most cougar inhabiting multiprey systems.

Simply removing cougars that overlap spatially with the population of interest also may not have the desired effect. Our data suggest that cougar territory that overlaps various types of ungulate-prey territory can specialize in, select for, use as available, or even avoid preying upon a particular species. Ross et al. (1997) and Ernest et al. (2002) similarly show that some cougars with home ranges overlapping bighorn range appeared to avoid them, rarely or never killing sheep. Spatial overlap by itself, while an obvious requirement of a specialist is, therefore, an insufficient basis for their identification. Indeed, removing cougar that overlap spatially with the prey species of interest but that avoid them as prey has the potential to create a vacancy that might be filled by a specialist predator.

Because of the importance of increasing the probability of correctly identifying specialist cougar for management purposes, it is essential that we better understand what drives prey selection in this species. Is individual-cougar predation a purely idiosyncratic and stochastic (i.e., unpredictable) phenomenon as some suggest (Festa-Bianchet 2006), or does it have a mechanistic and predictable basis that can help managers identify and prevent problems? Unfortunately, little is known about the drivers of cougar predation. Even population-level prey selection in cougars remains poorly understood. At some study locations, deer are selected at a rate greater than their availability in the environment would suggest (Kunkel et al. 1999) while, at other sites cougars focus on elk, even when deer are more abundant (Hornocker 1970). What is the basis for these differences and for the differences observed at the level of the individual? And, how much do habitat, alternate prey densities, age-sex structure of the cougar population or individual idiosyncrasies weigh in? Through our continuing research efforts in westcentral Alberta, we hope to provide some of the answers to these questions.

If specialist cougars have been identified as a management concern, methods for improving the probability of correctly identifying specialists are available. And, removal of these specialist cougars is recommended by management agencies to reduce impacts on ungulate populations. A removal method must be chosen. Within an appropriate management framework, hunting with hounds can be very selective and precise, allowing for specific regions, age-sex classes, or even individuals to be targeted. Consequently, this might be the best method available for managing problematic prey specialization by individual cougar. Hunting with hounds has been advocated as a cougar-harvest method (Cougar Management Guidelines Working Group 2005), and it has several advantages over removal methods which are not selective (e.g., general hunting seasons, widespread snaring, poisoning) because using nonselective removal methods makes it less likely that the intended targets will be missed, preventing unnecessary and undesirable reduction of cougar populations. By using appropriate identification and selective removal techniques to manage specialist cougar predation, it might be possible to avoid undesirable declines in endangered and or economically valuable populations of secondary ungulates while simultaneously maintaining the ecological benefits associated with a healthy cougar population.

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