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Management and Conservation Article

Scavenging Makes Cougars Susceptible to Snaring at Wolf Bait Stations

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ABSTRACT In western Canada it is illegal to trap or snare cougars (*Puma concolor*), but cougars are sometimes caught accidentally in snares placed near carrion baits, a technique commonly used by trappers to harvest wolves (*Canis lupus*). We studied cougar foraging ecology and survival in west-central Alberta to estimate the propensity for cougars to scavenge, their susceptibility to snaring at trapper bait stations, and the implications these have for managing cougar populations. During 2005–2008, we used data from visits to 3,407 Global Positioning System (GPS) location clusters and >400 km of snow tracking of 44 cougars to locate foraging events and calculate scavenging rates. We identified 83 instances of scavenging, and 64% of monitored cougars scavenged at least once. Scavenging rates were higher in winter (0.12 events/week) than in summer (0.04 events/week), reflecting seasonal variation in carrion availability. Individual cougars scavenged at different rates, and winter feeding on carrion occupied up to 50% of total carcass handling time for some cougars. Based on these results we conclude that cougars are facultative scavengers. A propensity to scavenge made cougars susceptible to snaring causing high annual mortality in radiocollared cougars (0.11, 95% CI = 0.03–0.21). Provincial cougar mortality data demonstrate that snaring has increased dramatically as a mortality source in Alberta over the last 2 decades. Mortalities of radiocollared cougars during our study were 100% human caused and the addition of snaring mortality to already high hunting mortality resulted in low annual survival (0.67, 95% CI = 0.53–0.81). Our study is one of the first to identify population-level consequences for nontarget animals killed unintentionally by indiscriminate harvest techniques in a terrestrial ecosystem. Maintaining sustainable cougar harvest where snaring at carrion baits is permitted may require flexible hunting quotas capable of accommodating high cougar snaring mortalities in some years.

KEY WORDS Alberta, Canada, *Canis lupus*, cougar, facultative scavenging, harvest management, hunting, *Puma concolor*, snaring, wolf.

Indiscriminate harvesting techniques capable of capturing both target and nontarget species are commonly employed in the commercial, recreational, and subsistence harvest of fish and wildlife. Nontarget harvest is especially common in fisheries, where efficient and economical harvesting techniques also tend to be indiscriminate (Jefferson and Curry 1994, Dayton et al. 1995, Stevens et al. 2000). Although less common in terrestrial systems, potentially indiscriminate harvest techniques in the form of traps and snares are occasionally employed (Phillips 1996, Shivik and Gruver 2002), and the ramifications of nontarget harvest as a consequence of their use can be significant. In a study of efficacy of neck snares for predator control in Texas, for instance, Guthery and Beasom (1978) reported nearly as many nontarget as target captures, and snaring was sufficient to cause unintentional extirpation of a local herd of collared peccaries (*Pecari tajacu*). In Africa, snaring targets a wide variety of species for the bush-meat trade and for subsistence (Noss 1998), but the lack of prey selectivity associated with snaring means that species that might otherwise be avoided (e.g., rare species of conservation concern but little economic value) are killed in snares meant to capture more profitable species (Rowcliffe et al. 2003).

In Alberta, Canada, cougars (*Puma concolor*) can be harvested legally by hunting, but they may not be trapped or snared. However, neck snares placed near carrion bait are often used to harvest wolves (*Canis lupus*) for management, recreation, and commercial purposes, and cougars, which are sympatric with wolves along the eastern slopes of Alberta's Rocky Mountains, are occasionally caught incidentally. Cougars killed by trappers may not be kept or sold, but are forfeit to the province (Alberta Fish and Wildlife 2008). Snaring mortalities thus detract from "optimum allocation of the cougar resource amongst recreational, commercial and other users," a primary goal of Alberta's cougar management plan (Jalkotzy et al. 1992:65). Accordingly, incidental cougar snaring is undesirable for both trappers and wildlife managers. The degree to which cougars are susceptible to capture at wolf bait stations, and the broader impacts of snaring on cougar population dynamics and its implications for cougar harvest management, however, have not been assessed.

Carrion bait provides a strong attractant for scavenging carnivores, and the inclination to scavenge determines susceptibility to capture in snares near bait. The propensity for wolves to scavenge has been well documented and makes them vulnerable to harvest at bait stations established by trappers (Huggard 1993, Hayes et al. 2000, Jedrzejewski et al. 2002, Stahler et al. 2006, Webb 2009). The evidence regarding the cougar's penchant for carrion is less clear, however. Most studies of cougar foraging indicate or assume that scavenging is rare, suggesting that susceptibility to snaring via attraction to baits should be low (Hornocker 1970, Ross and Jalkotzy 1996, Murphy 1998, Anderson and Lindzey 2003, Laundré 2008). Indeed, in a study of scavenger use of hunter- and wolf-killed carcasses in the Greater Yellowstone Ecosystem, all large and medium-sized carnivores present, except cougars, were observed scavenging (Wilmers et al. 2003). However, carcasses left out as bait in California were frequently scavenged by cougars, and a

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report of a cougar in Oregon consuming only carrion for >3 weeks suggests that scavenging might play an important role in the diets of some cougars (Nowak et al. 2000, Bauer et al. 2005). Studies that focus on measuring the prevalence of scavenging behavior among individuals, the frequency with which individuals scavenge, and the dietary importance of scavenging are needed to clarify the role scavenging plays in cougar foraging ecology.

We studied foraging behavior, survival, and cause-specific mortality of cougars in west-central Alberta where snaring for wolves is prevalent. Our primary objectives were to establish the role of scavenging in cougar foraging ecology, assess susceptibility to snaring at wolf bait stations, and evaluate the implications of this source of mortality for cougar population dynamics and harvest management. We hypothesized that cougars, like most vertebrate predators, would prove to be facultative scavengers (i.e., exploiting carrion opportunistically when encountered; DeVault et al. 2003, Selva et al. 2005). Specifically, we made the following predictions that conform to the principles of the facultative scavenger hypothesis (DeVault et al. 2003). First, scavenging would be a common foraging strategy at the population level (i.e., most individuals would scavenge). Second, scavenging rates would increase as carrion availability increased and carrion would constitute an important component of the diet where it was abundant and accessible to cougars (i.e., cougars would not pass up a free lunch). Third, scavenging would be incorporated into the foraging strategies of healthy cougars and not simply used as a last resort by energetically compromised animals that were forced to scavenge to survive. If these predictions held, we further expected cougars to be attracted to wolf bait stations and hence susceptible to snaring.

STUDY AREA

Our study area consisted of 16,900 km^2 of mountains, foothills, and agricultural lands located just east of Banff and Jasper National Parks in western Alberta, Canada (centered at approx. 52°18′N, 115°48′W). The region's climate over the course of our study was characterized by wet springs, warm dry summers, and cold snowy winters. Warm dry winds from the west (known locally as Chinooks) periodically eliminated the snow-pack from south-facing slopes. Conifer forests composed primarily of lodgepole pine (*Pinus contorta*) and white spruce (*Picea glauca*) dominated the study area. Both forestry and oil and gas industries were active on the landscape, creating networks of roads, seismic lines, well sites, and clear-cuts. Snaring for wolves was permitted on public lands in the study area between 1 December and 31 March under Alberta's Registered Fur Management Area (RFMA) program (Alberta Fish and Wildlife 2008). The study area contained 66 RFMAs, but a recent survey of trappers in the area indicates that only about 56% of those holding RFMAs actively trapped for wolves (Webb et al. 2008). Trappers who pursued wolves usually had $\geq$1 wolf bait station on their RFMA each year. Wolf bait stations consisted of carrion bait (most often >1 ungulate carcass plus occasional scraps and small mammal remains) and 20–60 snares set within a radius of a few hundred meters. Trappers usually replenished baits regularly during the season. Wolves were trapped most actively in December–February, when pelts were prime, and much less actively in March, when pelts were rubbed and had lower value (Barrus et al. 1997).

Big game hunting also was popular in the region and licensed ungulate harvest occurred in the fall (Aug–Dec). Treaty Indians were exempt from normal hunting regulations but harvested animals most frequently in fall and winter (Aug–Mar). Both licensed and unlicensed hunters regularly left gut-piles, bones, and hide in the field, providing opportunities for scavengers. Carrion derived from human activities therefore was more abundant in fall and winter than in summer. Other scavenging opportunities for cougars were created, year round, by vehicle–wildlife collisions on roads, by predatory activities of other carnivores (e.g., wolves), and at domestic animal carcass dumps on agricultural lands. Cougars were managed as a big-game animal and were hunted according to a quota system with seasons running from 1 December to 28 February or until the quota filled (Ross et al. 1996). In addition, landowners were permitted to shoot cougars on their private land at any time of year.

METHODS

Capture and Monitoring

We captured 44 cougars, some more than once (totaling 57 captures), between December 2005 and May 2008 under the authority of a provincial research and collection license (no. 19872-CN) and an approved University of Alberta Animal Care Protocol (no. 479505). We used trained hounds to track and tree cougars and then chemically immobilized them by administering 3 mg/kg zolazepam-tiletamine (Telazol®; Fort Dodge Animal Health, Fort Dodge, IA) and 2 mg/kg xylazine (Rompun®; Bayer, Inc., Toronto, ON, Canada). Once immobilized, we weighed, measured, sexed, and aged cougars. We estimated age using a combination of tooth color and wear characteristics (Ashman et al. 1983, Shaw 1986), pelage spotting progression (Shaw 1986), and gum-line recession (Laundré et al. 2000). We assigned cougars to 1 of 3 age brackets: kitten (still with mother), subadult (dispersal, usually around 12–18 months to 2.5–3 yr), or adult (>2.5–3 yr). Our sample of collared cougars included 23 adult females, 6 adult males, 6 subadult females, and 9 subadult males at capture. Three of the subadult females and 2 of the subadult males transitioned to adults during the study. On most capture occasions (n = 46), we fitted cougars with Lotek 4400s Global Positioning System (GPS) collars (Lotek Engineering, Newmarket, ON, Canada), but we also deployed 6 H.A.B.I.T GPS–very high frequency (VHF) collars (H.A.B.I.T research, Victoria, BC, Canada) and 5 Lotek VHF collars. At the completion of the handling procedure, we gave cougars 0.125 mg/kg yohimbine (Yobine®; Lloyd Laboratories, Shenandoah, IA) to reverse effects of xylazine, and we released them.

All collars deployed on cougars were equipped with mortality sensors that caused the VHF pulse rate to double if the collar was immobile for >18 hours, facilitating identification of mortality events. We monitored collared cougars intensively between December 2005 and August 2008 using a combination of ground and aerial VHF telemetry (we attempted $\geq$1 relocation/cougar/week). In addition, we programmed GPS collars to obtain a location fix every 3 hours and we downloaded these data from the ground and occasionally from the air every 2–3 weeks. We investigated mortality signals as soon as possible after we detected them and assigned date of death using the first GPS location at the mortality site. When cougars were killed by hunters, we assigned date of death using information provided by the hunter and confirmed by the last GPS location fix in the cougar's home range.

Scavenging Behavior

We used a rule-based algorithm to identify clusters of location fixes from GPS data and then systematically searched clusters in the field for evidence of predation and scavenging events (Knopff et al. 2009). Prior to November 2007 we visited nearly all clusters of $\geq$2 locations occurring within 200 m of each other and within a temporal window of 6 days. From November 2007 to August 2008 we used a logistic regression model to screen clusters with a near zero probability of a kill site from the set we visited in the field. If the model estimated a probability of a kill <0.15 in winter (defined here as 15 Oct–14 Apr) or <0.1 in summer (15 Apr–14 Oct) we did not visit the cluster. Specific details of cluster visitation techniques and models used to guide field efforts are described in Knopff et al. (2009). We visited clusters of each collared cougar for as long as the collar continued to function. Although cluster visitation was our primary means of data collection accounting for most of the cougar foraging events we located, we also occasionally snowtracked collared and uncollared cougars to identify predation or scavenging events.

We classified feeding on a carcass as a scavenging event only if there was clear evidence that the animal had been killed by something other than the focal cougar. Evidence for scavenging included 1) identification of an animal that had clearly died before the date that the collared cougar visited the site, 2) evidence that the carcass was of an animal that had been wounded or killed by a hunter (arrow or bullet wound), 3) evidence that the carcass had been dumped by humans (trapper bait station, livestock dump site, knife or saw marks on bones of wild ungulates), 4) broken bones and carcass proximity to a road that would indicate a collision with a vehicle, or 5) evidence that the animal had been killed by another predator.

Once we determined that carrion had been scavenged by a cougar, we identified the species and age-sex class of the carcass. We also estimated the type of foraging opportunity the carcass presented to the cougar (e.g., whole animal or any combination of meat, hide, or bone) by carefully investigating the carcass remains and by examining cougar scat associated with the cluster. Global Positioning System data allowed us to estimate the amount of time cougars spent accessing foraging locations, delineating handling time for 73 scavenging events and 1,254 predation events. Cougar handling time was significantly and positively related to prey size (i.e., available biomass) at predation events in west-central Alberta, leading us to assume that handling times can be used to approximate the energetic value of a foraging opportunity (K. H. Knopff, University of Alberta, unpublished data). We used a single-factor analysis of variance (ANOVA) followed by nonorthogonal planned comparisons, evaluated using the Dunn–Sidàk method (Day and Quinn 1989), to compare handling times among 4 classes of scavenging events: 1) kills made by other carnivores, 2) hunter carcasses, 3) trapper bait stations, and 4) all other scavenging events.

We calculated scavenging rates for each GPS-collared cougar separately for summer and winter. Because short monitoring periods might not provide a representative sample of feeding behavior, we used data only from cougars with $\geq$28 days of continuous monitoring in a given season (Knopff et al. 2009). We calculated scavenging rates in 2 ways. First, we simply divided the number of scavenging events we observed during a seasonal monitoring period by total number of days monitored (Hebblewhite et al. 2003), which gave a measure of frequency but no measure of the relative energetic importance of scavenging for each cougar. We therefore also divided handling time at scavenging events by number of days monitored to obtain a rate (hr/day) that measured the amount of time different cougars invested in scavenging.

A prediction of the facultative scavenging hypothesis is that cougars will scavenge more frequently when carrion is more abundant. In our study area, humans deposited carrion on the landscape more commonly in winter during the trapping and hunting seasons than in summer. Although we did not directly estimate the biomass of carrion provided by hunters and trappers, other studies in similar systems have shown that it can be substantial (Wilmers et al. 2003). Winter-killed ungulates and slow carcass decomposition in cold weather also increase carrion availability in winter. Consequently, we predicted that cougars would scavenge more often during winter (15 Oct–14 Apr). We tested this prediction using a one-tailed paired t-test for individual cougars for which we were able to calculate a scavenging rate in both summer and winter. Differences in hunting efficiency and energetic needs among cougar age-sex classes also may influence scavenging behavior. We therefore compared scavenging rates between adult males, adult females, and subadults and used a two-tailed t-test to determine whether adult and subadult animals scavenged at significantly different rates ($P < 0.05$).

Survival and Cause-Specific Mortality

Like many species of harvested wildlife (e.g., Hasbrouck et al. 1992), cougars do not experience constant survival throughout the year, but exhibit a strong mortality pulse associated with the hunting season (Ross and Jalkotzy 1992, Lambert et al. 2006). For populations with identifiable mortality pulses such as these a modification of the binomial Mayfield (1975) estimator by Heisey and Fuller (1985) using defined mortality periods may be the most appropriate technique for simultaneously estimating annual survival and cause-specific mortality (Heisey and Patterson 2006, Murray 2006). However, this method assumes constant mortality risk within periods, violations of which can result in poor survival estimates (Tsai et al. 1999). Alternative estimators are Kaplan–Meier (Pollock et al. 1989) for survival and Heisey–Patterson (Heisey and Patterson 2006) for cause-specific mortality. These estimators make no assumptions about constant mortality but are sensitive to the sample size of radiomarked animals on days where mortalities occur (i.e., animals collared on a given day are assumed to be representative of the population), and cause-specific mortality estimated this way can have unacceptably high variance or even be undefined (Heisey and Patterson 2006).

The Heisey–Fuller method reduces to the Kaplan–Meier survival estimator and the Heisey–Patterson cause-specific mortality estimator when the mortality period is defined to be a day (Heisey and Patterson 2006), making it easy to calculate survival and mortality estimates using different approaches. We used equations given in Heisey and Fuller (1985) to calculate annual survival, S^*, and cause-specific mortality, M_j^*. We calculated variance and 95% confidence intervals around S^* and M_j^* by bootstrapping the estimate using 10,000 resampling iterations where we randomly selected with replacement individual cougars from our original sample for each iteration. We calculated S^* and M_j^* for the cougar population as a whole and for males and females separately.

When applying the Heisey–Fuller approach to populations with clear mortality pulses, mortality periods (i) should be chosen in such a way that probability of death varies between periods but remains constant within them. Heisey and Fuller (1985) recommend using the least number of periods possible for the sake of parsimony. We therefore divided the year into 2 periods, a high-mortality period (1 Dec–28 Feb, which encompassed the entire cougar hunting season and the most active part of the wolf snaring season) and a low-mortality period (1 Mar–30 Nov). We also estimated survival and cause-specific mortality using day as the mortality period (i.e., Kaplan–Meier and Heisey–Patterson). The techniques should yield similar results provided their respective assumptions are met and sample sizes are sufficiently large (Heisey and Patterson 2006, Murray 2006). Substantial deviations would indicate that assumptions of ≥ 1 methods were violated and would require further scrutiny.

All human-caused cougar mortalities in Alberta must, by law, be registered with the provincial government. We used these registered mortality incidents to assess temporal variation in mortality patterns between 1990 and 2008 in the provincial Wildlife Management Units (WMUs) that partially or completely overlapped our study area (i.e., Alberta's WMUs 318, 320, 322, 324, 326, 328, 330, 417, 418, 420, 422, 426, 428, 429, 430, 432, and 434). We also obtained annual wolf harvest data from all RFMAs in our study area and correlated these data with the proportion of human-caused cougar mortality due to snaring to test the assumption that the relative importance of snaring as a cause of cougar mortality would be related to trapper effort and success at wolf snaring in a given year. Because both cougar hunting and wolf snaring seasons begin 1 December, we treated that date as the start of a new year for grouping mortality data.

RESULTS

Monitoring yielded 12,080 cougar radiodays and 47,998 GPS locations. We visited 3,407 cougar GPS location clusters (1,776 in summer and 1,629 in winter) and also tracked VHF-collared and uncollared cougars through the snow in winter, amassing >400 km of snowtracking data. We located 1,455 cougar feeding events (on average 25.7 days after the first GPS location at a cluster, SD = 23) and classified 83 of these as scavenging. We calculated 42 winter and 33 summer scavenging rates (we calculated rates once in each age class for individuals that transitioned to an older age class during the study). Most individual cougars (64%) scavenged at least once. We excluded 4 cougars from scavenging rate analyses because their foraging behavior was affected by collaring (K. H. Knopff, unpublished data) and we excluded one cougar because his collar failed before we accumulated 28 days of continuous monitoring.

Cougars of all age-sex classes scavenged but subadults did so most often (0.144 events/week, SD = 0.17, n = 13), followed by adult females (0.043 events/week, SD = 0.097, n = 22) and adult males (0.021 events/week, SD = 0.023 , n = 7). On average, subadults scavenged approximately 4 times more frequently than adults ($t_{40} = 2.7$, $P = 0.01$), and scavenging also occurred 4 times more frequently in winter (0.13 events/week) than in summer (0.03 events/week; $t_{29} = 2.09$, $P = 0.02$). Amount of time cougars spent at scavenging events tended to be longer in winter ($\bar{x}$ = 59.3 hr, SD = 70.0, n = 55) than in summer ($\bar{x}$ = 31.0 hr, SD = 32.1, n = 18), but this difference was not significant ($t_{71} = 1.65$, $P = 0.10$). Frequency of scavenging events varied by month and scavenging was most common in February–April (Fig. 1).

Cougars cached kills by covering carcasses with woody debris, grass, or snow between feeding events, and we noted that this behavior was also common at scavenging locations, provided there was sufficient carrion available to permit multiple feedings. Of the 83 carcasses scavenged by cougars most were at trapper bait stations (29%), followed by hunter-killed animals (23%), and other carnivores (14%). A single-factor ANOVA showed that scavenging sources differed in handling time ($F_{3,69} = 6.49$, $P < 0.001$; Fig. 2) and Dunn–Sidàk tests revealed that this difference was driven by higher handling times at bait stations. Although unequal variance and substantial difference in sample size did not permit statistical comparisons between handling time at different scavenging types and predation events (Day and Quinn 1989), mean time spent at bait

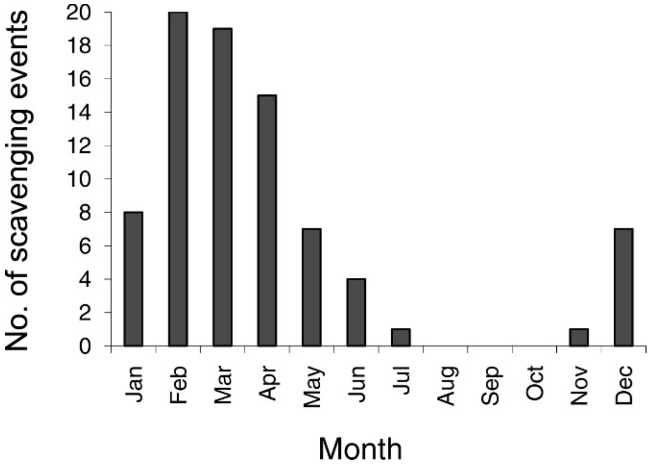

Figure 1. Number of cougar scavenging events identified at Global Positioning System telemetry clusters in each month in west-central Alberta, Canada, during 2005–2008.

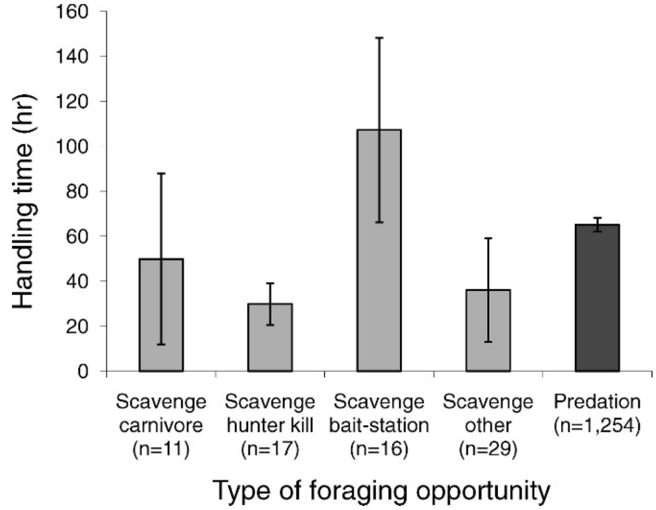

Figure 2. Mean handling time of cougars feeding at scavenging locations classed by carcass source and at predation locations (shown with 95% CI) in west-central Alberta, Canada, during 2005–2008.

stations also was longer than time spent at predation events (Fig. 2). Bait stations where cougars fed often included >1 entire ungulate carcass plus meat scraps and small mammal carcasses, whereas predation normally resulted in one ungulate prey, and carcasses left by other carnivores or hunters typically consisted of only portions of an ungulate. Handling times therefore match the available biomass of the various foraging types (Fig. 2).

Some cougars spent substantial time feeding on carrion. For example, 5 cougars spent >35% of their total handling time during winter scavenging (2 of these were subadult females that spent close to 50% of their handling time consuming carrion). Moreover, scavenging is not a strategy employed only by cougars that have depleted energy reserves and so must scavenge to survive. Healthy cougars with demonstrated killing ability also scavenged frequently and so were susceptible to snaring (Fig. 3).

We recorded 16 mortalities of radiocollared cougars during our study. We excluded 4 of these cougars from inferences of population-level survival and cause-specific mortality because their deaths were attributed to delayed effects of capture and collaring and hence were not considered representative. Cougars were susceptible to snaring at wolf bait stations and 33.3% ($n = 4$) of mortalities were a result of snaring. Other mortality sources were licensed hunting ($n = 6$), poaching ($n = 1$), and landowner harvest ($n = 1$). Thus, 100% of radiocollared cougar mortality during our study was human caused.

We calculated survival and cause-specific mortality using a sample of 40 cougars (11,907 radiodays). We combined poaching, hunting, and landowner harvest together into one cause-specific category (shooting), and snaring made up the other category. All mortalities of radiocollared cougars occurred during the high mortality period (1 Dec–28 Feb). We calculated an annual survival of 0.67 using the Heisey–Fuller approach with 2 mortality periods (Table 1) and 0.68 when we used day as the mortality period (i.e., Kaplan–Meier), indicating that the assumption of constant mortality during the high harvest season was met by our data. Likewise, Heisey–Fuller estimates of cause-specific mortality (snaring = 0.11, shooting = 0.22) were similar to those estimated using Heisey–Patterson (snaring = 0.12, shooting = 0.20). For the sake of brevity and consistency, all other results are given only using Heisey–Fuller estimates (Table 1). There was a nonsignificant tendency for males to have lower annual survival than females (Table 1). However, although males tended to have a higher annual probability of being killed by a hunter, females were more likely to be snared (Table 1).

Provincial records were consistent with our radiotelemetry results. Most of the 579 human-caused mortalities (94%) reported to the province in our study area during 1991–2008

Figure 3. Heavy deposition of subcutaneous and visceral fat revealed during the field necropsy of an adult female cougar snared at a wolf bait station in west-central Alberta, Canada, in 2008. Fat stores on this cougar, which spent 20% of its foraging time scavenging (over the 80 days it wore a Global Positioning System collar), suggests that carrion can be incorporated into successful foraging strategies employed by healthy cougars.

Table 1. Survival and cause-specific mortality of 40 radiocollared cougars calculated using the Heisey–Fuller method with 2 mortality periods in west-central Alberta, Canada, during 2005–2008. Results are given at the population level and for males and females separately.

Survival and mortality	Mar–Nov		Dec–Feb		Annual	
	Rate	95% CI	Rate	95% CI	Rate	95% CI
Survival						
Population	1.00	1.00–1.00	0.67	0.53–0.81	0.67	0.53–0.81
M	1.00	1.00–1.00	0.60	0.38–0.84	0.60	0.38–0.84
F	1.00	1.00–1.00	0.70	0.53–0.87	0.70	0.53–0.87
Snaring mortality						
Population	0.00	0.00–0.00	0.11	0.02–0.21	0.11	0.02–0.21
M	0.00	0.00–0.00	0.07	0.00–0.26	0.07	0.00–0.26
F	0.00	0.00–0.00	0.12	0.00–0.23	0.12	0.00–0.23
Shooting mortality						
Population	0.00	0.00–0.00	0.22	0.09–0.35	0.22	0.09–0.35
M	0.00	0.00–0.00	0.32	0.08–0.59	0.32	0.08–0.59
F	0.00	0.00–0.00	0.17	0.04–0.32	0.17	0.04–0.32

occurred during the cougar-hunting season and active portion of the wolf-trapping season (i.e., 1 Dec–28 Feb). Hunting was the most important source of human-caused mortality, but up to 27% of annual registrations resulted from incidental snaring (Fig. 4). Most cougars (60%) taken incidentally by trappers were female. These consistencies were evident even though registered mortalities can underestimate the importance of snaring if trappers fail to report snaring incidents or if cougars break snares and die away from the bait station, leaving the trapper with nothing to report. One of the radiocollared cougars we monitored, for instance, broke the snare below the lock, escaping the bait station only to have the snare eventually kill her. In a second case, we captured a cougar that had a snare (broken at the lock and unable to tighten) attached to her neck, indicating that breaking snares may not be uncommon. Thus, snaring

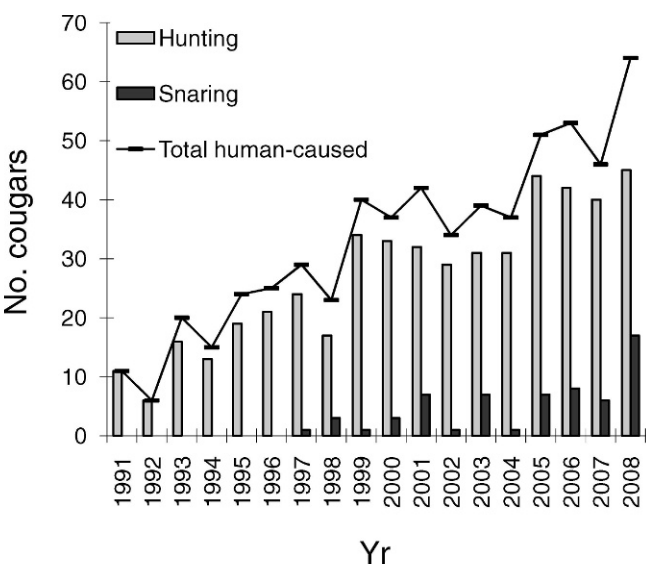

Figure 4. Number of cougars snared and hunted and total annual mortality of cougars reported through a mandatory provincial cougar registration program in west-central Alberta, Canada, during 1991–2008.

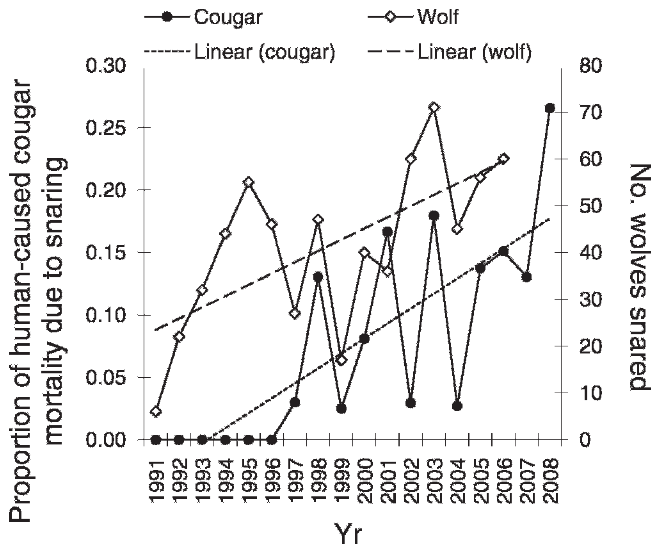

Figure 5. Proportion of total annual human-caused cougar mortality resulting from nontarget snaring and total number of wolves snared annually as reported through mandatory provincial registration programs in west-central Alberta, Canada, during 1991–2008. The best-fit regressions against year are displayed for cougars (proportion of mortality due to snaring increasing at 0.012/yr) and for wolves (no. snared increasing at 2.4 wolves/yr).

might be a more important source of mortality than provincial records indicate.

Both hunting and snaring mortalities increased substantially over the past 2 decades, with total number of human-caused cougar deaths escalating by approximately 600% between 1991 and 2008 (Fig. 4). Whereas snaring mortality is highly variable among years (Fig. 4), the general trend nevertheless indicates that snaring has made up an increasingly important proportion of all human-caused mortality over time (increasing at 1.2%/year, $r^2 = 0.61$; Fig. 5). This increase is mirrored by an increasing wolf harvest (increasing at 2.4 wolves/year, $r^2 = 0.43$; Fig. 5), and we identified a positive correlation between number of wolves snared and annual proportion of human-caused cougar mortality due to snaring ($P = 0.04$, $r^2 = 0.27$, $n = 16$).

DISCUSSION

Scavenging Behavior

Our results support the hypothesis that cougars, like most predators, are naturally inclined to scavenge (DeVault et al. 2003, Bauer et al. 2005). Cougars in west-central Alberta conformed to all 3 predictions for facultative scavengers: 1) scavenging was a common foraging strategy employed by most cougars in the population, 2) scavenging increased during winter when carrion availability was higher and some cougars spent a substantial portion of their foraging time consuming carrion during winter, and 3) healthy adult cougars with demonstrated killing ability incorporated scavenging into their foraging strategy. Indeed, we probably underestimated the true importance of scavenging because GPS cluster visitation does not always detect feeding events where available biomass is low (Knopff et al. 2009), and some cougar scavenging opportunities might have involved carcasses with limited edible material.

Inclination for cougars to scavenge should not be surprising since scavenging allows cougars to take advantage of foraging opportunities while avoiding risks associated with predation (e.g., Ross et al. 1995, Logan and Sweanor 2001). Given this benefit, cougars might scavenge whenever edible carrion is encountered and has not been monopolized by a competitor. The reason that we observed higher scavenging rates for subadults might be because they are less-efficient predators (Murphy 1998; K. H. Knopff, unpublished data) and are forced to spend more time searching for food, increasing their encounter rate with carrion. Spoilage of animal carcasses in warm weather imposes costs because of possible toxicity that will eventually outweigh the benefits of scavenging, partially explaining the observed reduction in scavenging rates and tendency to shorter handling times in summer (DeVault et al. 2003, Bauer et al. 2005).

Scavenging in west-central Alberta also confirms the suspicions of Bauer et al. (2005) that misclassified scavenging events can influence kill rate estimation for cougars. Kill rate estimators that rely on telemetry data alone (e.g., Anderson and Lindzey 2003, Laundré 2008), delayed visitation of telemetry clusters (e.g., Anderson and Lindzey 2003), or energetics models (e.g., Laundré 2005) may overestimate the importance of predation. Indeed, using the logistic regression model and optimal probability cutoff proposed by Knopff et al. (2009) to calculate kill rate without field visitation would have inflated winter kill rate estimates by $\geq$25% for the 5 individual cougars that scavenged most frequently. Even when clusters are visited in the field, conservative estimates of scavenging rates (and overestimated kill rates) are possible because of the potential to misclassify as predation fresh carcasses that cannot be clearly identified as being killed by something other than a cougar.

Although scavenging was reported in some of the earliest studies of cougar diet (Young 1946), its importance has remained obscure, probably because scavenging rates have been difficult to estimate. Estimating foraging patterns via scat analysis, for instance, does not permit differentiation between predation and scavenging events (e.g., Rosas-Rosas et al. 2003), nor does visiting GPS location clusters if the delay between cluster creation and visitation is long (e.g., Anderson and Lindzey 2003). In such cases predation is often assumed. Indeed, failure to recognize the importance of scavenging is a common problem in studies of vertebrate predators, precisely because ecologists tend to focus their attention on predation (DeVault et al. 2003). Monitoring cougar foraging behavior using daily radiotelemetry and regular field checks of radiolocations allows researchers to identify scavenging events, but logistical challenges associated with these techniques tend to yield short monitoring periods and low sample sizes (Murphy 1998, Nowak 1999, Cooley et al. 2008). Downloadable GPS collars permitted us to visit large numbers of telemetry location clusters shortly after they were made, allowing us to circumvent many of these problems and calculate cougar scavenging rates for the first time. Similar techniques might be applied for estimating scavenging rates in other large carnivores.

Susceptibility to Snares and Harvest Management

The propensity for cougars to scavenge makes them vulnerable to snaring at bait stations, with important implications for cougar populations and harvest management. Eleven percent of the cougar population was removed annually as a result of incidental snaring alone, and our estimated annual human-caused mortality of 33% of independent cougars more than doubles the maximum annual human-caused mortality of 15% recommended in Alberta's cougar management plan (Jalkotzy et al. 1992). Although cougar populations are capable of rapid growth (Ross and Jalkotzy 1992, Logan and Sweanor 2001), annual harvest of 30–50% of independent cougars has been shown to cause decline (Anderson and Lindzey 2005, Lambert et al. 2006, Stoner et al. 2006). This is especially true if, as we found in west-central Alberta, annual mortality of independent and potentially reproductive females exceeds 20–25% (Anderson and Lindzey 2005, Lambert et al. 2006).

Although we did not measure it directly, survival of dependent kittens and juveniles also can be reduced in heavily harvested populations. Females traveling with spotted kittens cannot legally be hunted in Alberta, but mothers often travel independently and thus are susceptible to harvest (e.g., Barnhurst and Lindzey 1989, Anderson and Lindzey 2005, Laundré and Hernàndez 2008). In our study, 29% of harvested females (2/7, one hunter harvest, one snared) had dependent kittens <8 months old. Therefore, although we recognize that the confidence interval around our annual survival estimate is wide and that true survival of independent cougars near the upper 95% limit (0.81) is compatible with stable or even increasing populations, we point out that our data are more consistent with a declining or sink population (Anderson and Lindzey 2005, Stoner et al. 2006, Robinson et al. 2008).

During our study, hunting quotas were set in advance and were usually filled; hence, hunting mortality was fixed. Natural mortalities tend to be rare in heavily harvested cougar populations, a pattern that is further supported by our results (Anderson and Lindzey 2005, Lambert et al. 2006, Robinson et al. 2008, but see Stoner et al. 2006). Thus, managing the substantial and variable nontarget mortality at wolf bait stations represents an important component of cougar population management in west-central Alberta. This is one of the first times population-level consequences for nontarget animals killed unintentionally by indiscriminate harvest techniques have been identified in a terrestrial ecosystem.

Incidental cougar capture at wolf bait stations is a new management concern in west-central Alberta and cougar mortality due to snaring only became prevalent after 1997 and has increased steadily since. In part, the increase in the number of cougars snared might be a result of a growing provincial cougar population. Increasing cougar numbers across North America in recent decades is apparent in genetic evidence and the recolonization of portions of cougar range east of the Rocky Mountains (Biek et al. 2006, Thompson and Jenks 2007, Bacon and Boyce 2009). Moreover, increased cougar harvest in western states and provinces is a response by management agencies to perceived growth in cougar populations. The approximately 600% growth in human-caused cougar mortality in west-central Alberta over the last 2 decades parallels similar patterns in other jurisdictions (e.g. Riley and Malecki 2001, Keister and Van Dyke 2002, Toweill et al. 2008). Density estimates based on intensive collaring efforts indicate that cougar populations as much as tripled in west-central Alberta during 1991–2006, although high harvests reported in this study might have begun to curb or even reverse that trend (K. Knopff, unpublished data).

The proportion of human-caused mortality attributed to snaring also increased over time, and we found a significant positive relationship between the annual proportion of cougars dying in snares and the number of wolves snared, suggesting that changes in trapper effort might be driving changes in incidental cougar harvest. Increasing wolf numbers in west-central Alberta and attempts by provincial agencies to increase efficacy of snaring as a wolf management tool by sponsoring snaring courses and helping licensed trappers to obtain road-killed ungulates for bait may have resulted in higher trapper effort (Webb 2009; J. Allen, Alberta Sustainable Resource Development, personal communication). Although reducing the number of bait stations on the landscape should reduce incidental cougar captures, reducing harvest of target species such as wolves may not be a desirable outcome for managers in many situations. Under these circumstances, strategies for maintaining wolf harvest while reducing incidental cougar capture are necessary.

Overall, snaring remained more effective at targeting wolves than cougars on a per capita basis. We report an annual snaring-specific mortality rate of 0.11 for cougars, and Webb (2009) found a rate of 0.26 for wolves in the same study area over approximately the same time period. A potential explanation for higher susceptibility of wolves to snaring is that they move further and over larger areas than cougars, increasing their encounter rates with bait stations (K. Knopff and N. Webb, University of Alberta, unpublished data). Further reductions in cougar susceptibility to wolf snares might be possible if differences in wolf and cougar habitat selection are exploited by trappers to diminish the probability that cougars will access areas where bait is placed and snares are set (Alexander et al. 2006, Atwood et al. 2007, Kortello et al. 2007). In addition, carrion bait can be used to attract wolves and maintain their presence in an area, but snares can be set near canid-specific lures several hundred meters away from bait carcasses to limit incidental capture of noncanid scavengers (G. Klassen, Alberta Trappers Association, personal communication). Trappers who check their bait stations frequently (e.g., daily instead of weekly) might be able to reduce the number of cougar captures by deactivating snares when they notice cougars accessing the bait.

MANAGEMENT IMPLICATIONS

Our study highlights the potential importance of indiscriminate harvest techniques for nontarget species captured incidentally in terrestrial systems. A strong propensity to scavenge makes cougars susceptible to carrion baiting techniques used to attract carnivores so that they can be trapped or snared. Managers working where snaring or trapping using carrion bait is permitted for species other than cougars, including snaring or trapping of coyote (*Canis latrans*), bobcat (*Lynx rufus*), and lynx (*Lynx canadensis*), might need to consider incidental mortalities when setting harvest quotas for cougars. Because incidental mortalities can vary among years, we recommend maintaining flexible hunting quotas that can be adjusted to compensate for the previous year's mortality.

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LITERATURE CITED

Alberta Fish and Wildlife. 2008. Alberta guide to trapping regulations. <http://www.albertaregulations.ca/Trapping-Regs-2008-2009.pdf>. Accessed 15 Apr 2009.

Alexander, S., T. Logan, and P. Paquet. 2006. Spatio-temporal co-occurrence of cougars (*Felis concolor*), wolves (*Canis lupus*), and their prey during winter: a comparison of two analytical methods. Journal of Biogeography 33:2001–2022.

Anderson, C. R., and F. G. Lindzey. 2003. Estimating cougar predation rates from GPS location clusters. Journal of Wildlife Management 67:307–316.

Anderson, C. R., and F. G. Lindzey. 2005. Experimental evaluation of population trend and harvest composition in a Wyoming cougar population. Wildlife Society Bulletin 33:179–188.

Ashman, D. L., C. Christensen, M. L. Hess, G. K. Tsukamoto, and M. S. Wichersham. 1983. The mountain lion in Nevada. Report W-48-15, Nevada Department of Wildlife, Reno, USA.

Atwood, T., E. Gese, and K. Kunkel. 2007. Comparative patterns of predation by cougars and recolonizing wolves in Montana's Madison Range. Journal of Wildlife Management 71:1098–1106.

Bacon M. M., and M. S. Boyce. 2009. The prairie cougar: examining the effects of a re-established predator population. Nature Alberta 38:20–23.

Barnhurst, D., and F. G. Lindzey. 1989. Detecting female mountain lions with kittens. Northwest Science 63:35–37.

Barrus, D., F. Neumann, E. Robertson, A. Rylaarsdam, and F. Sedmak. 1997. Alberta Trapper Training Manual. Lakeland College, Lloydminster, Alberta, Canada.

Bauer, J. W., K. A. Logan, L. L. Sweanor, and W. M. Boyce. 2005. Scavenging behavior in puma. Southwestern Naturalist 50:466–471.

Biek, R., A. J. Drummond, and M. Poss. 2006. A virus reveals population structure and recent demographic history of its carnivore host. Science 311:538–541.

Cooley, H. S., H. S. Robinson, R. B. Wielgus, and C. S. Lambert. 2008. Cougar prey selection in a white-tailed deer and mule deer community. Journal of Wildlife Management 72:99–106.

Day, R. W., and C. P. Quinn. 1989. Comparisons of treatments after an analysis of variance in ecology. Ecological Monographs 59:433–463.

Dayton, P. K., S. F. Thrush, M. T. Agardy, and R. J. Hofman. 1995. Environmental effects of marine fishing. Aquatic Conservation: Marine and Freshwater Ecosystems 5:205–232.

DeVault, T. L., O. E. Rhodes, Jr., and J. A. Shivik. 2003. Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. Oikos 102:225–234.

Guthery, F. S., and S. L. Beasom. 1978. Effectiveness and selectivity of neck snares in predator control. Journal of Wildlife Management 42:457–459.

Hasbrouck, J. J., W. R. Clark, and R. D. Andrews. 1992. Factors associated with raccoon mortality in Iowa. Journal of Wildlife Management 56:693–699.

Hayes, R. D., A. M. Baer, U. Wotschikowsky, and A. S. Harestad. 2000. Kill rate by wolves on moose in the Yukon. Canadian Journal of Zoology 78:49–59.

Hebblewhite, M., P. C. Paquet, D. Pletscher, R. B. Lessard, and C. J. Callaghan. 2003. Development and application of a ratio estimator to estimate wolf kill rates and variance in a multiple-prey system. Wildlife Society Bulletin 31:933–946.

Heisey, D. M., and T. K. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. Journal of Wildlife Management 49:668–674.

Heisey, D. M., and B. R. Patterson. 2006. A review of methods to estimate cause-specific mortality in presence of competing risks. Journal of Wildlife Management 70:1544–1555.

Hornocker, M. G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. Wildlife Monograph 21.

Huggard, D. J. 1993. Effect of snow depth on predation and scavenging by gray wolves. Journal of Wildlife Management 57:382–388.

Jalkotzy, M., I. Ross, and J. R. Gunson. 1992. Management plan for cougars in Alberta. Wildlife Management Planning Series Number 5, Edmonton, Alberta, Canada.

Jedrzejewski, W., K. Schmidt, J. Theurkauf, B. Jedrzejewska, N. Selva, K. Zub, and L. Szymura. 2002. Kill rates and predation by wolves on ungulate populations in Biołoweiża Primeval Forest (Poland). Ecology 83:1341–1356.

Jefferson, T. A., and B. E. Curry. 1994. A global review of porpoise (Cetacea, Phocoenidae) mortality in gillnets. Biological Conservation 67:167–183.

Keister, G. P., and W. A. Van Dyke. 2002. A predictive population model for cougars in Oregon. Northwest Science 76:15–25.

Knopff, K. H., A. A. Knopff, M. B. Warren, and M. S. Boyce. 2009. Evaluating global positioning system telemetry techniques for estimating cougar predation parameters. Journal of Wildlife Management 73:586–597.

Kortello, A. D., T. E. Hurd, and D. L. Murray. 2007. Interactions between cougars (*Puma concolor*) and gray wolves (*Canis lupus*) in Banff National Park, Alberta. Ecoscience 14:214–222.

Lambert, C. M. S., R. B. Wielgus, H. S. Robinson, D. D. Katnik, H. S. Cruickshank, R. Clark, and J. Almack. 2006. Cougar population dynamics and viability in the Pacific Northwest. Journal of Wildlife Management 70:246–254.

Laundré, J. W. 2005. Puma energetics: a recalculation. Journal of Wildlife Management 69:723–732.

Laundré, J. W. 2008. Summer predation rates on ungulate prey by a large keystone predator: how many ungulates does a large predator kill? Journal of Zoology 275:341–348.

Laundré, J. W., and L. Hernández. 2008. The amount of time female pumas *Puma concolor* spend with their kittens. Wildlife Biology 14:221–227.

Laundré, J. W., L. Hernández, D. Streubel, K. Altendorf, and C. López González. 2000. Aging mountain lions using gum-line recession. Wildlife Society Bulletin 28:963–966.

Logan, K. L., and L. L. Sweanor. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington, D.C., USA.

Mayfield, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456–466.

Murphy, K. M. 1998. The ecology of the cougar (*Puma concolor*) in the northern Yellowstone Ecosystem: interactions with prey, bears, and humans. Dissertation, University of Idaho, Moscow, USA.

Murray, D. L. 2006. On improving telemetry-based survival estimation. Journal of Wildlife Management 70:1530–1543.

Noss, A. J. 1998. Cable snares and bushmeat markets in a central African forest. Environmental Conservation 25:228–233.

Nowak, M. C. 1999. Predation rates and foraging ecology of adult female mountain lions in northeast Oregon. Thesis, Washington State University, Pullman, USA.

Nowak, M. C., T. E. Taylor, and G. W. Witmer. 2000. Prolonged scavenging by a female mountain lion in northeastern Oregon. Northwestern Naturalist 81:63–65.

Phillips, R. L. 1996. Evaluation of 3 types of snares for capturing coyotes. Wildlife Society Bulletin 24:107–110.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7–15.

Riley, S. J., and T. A. Malecki. 2001. A landscape analysis of cougar distribution and abundance in Montana, USA. Environmental Management 28:317–323.

Robinson, H. S., R. B. Wielgus, H. S. Cooley, and S. W. Cooley. 2008. Sink populations in carnivore management: cougar demography and immigration in a hunted population. Ecological Applications 18:1028–1037.

Rosas-Rosas, O. C., R. Valdez, L. C. Bender, and D. Daniel. 2003. Food habits of pumas in northwestern Sonora, Mexico. Wildlife Society Bulletin 31:528–535.

Ross, P. I., and M. G. Jalkotzy. 1992. Characteristics of a hunted population of cougars in southwestern Alberta. Journal of Wildlife Management 56:417–426.

Ross, P. I., and M. G. Jalkotzy. 1996. Cougar predation on moose in southwestern Alberta. Alces 32:1–8.

Ross, P. I., M. G. Jalkotzy, and P. Y. Daoust. 1995. Fatal trauma sustained by cougars, *Felis concolor*, while attacking prey in southern Alberta. Canadian Field Naturalist 109:261–263.

Ross, P. I., M. G. Jalkotzy, and J. R. Gunson. 1996. The quota system of cougar harvest management in Alberta. Wildlife Society Bulletin 24:490–494.

Rowcliffe, J. M., G. Cowlishaw, and J. Long. 2003. A model of human hunting impacts in multi-prey communities. Journal of Applied Ecology 40:872–889.

Selva, N., B. Jedrzejewska, W. Jedrzejewski, and A. Wajrak. 2005. Factors affecting carcass use by a guild of scavengers in European temperate woodland. Canadian Journal of Zoology 83:1590–1601.

Shaw, H. G. 1986. Mountain lion field guide. Special Report No 9. Arizona Game and Fish Department, Phoenix, USA.

Shivik, J. A., and K. S. Gruver. 2002. Animal attendance at coyote trap sites in Texas. Wildlife Society Bulletin 30:502–507.

Stahler, D. R., D. W. Smith, and D. S. Guernsey. 2006. Foraging and feeding ecology of the gray wolf (*Canis lupus*): lessons from Yellowstone National Park, Wyoming, USA. Journal of Nutrition 136:1923–1926.

Stevens, J. D., R. Bonfil, N. K. Dulvy, and P. A. Walker. 2000. The effects of fishing on sharks, rays, and chimaeras (Chondrichthyans), and the implications for marine ecosystems. Journal of Marine Science 57:476–494.

Stoner, D. C., M. L. Wolfe, and D. M. Choate. 2006. Cougar exploitation levels in Utah: implications for demographic structure, population

recovery, and metapopulation dynamics. Journal of Wildlife Management 70:1588–1600.
Thompson, D. J., and J. A. Jenks. 2007. Spirits in the hills: the black hills cougar. Wild Cat News 3:1–4.
Toweill, D. E., S. Nadeau, and D. Smith, editors. 2008. Proceedings of the ninth mountain lion workshop, 5–8 May 2008, Sun Valley, Idaho, USA.
Tsai, K., K. H. Pollock, and C. Brownie. 1999. Effects of violation of assumptions for survival analysis methods in radiotelemetry studies. Journal of Wildlife Management 63:1369–1375.
Webb, N. 2009. Density, demography, and functional response of a harvested wolf population in west-central Alberta, Canada. Thesis, University of Alberta, Edmonton, Canada.
Webb, S. M., D. J. Davidson, and M. S. Boyce. 2008. Trapper attitudes and industrial development on registered traplines in west-central Alberta. Human Dimensions of Wildlife 13:115–126.
Wilmers, C. C., D. R. Stahler, R. L. Crabtree, D. W. Smith, and W. M. Getz. 2003. Resource dispersion and consumer dominance: scavenging at wolf- and hunter-killed carcasses in Greater Yellowstone, USA. Ecology Letters 6:996–1003.
Young, S. P. 1946. Economic status. Pages 127–131 *in* S. P. Young and E. A. Goldman, editors. The puma, mysterious American cat. American Wildlife Institute, Washington, D.C., USA.

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