Research Article

Cougar Exploitation Levels in Utah: Implications for Demographic Structure, Population Recovery, and Metapopulation Dynamics

DAVID C. STONER,[1] *Department of Wildland Resources, Utah State University, Logan, UT 84322, USA*
MICHAEL L. WOLFE, *Department of Wildland Resources, Utah State University, Logan, UT 84322, USA*
DAVID M. CHOATE,[2] *Department of Wildland Resources, Utah State University, Logan, UT 84322, USA*

Abstract

*Currently, 11 western states and 2 Canadian provinces use sport hunting as the primary mechanism for managing cougar (*Puma concolor*) populations. Yet the impacts of sustained harvest on cougar population dynamics and demographic structure are not well understood. We evaluated the effects of hunting on cougar populations by comparing the dynamics and demographic composition of 2 populations exposed to different levels of harvest. We monitored the cougar populations on Monroe Mountain in south-central Utah, USA, and in the Oquirrh Mountains of north-central Utah from 1996 to 2004. Over this interval the Monroe population was subjected to annual removals ranging from 17.6–51.5% (mean $\pm$ SE $= 35.4 \pm 4.3\%$) of the population, resulting in a $>60\%$ decline in cougar population density. Concurrently, the Oquirrh study area was closed to hunting and the population remained stationary. Mean age in the hunted population was lower than in the protected population ($F = 9.0$; $df = 1, 60.3$; $P = 0.004$), and in a pooled sample of all study animals, females were older than males ($F = 13.8$; $df = 1, 60.3$; $P < 0.001$). Females from the hunted population were significantly younger than those from the protected population (3.7 vs. 5.9 yr), whereas male ages did not differ between sites (3.1 vs. 3.4 yr), suggesting that male spatial requirements may put a lower limit on the area necessary to protect a subpopulation. Survival tracked trends in density on both sites. Levels of human-caused mortality were significantly different between sites ($\chi^2 = 7.5$; $P = 0.006$). Fecundity rates were highly variable in the protected population but appeared to track density trends with a 1-year lag on the hunted site. Results indicate that harvest exceeding 40% of the population, sustained for $\geq$4 years, can have significant impacts on cougar population dynamics and demographic composition. Patterns of recruitment resembled a source–sink population structure due in part to spatially variable management strategies. Based on these observations, the temporal scale of population recovery will most likely be a function of local harvest levels, the productivity of potential source populations, and the degree of landscape connectivity among demes. Under these conditions the metapopulation perspective holds promise for broad-scale management of this species.* (JOURNAL OF WILDLIFE MANAGEMENT 70(6):1588–1600; 2006)

Key words

connectivity, cougar, demographics, hunting, metapopulation, population dynamics, Puma concolor*, radiotelemetry, refuge, source–sink dynamics, Utah.*

Across western North America sport harvest is the primary mechanism for the population-scale management of *Puma concolor* (Pierce and Bleich 2003). Management regimes vary from public safety and depredation control only in California, to a year-round open season in Texas (Nowell and Jackson 1996). In order to balance hunting opportunities with protection of big game and livestock, most states manage cougar populations at some intermediate level. However, cougars are secretive, long-lived, and utilize large home ranges, making them difficult to manage with precision (Ross et al. 1996). At present, there are no widely accepted methods for the enumeration of cougars across diverse habitat types and climatic regimes (Anderson et al. 1992, Ross et al. 1996). Most techniques (e.g., track counts, scent stations, probability sampling) have limitations that render them marginally useful (Choate et al. 2006) or capable of detecting only large and rapid changes in population size (Van Sickle and Lindzey 1992, Beier and Cunningham 1996). Additionally, cougars occur at low population densities relative to their primary prey, making them sensitive both to bottom-up (e.g., prey declines; Logan and Sweanor 2001, Bowyer et al. 2005) and top-down (e.g., overexploitation; Murphy 1998) perturbations. Assessing cougar population trends is complicated by annual removals of varying intensity. Changes in population size and composition are generally indexed through harvest data and are therefore confounded by nonrandom sampling biases, further hindering reliable trend estimation (Wolfe et al. 2004).

Cougar management in Utah is spatially organized, with 4 broad ecoregions subdivided into 30 different hunting units. Each unit is managed independently in order to apply harvest pressure according to local priorities, which can include density reductions aimed at increasing survival in mule deer (*Odocoileus hemionus*) or bighorn sheep (*Ovis canadensis*) populations. Cougars are therefore managed at 2 different spatial scales. Locally, they are either managed conservatively as a trophy species or liberally as a limiting factor in the population dynamics of native ungulates. The statewide population, however, is managed for sustainable

[1] *E-mail: dstoner@cc.usu.edu*
[2] *Present address: Department of Biological Sciences, University of Notre Dame, Notre Dame, IN 46556 USA*

hunting opportunities and persistence across its currently occupied range (Mason et al. 1999).

Cougar hunting in Utah is conducted by means of pursuit with trained hounds. The hunting season extends from mid-December to early June, but approximately 75% of the kill occurs during December to March, when snow cover facilitates tracking and pursuit (Mason et al. 1999). Prior to 1998 the sport harvest of cougars occurred under a Limited Entry (i.e., lottery) system in which the number of permits for individual units is restricted. The long-term mean hunter success for this system is 64%. Beginning with the 1997–1998 season the Harvest Objective (i.e., quota) system was introduced for some units. This system employs an unlimited availability of permits to achieve a prescribed level of kill. Hunters are required to report their kill within 48 hours and the unit is closed once the quota is reached. Typically 74% of the quota is achieved, but instances of overharvest do occur. Between 1995 and 2003 legal harvest accounted for 90.0% of the total statewide cougar kill (Hill and Bunnell 2005). The remaining known mortality was distributed among animals killed in response to livestock depredation (6.2%) and other human-caused mortality, including roadkill and accidental trappings (3.8%). Additional unreported mortality such as incidental take during big game hunting seasons and illegal snaring occurs, but the magnitude of this impact is probably small relative to legal harvest. Individual cougars involved in livestock depredation are managed by the Wildlife Services Division of the United States Department of Agriculture, who may employ foothold snares as well as hounds to remove offending individuals. Nuisance cougars are defined as animals in urban settings that constitute a potential threat to human safety. These animals are generally controlled by Utah Division of Wildlife Resources (UDWR) personnel using lethal or nonlethal means, as circumstances warrant.

Little is known about both the immediate and long-term effects of sustained harvest on cougar populations (Anderson 1983, Ross et al. 1996). Numerous studies have been conducted on exploited populations (Murphy 1983, Barnhurst 1986, Logan et al. 1986, Ross and Jalkotzy 1992, Cunningham et al. 2000), including 2 removal experiments (Lindzey et al. 1992, Logan and Sweanor 2001), but few of these studies directly addressed the questions of: 1) how harvest affects the demographic structure of a population, and 2) what the long-term implications are for persistence and recovery of exploited populations within a metapopulation context. Moreover, habitat configuration and connectivity are important factors influencing cougar recruitment patterns, but with few exceptions (Beier 1993, 1995, Maehr et al. 2002) this relationship has been largely overlooked.

Recent years have seen the emergence of the idea of managing cougars as a metapopulation based on the effects of natural habitat patchiness (Sweanor et al. 2000, Laundré and Clark 2003) or anthropogenic fragmentation (Beier 1996, Ernest et al. 2003). Because metapopulations transcend administrative boundaries, understanding population response to sustained harvest is vital in order to manage for persistence across landscapes exhibiting varying degrees of natural and human-caused fragmentation.

We assessed the impacts of exploitation on cougar population dynamics by comparing demographic characteristics between an exploited and a semiprotected population. Specific objectives of this study were: 1) determine how harvest levels might influence the dynamics and demographic structure of individual populations, 2) identify the factors that may influence the rate of population recovery, and 3) assess how the distribution of harvest impacts might affect recruitment within a metapopulation context.

Study Area

Cougar habitat in Utah is geographically fragmented, being broadly associated with mesic regions between 1500 m and 3000 m. The Wasatch Mountains and associated high plateaus form the core habitat, longitudinally bisecting the state, whereas the Colorado Plateau and Great Basin ecoregions consist primarily of desert ecosystems, with suitable habitat sparsely distributed among insular mountain ranges (Fig. 1). We selected Monroe Mountain and the Oquirrh Mountains as study areas for this research (Fig. 1). Although differences existed between these sites in terms of size and plant community composition, they were located within 190 km of each other, making them climatically and ecologically similar in a broad sense, but far enough apart to be treated demographically as independent populations. The most pronounced difference between these populations was the level of exploitation to which each was subjected.

Exploited Area

Monroe Mountain comprises part of the Sevier Plateau in the Southern Mountains ecoregion of south-central Utah (38.5°N, 112°W). The site is a high volcanic plateau extending 75 km in a north–south orientation and lies within a west–east geologic transition from basin and range topography to the Colorado Plateau. Hydrologically, Monroe is part of the Great Basin, but climatically and biologically it is more closely associated with other high-elevation regions of the Colorado Plateau and southern Rocky Mountains. The study site covered approximately 1,300 km^2 and encompassed the central unit of the Fishlake National Forest, southeast of Richfield. Other landholders included the Bureau of Land Management (BLM), State of Utah, and various private interests.

The terrain is mountainous with elevations ranging from 1,600–3,400 m. Annual precipitation ranged from 15–20 cm at lower elevations to 60–120 cm on the plateaus above 2,700 m. Approximately 60% of the annual precipitation occurred as snow in January and February, with most of the remainder derived from summer thunderstorms (Ashcroft et al. 1992). Snowpack typically persisted until mid-June at elevations $>$3,000 m. Mean monthly temperatures ranged from −4.6° C in January to 18.7° C in July (Ashcroft et al. 1992).

Plant communities were diverse and varied with elevation and aspect (Edwards et al. 1995). Piñon-juniper woodlands

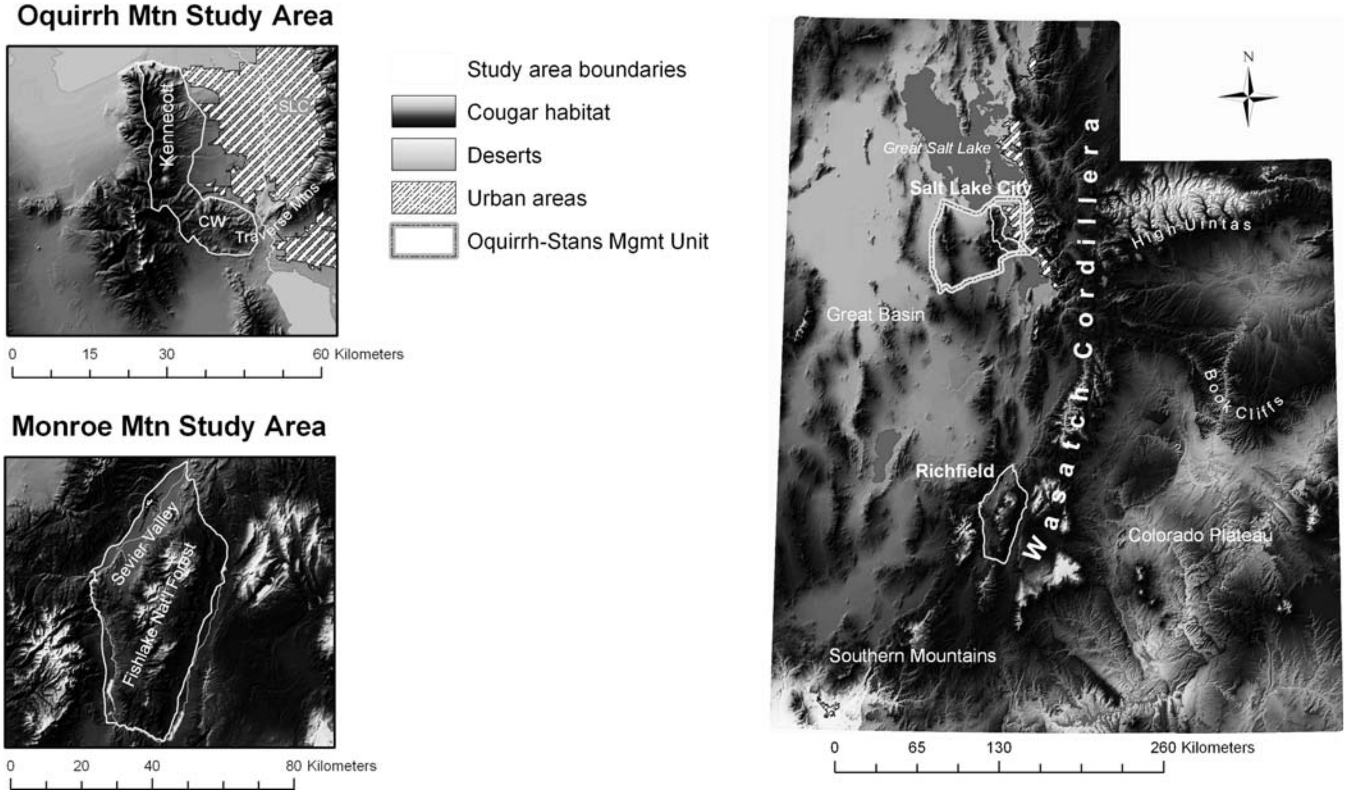

Figure 1. Study-area locations and cougar habitat across Utah, USA, 1996–2004.

(*Pinus edulis, Juniperus scopulorum, Juniperus osteosperma*) comprised the single largest vegetation type covering approximately 44% of the area. Mixed conifer and aspen (*Populus tremuloides*) stands occurred at higher elevations, with gambel oak (*Quercus gambelii*), mountain shrub (e.g., *Cercocarpus ledifolius, Rosa woodsii, Purshia tridentata*), and mixed sagebrush (*Artemisia tridentata*) –grassland meadows interspersed throughout.

Resource exploitation included livestock grazing, logging, and recreation. The UDWR classified Monroe Mountain as Cougar Management Unit 23. Mule deer and elk (*Cervus elaphus*), the primary cougar prey species on this site, were also managed for annual harvests. Human densities around the site varied from 73/100 km^2 to 382/100 km^2 (U.S. Census Bureau), with most of the population scattered among small agricultural communities in the Sevier Valley on the northwestern boundary of the study site.

Protected Area

The Oquirrh-Traverse Mountains complex (hereafter the Oquirrhs) extends 55 km in a north–south orientation on the eastern edge of the Great Basin ecoregion in north-central Utah (40.5°N, 112.2°W). The Oquirrhs are typical of other mountain ranges within this ecoregion in that they form islands of high productivity relative to the surrounding desert basins (Brown 1971) and thus represented the majority of cougar habitat in this area.

The total area of the Oquirrhs measures approximately 950 km^2, but we conducted fieldwork primarily on the northeastern slope of the range on properties owned and managed by the Utah Army National Guard (Camp Williams, Traverse Mountains, 100 km^2) and the Kennecott Utah Copper Corporation (Oquirrh Mountains, 380 km^2). The site was situated at the southern end of the Great Salt Lake, abutting the southwestern side of the greater Salt Lake metro area. Ownership on the southern and western portions of the Oquirrhs was a conglomeration of BLM, grazing associations, and small mining interests, with approximately 45% of the range residing in private ownership.

Elevations on the site vary from lake level at 1,280 m up to 3,200 m. The Traverse Mountains run perpendicular to the Oquirrhs, and range in elevation from 1,650 m to 2,100 m. Annual precipitation ranged from 30–40 cm in the Salt Lake and Tooele valleys to 100–130 cm on the highest ridges and peaks. Most precipitation fell as snow between December and April, with approximately 25% occurring in the form of summer thunderstorms. Mean monthly temperatures ranged from −2.4° C in January to 22.2° C in July (Ashcroft et al. 1992).

Gambel oak and sagebrush were the predominant vegetation on the site. Also prevalent were Utah juniper in the foothills, and canyon maple (*Acer grandidentatum*) in the drainages at low elevations, and across broader areas above 1,800 m. Mountain mahogany (*Cercocarpus spp.*) was present, but relegated to well-drained soils along ridges. North-facing slopes above 2,200 m supported localized montane communities of aspen and Douglas fir (Edwards et al. 1995).

Mining activities have dominated the Kennecott property for >100 years (Roylance 1982), and the site included 2 large open pit mines and attendant infrastructure. Camp Williams was used for military training activities, and consequently exhibited brief fire return intervals. All prominent peaks on the study site supported commercial radio and television transmitters with associated access roads. A limited amount of livestock grazing occurred seasonally. Mule deer and elk were present on this study area as well; however deer were not hunted, whereas elk were subject to intensive management through annual harvests and active translocation projects. The study site was part of the Oquirrh-Stansbury Cougar Management Unit 18, but both of these properties were closed to the public and cougar hunting was prohibited. Human density adjoining the study area varied from 232/100 km^2 in rural Tooele County to 47,259/100 km^2 in urban Salt Lake County (United States Census Bureau).

Methods

We monitored cougar populations within the 2 study areas simultaneously from early 1997 to December 2004. We estimated demographic parameters for each population based on radiotelemetry data collected between 1996 and 2004 on Monroe and from 1997 and 2004 on the Oquirrhs. We calculated estimates of life-history parameters for cougars on the Oquirrh site during 1997 and 1998 from raw data presented in Leidolf and Wolfe (Utah State University, unpublished data). We performed statistical comparisons with the use of SAS (V.8) software. We report all descriptive statistics as mean ± SE unless otherwise noted.

Radiotelemetry and Harvest

We conducted intensive capture efforts during winter (Nov–Apr) each year of the study. We captured cougars by pursuing them into trees, culverts, cliffs, or mine shafts with trained hounds (Hemker et al. 1984). We immobilized each animal with a 5:1 combination of ketamine HCl and xylazine HCl (Kreeger 1996) at a dose of 10 mg ketamine plus 2 mg xylazine/kg of body weight. We administered immobilizing drugs with a Palmer CO_2 pistol (Powder Springs, Georgia), jab stick, or hand-held syringe. We collected tooth (vestigial premolar, P2) samples for age determination by counts of cementum annulations. We sexed, aged, weighed, measured, tattooed with a unique identifier, and equipped with a radiocollar (Advanced Telemetry Solutions, Isanti, Minnesota) and a microchip (AVID Co., Norco, California) every adult animal captured. We checked adult females for evidence of lactation during handling. We tattooed, microchipped, and released all kittens too small to wear a radiocollar. We conducted all procedures in accordance with Utah State University Institutional Animal Care and Use Committee standards (Approval No. 937-R).

We relocated all radio-collared cougars with the use of aerial and ground-based telemetry techniques (Mech 1983). We conducted telemetry flights bimonthly on both sites as weather conditions permitted. We also relocated cougars opportunistically with ground-based telemetry by plotting radiotriangulated locations on United States Geological Survey 7.5′ topographic quads with the use of Universal Transverse Mercator coordinates (zone 12, North American Datum 1927). We stored all locations in a Geographic Information Systems (GIS) database (ArcView, ESRI Products, Redlands, California).

Over the course of the study, radiocollared cougars on Monroe Mountain were not protected from harvest beyond normal legal stipulations outlined in the UDWR hunting proclamations. Annual hunter-kill was regulated by apportionment of a limited number of hunter permits, issued by the UDWR on the decision of the State Wildlife Board. The Camp Williams and Kennecott properties were closed to hunting throughout the study; however, radiocollared cougars leaving those properties were considered legal take on adjacent private and public lands within Unit 18 during the 1997–2001 hunting seasons. Radiocollared cougars on that unit were protected after 2002.

Demographic Parameters

Density.—We measured cougar density as the total number of adult and subadult cougars/100 km^2 present during winter. Our a priori goal was to capture and collar as many individuals as possible. In this sense, we attempted to conduct a census of the population during winter, but during no year were we able to capture all independent cougars. To derive a conservative estimate of the number of unmarked animals on the site, we used 2 methods. First, because males and females can generally be differentiated by track size (Fjelline and Mansfield 1989), we considered multiple track sets of same-sexed animals encountered in the same watershed one individual. Given the large ranges of cougars, we felt that the primary watersheds on the site ($n = 4$; mean ± SD = 361 ± 95 km^2, range = 237–462 km^2) provided a practical threshold for differentiating individuals, as these basins approximated the size of a male home range. This does not negate the possibility that some individuals were double-counted; however, the effect of this error on the population estimate was small due to the number of animals that fell into this category annually. Second, we back-calculated birthdates of radiocollared cougars from age estimations based on tooth wear and counts of cementum annulations and used this information to assess our estimates of uncollared individuals from track evidence and hunter harvest. We excluded males backdated in this manner from the population estimate when they were <3 years old because of the likelihood that they were recent immigrants. Because females tend to be philopatric (Sweanor et al. 2000), we included them in the population estimate as resident subadults at the backcalculated age of 1–2 years. Although there are exceptions to these arbitrary dispersal rules, they provide a reasonable cutoff point for population estimates based on known cougar behavior (Beier 1995, Sweanor et al. 2000). We summed the total number of animals detected (from all means: capture, deaths, tracks) in June at the end of the capture and hunting seasons. This number most accurately represented the population during the period June to December of the preceding year (Choate et al. 2006).

Road densities were high across both study areas. In addition to using 4-wheel-drive vehicles, we conducted winter tracking efforts on horseback and snowmachine in order to reduce bias associated with different levels of access. Using multiple methods also helped to reduce bias in terms of the social classes most vulnerable to detection due to frequent road crossings or small home ranges (Barnhurst 1986). Snow conditions influenced our ability to detect tracks, and therefore dry winters may have some bias associated with population counts; however, this bias was likely consistent between sites, as both study areas are subject to similar weather patterns.

We based study-area boundaries on major roads surrounding the site; therefore we used ecologically relevant vegetative and topographic features to delineate and quantify habitat within the study-site perimeter. We used the criteria of Laing and Lindzey (1991), which excluded valley bottoms and landcover types dominated by urban and agricultural uses. Maps represent geographical area on the planar surface and do not account for slope differences in mountainous terrain where actual surface area is greater. This discrepancy in area calculation leads to an increasing overestimation of population density as the ruggedness of the terrain increases. In order to increase the accuracy of the density estimates we used GIS software (ArcView surface to area ratio extension, Jenness Enterprises, Flagstaff, Arizona) to calculate the surface areas of habitat within study-site perimeters.

Age structure.—We determined age at the time of capture by visual inspection of tooth wear and gumline recession (Ashman et al. 1983, Laundré et al. 2000). In a few cases we used counts of cementum annulations (Matson's Lab, Milltown, Montana). To test for age differences among treatment groups (site and sex combinations), we used a 2-way factorial analysis of variance in a completely randomized design with unequal variances. We adjusted significance levels for pairwise mean comparisons to control experimentwise Type I error with the Tukey-Kramer method.

Cause-specific mortality.—We determined causes of mortality through visual inspection and necropsy of carcasses. When we could not determine cause of death in the field, we submitted the carcass to the Utah State University Veterinary Diagnostics Lab for detailed analysis. We calculated mortality by tallying cause of death among radiocollared animals and unmarked animals found opportunistically during tracking sequences. We pooled all human-related causes by site and tested for proportional differences with the use of chi-square (χ^2) tests.

Survival.—We calculated survival annually for all radiocollared adult and subadult animals from each population. To account for staggered entry and censoring due to the additions and losses of radiocollared animals to the sample, we used a Kaplan-Meier product limit estimator (Kaplan and Meier 1958). We estimated annual survival by defining the start of sample intervals as 1 December of each year. By beginning the sampling interval prior to the beginning of the hunting season (15 Dec), we ensured that human-related mortality is accounted for only once during a single nonoverlapping period in each year. We calculated measures of precision for the computed survival rates from procedures described by Cox and Oakes (1984; cited in Pollock et al. 1989). We compared survival curves between sites with the use of the log-rank test (Pollock et al. 1989).

Fecundity.—We measured fecundity as the proportion of sexually mature females detected with litters-of-the-year (kittens <1 yr) on site during winter. We counted litters during snow tracking and capture efforts. We checked all females taken in the hunt for signs of lactation, which helped account for otherwise undocumented reproduction. Kittens >3 months old are only found with their mothers 20–43% of the time (Barnhurst 1986), but we tracked many female cougars on multiple occasions, thereby increasing the probability of detecting kittens, if present. We did not attempt any analyses on the actual number of kittens born per litter, because of the difficulty in determining the actual number of kittens when ≥ 2 track sets were found. There are 2 potential sources of error in this estimate. First, it is possible that some maternal females experienced whole-litter loss prior to the winter tracking season, and therefore a proportion of nonlactating females or those without kittens may actually have been reproductively active that season. Second, kittens <2 months old are not mobile, and so this cohort would also have been missed through track-based counts. Consequently, both the number of kittens per litter and the proportion of reproductively active females are biased low. The minimum percentage of females caring for young provided an annual estimate of productivity for each population (Barnhurst 1986). We used paired t-tests to detect differences in mean fecundity rates pooled over the entire study interval.

Dispersal.—We tattooed the ears of all kittens handled on the Oquirrh mountain site in the event that they were recaptured as adults. For the Oquirrh Mountain animals, we were able to calculate several crude estimates of dispersal distance and direction opportunistically based on harvest returns of animals marked as kittens. In addition, we monitored subadults captured as transients on Monroe via radiotelemetry for extrasite movements, thus providing some information on coarse-scale movement patterns. We calculated distances as a straight line between capture site and death site or the center of the home range.

Landscape Configuration

We used measures of landscape configuration to assess the overall degree of connectivity of the study sites to surrounding habitats within their respective ecoregions. Connectivity is defined here as "the degree to which the landscape facilitates or impedes [animal] movement among resource patches" (Taylor et al. 1993). We used descriptions provided by Laing and Lindzey (1991) to delineate potential connective habitats between the study areas and neighboring patches. In assessing connectivity for cougars we used only easily quantifiable landscape variables and did not consider potential psychological barriers, although there is some evidence that outdoor lighting may function as such (Beier 1995). We derived the following metrics: size (km^2), shape (perimeter–area ratios), greatest interpatch distance, percent of perimeter connected to neighboring habitat patches, width of connective habitat, and percent of perimeter impermeable to cougar movement. Impermeability refers to landscape features that prohibited, filtered, or redirected animal movement (Ernest et al. 2003, Forman et al. 2003), such as the Great Salt Lake, interstate highways, and urban areas. Some of these features may not form absolute barriers, but they can act as an impediment to animal movement. Perimeter-area ratios are a unitless metric that provided a relative measure of how circular (or how much edge) one study area had relative to the other. We derived these measures in ArcView using the spatial analyst extension and a 30-m digital elevation model of the state of Utah.

Results

Radiotelemetry and Harvest

Capture.—We captured and marked 110 individual cougars on the 2 study sites, representing 145 capture events (Table 1). In addition, we found one dead cougar opportunistically during tracking on the Oquirrh site. We conducted captures on Monroe Mountain from January 1996 to March 2004 and on the Oquirrh site from February 1997 to March 2004. Rugged terrain and frequent animal use of culverts, mine shafts, and lava tubes hindered the collection of ground-based telemetry observations. Consequently most telemetry data were derived from aerial surveys. Monitoring times for Monroe cougars averaged 758 days (range = 2–3140 days) for females, and 194 days (range = 3–662 days) for males. On the Oquirrh site we monitored females for a mean of 810 days (range = 14–2674 days) and males for 399 days (range = 76–1173 days). Differences between sexes reflected the smaller sample of males, their greater tendency to emigrate, and shorter residence times.

Monroe Mountain cougar harvest.—For the period 1990–1995, prior to initiation of this study, a mean of 15.6 (range = 14–19) hunting permits were issued annually, corresponding to a mean kill of 8.7 cougars per year (range = 6–12), and a mean hunter success of 54.0% (range = 40.7–64.9%). In 1996, the number of permits issued increased 33.7% over the 1990–1995 mean. In 1997, the number of permits increased 40% over 1996 levels and 151% over the 1990–1995 mean. Between 1999 and 2000, the number of permits issued decreased to 1990–1995 mean levels and was again decreased for the 2001 season. During the years of heavy harvest (1996–2001), mean per-capita hunting pressure (i.e., the proportion of the population that was legally harvestable) was 87% (range = 68.5–100%). During the years of reduced harvest (2002–2004) mean per-capita hunting pressure was 25.7% (range = 22.7–29.4%; Table 2). During the study 164 permits were issued, 79 cougars were killed (51 M, 28 F), and total hunter success was 48.1%, whereas mean annual hunter success was 46.5% (1996–2001) and 73.3% (2002–2004; Hill and Bunnell 2005). The general decline in the number of hunting tags issued over time was partially in response to preliminary study results.

Table 1. Number of cougars captured according to age and sex classes, Monroe and Oquirrh Mountain study sites, Utah, USA, 1996–2004.

Age and sex	Monroe	Oquirrhs
Adults		
F	16	20
M	12	7
Subadults		
F	14	2
M	15	3
Kittens		
F	2	9
M	1	9
Totals	60	50

Oquirrh Mountain cougar harvest.—From 1996 to 2001 radiocollared animals on Unit 18 were considered legally harvestable. Cougars on the Camp Williams and Kennecott properties were protected, but these areas were surrounded by private and public lands open to hunting, making any study animal found offsite legal quarry. Beginning in 2002, all radiocollared animals on the unit were protected by law regardless of property ownership to facilitate a concurrent study. During our study 5 radiocollared cougars were killed just outside the study site boundaries (4 M, 1 F). Of these, the 4 males were legally harvested, whereas the female was taken after the 2002 moratorium on radiocollared study animals.

Demographic Parameters

Density.—Estimated high densities (cougars/100 km^2) were similar between sites (Oquirrhs, 2.9; Monroe, 3.2); however, trends in this parameter differed markedly (Fig. 2). Density on Monroe showed a consistent decline during the years of heavy harvest (1997–2001), which leveled off when permits were reduced by 80%, averaging 2.0 ± 0.3 (2002–2004). Oquirrh density showed minimal variation over the study interval averaging 2.8 ± 0.1 (Fig. 2).

Age structure.—Age estimates determined upon initial capture were pooled by sex and site for the entire study period (Table 1). Sexually mature cougars from the Monroe population ($n = 57$) averaged 3.4 ± 0.2 years (F = 3.7 ± 0.4; M = 3.1 ± 0.3). Adult cougars from the Oquirrh population ($n = 33$) averaged 4.6 ± 0.3 years (F = 5.9 ± 0.5; M = 3.4 ± 0.4; Fig. 3). Mean cougar ages differed both by study site (Monroe cougars < Oquirrh cougars; $F = 9.0$, df = 1,60.3, $P = 0.004$) and by sex (F > M; $F = 13.8$; df = 1, 60.3; $P < 0.001$). Further, we found evidence of an interaction between sex and site ($F = 5.31$; df = 1, 60.3; $P = 0.025$). Within the Monroe population male and female mean ages did not differ ($t = 1.21$; df = 54.6; $P = 0.625$), whereas Oquirrh females were significantly older than their male counterparts ($t = 3.70$; df = 30.2; $P = 0.003$). Between sites, Oquirrh females were older than Monroe females ($t =$

Table 2. Cougar harvest characteristics from Monroe Mountain (Unit 23), Utah, USA, 1996–2004.

Hunting season	Estimated population[a]	Permits issued	Cougars killed[b]	% hunter success	% F	% population Hunted[c]	% population Killed
1995–96	35	24	14	58.3	42.9	68.5	40.0
1996–97	42	40	17	42.5	47.1	95.2	40.5
1997–98	33	30	15	50.0	26.7	90.9	45.5
1998–99	26	25	7	28.0	28.6	96.1	26.9
1999–00	21	15	9	60.0	44.4	71.4	42.9
2000–01	15	15	6	40.0	33.3	100.0	40.0
2001–02	17	5	3	60.0	33.3	29.4	17.6
2002–03	20	5	4	80.0	00.0	25.0	20.0
2003–04	22	5	4	80.0	25.0	22.7	18.2
Mean	25.6	18.2	8.8	55.4	31.2	66.6	32.4
SE	3.0	4.1	1.8	17.5	5.0	10.8	3.8

[a] Estimated number of adults and independent subadults from winter capture and tracking efforts.
[b] Legal sport harvest only (Hill and Bunnell 2005).
[c] Per capita hunting pressure, i.e., the ratio of the number of permits issued to the estimated population size (column 3/column 2).

−3.53; df = 38.8; $P = 0.004$), but male ages did not differ between sites ($t = -0.54$; df = 22.5; $P = 0.949$).

Cause-specific mortality.—Mortality on the Monroe site was predominantly human caused (74%), with legal harvest accounting for 81% of human-caused ($n = 26$) and 60% of total mortality ($n = 35$) (Fig. 4). Causes of mortality on the Oquirrh site varied (Fig. 4). All human causes (including roadkill) comprised 53% of the total mortality ($n = 17$) and of this, legal harvest accounted for 44% of all human-caused mortality ($n = 9$) but only 24% of the total. Levels of human-caused mortality differed between sites ($\chi^2 = 7.5$; $P = 0.006$). Various forms of poaching (neck snares, illegal hunter-kill) occurred sporadically on both sites (Monroe, $n = 2$; Oquirrhs, $n = 1$), though alone, this did not represent a significant source of mortality for radio-collared animals.

The second leading cause of death on both sites was intraspecific predation, comprising 17% ($n = 6$) and 18% ($n = 3$) of total mortality on the Monroe and Oquirrh sites, respectively. During the years of high per-capita harvest pressure on Monroe, all victims of intraspecific aggression were resident adult females ($n = 4$), whereas during the period of light harvest all victims were subadult males ($n = 2$). On the Oquirrhs, 1 victim was a predispersal subadult male and 2 were adult females. Notably, one of these instances was an adult female cannibalizing another female with dependent young. Two years later, the survivor in this encounter was killed by an unidentified cougar. Cause of death could not be determined in three cases (2 F, 1 M), but did not appear to be human-related.

In addition to direct mortality, ≥11 kittens from 5 different litters on Monroe were orphaned when their mothers were killed during the winter hunt ($n = 10$) or during summer depredation control actions ($n = 1$). We confirmed the death of one orphaned litter (2 kittens, approx. 6 months old) due to dehydration and malnutrition. On the Oquirrhs, one male kitten was orphaned at the estimated age of 9 months when its mother was killed by an automobile. This animal survived 6 weeks before being taken in a depredation control action on a small ranch just outside of Salt Lake City. A litter of 3 4-month-old kittens died following the disease-related death of their mother. One other male kitten was marked at the age of 7 months following the poaching-related death of its mother in January 2002. It survived at least 2 months before radio contact was lost. Aside from this individual, no other orphans were detected following the deaths of their mothers or as adults on either study area in subsequent years.

Survival.—Adult survival varied between sites and among years (Fig. 5). On Monroe, survival tracked harvest

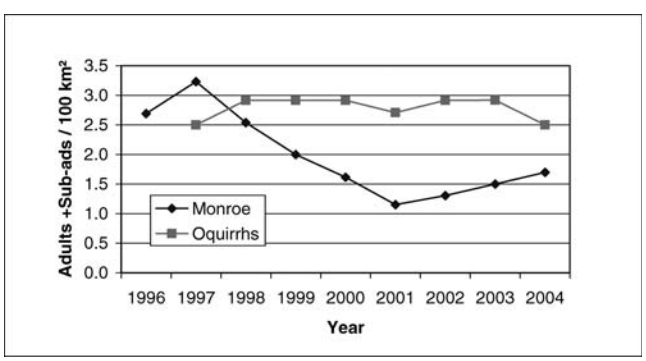

Figure 2. Annual nonjuvenile cougar density as determined from capture, tracking, and harvest, Monroe and Oquirrh Mountain study sites, Utah, USA, 1996–2004.

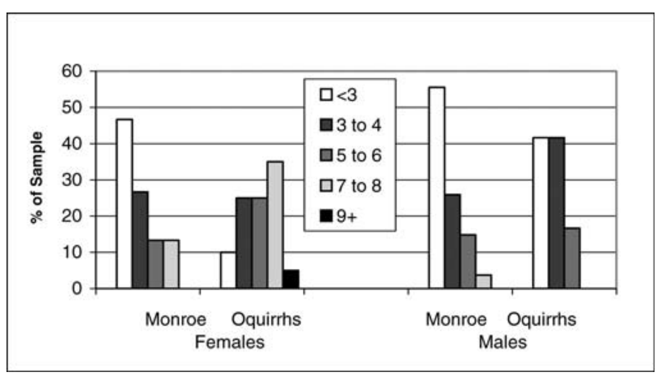

Figure 3. Age distribution of radiocollared cougars by sex, Monroe ($n = 57$) and Oquirrh ($n = 30$) Mountain study sites, Utah, USA, 1996–2004.

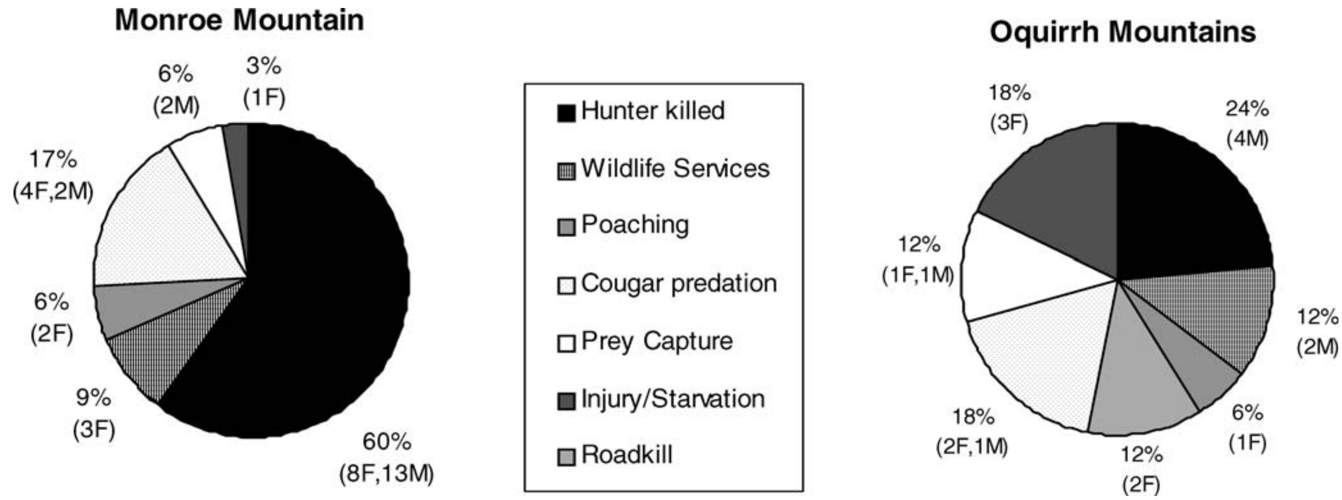

Figure 4. Cause-specific mortality among radiocollared cougars from the Monroe ($n = 35$) and Oquirrh Mountain ($n = 17$), study sites, Utah, USA, 1996–2004.

intensity, ranging from a high of 1.0 in 1996, just prior to the initiation of the treatment period, and declining to a low of 0.36 ± 0.33 (95% CI) in 2001, the end of high per-capita hunting pressure. Survival on the Oquirrhs showed moderate variation, ranging from 0.63 ± 0.28 to 0.91 ± 0.17. Trends in survival mirrored those of density on both sites, averaging 0.64 ± 0.07 (± SE) on Monroe and 0.76 ± 0.04 on the Oquirrhs. Analysis of trends over the entire interval suggested a difference in survival between sites ($\chi^2 = 3.41$; df = 1, $P = 0.068$).

Fecundity.—Reproduction varied between sites and years (Fig. 6). The number of litters detected annually ranged from 0–9 on Monroe and from 1–5 on the Oquirrhs, averaging 0.24 ± 0.04 (Monroe) and 0.34 ± 0.05 (Oquirrhs) litters per sexually mature female. Although rates did not differ statistically between sites ($t = -1.23$; df = 7; $P = 0.258$), fecundity on Monroe tracked the population decline and included a zero detection rate in 2002, the year following the lowest population estimate. At that time there were ≥ 5 sexually mature females present. The lowest fecundity estimate for the Oquirrh population was recorded the year after a 50% reduction in elk numbers. These animals were removed for reintroductions in other states. The removal was conducted over 2 years and was comprised primarily of cows and calves, the sex and age classes most vulnerable to cougar predation (Murphy 1998). The number of resident females on the Oquirrh site was smaller ($\bar{x} = 9.6$/yr) than on Monroe ($\bar{x} = 15.7$/yr), which may have influenced the variability in fecundity. Litter sizes averaged 1.7 and 1.9 kittens per litter on Monroe and the Oquirrhs, respectively. Based exclusively on the Oquirrh site using only kittens handled and marked (4–10 months post partum), the sex ratio was even (9 F, 9 M).

Dispersal.—Several animals were captured and marked either just prior to, or during dispersal. Four cougars (1 F, 3 M) moved from Monroe to neighboring mountain ranges 19–55 km distant. Two of these (1 F, 1 M) established residency in habitat adjacent to the study area; one was recaptured and his collar removed (fate unknown); and one was harvested 42 km northeast on the Fishlake Plateau (Fig. 7).

Seven dispersals were documented on the Oquirrh site (2 F, 5 M), ranging in distance from 13 to 85 km (Fig. 7). Of these, 3 (1 F, 2 M) settled elsewhere in the Oquirrh Mountains; 1 female moved to the Simpson-Sheeprock Mountains; 2 males moved to the Stansbury Mountains where they were hunter-killed as transients; and 1 male dispersed to the Mt. Timpanogos region of the southern

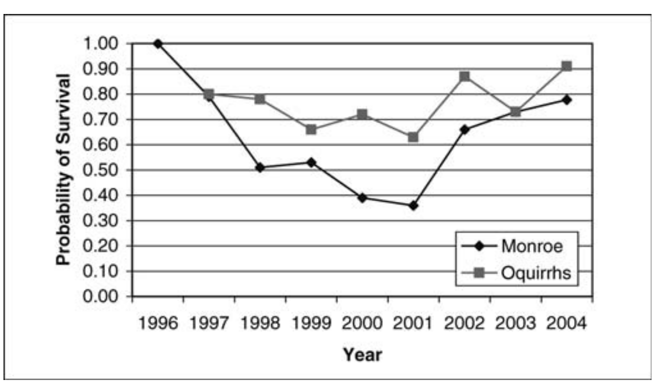

Figure 5. Estimated annual survival rates for radiocollared cougars, Monroe and Oquirrh Mountain study sites, Utah, USA, 1996–2004.

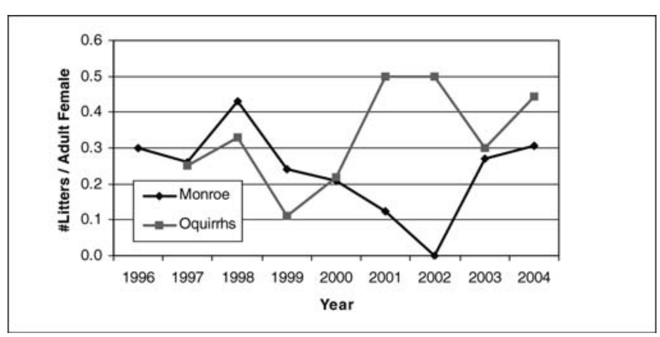

Figure 6. Annual fecundity rates for adult cougars on the Monroe and Oquirrh Mountain study sites, Utah, USA, 1996–2004.

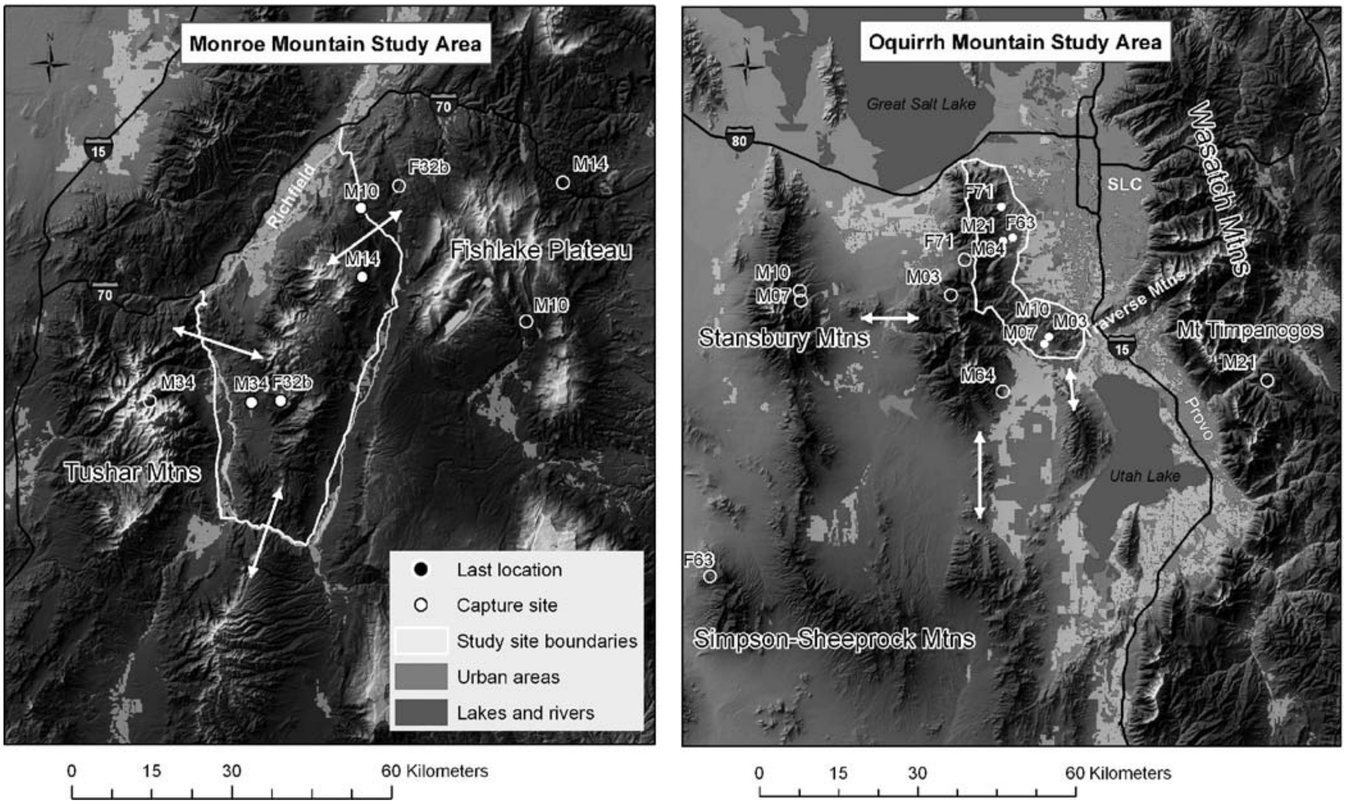

Figure 7. Dispersal patterns and landscape connectivity, Monroe and Oquirrh Mountain study sites, Utah, USA, 1996–2004. Arrows represent points of habitat connectivity.

Wasatch Mountains, crossing a 6-lane interstate and ≥5 km of city streets to get there.

Landscape Configuration

The study sites exhibited similar perimeter-area indices, but notable differences in connectivity and perimeter permeability (Table 3). During the study, no substantial movement barriers existed along the perimeter of Monroe Mountain, and in general, the unit was well connected to other habitats of similar quality within the Southern Mountains ecoregion (Fig. 7).

In contrast, only 5% of the Oquirrhs' perimeter was connected to neighboring habitat and approximately 40% was nearly impermeable to cougar movement. Movement barriers included the southern shore of the Great Salt Lake (7 km), the Salt Lake metro area (50 km), and a heavily traveled segment of Interstate 15 (2 km), which bisected the Traverse Mountains (Fig. 7). The remaining 55% graded into salt desert scrub communities offering little vegetative cover or surface water (West 1983). Additionally, residential development emanating from the Salt Lake–Provo metropolitan corridor was much greater around the Oquirrh site.

Overall, the Oquirrhs exhibited much thinner and more tenuous connectivity to neighboring patches of generally poorer quality (i.e., lower primary production), a pattern typical of basin and range topography (Fig. 1). This topographic fragmentation combined with anthropogenic fragmentation in the foothills and valleys around the site rendered this area susceptible to isolation (see Beier 1995).

Discussion

Influence of Harvest on Cougar Populations

Demographic differences between study populations reflected the prevailing management strategies. Cougar removal on Monroe Mountain ranged from 17.6–54.5% of the adult population exceeding 40% for 4 of the 5 years of high per-capita hunting pressure. Females comprised 32% of the harvest but 100% of depredation control and poaching mortality. Under this regime the population declined by >60%, whereas the Oquirrh Mountain population remained stationary. Moreover, the Oquirrh population had a significantly higher mean age among females and a smaller proportion of subadults. Age structure of males did not differ between sites, suggesting either: 1) males and females had a fundamentally different age distribution in the general population, or 2) the unhunted portion of the Oquirrhs was too small to adequately protect males. Density, survival, and fecundity were all negatively associated with sustained high per-capita hunting pressure on Monroe Mountain, whereas, with the exception of fecundity, these measures remained relatively constant over the same interval on the Oquirrh site. Though humans represented the single greatest source of mortality for animals traveling outside the Oquirrh study site, the absence of harvest within the study area suggests that the Camp Williams–Kennecott properties collectively acted as a functional refuge. Resident females were the primary beneficiaries of this protection. On the Monroe site, the prevalence

Table 3. Measures of landscape connectivity, Monroe and Oquirrh Mountain study sites, Utah, USA, 1996–2004.

Landscape metrics	Monroe	Oquirrhs
Perimeter (km)	178	150
Area (km^2)	1300	950
Perimeter:area	0.137	0.157
Greatest interpatch distance (km)	7	25
Perimeter impermeable (%)	0	40
Perimeter connected (%)	33	5
Width connective habitat (km)	7–21	2–4.5

of human-caused mortality, lack of starvation as a mortality cause, and moderately stable prey populations (UDWR, unpublished data) suggest that this level of mortality was largely additive. Annual harvests exceeding 30% of the adult population consisting of 42% females, carried out continuously for >3 years, can reduce density, fecundity, and skew age structure.

The consequences of sustained exploitation may not be limited to numeric population changes. Fecundity rates on Monroe tracked per-capita harvest pressure with a 1-year lag. We did not observe compensatory reproduction under increased harvest levels, as has been noted for some monogamous carnivores (Knowlton 1972, Frank and Woodroffe 2001). Smuts (1978), Knick (1990), and Wielgus and Bunnell (2000) reported analogous findings for hunted populations of African lions (*Panthera leo*), bobcats (*Lynx rufus*), and brown bears (*Ursus arctos*), respectively. One hypothesized function of male territoriality among polygynous carnivores is to increase offspring survival by excluding nonsire males from the natal range (Bertram 1975, Ross and Jalkotzy 1992), thereby reducing infanticide and optimizing fitness (Packer and Pusey 1984, Swenson 2003). Cougars are known to exhibit this behavior (Hornocker 1970, Hemker et al. 1986, Pierce et al. 1998) suggesting that hunted populations may experience increased levels of infanticide (Swenson 2003). On Monroe heavy harvest and subsequent social instability may have reduced the reproductive capacity of the population and therefore its ability to compensate losses.

Factors Influencing the Rate of Population Recovery

From 2002 to 2004 per capita hunting pressure on Monroe Mountain was reduced to <30%, during which survival and fecundity increased. Nevertheless, following 3 seasons of light harvest the population had only recovered to 52.4% of its 1997 levels, with nearly equal sex ratios and reproduction lagging behind resident replacement.

Lindzey et al. (1992) in Utah and Logan and Sweanor (2001) in New Mexico conducted controlled removals to examine the demographic mechanisms and time scales of population recovery. These authors noted that female recruitment was achieved via philopatric behavior or diffuse dispersal, whereas male recruitment was solely the product of immigration. Further, they suggested that recovery from 27–58% population reductions could be attained within 2–3 years under complete protection. However, those removals spanned only a single season and large sanctuaries (>1,000 km^2) buffered the treatment areas. In contrast, the Monroe population had only a 7-month annual reprieve from hunting pressure and was surrounded by units subjected to similar levels of exploitation.

The degree of landscape connectivity can mediate demographic connectivity, and is thus an important factor in population recovery or persistence (Beier 1993). Strong connectivity is the most likely reason we detected transients on Monroe each winter. These animals buffered population declines (Brown and Kodric-Brown 1977) but may have contributed to social instability. It has been hypothesized that the removal of resident males may induce a "vacuum effect" in which multiple transients vie for a vacant home range, potentially leading to an increase in population density (Shaw 1981, Logan et al. 1986). Our results lend only limited support to this argument. We observed an increase in the relative proportion of subadult males subsequent to removal of resident males, whereas the overall population declined. In general, males tend to disperse farther than females, remain transient longer, and are less tolerant of other males (Cunningham et al. 2001, Logan and Sweanor 2001, Maehr et al. 2002). Conversely, females often exhibit philopatric behavior, reproduce at an earlier age than males, and tolerate spatial overlap with other females (Murphy 1998, Pierce et al. 2000). Therefore, the transient segment of the cougar population is likely to be male biased (Hansson 1991). Removal of resident males provides territory vacancies that may be contested by multiple immigrants, thereby temporarily increasing the proportion of males in the population but not the overall density of males in the general population. Based on preliminary data from the post-treatment period, we hypothesize that following sustained disturbance, population recovery will proceed in 2 general phases: numerical and functional. Functional recovery implies not simply increases in absolute density but rather stabilization of social relationships and decreases in the variability of vital life-history rates. Female-biased sex ratios, low male turnover rates, and higher per-capita productivity may be used as relative indices of functional recovery.

Harvest Dynamics and the Regional Metapopulation

The metapopulation concept has been proposed as a framework for large-scale management of cougars (Beier 1996, Sweanor et al. 2000, Laundré and Clark 2003). In the strictest sense, a metapopulation is the composite of numerous spatially discrete subpopulations exhibiting independent behavior over time. The dynamics of the metapopulation are the net result of the shifting balance between local extinctions and recolonizations facilitated by intermittent dispersal events. The latter quality defines the classic metapopulation (Levins 1969, Hanski and Simberloff 1997).

The source–sink model provides a mechanism for metapopulation dynamics by emphasizing recruitment patterns within and among populations. The more general definition describes a sink as a net importer and a source as a net exporter of individuals over time (Pulliam 1988). Demographically, the Monroe and Oquirrh populations approximate the sink–source archetypes, respectively, albeit as a result of exploitation levels rather than habitat quality (e.g., Novaro et al. 2000). When harvest and its apparent impacts are considered, the Monroe population exhibited sink-like mortality. Notwithstanding low kitten production, each winter new animals, primarily subadult males, were captured on the site. Some of these individuals may have been resident progeny but mammalian dispersal patterns tend to be male-biased (Greenwood 1980). Low productivity and high immigration rates are the essence of a sink population.

In contrast, the Oquirrh population exhibited static density and emigration of resident progeny. No marked female kittens were detected as adults on the site. Indeed, 5 tattooed kittens (2 F, 3 M) were later killed elsewhere in the Oquirrhs or on neighboring mountain ranges up to 85 km distant. Solely based on age (4 yr) the female emigrants could have raised one litter to independence, whereas the males were killed immediately upon leaving their natal ranges, thereby subsidizing the harvest in adjacent units. On the Oquirrh site female dispersal appeared to be related to the saturation of available habitat, suggesting a source-like population structure.

When the prevailing harvest rate is considered a component of habitat quality, then a spatially clumped harvest distribution can promote source–sink dynamics. This may result in an immigration gradient directed toward patches such as Monroe Mountain, where strong connectivity coupled with low population density create an ecological trap (i.e., a productive habitat that displays sink-like mortality patterns, e.g., Bailey et al. 1986, Kokko and Sutherland 2001). These sites represent examples of populations exhibiting different dynamics simultaneously within a metapopulation. Importantly, source–sink characteristics may be dynamic and interchangeable depending on how prevailing management interacts with habitat productivity and connectivity. For example, the Monroe population illustrates the potential consequences of overharvest, yet is situated within a large semicontiguous tract of habitat spanning the state with extensions into Colorado, Idaho, and Arizona. Conversely, the Oquirrh population appears demographically stable, but lies within an ecoregion defined by weak connectivity among sparsely distributed desert ranges. Under different objectives, conservative management could render the Monroe population a source, whereas the Oquirrh population should be managed under the small population paradigm (Caughley 1994).

Management Implications

At the scale of the local population or management unit, annual harvests exceeding 40% of the nonjuvenile population for $\geq$4 years can not only reduce density but may also promote or maintain a demographic structure that is younger, less productive, and socially unstable. At an ecoregional scale the difficulties of reliably delineating discrete populations (Pierce and Bleich 2003) and their respective sizes (Choate et al. 2006) emphasize the importance of managing cougars in a metapopulation context. That said, source–sink characteristics may be more amenable to field evaluation than the extinction and recolonization events that define classic metapopulations. Numeric recovery of overexploited populations may initially depend more on immigration than in situ reproduction. Under moderate to heavy exploitation this tack may require: 1) an assessment of habitat connectivity between identified sources and sinks, and 2) the presence of truly functional source populations, most readily managed through the establishment of refugia.

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Literature Cited

Anderson, A. E. 1983. A critical review of literature on puma (*Felis concolor*). Colorado Division of Wildlife, Special Report No. 54, Denver, USA.

Anderson, A. E., D. C. Bowden, and D. M. Kattner. 1992. The puma on the Uncompahgre Plateau, Colorado. Colorado Division of Wildlife, Technical Publication No. 40, Denver, USA.

Ashcroft, G. L., D. T. Jensen, and J. L. Brown. 1992. Utah climate. Utah Climate Center, Utah State University, Logan, USA.

Ashman, D. L., G. C. Christensen, M. L. Hess, G. K. Tsukamoto, and M. S. Wickersham. 1983. The mountain lion in Nevada. Nevada Department of Wildlife, Carson City, USA.

Bailey, T. N., E. E. Bangs, M. F. Portner, J. C. Malloy, and R. J. McAvinchey. 1986. An apparent overexploited lynx population on the Kenai Peninsula, Alaska. Journal of Wildlife Management 50:279–290.

Barnhurst, D. 1986. Vulnerability of cougars to hunting. Thesis, Utah State University, Logan, USA.
Beier, P. 1993. Determining minimum habitat areas and habitat corridors for cougars. Conservation Biology 7:94–108.
Beier, P. 1995. Dispersal of juvenile cougars in fragmented habitat. Journal of Wildlife Management 59:228–237.
Beier, P. 1996. Metapopulation models, tenacious tracking, and cougar conservation. Pages 293–323 *in* D. R. McCullough, editor. Metapopulations and wildlife conservation. Island, Covelo, California, USA.
Beier, P., and S. C. Cunningham. 1996. Power of track surveys to detect changes in cougar populations. Wildlife Society Bulletin 24: 540–546.
Bertram, B. C. R. 1975. Social factors influencing reproduction in wild lions. Journal of Zoology, London 177:463–482.
Bowyer, R. T., D. K. Person, and B. M. Pierce. 2005. Detecting top-down versus bottom up regulation of ungulates by large carnivores: implications for conservation of biodiversity. Pages 342–361 *in* J. C. Ray, K. H. Redford, R. S. Steneck, and J. Berger, editors. Large carnivores and the conservation of biodiversity. Island, Covelo, California, USA.
Brown, J. H. 1971. Mammals on mountaintops: nonequilibrium insular biogeography. American Naturalist 105:467–478.
Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58:445–449.
Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology 63:215–244.
Choate, D. M., M. L. Wolfe, and D. C. Stoner. 2006. Evaluation of cougar population estimators in Utah. Wildlife Society Bulletin 34: 782–799.
Cox, D. R., and D. Oakes. 1984. Analysis of survival data. Chapman & Hall, New York, USA.
Cunningham, S. C., W. B. Ballard, and H. A. Whitlaw. 2001. Age structure, survival, and mortality of mountain lions in southeastern Arizona. Southwestern Naturalist 46:76–80.
Edwards, T. C., C. G. Homer, S. D. Bassett, A. Falconer, R. D. Ramsey, and D. W. Wight. 1995. Utah gap analysis: an environmental information system. Utah Cooperative Fish and Wildlife Research Unit, Technical Report 95–1. Utah State University, Logan, USA.
Ernest, H. B., W. M. Boyce, V. C. Bleich, B. May, S. J. Stiver, and S. G. Torres. 2003. Genetic structure of mountain lion (*Puma concolor*) populations in California. Conservation Genetics 4:353–366.
Fjelline, D. P., and T. M. Mansfield. 1989. Method to standardize the procedure for measuring mountain lion tracks. Pages 49–51 *in* R. H. Smith, editor. Proceedings of the Third Mountain Lion Workshop. Arizona Game and Fish Department, Phoenix, USA.
Forman, R. T. T., D. Sperling, J. A. Bissonette, A. P. Clevenger, C. D. Cutshall, V. H. Dale, L. Fahrig, R. France, C. R. Goldman, K. Heanue, J. A. Jones, F. J. Swanson, T. Turrentine, and T. C. Winter. 2003. Road ecology—science and solutions. Island, Covelo, California, USA.
Frank, L. G., and R. Woodroffe. 2001. Behavior of carnivores in exploited and controlled populations. Pages 419–442 *in* J. L. Gittleman, S. M. Funk, D. MacDonald, and R. K. Wayne, editors. Carnivore conservation. University of Cambridge, United Kingdom.
Greenwood, P. J. 1980. Mating systems, philopatry, and dispersal in birds and mammals. Animal Behavior 28:1140–1162.
Hanski, I., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. Pages 5–26 *in* I. Hanski and M. E. Gilpin, editors. Metapopulation biology: ecology, genetics, and evolution. Academic, San Diego, California, USA.
Hansson, L. 1991. Dispersal and connectivity in metapopulations. Biological Journal of the Linnean Society 42:89–103.
Hemker, T. P., F. G. Lindzey, and B. B. Ackerman. 1984. Population characteristics and movement patterns of cougars in southern Utah. Journal of Wildlife Management 48:1275–1284.
Hemker, T. P., F. G. Lindzey, B. B. Ackerman, and A. J. Button. 1986. Survival of cougar cubs in a non-hunted population. Pages 327–332 *in* S. D. Miller and D. D. Everett, editors. Cats of the world: biology, conservation, and management. National Wildlife Federation, Washington, D.C., USA.
Hill, H., and K. Bunnell. 2005. Utah Cougar harvest report, 2001–2002 to 2004–2005. Utah Department of Natural Resources, Publication No. 05-39. Salt Lake City, USA.
Hornocker, M. G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. Wildlife Monographs 21:1–39.
Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. Journal of the American Statistical Association 53:457–481.
Knick, S. T. 1990. Ecology of bobcats relative to exploitation and a prey decline in southeastern Idaho. Wildlife Monographs 108:1–42.
Knowlton, F. F. 1972. Preliminary interpretations of coyote population mechanics with some management implications. Journal of Wildlife Management 36:369–382.
Kokko, H., and W. J. Sutherland. 2001. Ecological traps in changing environments: ecological and evolutionary consequences of a behaviourally mediated Allee effect. Evolutionary Ecology Research 3:537–551.
Kreeger, T. J. 1996. Handbook of wildlife chemical immobilization. Wildlife Pharmaceuticals, Inc., Fort Collins, Colorado, USA.
Laing, S. P., and F. G. Lindzey. 1991. Cougar habitat selection in south-central Utah. Pages 27–37 *in* C. S. Braun, editor. Proceedings of the mountain lion–human interaction workshop. Colorado Division of Wildlife, Denver, USA.
Laundré, J., and T. W. Clark. 2003. Managing puma hunting in the western United States: through a metapopulation approach. Animal Conservation 6:159–170.
Laundré, J., L. Hernández, D. Streubel, K. Altendorf, and C. A. López-González. 2000. Aging mountain lions using gum-line recession. Wildlife Society Bulletin 28:963–966.
Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15:237–240.
Lindzey, F. G., W. D. Van Sickle, S. P. Laing, and C. S. Mecham. 1992. Cougar population response to manipulation in southern Utah. Wildlife Society Bulletin 20:224–227.
Logan, K. A., L. L. Irwin, and R. Skinner. 1986. Characteristics of a hunted mountain lion population in Wyoming. Journal of Wildlife Management 50:648–654.
Logan, K. A., and L. L. Sweanor. 2001. Desert puma—evolutionary ecology and conservation of an enduring carnivore. Island, Washington, D.C., USA.
Maehr, D. S., E. D. Land, D. B. Shindle, O. L. Bass, and T. S. Hoctor. 2002. Florida panther dispersal and conservation. Biological Conservation 106:187–197.
Mason, J., D. Peay, K. Robinson, R. Danvir, B. Bateman, M. Bodenchuk, M. Wolfe, L. Shirley, B. Bates, L. Cornicelli, B. Giunta, S. Cranney, J. Karpowitz, and J. Grandison. 1999. Utah cougar management plan. Utah Department of Natural Resources, Salt Lake City, USA.
Mech, L. D. 1983. Handbook of animal radio-tracking. University of Minnesota, Minneapolis, USA.
Murphy, K. M. 1983. Relationships between a mountain lion population and hunting pressure in western Montana. Thesis, University of Montana, Missoula, USA.
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.
Novaro, A. J., K. H. Redford, and R. Bodmer. 2000. Effect of hunting in source–sink systems in the neotropics. Conservation Biology 14:713–721.
Nowell, K., and P. Jackson, editors. 1996. Puma, *Puma concolor* (Linnaeus 1771). Pages 131–137 *in* Wild cats: status survey and conservation action plan. International Union for the Conservation of Nature. Burlington, Cambridge, United Kingdom.
Packer, C., and A. E. Pusey. 1984. Infanticide in carnivores. Pages 31–42 *in* G. Hausfater and S. B. Hrdy, editors. Infanticide—comparative and evolutionary perspectives. Aldine, New York, New York, USA.
Pierce, B. M., and V. C. Bleich. 2003. Mountain lion. Pages 744–757 *in* G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Wild mammals of North America: biology, management, and conservation.

Second edition. The Johns Hopkins University, Baltimore, Maryland, USA.
Pierce, B. M., V. C. Bleich, and R. T. Bowyer. 2000. Social organization of mountain lions: does a land tenure system regulate population size? Ecology 81:1533–1543.
Pierce, B. M., V. C. Bleich, C. B. Chetkiewicz, and J. D. Wehausen. 1998. Timing of feeding bouts of mountain lions. Journal of Mammalogy 79:222–226.
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.
Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652–661.
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., M. G. Jalkotzy, and J. R. Gunson. 1996. The quota system of cougar harvest management in Alberta. Wildlife Society Bulletin 24: 490–494.
Roylance, W. J. 1982. Utah: a guide to the state. Utah Arts Council, Salt Lake City, USA.
Shaw, H. G. 1981. Comparison of mountain lion predation on cattle on two study areas in Arizona. Pages 306–318 *in* L. Nelson Jr. and J. M. Peek, editors. Proceedings of the wildlife–livestock relationships symposium. Forest, Wildlife, & Range Experiment Station, University of Idaho, Moscow, USA.
Smuts, G. L. 1978. Effects of population reduction on the travels and reproduction of lions in Kruger National Park. Carnivore 2:61–72.
Sweanor, L. L., K. A. Logan, and M. G. Hornocker. 2000. Cougar dispersal patterns, metapopulation dynamics, and conservation. Conservation Biology 14:798–808.
Swenson, J. E. 2003. Implications of sexually selected infanticide for the hunting of large carnivores. Pages 171–189 *in* M. Festa-Bianchet and M. Apollonio, editors. Animal behavior and wildlife management. Island, Washington, D.C., USA.
Taylor, P. D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. Oikos 68:571–573.
Van Sickle, W. D., and F. G. Lindzey. 1992. Evaluation of road track surveys for cougars (*Felis concolor*). Great Basin Naturalist 52:232–236.
West, N. E., editor. 1983. Intermountain salt-desert shrubland. Pages 375–397 *in* Temperate deserts and semi-deserts. Vol. 5: Ecosystems of the world. Elsevier, Amsterdam, Netherlands.
Wielgus, R. B., and F. L. Bunnell. 2000. Possible negative effects of adult male mortality on female grizzly bear reproduction. Biological Conservation 93:145–154.
Wolfe, M. L., D. M. Choate, and D. C. Stoner. 2004. USU/UDWR statewide cougar study—final report. Utah Division of Wildlife Resources, Salt Lake City.

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