Evaluation of Cougar Population Estimators in Utah

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Abstract

*Numerous techniques have been proposed to estimate or index cougar (*Puma concolor*) populations, but few have been applied simultaneously to populations with reliable estimates of population size. Between 1996 and 2003, we evaluated the relative efficacy and accuracy of multiple estimation and index techniques for populations at 2 locations in Utah, USA: Monroe Mountain and the Oquirrh Mountains. We used radiotagging followed by intensive monitoring and repeated capture efforts to approach a complete enumeration of the populations. We used these benchmarks to evaluate other population estimates (Lincoln–Petersen mark–recapture, helicopter-survey probability sampling, catch-per-unit-effort) and indices (scent-station visits, track counts, hunter harvest). Monitoring over 600 scent-station-nights using different attractants June–September in 1996 and 1997 yielded a single cougar visit. Summer track-based indices reflected a 54–69% reduction in population size on the Monroe site and a numerically stable population on the Oquirrhs, but relationships between indices and the benchmark population estimates varied among techniques. Aerial track surveys required sufficient fresh snowfall accumulations for adequate tracking coverage of a given unit, conditions that were met only once on one study site in each of 3 years. Population estimates derived from helicopter-survey probability sampling exceeded reference population estimates by 120–284%, and bootstrapped estimates of standard error encompassed 25–55% of the population estimates (e.g., 5.6 ± 1.4 cougars/100 km^2). Despite poor performance in predicting cougar population sizes, track-based estimates may provide better indices for monitoring large changes in population trends (i.e., with low precision). However, we recommend using multiple indices after determination of a more rigorous initial population estimate for managing populations of conservation concern and when considering connectivity to determine potential refuge sites for regional management (e.g., management by zones).*
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Key words

catch-per-unit-effort, cougar, indices, mountain lion, population estimation, population monitoring, probability sampling, Puma concolor*, scent station, track survey, Utah.*

Reliable estimation of abundance poses a perennial problem in managing large carnivores (Linnell et al. 1998, Gese 2001). The cougar (*Puma concolor*) exemplifies the difficulties of enumeration of a long-lived, wide-ranging, and secretive mammal. Although numerous techniques have been proposed for the estimation of cougar populations (Johnson and Couch 1954, Currier et al. 1977, Van Dyke et al. 1986, Smallwood and Fitzhugh 1995), few have been applied simultaneously and tested against populations of known density to evaluate their accuracy or precision (Van Sickle and Lindzey 1991, 1992). Aside from costly capture and radiotelemetry studies that may approximate a census, population metrics for cougars include estimates of absolute and indices of relative abundance. Several authors (Caughley 1977, Seber 1982, Lancia et al. 1996*b*, Williams et al. 2001) have noted the distinction between the 2 metrics, both of which may be used to assess numerical trends for monitoring and management. Generally, population estimators are derived from sampling methods and based on well-established theory (e.g., Seber 1982, Pollock et al. 1990). By contrast, indices frequently involve techniques based on indirect evidence of the animals' presence such as track counts or kill statistics and are used to compare different populations or a specific population over time. However, the relationship between an index and actual population size is not always known. The objectives of this study included 1) evaluating the efficacy and accuracy of cougar population estimators, and 2) investigating the potential for indirect enumeration methodology for long-term monitoring and management purposes. The techniques we employed included 1) scent-station surveys, 2) track-count surveys, 3) hunter kill, 4) hunter catch-per-unit-effort, and 5) capture–mark–release population estimators involving both invasive (i.e., radiocollaring cougars) and noninvasive (i.e., encounter rates with tracks) sampling.

Study Areas

Monroe Mountain

Occupying approximately 1,300 km^2, the Monroe Mountain study site was located near Richfield in south-central Utah (Fig. 1) and comprised the central unit of the Fishlake National Forest. Terrain is mountainous with elevations spanning 1,600–3,300 m. Annual precipitation ranged from 15–20 cm at lower elevations to 60–120 cm on the plateaus above 2,800 m (Ashcroft et al. 1992). The area supported 19 vegetative types (Edwards et al. 1995), with the largest (44%) area dominated by piñon (*Pinus edulis*)–juniper (*Juniperus* spp.) woodlands. Mixed conifer and aspen (*Populus tremuloides*) stands occurred at higher elevations, interspersed throughout with Gambel oak (*Quercus gambelii*), mountain brush, and sagebrush (*Artemisia* spp.)–grassland communities. The Utah Division of Wildlife Resources (UDWR) managed Monroe Mountain as a limited-entry cougar hunt unit (No. 24). During the study, Monroe was open to cougar hunting, and radiocollared individuals were not protected from harvest beyond the normal legal stipulations outlined by the UDWR.

Oquirrh Mountains

The Oquirrh–Traverse mountain complex comprises approximately 950 km^2 located in north-central Utah. Fieldwork was

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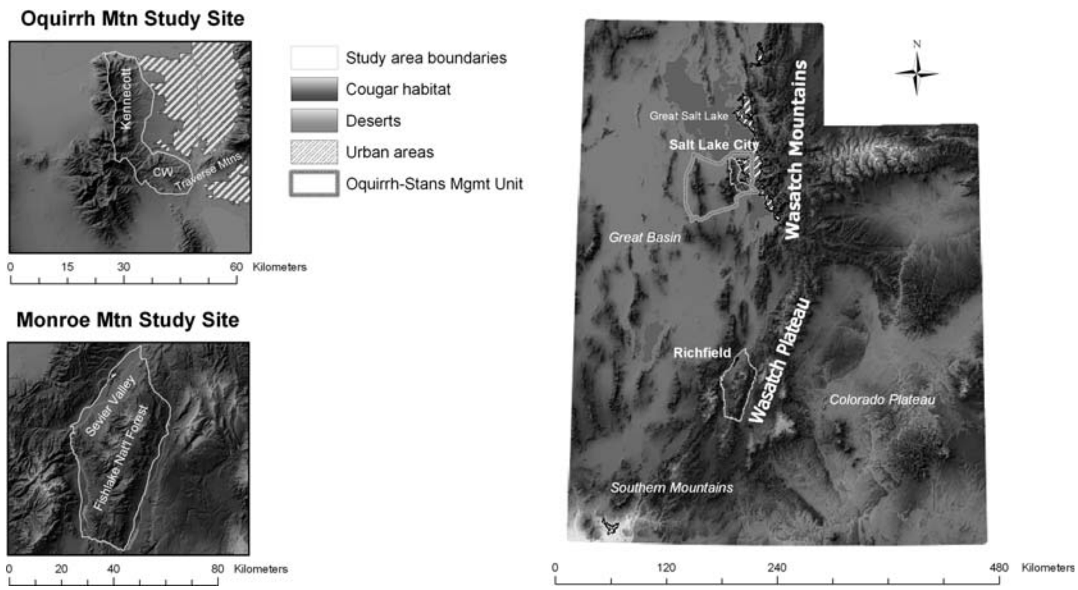

Figure 1. Locations in Utah, USA, of primary study sites (Monroe Mountain, Oquirrh Mountains) investigated during evaluation of cougar population estimators. Both study sites lie on the eastern edge of the Great Basin. Note that the Oquirrhs study site was restricted to Camp Williams and Kennecott Copper properties in the northeastern portion of the Oquirrh–Stansbury Cougar Management Unit No. 18.

restricted to the northeastern slope, on lands owned and managed by the Utah National Guard (Camp Williams [CW]; Traverse Mountains ca. 100 km^2) and Kennecott Utah Copper (KUC; ca. 380 km^2), which bordered the southwestern side of the greater Salt Lake metropolitan area. Elevations on the Oquirrh site vary from lake level (1,280 m) to peaks on the south end of the range at 3,200 m. In contrast to the steep canyons on the west side, the east side of the mountain descends as gently rolling foothills interspersed with shallow drainages. Annual precipitation ranged from 30–40 cm in the Salt Lake and Tooele valleys to 100–130 cm on the ridges and peaks (Ashcroft et al. 1992). Major vegetation types were composed of Gambel oak (23%, Edwards et al. 1995), juniper woodlands (3%), and canyon maple (*Acer grandidentatum*; 2.6%). Communities of aspen and mixed conifer appeared on the north-facing slopes above 2,200 m, and sagebrush was interspersed throughout. Mining activities have dominated the KUC property for over 100 years (Roylance 1982), and the site included 2 large open pit mines with attendant infrastructure Camp Williams was used primarily for military training. The study site was included in the Oquirrh–Stansbury Cougar Management Unit (No. 18), but CW and KUC properties were closed to hunting throughout the study. However, cougars leaving those properties were subject to harvest during the hunting season on adjacent private and public lands.

Methods

Estimation of Reference Population Size

We monitored cougar populations on both sites simultaneously from early 1997 to 2003. We conducted intensive capture efforts from November to April during 1995– 2003. We captured cougars by pursuing them into trees, culverts, or mineshafts with trained hounds (Hemker et al. 1984) and then immobilized them with a combination of 10 mg ketamine HCl and 2 mg xylazine HCl per kilogram body weight (Logan et al. 1986). We administered immobilizing drugs with a Palmer CO_2 pistol (Powder Springs, Georgia), jab-stick, or handheld syringe. When possible we removed a vestigial premolar (P2) for age-determination cementum annulation counts (Trainer and Matson 1988) and drew a blood sample for genetic analyses. We sexed, weighed, and measured cougars, tattooed them with a unique identifier, and equipped them with a radiocollar (Lotek, New Market, Ontario, Canada) and a microchip (AVID Co., Norco, California). Because accuracy of age estimation from cementum annuli counts is low for cougars (70–75%; Matson' s Laboratory, Milltown, Montana, unpublished data), although agreement with other methods varies from 78% to 93% (Anderson and Lindzey 2005), we estimated age using visual inspection of tooth wear and gum-line recession (Shaw 1979, Ashman et al. 1983, Laundré et al. 2000), pelage spotting, or known kitten births from radiocollared females. We classified each animal as an adult (>2.5 yr), subadult (1.5– 2.5 yr), or kitten (<1.5 yr). On the Oquirrh site we microchipped, tattooed, and released kittens too small to wear a radiocollar. We relocated radiocollared cougars using ground-based and aerial telemetry flights (Mech 1983). Telemetry flights were conducted bimonthly as weather conditions permitted. We relocated cougars with ground-based telemetry concurrent with other activities, by plotting radiotriangulated locations on United States Geological Survey (USGS) 7.5-minute topographic quadrangles using Universal Transverse Mercator coordinates (zone 12, NAD 27). We entered all locations into a geographic information system (GIS) database (ArcView; ESRI Products, Redlands, California). All procedures were conducted in accordance with Utah State University Institutional Animal Care and Use Committee, approval number 937-R.

Our reference estimates are analogous to the "complete enumeration" scenario described by the Cougar Management

Guidelines Working Group ([CMGWG] 2005) and consist of the number of adults and subadults present on a given site during winter. We included subadults in the population estimate because hunters are not likely to discriminate between these age classes. We derived reference population estimates from the combination of captured animals marked or equipped with radiocollars, unmarked hunter- or depredation-killed animals, and evidence based on intensive tracking efforts of unmarked individuals. Roads provided sufficient access to both study sites, but we also conducted winter tracking efforts by horseback and snowmobile to reduce detection bias associated with degree of access. This also reduced bias associated with the differential detection of resident females due to frequent road crossings or small home ranges (Barnhurst 1986). To derive a conservative estimate of the number of unmarked animals on the site and because males and females can often be differentiated by track size (Fjelline and Mansfield 1989), we counted multiple track sets of same-sexed animals encountered in the same watershed between November and April as one individual. We used the primary watersheds on the site ($n = 4$, mean $\pm$ SD $= 361 \pm 95$ km^2, range $= 237$–462 km^2) as a practical threshold for differentiating individuals, as these basins approximated the larger size of a male home range. We used this approach only if we could not assign a unique identity to a set of tracks during our cumulative capture and radiotelemetry effort.

We refined our population estimates by back-calculating birth dates of radiocollared cougars from the age at capture and used this information to adjust our estimates of uncollared individuals from track evidence and hunter harvest. We did not include males back-dated in this manner in the population when <3 years old because they might have immigrated to the site at that age. We considered females resident subadults at the back-calculated age 1.5–2.5 years and included them in the population estimate because females tend to be philopatric (Beier 1995, Ruth et al. 1998, Sweanor et al. 2000). Back-calculated birth dates also helped to correct for track-detection bias between years that might be associated with differences in snow conditions. Because population losses were greatest during the hunting season (Stoner et al. 2006), the population reference estimate represents the population resident on a site immediately prior to the hunting season—estimates are derived from the interval November–April. Funding and the logistics of applying multiple surveys to each site limited our capture efforts to winter periods; therefore, we used data from radiocollared cougars and all tracking efforts to evaluate the assumption that a winter population estimate was valid for comparison with summer surveys. We used radiotelemetry data to determine movements of cougars on or off of the study site; however, we could not directly evaluate summer immigration of new individuals. To account for immigration into the subadult or adult classes, we determined first if new individuals during the winter were resident offspring from the previous year or could be attributed to tracks of an individual not captured in the previous year. We considered new individuals that could not be accounted for as offspring or through track evidence as immigrants to the population. If these new individuals were present at the start of a capture season, we assumed that they entered and were present in the population during the previous summer.

We calculated cougar density from the reference population estimates and study site area. This convention is used for consistency in comparing reference population estimates with population estimators that might vary in area surveyed (e.g., helicopter surveys) and because managers typically consider density on a management unit basis (e.g., unit-specific harvest objectives; UDWR 1999). Because this conversion divides reference $\hat{N}$ by a constant, any error in calculating area will not affect subsequent evaluations. We based study area boundaries on major roads; therefore, we used ecologically relevant vegetative and topographic features to delineate and quantify habitat within the study site perimeter. We followed the criteria of Laing and Lindzey (1991), which excluded unforested valley bottoms and land-cover types dominated by urban and agricultural uses.

Other Population Estimators

Aerial snow track surveys.—We conducted censuses of cougar tracks left after fresh snowfall on Monroe Mountain using procedures described by Becker (1991) and Van Sickle and Lindzey (1991). Even though we planned to conduct multiple surveys on both Monroe and the Oquirrhs during each winter of the study, suitable weather conditions and helicopter availability were met on only 3 occasions for the Monroe site. We established a baseline at the southernmost edge of the Monroe site that extended to the east and westernmost edges of the site boundaries. A series of parallel north–south transects extended from this baseline to the northernmost edge of the site (mean length $= 41.4 \pm 2.0$ km). We randomly determined the initial location of the first transect, with each subsequent transect spaced at 2-km intervals. Within 72 hours of a $\geq$10–12-cm snowfall, a 3-person team assembled to conduct each survey: pilot, tracker, and navigator–second tracker. We conducted the first survey in a UH1 (Huey) military helicopter (Bell Helicopter Textron, Hurst, Texas) to facilitate training with additional researchers. We conducted subsequent flights using a Bell JetRanger III. We surveyed transects until we encountered a track set, then followed the track set to its origin and completion. We recorded the detailed route of each track set using Global Positioning System (GPS) navigation systems visually confirmed with known landmarks and plotted on USGS 7.5-minute topographic maps.

We estimated population size T_j using probability sampling (Becker 1991) under similar conditions as described by Van Sickle and Lindzey (1991). We determined the baseline length D for each survey as the number of transects flown multiplied by the distance between adjacent transects. Using the distance, x_i, parallel to the baseline, traveled by each (ith) cougar, the probability (p_i) that the ith cougar is contained in the jth sample was calculated as $p_i = x_i/(D/q)$, where q is the number of transects surveyed during a sample. The population estimate for the jth systematic sample is $T_j = (1/p_i)$. For greatest precision and accuracy, we counted cougars traveling together as a single individual (Van Sickle and Lindzey 1991). Although we anticipated multiple surveys within a season for each unit, we met appropriate weather tracking conditions only once in each of 3 winters, thereby precluding direct estimation of variance for the population size. Consequently, we derived standard errors for the population estimates using bootstrapping methods ($\beta = 1{,}000$; Efron and Tibshirani 1986), by sampling with replacement of the $1/p_i$ estimates from each cougar detected to derive a sample of T_j.

Anderson (2003) simulated the relative accuracy and precision of aerial probability sampling using this track-intercept method (line-intercept estimator; Becker 1991, Van Sickle and Lindzey 1991) and a variation using block sampling (Becker et al. 1998). Of these techniques, track-intercept performed better, particularly when he used a correction factor to adjust the x_i values, accounting for short movements (low x_i). Based on empirical evidence that short track sets may result from a cougar's remaining near a kill site, Anderson (2003) calculated an adjusted T_a as

$$T_a = \frac{\sum[(1/p_i)(1 - \pi_i)]}{1 - \hat{P}},$$

where p_i is the probability that the ith cougar is contained in the jth sample (defined earlier), and $\hat{P}$ is the proportion of tracks expected to be at kill sites, with values of 0.204 based on sampling 1 night after a snowfall event and 0.113 after 2 nights. The probability that a track set will be at a kill site, $\pi_i = e^u/(1 + e^u)$, where u is derived from Anderson's (2003) tracking data as either $u = 5.0176 - 0.0053 \times$ (total track length) for surveys conducted 1 night after snowfall or $u = 6.3315 - 0.0039 \times$ (total track length) for surveys conducted after 2 nights. To assess the efficacy of this approach, we calculated the adjusted population T_a for each survey using Anderson's method. In addition, Anderson (2003) suggested that management agencies can derive more time- and cost-efficient population estimates (T_e) by omitting the tracking of individuals during the aerial surveys and simply inserting perpendicular movement distances (x_i) chosen randomly from the track distances presented in his study for each encountered track set, as a reasonable approximation of x_i. We tested this approach by randomly sampling x_i from Anderson's (2003) data and using these values for each track set encountered during our surveys to calculate T_e for each survey. We derived standard errors of the T_a and T_e estimates using bootstrap methods as described for T_j and compared these estimates with the reference population size.

Catch-per-unit-effort as an estimator.—Since 1978 the UDWR has issued questionnaires following each hunting season to each permit holder (either hunting or pursuit), requesting information concerning the number of days spent hunting, animals captured, and related details. Due to a limited response rate (25-yr [1979–2003] statewide mean $\pm$ SD = 54 $\pm$ 16%), the UDWR uses the statewide proportion responding to adjust hunting-unit-specific catch-per-unit-effort (CPUE). Because this assumes that nonrespondents equal respondents, in 1997 we attempted to test this assumption; however, a low response rate during our trial survey required using UDWR survey data. Catch-per-unit-effort is estimated as the number of cougars brought to bay per day of hunting effort, presented in annual harvest reports for management purposes (e.g., Maxfield 2001). We only used data from pursuit permit holders for this analysis because effort was less likely to change across the season than effort expended by hunters. As an additional comparison, we kept detailed capture logs of research efforts on each study site in an attempt to evaluate recapture rates of radiocollared animals. Because the sample was biased by efforts directed at capturing new animals, we calculated CPUE based on both all animals captured (more similar to hunter-effort) and only efforts directed at capturing new individuals. Because cougar density on Monroe varied during the study, we tested whether changes in hunter harvest rate or CPUE by researchers or hunters directly tracked population changes by using regression analyses. We determined annual research CPUE for each study site for the intervals during which capture work was conducted, November–April. For the Oquirrh site, we did not compare harvest-related CPUE with research CPUE because the research capture effort was directed only at a protected portion of that population.

A simple relationship between CPUE and population size can be estimated from the equation $C = k \times N$, where C = number of cougars killed per day, N is the population size, and the parameter k is a constant (e.g., Williams et al. 2001). True population size is the unknown, and either least squares or maximum likelihood methods are used incorporating CPUE information to estimate N_o, the initial population size during a catch–removal sampling period. The parameter k can be estimated by regressing CPUE on population size when population size is known or against known removals, in this case the number of cougars killed during the sampling interval. This provides a population estimator model based on the index, CPUE. Subsequent population estimates using this model can be compared with the capture–telemetry-based reference population estimates. Catch-effort models assume that a population is closed and that the probability of capture is equal among individuals. As a partial test for constant k, we regressed CPUE against the hunter harvest for a given season. Because daily capture-effort logs were unavailable, we collapsed the sampling effort into a yearly average. Consequently, data consist of a yearly CPUE and removal (i.e., annual harvest) estimate. This approach is inferior to a within-season series of samples (eg., Lancia et al. 1996*a*), but hunting effort for cougars spans months rather than the days or weeks used for other taxa. Consequently, sample size is prohibitively limited if shorter intervals are used to estimate CPUE.

Mark–recapture.—We investigated the use of mark–recapture methods using encounter rates with tracks during all winter search and capture efforts. We determined the identity of an animal through pursuit until the individual was observed or radio-telemetry could be used for positive identification. We estimated population size and 95% confidence intervals by Chapman's (1951) modification of the basic Lincoln–Petersen (L-P) relationship derived from encounter rates with tracks of radiocollared (m_i) individuals and uncollared (n_i) individuals in year i, and collared (n_1) individuals present on the study site prior to the hunting or winter-tracking season. This estimator for $\hat{N}_i$ is essentially the same as the radiotelemetry-based estimator proposed by Hallett et al. (1991); however, we used track encounters rather than actual trap-based recaptures of marked and unmarked individuals. Even though this estimate requires population closure, an assumption violated for this study by the large dispersal distances of radiocollared cougars, we present L-P estimates for comparative purposes.

Indices

Hunter harvest.—Because cougar density on Monroe varied during the study, we evaluated whether changes in typical hunter harvest statistics (hunter harvest rate, percent females in the harvest, age of animals in the harvest) reported by the UDWR (e.g., Maxfield 2001) directly tracked population changes. The UDWR reports ages of hunter-killed cougar based on counts of cementum annulations. To evaluate the accuracy and precision of this method, we compared our age estimates of radiocollared cougars with ages determined from cementum counts and compared results of counts from premolar pairs from harvested cougars. As suggested by Anderson and Lindzey (2005), we predicted that the proportion of individuals in the harvest from the least vulnerable age and sex classes (i.e., adult females) would increase as population size declines.

Scent-station surveys.—We conducted scent-station surveys only on the Monroe Mountain study site during 2 summer (Jun–Sep) seasons (1996–1997). In 1996 we designed sampling to test if cougars would respond to any of 3 olfactory attractants: a commercially produced fatty-acid scent (FAS; U.S. Department of Agriculture Supply Depot, Pocatello, Idaho), bobcat urine (Montgomery Fur Co., Ogden, Utah), and catnip extract (St. Aubrey Vet Labs, Hauppauge, New York).

We established 16-km transects ($n = 5$), along dirt roads, all-terrain-vehicle (ATV) routes, and foot trails with each transect comprising 20 stations placed at 0.8-km intervals on alternating sides of the transects. Human interference precluded placement of scent-station sets directly on roads or trails. Consistent with other studies (Dickson and Beier 2002), preliminary radiotelemetry and tracking data demonstrated that cougars did not avoid the use of unpaved roads within their home ranges. We distributed transects throughout the study site and placed them as far from each other as possible (6.73 ± 1.06 km, mean distance $\pm$ SE) in an attempt to reduce the probability that an individual cougar would encounter multiple transects during a trial (Roughton and Sweeny 1982, Sargeant et al. 2003). Beier et al. (1995) demonstrated that on average, cougars move 6.4 km ($SD = 4.2$) during diel periods, and Hemker et al. (1984) noted that the greatest average distance moved in 1 day in a similar site in southern Utah, USA, was 4.8 km (range 0.3–10.8 km). However, the potential for a single cougar to visit multiple transects in one evening was not eliminated because cougars can travel greater distances in a diel period (Dickson et al. 2005). Individual stations consisted of a 1.5-m-diameter plot cleared of surface material and covered with sifted soil. We placed a scent-impregnated plaster tab in the center of each plot on the day prior to each survey. We selected a plot diameter that would be 0.5 m greater than the average stride of a cougar (Halfpenny and Biesot 1986), thereby preventing a cougar from leaning over the tracking medium to investigate a tab without leaving a track. In each survey we examined each scent station in the 2 mornings following the placement of the lure. We recorded tracks present at each station during each examination, then cleared them and replaced missing attractants. We operated scent stations during different days from those used for track-count surveys to eliminate any potential attractant bias to track-survey routes. We surveyed each transect 1–3 times ($mean = 1.8$) using a single lure for each survey.

In 1997 we modified sampling design to compare the efficacy of different lures. We established 9 9.6-km-long transects, each with 12 stations placed at 0.8-km intervals. We constructed stations as in 1996 with the following modifications. We suspended 2 reflective mylar strips (5×30 cm) in vegetation near the set to serve as a visual attractant (e.g., McDaniel et al. 2000). In addition to the FAS and catnip lures, we tested a commercial lure, Pro's Choice® (Russ Carman's, New Milford, Pennsylvania) as an olfactory attractant, and a control consisting of a plain plaster tab. We randomly assigned scents to a station within blocks of 4 stations, resulting in the placement of each lure and the control at 3 stations per transect line, for a total of 27 stations per lure. We checked each station on 3 consecutive days following placement of the scent tabs.

Ground-based track counts.—We conducted systematic track counts on both sites during summer months during 1996–2001 on Monroe and 1998–2001 on the Oquirrhs, as described by several investigators (e.g., Van Dyke et al. 1986, Van Sickle and Lindzey 1992, Smallwood and Fitzhugh 1995, Beier and Cunningham 1996). We selected 16-km- (1996–1997) and 8-km (>1997)-long track-survey transects and prepared road transects by dragging a 1×2-m segment of chain-link fence along the transect 1–3 days prior to each survey. We tracked routes on foot, by ATV, or by 4-wheel-drive pickup truck, traveling at ≤ 8 km/hour. On the Oquirrhs 34% of routes consisted of walking dry washes, due to terrain and interspersion of gravel and paved roads. By comparison, 5% of routes on Monroe consisted of walking dry washes or trails. Due to this difference, we evaluated track counts as an index by comparing years within a site rather than by comparing sites.

For each set of tracks from an individual cougar, we measured the interdigital pad width for several tracks for each foot using the minimum outline method (Fjelline and Mansfield 1989). We used multiple measurements from each foot to calculate means and recorded a combination track measure for each track set. Although left and right foot measurements for either the front or rear feet do not differ significantly (Halfpenny 1998), cougar front feet are significantly larger than rear feet. In preliminary training, we determined that the track size ratio of front feet to rear feet remained consistent for individual cougars. This ratio provided another way to infer individual identity and, thus, decreased the risk that interobserver variation in measurements would lead to unreliable conclusions that a track set represented a new individual. Contrary to the findings of Grigione et al. (1999), we determined that individual cougars could often be identified from heel pad measures by creating an individual track-set profile incorporating data from all 4 feet. This approach provides a minimum estimate because, lacking other unique features for differentiation (e.g., missing or misshaped toes; Rosas-Rosas et al. 2003), the size ratio of 2 individuals may overlap.

In addition to track measurements, we geo-referenced the location of the track sets with handheld GPS instruments. We evaluated the condition of the tracking substrate for each transect at 1.6-km intervals similar to Van Dyke et al.'s (1986) subjective boot impression criteria. At each interval we walked 10 steps diagonally across the road or trail and evaluated each boot print on a scale of 0–4, with 0 assigned for no trace of the print and 4 when complete detail of the track was present. Each interval received a score of 0–40 and a mean was then determined for each transect. Substrate condition can influence the ability to detect tracks; therefore, we attempted to develop correction factors for track detection based on substrate conditions (BT score: boot track condition rating) and used these to adjust for differences among sites, surveys, and years using regression methods. Because transects crossed elevation gradients and substrate types, we could not assume a constant probability of track detection along transects. The data were insufficient to compare track-detection frequencies across transects or evaluate for possible serial autocorrelation. Consequently, we pooled data from all years and tested the fit of track-finding frequency along transects against Poisson and the more general negative binomial distributions using Kolmogorov–Smirnov 1-sample tests. We used regression analyses to test for relationships between summer-season cougar density as back-adjusted from the winter reference-population estimate and either the number of tracks or minimum number of cougars encountered per kilometer of transect searched in a summer season.

Descriptive statistics are reported as mean ± SE unless otherwise noted. We calculated analyses and statistical comparisons using SYSTAT 10.0 (SPSS 2000). We tested all variables for normality prior to parametric statistical analyses and described transformations where appropriate.

Results

Estimation of Reference Population Size and Density

Between January 1996 and April 2003, we captured 93 individual cougars, including 24 adults, 23 subadults, and 2 kittens on Monroe Mountain, and 22 adults, 4 subadults, and 18 kittens on the Oquirrh Mountains. Annual population estimates for each site are presented in Table 1, excluding years 1997–1999 for the Oquirrhs when track-based mark– recapture data on that site were unavailable. The estimate of the unmarked proportion of the population derived from track evidence closely agreed with the estimate derived from back-calculation of the ages of radiocollared cougars for both sites (i.e., difference = −0.25 ± 2.4 individuals/yr). However, on Monroe the bias from track-based estimations slightly overestimated (+0.7 ± 1.5) and on the Oquirrhs the bias slightly underestimated (−1.6 ± 2.9) population size based on back-calculations. Cougar dispersal estimated from radiocollared individuals from either site occurred at an equally low rate across all seasons and years of the study (Monroe: 0.5 ± 0.26 individuals/yr, $n = 4$; Oquirrhs: 0.88 ± 0.35 individuals/yr, $n = 7$) and did not appear to bias winter-based population estimates. Excluding known dispersals and transients, 3 radiocollared cougars on Monroe were part-time residents, and home ranges of 5 extended slightly beyond the site boundaries such that 99 ± 0.6% of relocations of radiocollared cougars were within the study-site boundaries across all years. Even though cougars moved down an elevation gradient in winter, this did not result in a seasonal difference in population estimates for Monroe. Consequently, we used our early winter–based population estimates for comparisons with the previous summer's track surveys (e.g., summer 1996 vs. winter 1996–1997). Unlike Monroe, the Oquirrh site included part of a larger, geographically isolable population. Home ranges of 2 male and 3 female radiocollared cougars extended beyond the site boundaries, such that 67 ± 6% of relocations of radiocollared cougars were within the study-site boundaries across all years. Therefore, we used our combined radiotelemetry and tracking information to adjust the winter estimates for comparison with summer track surveys. Demographic details for both sites are presented in Stoner et al. (2006). During the study cougar density on Monroe declined from a high of 3.2 adult and subadult cougars/100 km^2 in 1997 to a low of 1.2/100 km^2 in 2001, concurrent with an increase in hunting pressure (Fig. 2). Conversely, cougar density on the Oquirrhs remained static at an average of 2.8 ± 0.06 cougars/100 km^2.

Other Population Estimators

Aerial snow track surveys.—Surveys required 6.1 ± 0.7 hours total flight time to complete (Table 2). In February 1998, 2 adult females were traveling with 2 kittens each, and 2 kittens were found traveling together without an adult female (orphaned by hunter-kill). We counted these track sets as single cougar track sets for analysis (Van Sickle 1990). Population estimates based on probability sampling exceeded the reference population by 120–284%. Reference population estimates fell outside of the 95% confidence intervals for each sampling estimate with 2 exceptions (Table 2). The reference estimate fell within the 95% confidence intervals for the 1997 adjusted and the December 1998 unadjusted sampling estimates; however, the latter interval included the range of 0–205 cougars/100 km^2. Each survey also displayed poor precision, with bootstrap standard errors of 25–55% of the population estimates (e.g., 5.6 ± 14 cougars/100 km^2). Adjusted population estimates using Anderson's (2003) method performed better; however, these underestimated the reference density for each of the surveys by 25.7–87.5%, with standard error comprising 24–52% of the estimates. Randomly selecting track lengths as suggested by Anderson (2003) resulted in inconsistent biases, with 1 year underestimating (<22.8% in 1998) and 2 years overestimating (>44–58.5%) reference population size. On average, the bootstrap means for each method displayed a negative bias relative to the survey estimates (e.g., Bootstrap T_j − Survey $T_j = -0.33$); however, this bias varied among years and adjustment methods.

Catch-per-unit-effort.—We calculated CPUE for each year as the days required to capture only uncollared animals and the days required to capture any cougar, including recapturing previously collared individuals (Table 1). We used the latter measure for comparisons. Catch-per-unit-effort was a poor predictor of population size for either Monroe ($r^2 = 0.021$, $F_{1,6} = 0.126$, $P = 0.734$) or the Oquirrhs ($r^2 = 0.148$, $F_{1,2} = 0.349$, $P = 0.615$), when based on research results, or hunter-efforts ($r^2 = 0.468$, $F_{1,4} = 3.520$, $P = 0.134$; Fig. 3). Similarly, there was no relationship between CPUE and hunter harvest on Monroe regardless of whether CPUE was based on research ($r^2 = 0.011$, $F_{1,6} = 0.066$, $P = 0.806$) or hunter-effort ($r^2 = 0.052$, $F_{1,4} = 0.219$, $P = 0.664$). Accounting for nonhunting losses (e.g., depredation-related removals) did not improve the regression measures. The poor fit of these regressions negate the assumption of equal probability of capture and preclude meaningful estimates of k.

Mark–recapture.—To evaluate the potential for a longer marking interval, or perhaps a season-long prehunt period, we investigated the use of encounters with tracks of previously captured cougars as a "marked" recapture, concurrent with our capture activities (Table 1). On average, track-based L-P estimates for Monroe underestimated reference population size by 17 ± 14%.

Table 1. Winter capture efforts and population estimates for cougars on Monroe Mountain and the Oquirrh Mountains, Utah, USA, 1996–2003.

			No. of track sets[b]								Reference estimate[c]		CPUE[d]		L-P estimate[e]	
			Total		Individuals											
Site/yr[a]	Days	Collared cougars (n_1)	Adults	Kittens	Collared (m_i)	New adult	Pursuits	Adults treed	New animals	Recaptures	No.	Cougars/100 km^2	Days/all cougars	Days/new cougars	$\hat{N}$	CI
Monroe																
1996	39	12	28	8	3	25	18	13	12	1	35	2.7	3	3.3	n/a	
1997	37	11	29	16	7	14	13	5	5	0	42	3.2	4.6	7.4	32	10
1998	65	11	52	25	8	14	20	9	1	8	33	2.5	7.2	65	30	7
1999	40	7	51	2	5	14	21	7	6	1	26	2	5.7	6.7	26	8
2000	35	7	27	2	3	7	12	3	2	0	21	1.6	11.7	17.5	21	11
2001	45	4	45	2	4	6	25	7	5	2	15	1.2	6.4	8	10	0[f]
2002	49	3	46	0	3	9	23	11	9	2	17	1.3	4.4	5.4	12	0[f]
2003	51	6	74	6	6	9	39	18	9	9	20	1.5	2.8	5.7	15	0[f]
Oquirrhs																
2000	16	6	38	3	5	6	9	7	5	2	14	2.9	2.3	3.2	13	3
2001	23	9	51	0	6	3	22	7 (18)[g]	3	2	13	2.7	3.3	4.6	13	2
2002	44	8	78	2	8	8	30	6 (16)[g]	4	2	14	2.9	2.8	11	16	0[f]
2003	40	7	63	2	6	6	22	12	5	6	14	2.9	3.6	8	14	2

[a] Year based on hunting season (e.g., 15 Dec 1995–15 Jun 1996 = 1996). Oquirrh Mountains track-set data were unavailable for 1998–1999; the population estimate for both years is 2.9/100 km^2 (M. L. Wolfe, D. M. Choate, and D. C. Stoner, unpublished data).

[b] The total number of track sets encountered may exceed the sum of the number radiocollared and number of new adults because individuals may be encountered more than once during a capture season.

[c] Population estimate includes adults and subadults based on all capture, radiotelemetry, tracking, and mortality data; the reference estimate.

[d] CPUE, catch-per-unit-effort measured in days required to capture a cougar.

[e] Lincoln–Petersen (L-P) estimates are derived from encounter rates with tracks of radiocollared individuals (m_i) and uncollared individuals (new adults) in year i ($n_i = m_i +$ new adults) and the collared (n_1) individuals (adults + subadults) present on the study site prior to the hunting–winter-tracking season: $\hat{N}_i = [(n_1 + 1)(n_i + 1)/(m_i + 1) - 1]$. Values are presented with a 95% CI (Chapman 1951).

[f] Tracks from all radiocollared cougars were encountered during surveys, resulting in no variance estimate ($n_1 - m_i = 0$).

[g] Numbers in parentheses indicate total number of times animals were treed, including multiple captures during a season; numbers outside parentheses indicate different individuals.

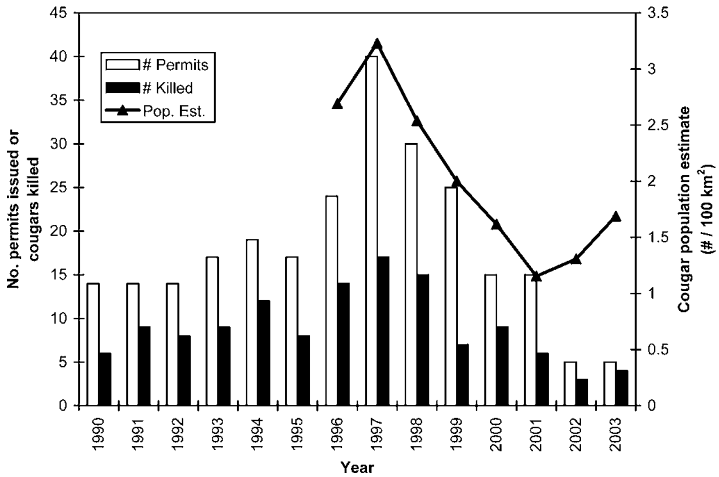

Figure 2. Comparison of hunter-kill and change in cougar density (adult + subadults) on the Monroe Mountain study site, Utah, USA, 1990–2003. Cougar permits issued and hunter harvest on Monroe Mountain Cougar Management Unit No. 23, 1990–2003, are depicted on the left axes, while cougar population estimates for the study period (1996–2003) are depicted on the right axes. Harvest data have been adjusted for the split with the Dutton Unit (No. 24) in 1994, such that only cougars killed on Monroe Mountain are included for 1994.

Indices

Hunter harvest.—Mean kill rate on Monroe (including legal harvest, depredation, and poaching related mortality) was 0.93/year/100 km^2 (Fig. 2; see also Stoner et al. 2006). The first decline in hunter success (28.0% permits filled) occurred in the second year of decline in population size. Average age of hunter-killed cougars declined from 3.8 years in 1996–1997 to a low $\bar{x} = 2.6$ ($\pm$0.06) years between 1997 and 2000 (Fig. 4). The relationship between age and the population estimate was not statistically significant ($r^2 = 0.015$, $F_{1,6} = 0.090$, $P = 0.774$) without removal of one outlier (2001, 4.4 yrs; $r^2 = 0.706$, $F_{1,5} = 12.030$, $P = 0.018$). Similarly, the adult female proportion of the harvest declined from 35.3% to 0 in 2002 (Fig. 4); however, the decline was not statistically correlated with the population estimate ($r^2 = 0.256$, $F_{1,6} = 2.067$, $P = 0.201$) and only marginally related after removal of one outlier (2000, 44%; $r^2 = 0.546$, $F_{1,5} = 6.008$, $P = 0.058$). We caution that statistical significance here may be misleading due to sensitivity to the outliers and that emphasis should be placed on monitoring the long-term trend in age or proportion of females in the harvest. In addition, 75% of cougar ages estimated from cementum annuli counts agreed within 2 years of our age estimates for radiocollared cougar ($n = 51$), primarily as under-estimates. Similarly, 46% of paired samples from harvested cougar matched exactly, and 24% matched within 1 year ($n = 37$).

Scent-station surveys.—In 1996 we operated scent stations for a total of 340 station-survey nights (FAS $n = 200$, catnip $n = 80$, bobcat urine $n = 60$). Only 40–50 stations could be operated simultaneously because of the distance between transect lines, with a complete survey of 100 stations requiring 6–12 days. None of the attractants produced any visits by cougars, but we observed tracks from several other species, including rodents, mule deer (*Odocoileus hemionus*), red fox (*Vulpes vulpes*), coyote (*Canis latrans*), and bobcat (*Lynx rufus*). Radiotelemetry locations of collared animals revealed that 5 cougars spent 1–2 nights each within 0.5–1.0 km of various stations. We also observed tracks of a cougar that had passed within only a few meters of a scent station without visiting it. In 1997 a total of 108 scent stations were operable on 88% of available station-nights ($n = 285$). Only a single control station was visited by a cougar on one night, with the animal leaving a scrape and scat. The extremely low visitation rates in both years precluded statistical comparisons and prompted discontinuation of these surveys in subsequent years.

Ground-based track counts.—Across study sites and all years, we conducted summer ground-based track surveys comprising 187 transects and totaling 2,028.5 km of roads searched. On these transects 28 individual cougars left 35 track sets. Between 1996 and 2001 track surveys on Monroe Mountain comprised 116 transects including 1,379.3 km of roads searched (Table 3). On the Oquirrh Mountains we searched 286.2 km of roads and washes along 38 transects between 1998 and 2001.

On the Oquirrhs 1998 was the first trial year for summer surveys, many of which were not viable due to extensive gravel; consequently, the Oquirrhs data from summer 1998 were excluded from further analyses. Otherwise, tracking conditions on both Monroe (all years) and the Oquirrhs (1999–2001) were fair (BT: 24.6 $\pm$ 4.2) when adjusted to Van Dyke et al.'s (1986) scale. Average tracking conditions were slightly better on the Oquirrhs (17.1 $\pm$ 3.3) than on Monroe (BT: 14.4 $\pm$ 4.0) Average track-condition scores for each site did not differ among years ($r^2 = 0.167$, $F_{1,6} = 1.201$, $P = 0.315$); however, density declined on Monroe across years. Because density was not static, we examined the frequency of finding tracks across transects at a site within a given year, in order to develop a correction factor for the influence of substrate on track detection rate. The extremely low overall detection rate (024 $\pm$ 0.14 tracks/8-km transect) limits practical inference about the relation between track deposition and substrate quality. For example, after pooling data across all years, on both Monroe and the Oquirrhs, neither the minimum number of cougars nor the total number of track sets found in a year were correlated with track-condition scores (Monroe: $r^2 = 0.055$, $F_{1,6} = 0.347$, $P = 0.577$; Oquirrhs: $r^2 = 0.004$, $F_{1,6} = 0.022$, $P = 0.887$). A slight positive correlation appears between track-condition score (BT) and the number of cougar track sets found, but the standard error of the estimate is quite large (3.983).

Because track detections across transects more closely fit a negative binomial rather than a Poisson distribution (Kolmogorov–Smirnov test; negative binomial-fit: $P = 1.000$, Poisson-fit: $P = 0.653$), we fit generalized linear models with a negative binomial distribution for the response variables track sets per kilometer searched or minimum number of cougars per 100 km searched, against the population estimates (PROC GENMOD in SAS version 9.1; SAS Institute, Cary, North Carolina). However, the model algorithms did not converge using Hessian criteria. Rather than drawing questionable inferences from the small data set, we transformed the standardized track-finding frequencies and regressed these values against the population estimates. We recognize that indices (e.g., track sets, expected counts $E(N)$) are usually regressed on an independent variable such as cougar density (Williams et al. 2001) in order to estimate the parameter β, for example where $E(N) = \beta \times N$. However, we chose to present our data using the index as the independent variable X (Fig. 5,

Table 2. Estimation of cougar population size from aerial snow-track surveys, Monroe Mountain, Utah, USA, 1997–1998.

											Cougars/100 km²[h]			
Transect[a]	No. of tracks intercepted	x_i[b]	p_i[c]	$1/p_i$	T_j[d]	SE[e]	T_a[f]	SE	T_e[g]	SE	Reference	Aerial	Adjusted	Random[g]
15 Jan 1997														
1	6	1.1	0.34	2.94										
		0.8	0.25	4										
		0.2	0.06	16.13										
		0.9	0.28	3.57										
		1.1	0.34	2.94										
6	1	0.3	0.09	10.87										
					40.45	12.55	9.47	2.25	18.42	2.48	3.23	10.24	2.4	4.66
17 Feb 1998														
1	2	0.3	0.09	10.87										
		0.5	0.15	6.67										
6	1	1.7	0.51	1.96										
9	2	1.4	0.43	2.33										
		0.4	0.12	8.33										
					30.16	7.46	2.18	1	10.6	1.56	2.54	5.59	0.4	1.96
23 Dec 1998														
1	2	0.5	0.15	6.67										
		0.2	0.06	16.13										
2	1	1.4	0.44	2.27										
9	2	0.5	0.15	6.67										
		0.05	0.02	66.67										
					98.41	54.36	1.19	0.62	13.11	1.8	2	23.82	0.29	3.17
				−66.67 =	31.74	10.02	1.03	0.61				7.68	0.25	

[a] The following transects were omitted ($x_i = 0$): 15 Jan 1997 No. 5, no tracks; No. 4, aborted due to low fuel; 17 Feb 1998 No 2, no tracks.
[b] x_i = distance (km), parallel to the baseline, traveled by *i*th cougar. Track sets left by cougars traveling together are counted as 1 track set.
[c] $p_i = x_i/(D/q)$ = probability that *i*th cougar is contained in *j*th sample; D = baseline length = 9.75 km in Jan 1997, 13.00 km in Feb 1998, 9.75 km in Dec 1998; q = No. transects/sample, 3 in Jan 1997, 4 in Feb 1998, 3 in Dec 1998.
[d] $T_j = \sum(1/p_i)$ = population estimate for the *j*th systematic sample.
[e] Standard error (SE) determined by bootstrapping methods (Efron and Tibshirani 1986)
[f] Adjusted population estimate from Anderson (2003), where $T_a = (\sum[(1/p_i)(1 - \pi_i)])/(1 - P)$; see text for explanation.
[g] Adjusted population estimate as above, however, using randomly selected x_i from Anderson's data (2003); see text for explanation.
[h] Aerial estimate derived from helicopter survey data; adjusted aerial estimates based on Anderson's (2003) correction factors; reference estimate derived from radiotelemetry data for comparison. Areas surveyed were 395 km² on 15 Jan 1997, 540 km² on 17 Feb 1998, and 413 km² on 23 Dec 1998.

inverse regression) for clarity in presentation We found a significant relationship between cougar density and track-finding frequency (Monroe: $r^2 = 0.883$, $F_{1,4} = 30.197$, $P = 0.005$; Monroe and Oquirrhs combined: $r^2 = 0.555$, $F_{1,7} = 8.737$, $P = 0.021$; Fig. 5), and between cougar density and track-finding frequency for individuals (Monroe: $r^2 = 0.899$, $F_{1,4} = 35.436$, $P = 0.004$; Monroe and Oquirrhs: $r^2 = 0.597$, $F_{1,7} = 10.388$, $P = 0.015$; Fig. 5). Inclusion of data from both sites resulted in a negative bias in the regression line that may reflect differences between sites or a more general saturation of tracks at higher population densities; therefore, we present the regression results not as a population estimator but as a general indicator of trend. We considered an alternative analysis that might be useful for detecting differences between years for a site by comparing count data from an underlying negative binomial distribution (e.g., White and Bennetts 1996), but the observed count data and number of transects surveyed each year were too small ($\bar{x} = 19.3$/yr; White and Eberhardt 1980) for the current analysis.

Discussion and Management Implications

Evaluation of Estimators and Indices

Overview.—In contrast to the relatively static harvest during the years prior to this study, total hunter-kill on the Monroe unit peaked in 1997 and reached a record low in 2002 (Fig. 2). The Monroe cougar population declined when hunter-kill exceeded 30% of the adults and subadults and comprised 42% females for 3 years, impacting fecundity and resulting in a skewed age structure (see also Stoner et al. 2006). Hunter success was influenced by the timing and duration of snowfall, but trend estimators displayed declines in the population prior to 2002. When standardized as the proportion of the first year count, track-count surveys demonstrated a decline of 69% in the rate of finding tracks between the summers of 1996 and 1997, followed by a second decline (20%) between 1998 and 1999 (Fig. 6B). Although the probability-based population estimates derived from helicopter surveys are suspect, the surveys provide an independent track estimate for Monroe during the winter. From this estimate (number of tracks per area searched), track evidence for cougar declined by 54.2% between the winters of 1996–1997 and 1997–1998, then increased by 3.2% between the winters of 1997–1998 and 1998–1999 (Fig. 6C). Proportional changes in the L-P estimates tracked the decline in cougar density (Fig. 6D), slightly underestimating the decline (Fig. 7). Despite the level of cougar harvest from Monroe Mountain between 1997 and 1998, trend estimators appeared to be comparable in detecting a population decline, consistent with the reference population estimates. Hunter success, often used as a metric for population trend, did not display a decline until the 1999 harvest by falling from 50% to

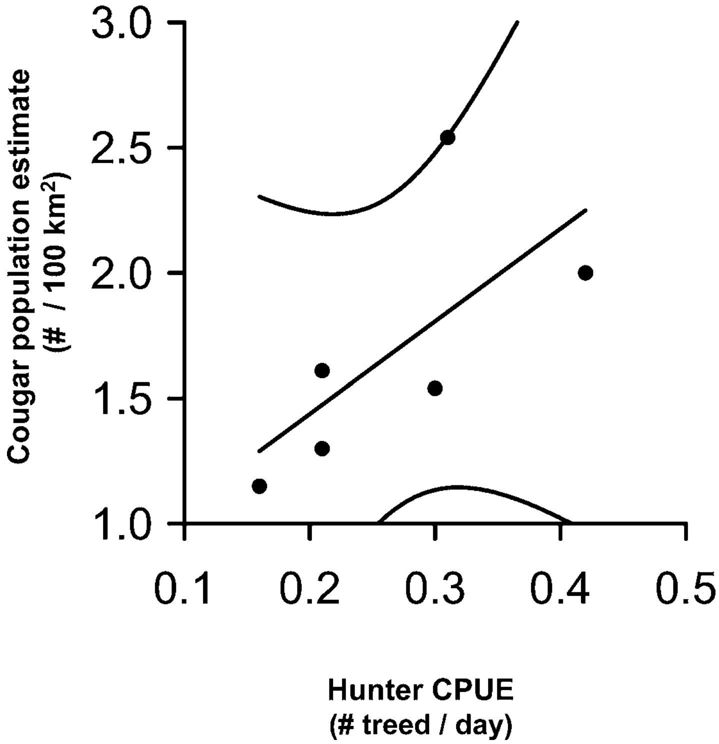

Figure 3. Relationship between cougar density and hunter catch-per-unit-effort (CPUE) in number of animals brought to bay in trees per day, Monroe Mountain, Utah, USA, 1998–2003 ($r^2 = 0.468$, $F_{1,4} = 3.520$, $P = 0.134$). Hunter CPUEs were unavailable for 1996 and 1997, the years of high cougar density, suggesting actual model fit might be less than plotted. Curved lines represent 95% CI.

28%. Although hunter success rose the next year to 60%, the increase resulted from the 40% reduction in permits issued for the unit. By comparison, during the periods that they were conducted, track counts on the Oquirrhs remained fairly constant.

Aerial snow track surveys.—As a cougar population estimator, aerial sampling still requires field validation for estimator precision. Although Van Sickle and Lindzey (1991) were successful in a field test trial validating their simulation model, their sample was limited to 1 survey with only 2 of 12 transects searched (in comparison to $\bar{x} = 3.5$ transects/survey, this study). Logistical difficulties challenge implementation of this technique, such as meeting sufficient snow tracking conditions while avoiding unstable air masses that can create hazardous flying conditions. In addition to the lack of survey replication, sensitivity of the population estimate to measurement error of short track sets (i.e., low x_i) may substantially inflate the probability-based estimates (Van Sickle and Lindzey 1991). Conceivably, sampling error may be reduced by landing the helicopter along each track-set route to determine a more accurate (immobile) GPS location for the endpoints of each track set. However, this may not be possible in difficult terrain and would considerably increase the time required to complete each survey. In addition, during our December 1998 survey, a single track set of <50 m increased the population estimate by 66.7 animals. During the survey period, a houndsman had kept this cougar in a tree, likely reducing the distance traveled by the cougar. Omitting this track set produced an estimate of 31.7 ± 10.0 (Table 2). Although omitting this track set may not be valid, it is impossible to estimate the distance the cougar might have moved and adjust for sampling error.

Anderson's (2003) correction for low x_i improved the aerial estimates but still underestimated the true density by 26–88% ± 54.6–115% (Table 2). This correction also may bias estimates due to the assumption that the lack of movement of a cougar depends on predation success, when a lack of movement might arise from other factors. In addition, a lack of movement of cougars might vary with the proportion of females in the population with suckling cubs (Logan and Sweanor 2001). Randomly selecting track lengths also resulted in inconsistent bias in the estimates, with 1 year underestimating (<23%, Feb 1998) and 2 years overestimating (>44–58%) reference estimates. Given this variability in the estimator, simply using the tracks detected along an aerial transect as another track-based index or as part of a mark–resight survey would appear more prudent and cost-effective. Despite the increased precision of the adjusted estimates, from both our survey estimates and Anderson's (2003) simulations, the confidence intervals are derived from resampling single surveys using bootstrap or jackknife techniques and should be viewed with caution. These techniques are based on resampling from the individual track sets ($1/p_i$) and do not provide an estimate of variation in encounter rates with track sets or the variability in the number of transects flown. Since it is the composite value used to estimate population size, how relevant is this measure of precision? Managers should be wary of attributing confidence to an estimate using this method for estimating precision until true field validation occurs, a prospect not likely in many geographic regions.

Catch-per-unit-effort.—Catch-per-unit-effort methods have met with some success in estimating population size, specifically for certain ungulates in game reserves (Lancia et al. 1996*a*). This notwithstanding, the approach might not be suited for estimation of cougar numbers. Violations of model assumptions are difficult to avoid. For example, our documentation of radiocollared animals dispersing from and onto the primary study sites indicated that the assumption of demographic closure during sampling was not met. The lack of a significant relationship between CPUE and hunter harvest or estimated population size arises in part due to the overlap in CPUE values for different population estimates. Specifically, both high (2.0–3.2 animals/100 km^2) and low (1.1–1.6 animals/100 km^2) cougar densities on Monroe correspond with a similar range of capture success (0.1–03 cougars treed/day). This may result from hunter selectivity for specific age–size classes of animals or concentration of hunting effort in either perceived better-quality habitat or regions with easier access. Either scenario constitutes a violation of the assumption of equal catchability. At high cougar densities, hunters are likely to focus their efforts on pursuing larger adult males. As the number of adult males and the overall density of cougars on a unit declines, hunters are more likely to pursue smaller cougars, including females, thereby maintaining a consistent capture rate. Evidence of a shift in hunter selectivity is demonstrated in the reduction in age class appearing in the harvest. However, Fig. 3 appears to suggest a relationship between hunter CPUE and cougar density and is worth further investigation. If the value at high density is a true outlier, a better correlation may be found; however, our data do

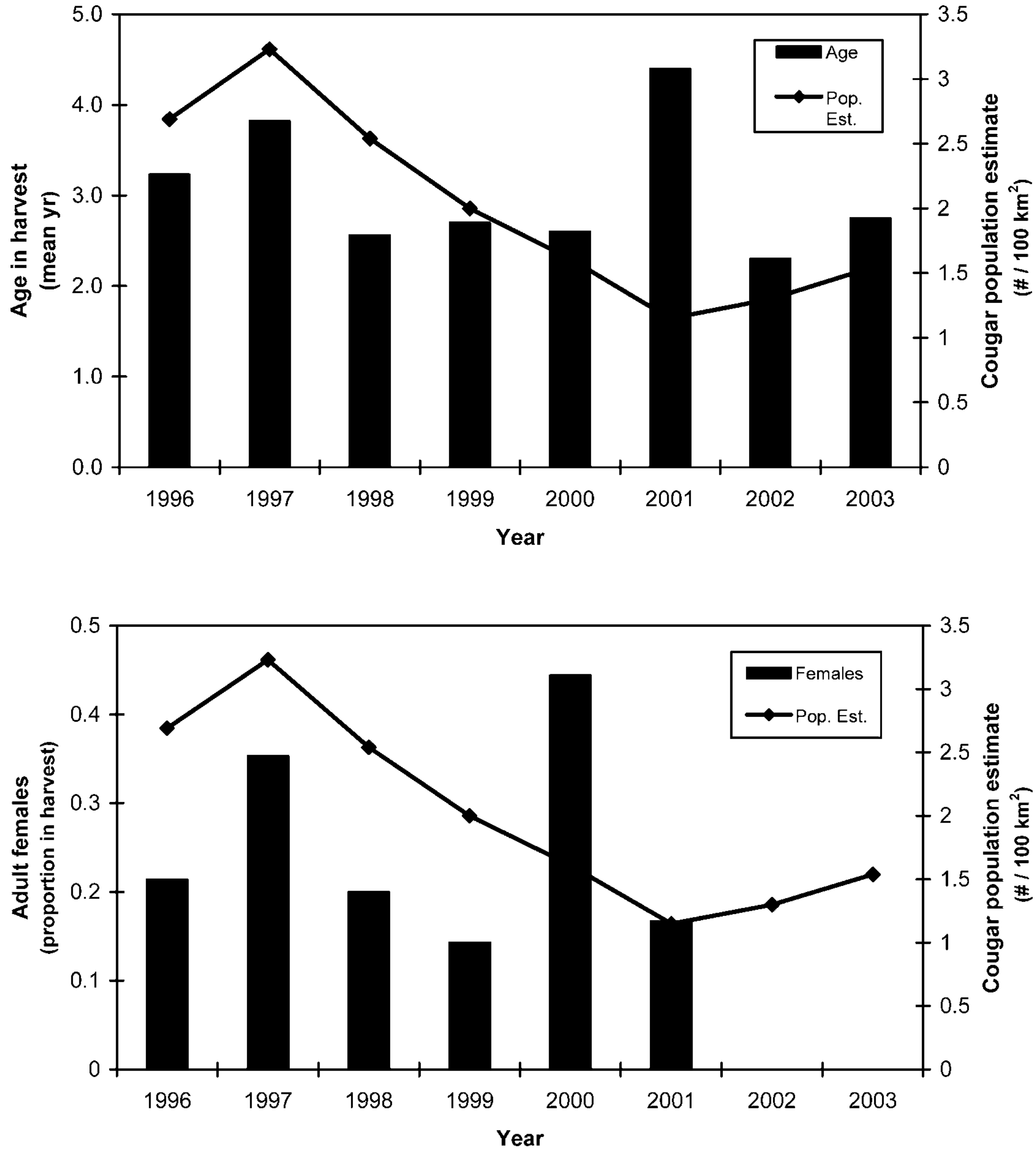

Figure 4. Harvest indices and cougar population estimates (adult + subadult cougars/100 km^2), Monroe Mountain, Utah, USA, 1996–2003. The average age of cougars in each year's harvest is shown in the upper panel on the left axis (bars), and the proportion of adult females in each year's total harvest is shown on the left axis of the lower panel. Cougar population estimates (lines) are shown on the right axis of each panel.

not support this prospect. Transformations did not normalize the variance in the residuals, and data were unavailable for 1996 and 1997, 2 years with the highest cougar density on Monroe.

Mark–recapture.—Intensive capture and radiotelemetry marking constitute the most reliable means for estimating local cougar abundance but likely are not feasible on a regional or statewide scale. Mark–recapture methods are subject to violations of underlying model assumptions. The assumption of equal catchability rarely is met in natural populations (Burnham and Overton 1979, Boersen et al. 2003) and was not met in this study. Natural populations seldom approximate closure (e.g., Woods et al. 1999, Boulanger and McLellan 2001); similarly, neither demographic nor geographic closure was maintained during our sampling periods. While dispersing individuals may decrease local population density, part-time residents can inflate density estimates (Garshelis 1992).

Seber (1970) also noted that the L-P population estimate $\hat{N}$ will remain reasonable, provided that the marked sample is representative of the unmarked population. Even though we systematically sampled each study site during capture and marking efforts, cougars that moved greater distances (i.e., left more tracks) were more likely to have been included in the marked sample. For the same reason, these individuals were more likely to have been encountered in subsequent samples, resulting in a correlation between the probability of being marked and subsequently detected. As a result, L-P estimates are negatively biased, as we observed. In addition, L-P estimates pertain to the first sample and, therefore, do not reflect the population size at the second sample, when deaths or removals occur during the interval.

Table 3. Summer track-count surveys for cougars on Monroe Mountain (1996–2001) and the Oquirrh Mountains (1998–2001), Utah, USA.

Study site	Year	No. of transects[a]	Total length (km)	Time[b] (hr)	No. of cougars	No. of track sets (TS)	Boot track score (0–40)	No. of km searched/TS	Min. No. of cougars/100 km
Monroe	1996	13	213.1	41.17	9	12		17.8	4.2
	1997	13	150.22	28.78	2	2	14	75.1	1.3
	1998	41	355	63.12	5	5	84	71	1.41
	1999	17	334	73	2	2	17.2	167	0.6
	2000	12	161	22.42	1	1	18.9	161	0.59
	2001	20	166	21.25	1	1	13.4	166	0.6
Oquirrhs	1998	17	106.3	26.28	0	0	8.5	0	0
	1999	8	91.25	32.42	4	5	18.6	18.25	4.38
	2000	6	42	10.32	2	5	13.4	8.4	4.76
	2001	7	46.6	7	2	2	19.4	23.3	4.29

[a] Based on 16-km-long transects in 1996 and 1997; 8-km thereafter.
[b] Total time required to conduct surveys for a site per year; all surveys conducted between 1 Jun and 1 Oct.

Bartmann et al. (1987) recommend marking at least 45% of the population when $N < 100$, in order to yield reliable estimates with useful confidence intervals (White and Garrott 1990). During the study we maintained radiocollars on 27 $\pm$ 5% of the population on Monroe at the start of each hunting season. However, hunting pressure resulted in losses of 1–5 radiocollared animals each year, making it difficult to maintain this level of marking. By comparison, on the Oquirrhs we maintained radiocollars on 58 $\pm$ 11% of the population, yet on average 0.7 radiocollared cougars were still removed annually from that site by hunters.

Currently several statistical procedures are available for analysis of mark–recapture data that relax assumptions of population closure (e.g., JOLLY; Pollock 1982) and provide tests for equal probabilities of capture or recapture (e.g., CAPTURE [White et al. 1982], MARK [White and Burnham 1999]). If there are more than 2 sampling occasions, estimates of bias and precision can be derived from these techniques and may provide more reliable estimates than conventional mark–recapture approaches. In this study low capture probability necessitated a longer sampling interval than days or weeks. Consequently we used only one marking (capture) and one sampling event. On Monroe a single-sample, track-based, mark–recapture L-P model underestimated population size by 17% ($\pm$14%; Table 1). Although the actual estimate may be suspect, the approach provides another index that may be useful for comparative purposes. Even though we intended to use relocation of radiocollared animals during the aerial surveys as another mark–resight sample, we did not detect radiocollared animals at the end of each survey due to probable equipment failure. In addition, inclement weather and logistics hindered follow-up aerial radiotelemetry, such that flights occurred 2–7 days after the helicopter surveys. Future studies that incorporate multiple independent sampling occasions by combining different techniques may provide more rigorous population estimates, within a shorter interval than required for back-dating captured cougars and making other adjustments to population estimates. This approach would be useful for populations targeted for specific management plans; however, suitable sample sizes might not be achievable for application in routine management situations.

Marking animals with genetic "tags" through DNA analysis of scat, tissue, or hair and subsequent recapture of genetic tags may provide an alternative tool for population estimation (e.g., Boulanger and McLellan 2001, Boersen et al. 2003); however, sampling issues may limit the applicability of this technique. For example, in a pilot study we conducted over 2 years on 2 additional study sites, a total of 64 hunters were issued 2-week special pursuit permits immediately prior to each hunting season (M. L. Wolfe, D. M. Choate, and D. C. Stoner, unpublished data). Participants were provided with equipment to capture hairs of animals brought to bay, so that DNA extracted from the hairs would constitute a genetic mark to be compared with DNA extracted from animals killed during the general cougar hunt using a mark–recapture estimator. This effort resulted in collection of 6 samples total, far less than the predicted initial (prehunt) sample of 15–20 individuals required to obtain an estimate of population size with modest precision.

Hunter harvest.—These limitations have implications for the harvest statistics currently used by many agencies in developing cougar management recommendations. Trends in population estimators may still be detected with careful adherence to rigorous sampling design. However absolute population estimates are likely to be negatively biased (Lancia et al. 1996*b*). Harvest reporting errors necessitate careful reconsideration of typical hunting statistics. The proportion of females recorded in the harvest (currently one of the performance measures used to evaluate harvest level effects) may be suspect, given the level of reporting errors (CMGWG 2005). Monitoring changes in the age of hunter-killed animals is appealing, but the reliability of ages determined by cementum annulation counts requires further evaluation. Even though precision was low for this study, in a "blind test" estimating 864 cougar tooth pairs, Kohlmann and Green (1999) found ages to agree or vary by 1 year in 93% of the pairs for <4-year-old cougars, but only 54% of pairs for older cougars. As a tool to differentiate between adult and subadult cougars in the harvest this may be sufficient, but few true tests of accuracy have been conducted to estimate bias for this technique. Monitoring the level of adult females in the harvest also is appealing because an increase in this index may indicate the loss of the most vulnerable age and sex classes (Barnhurst 1986) and a reduction in population size. For example, Anderson and Lindzey (2005) noted a population decline when the level of adult females in the harvest reached 25%, while levels of 10–15% appeared sustainable. In comparison, the level of adult females in the Monroe harvest declined from 35% to 0% over a 5-year period. We suggest that this reflects the history of frequent high harvest

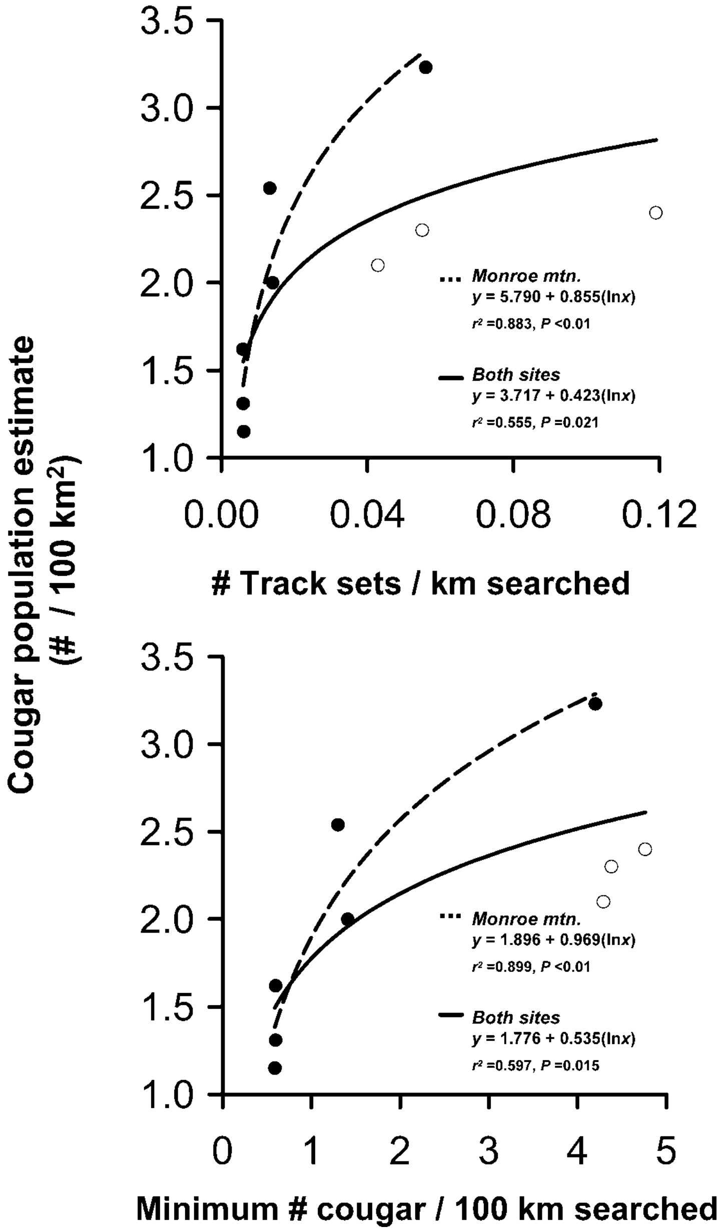

Figure 5. Relationship between the reference cougar population estimate and either the number of track sets encountered per kilometer of route searched (upper panel) or the minimum number of cougars per 100 km of route searched (lower panel) for surveys conducted on either Monroe Mountain (– – –) or Monroe Mountain and the Oquirrh Mountains study sites combined (—), Utah, USA, 1996–2001. Open circles (○) denote data from the Oquirrh Mountains study site.

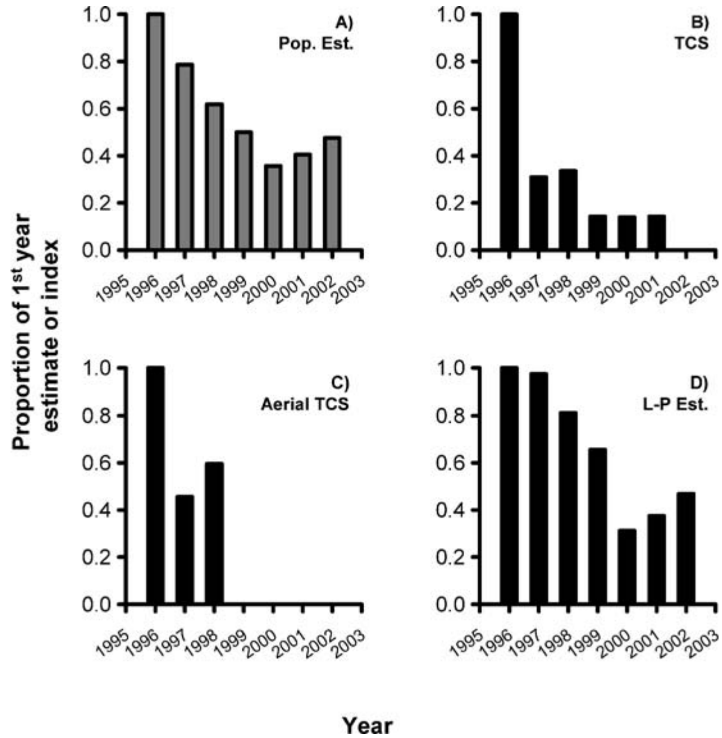

Figure 6. Proportional changes in cougar population estimates or indices relative to the first year of each survey on Monroe Mountain, Utah, USA. Track-count surveys (B), aerial surveys (C), and Lincoln–Petersen (L-P) estimates (D) are compared with changes in population estimates for Monroe Mountain (A).

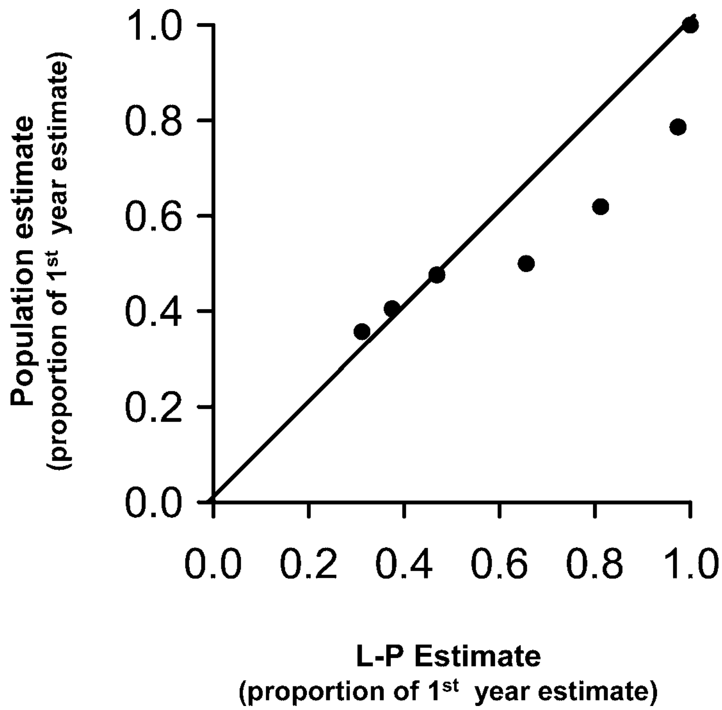

Figure 7. Relationship of proportional changes in the cougar population estimates for the study site, Monroe Mountain, Utah, USA, scaled to the first year's estimate, and proportional changes in the corresponding Lincoln–Petersen (L-P) estimates. The 45° reference line is drawn for comparison.

levels on the unit; adult females comprised 22 ± 2% of the harvest from 1990 to 1994, then rose to 31% in 1995. The subsequent decline in adult females in the harvest may reflect the overall reduction in population size and replacement with young individuals. Therefore, we reiterate Anderson and Lindzey's (2005) warning that harvest composition should be monitored over a number of years prior to drawing inferences about population trend.

Scent-station surveys and related techniques.—The efficacy of scent-station surveys as a population metric remains controversial. Sargeant et al. (1998) suggested that the technique might be useful as a supplement to other monitoring efforts, but evidence supporting a relationship between scent-station indices and actual abundance has not been demonstrated conclusively. Studies with canids and other smaller carnivores indicate disparate results (Conner et al. 1983, Minser 1984, Diefenbach et al. 1994, Novaro et al. 2000). Further, Sargeant et al. (2003) concluded that the index method may not perform well in monitoring wide-ranging carnivores with low probability of detection. Increasing the length of time stations are observed from the 2 nights used in this study and increasing the density of stations would increase the probability that a cougar would encounter a station, but might not increase the likelihood that an individual would leave tracks on a station. The lack of visitation at scent-station sets by radiocollared cougars suggests that the lures were ineffective. Harrison (1997) obtained similar results for scent-station visitation by cougars in Central America using similar attractants. In northeastern Utah, K. Bunnell et al. (Utah State University, unpublished data) detected only 2 visits by cougars during 91,800 trap-nights to hair-snare stations using a lure of castoreum and catnip oil (McKelvey et al. 1999, McDaniel et al. 2000). In addition, P. Beier and D. Mattson (Northern Arizona University, personal communication) placed scent stations 10–30 m from 4 fresh cougar kills (a different radiotagged cougar on each kill) and used a video camera to monitor cougar behavior with respect to the stations on the second night of feeding. In each case the cougar fed on the nearby kill and walked past the scent station several times en route to or from the kill but never rubbed or otherwise interacted with the station Alternatives employing presence–absence metrics with camera traps may have potential (but see Long et al. 2003); however, the success of camera traps may rely more on careful placement than on the attractant. For example, cameras have been successfully deployed on kill sites (e.g., Pierce et al. 1998) and along known travel routes over long time intervals ($\geq$3 weeks; D. Krucki, unpublished data). While saturation of a site with traps will increase the probability of detection, carefully selecting trap sites would require a priori information of cougar travel routes and consideration of overall sampling design in order to limit bias due to selective trap placement. We conclude that scent stations alone do not constitute a viable survey technique for cougars.

Ground-based track counts.—That track surveys can reliably detect only large changes in density is well documented (Van Sickle and Lindzey 1992, Beier and Cunningham 1996, Hayward et al. 2002). However, this does not diminish the utility of track surveys for detecting large and potentially threatening declines of carnivore populations (e.g., Kendall et al. 1992). As argued by Caughley (1977) and suggested by Hayward et al. (2002), an index can still provide adequate information for management purposes. However, as an index of abundance, track counts also demonstrate disparate results. Van Sickle and Lindzey (1992) found a significant relationship between the number of cougar home ranges overlapping with transects and the number of track sets found per kilometer searched; however, density was not related to track-finding frequency. Conversely, we found a significant relationship between cougar density and track-detection frequency in environments with tracking conditions similar to Van Sickle and Lindzey's (1992) study area (Fig. 5). Although our results are encouraging, we caution against ready application of these regression models for predicting population sizes. The nonlinear relationship between cougar density and track-finding frequency suggests a lower limit to detection and an upper limit to resolution of cougar density. Track surveys may be unable to detect differences in population size below densities of 1.6 cougars/100 km^2 and above densities of 3.0 cougars/100 km^2. Behaviorally this result may arise from the saturation of available habitat at greater densities, thereby imposing a limit on how many individuals may travel across a given space or from the difficulty in distinguishing among overlapping track sets. At low densities the probability of detection may be insufficient for detecting any track evidence or differentiating among population estimates, being prone to bias from chance or poor tracking conditions (e.g., substrate, weather) Adult cougar densities reported in radiotelemetry studies vary across different environments in North America from 0.3–0.5/100 km^2 in the Boulder-Escalante region of southern Utah (Hemker et al. 1984) to 1.5–2.2/100 km^2 in Alberta (Ross and Jalkotzy 1992; see also Logan and Sweanor 2001). Therefore, track surveys may provide reliable information only for populations that display a much smaller range of densities. Considering conservation priorities, this may be sufficient.

Track surveys incorporating information from track measures explained more variation in cougar population estimates (Fig. 5), than presence–absence measures of track sets per kilometer searched. However, determination of individual identity from tracks is not infallible. Our track ratio of front and rear feet measurements, conducted by a trained research team performed well, but consistency in measurements varied by as much as $\pm$2 mm among individuals (D. M. Choate, unpublished data). Other investigators (Smallwood and Fitzhugh 1993, Grigione et al. 1999, Lewison et al. 2001, Rosas-Rosas et al. 2003) have been able to correctly identify individual cougars using track measures. Despite increased variation from tracing track edges from photographs as opposed to physically measuring tracks in situ, multiple-track measures may provide more certainty for discriminating among individuals (Riordan 1998, Grigione et al. 1999, Lewison et al. 2001). However fewer but reliable measures as used in this and other studies (Smith et al. 1999) may provide greater utility among field personnel. Temporary residency of unmarked individuals (i.e., transients) may inflate population estimates derived using this technique. Even though we developed a regression model for predicting cougar abundance based on estimates of track counts, a better understanding is required of how ubiquitous the negative binomial distribution is for describing cougar track counts, across a greater variety of environments and cougar densities than those used in this study.

Cost comparisons.—Capture and marking of animals with radiotelemetry was the most costly of the techniques employed in this study (Table 4), but it also was the most sensitive for estimating population size. The difference in cost between capture and aerial surveys, even when a minimum of 3 aerial surveys are conducted, is substantial (approx. $10,000). The cost-efficiency difference is widened by the reduction in field time, however, because helicopter surveys require fewer person-hours to conduct than a mark–recapture study. In addition, aerial population estimates can be derived immediately following the survey

Table 4. Cost comparison of different survey techniques for cougars on Monroe Mountain, Utah, USA, 1996–2001.

Survey method	Equipment and personnel	Cost	Total costs
Summer track surveys	Technician	\$8.00/hr × 52 hr	\$416.00
	Vehicle (gasoline)	\$0.22/km × ~2,900 km/month	\$640.00
			~\$1,056.00/survey[a]
Scent-station surveys	Technician	\$8.00/hr × 240 hr	\$1,920.00
	Scent discs	\$0.40/tab × 110 tabs	\$44.00
	Scent	\$20.00 for 3 lures	\$20.00
	Misc. tools, equipment		\$50.00
	Vehicle	\$0.22/km × ~1,800 km	\$396.00
			~\$2,430.00/survey[a]
Helicopter surveys	Helicopter, pilot, fuel	\$500.00/hr × 8 hr	\$4,000.00
	Tracker	\$150/d	\$150.00
	Technician	\$8.00/hr	\$80.00
			~\$4,230.00/survey[b]
Capture–mark–recapture	Radiocollars	\$280.00/collar × 10	\$2,800.00
	Gasoline	\$0.22/km × ~3,220 km/month	\$880.00
	Houndsman's services	\$150.00/day × 40 d	\$6,000.00
	Air time	\$200.00/hr × 24 flights[c]	\$9,600.00
	Technician	\$8.00/hr × 8 hr/d × 40 days	\$2,560.00
	Misc. capture supplies		\$500.00
	Misc. vehicle expenses		\$500.00
			\$22,840/40-d effort

[a] Each survey was completed during a 4-month period: 1 Jun–30 Sep.
[b] To reliably estimate sampling variance a minimum of 3 surveys/site is required; on average 1 survey requiring 6 hr of flight time was completed each day.
[c] Estimated 1 yr of flight time = [(2 flights/month) × (2 hr/flight)].

providing information more rapidly than season-long surveys. Aside from the significant constraints of orchestrating helicopter availability with suitable survey conditions as demonstrated by this study, aerial surveys are inherently the most dangerous. Although noninvasive techniques such as genetic sampling may become a cost-effective method after development of primers for sample analyses, issues concerning effectively marking an appropriate sample of cougars and sufficient recapture rate may offset this cost reduction. Ground-based track surveys remain the least expensive survey technique and might be the most cost-efficient method, but with 2 important caveats. First, although our regression model may predict densities well within a limited range of population size, it may not apply to other sites with different tracking conditions. Second, as an index rather than an estimator, track surveys may be sufficient for monitoring population change across years; however, we would still recommend calibrating the index with at least an initial estimate using other methods (i.e., capture–mark–recapture). Winter track counts may be more efficient than summer counts due to better tracking conditions and could be conducted immediately prior to a hunting season to more closely relate the index to management objectives. While winter surveys remain to be tested, 2 related sampling issues should be considered. First, for low-density sites, surveys would need to be conducted over a sufficiently long interval(s) to increase track-detection rates; single day or weekend surveys employing many field personnel may result in an underestimate depending on movement rates of cougars, for example, relative to time since the last snowfall. Seasonal differences in snowfall may preclude this option for sites that are managed for hunting if the season opens prior to the first snowfall. Second, losses of animals during a hunting season may bias survey results. Similar considerations hold as discussed for the aerial track methods. Finally, track-based surveys in either season trade off cost for sensitivity to changes in population size. As well recalled by a reviewer, the old adage that you get what you pay for is most pertinent here.

Summary

Despite extensive research there remains no single reliable and cost-effective technique for estimating cougar abundance. Track estimators performed poorly as individual indices of population size; however, proportional changes over time were well related to similar proportional changes in indices. No single method other than costly capture and radiotelemetry study provides a panacea to the problem of enumerating cougar populations. Conservative application of indices derived from multiple techniques will provide the most confidence in short-term management decisions; however, better estimates require an initial population estimation period employing marking techniques to establish a baseline for comparison in subsequent years. Despite the allure of lower-cost index measures, the lack of sensitivity to population changes by indices, particularly over time scales involved in management decisions (e.g., annual harvests), warrants considerable caution in their application. Where surveys of any form are not possible, alternative approaches may be used to assist in guarding against uncertainty in management decisions. For example, careful timing of hunting seasons to protect young cougars and females, limiting the level of females harvested, and monitoring the age and sex class of animals in the harvest may help prevent population declines (CMGWG 2005). In addition, 2 large-scale options have been proposed that recognize the interconnected but patchy distribution of cougar populations: a metapopulation approach (Laundré and Clark 2003, Stoner et al. 2006) and zone management (Logan and Sweanor 2001, CMGWG 2005). A metapopulation approach considers the spatial arrangement and connectivity of subpopulations to allow for several to serve as sources or refuges relative to more heavily hunted sinks. Zone management extends this functionally to larger regions, which are adaptively managed for hunting, for control (i.e., predator reduction), or as a refuge. Monitoring plans that target specific populations within these frameworks for more accurate estimation may provide a reasonable compromise.

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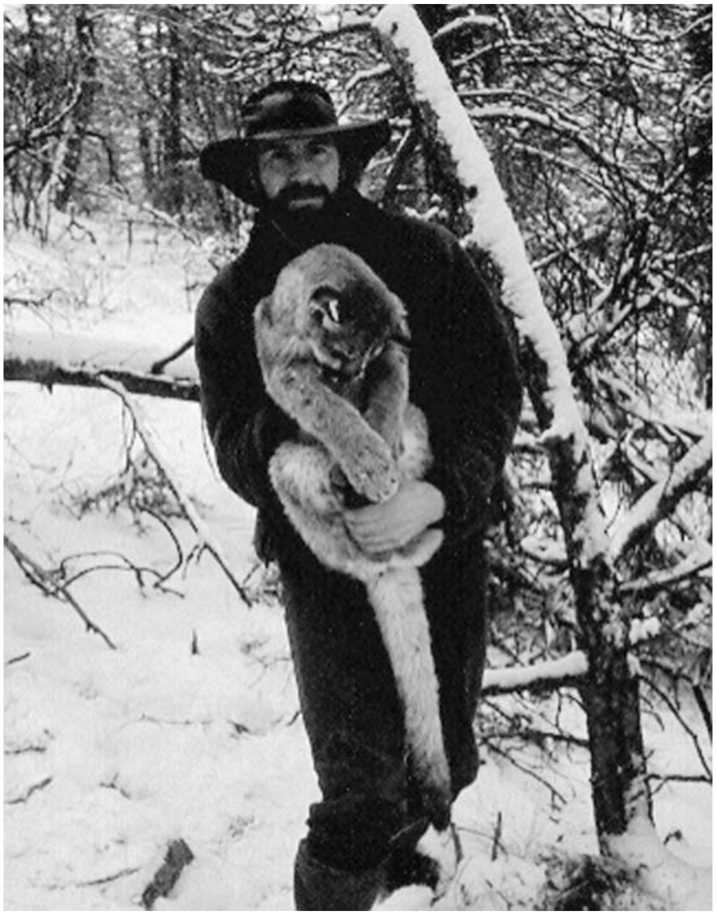

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