The Journal of Wildlife Management 80(1):27–36; 2016; DOI: 10.1002/jwmg.985

Research Article

Evaluation of Harvest Indices for Monitoring Cougar Survival and Abundance

MICHAEL L. WOLFE, *Department of Wildland Resources, Utah State University, Logan, UT 84322-5230, USA*
ERIC M. GESE, *U.S. Department of Agriculture, Wildlife Services, National Wildlife Research Center, Department of Wildland Resources, Utah State University, Logan, UT 84322-5230, USA*
PAT TERLETZKY, *Department of Wildland Resources, Utah State University, Logan, UT 84322-5230, USA*
DAVID C. STONER, *Department of Wildland Resources, Utah State University, Logan, UT 84322-5230, USA*
LISE M. AUBRY,[1] *Department of Wildland Resources & the Ecology Center, Utah State University, Logan, UT 84322-5230, USA*

ABSTRACT Harvest indices are used by state wildlife management agencies to monitor population trends and set harvest quotas for furbearer species. Although harvest indices may be readily collected from hunters, the reliability of harvest indices for monitoring demography and abundance of the harvested species is rarely examined, particularly amongst large carnivores. The overall objective of this study was to assess whether cougar (*Puma concolor*) harvest statistics collected by wildlife managers were correlated with changes in cougar demography, mainly survival rates and abundance. We estimated key demographic parameters for 2 cougar populations in Utah over 17 years during which we monitored 235 radio-collared cougars. We then compared these demographic parameters to harvest statistics provided by the Utah Division of Wildlife Resources over the same time period for the Oquirrh-Stansbury (lightly harvested population) and Monroe (heavily harvested population) harvest management units. In the Oquirrh-Stansbury unit, the percent of harvested cougars >6 years old was positively correlated with annual survival, indicative of a population experiencing several years of high survival resulting in an older age structure. Percent of permits filled and cougar abundance were also significantly correlated, suggesting higher hunting success with increased density. In the Monroe management unit, the annual percent of permits filled was correlated with changes in overall annual survival and male and female annual survival. Of utmost importance, pursuit success (cougars treed/day) increased with the number of cougars on the unit suggesting that pursuit indices may be an informative metric for wildlife managers to determine cougar population trends. Because both management units were subjected to contrasting mortality regimes, results provided by this assessment could potentially be applied to additional management areas sharing similar ecological characteristics and harvest metrics. Published 2015. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS abundance, competing risks, exploitation, harvest statistics, management, mortality, *Puma concolor*, survival.

Knowledge of the status of a carnivore population is essential for the development and implementation of an effective management plan (Ginsberg 2001, Pollock et al. 2012). Carnivores are often managed through regulated sport hunting to maintain viable populations (Sillero-Zubiri and Laurenson 2001, Keefover-Ring 2005), and reduce impacts of predation on their principal prey species and domestic livestock (Treves and Karanth 2003, Anderson et al. 2010, Loveridge et al. 2010). Management agencies often face the difficulty of opposing demands for more effective carnivore control to protect human safety, big game populations, and domestic livestock, and the demand for additional carnivore-hunting opportunities by sportsmen and outfitters and even societal demands for protection from exploitation (Sillero-Zubiri and Laurenson 2001, Anderson et al. 2010, Funston et al. 2013).

Given their large spatial requirements, low densities, and elusiveness, the management of large carnivores is often challenging because of the difficulties in estimating vital rates and population abundance (Gese 2001, Pollock et al. 2012). Cougar (*Puma concolor*) management nevertheless depends on the ability to monitor demographic responses to changing policies and management actions (Anderson et al. 2010). Unfortunately, state and provincial wildlife agencies are often required to make management decisions without the demographic information needed to monitor and maintain sustainable cougar population levels from one harvest season to the next (i.e., adaptive harvest management) because this information is often unavailable. Frequently, harvest

Received: 1 December 2014; Accepted: 13 August 2015

[1]*E-mail: lise.aubry@usu.edu*

composition statistics (e.g., age structure and sex composition) are used in lieu of measured demographic variables of population performance and abundance (Whittaker and Wolfe 2011). Harvest data alone is not sufficient for estimation of population size but rather should be used in conjunction with additional demographic data such as annual survival rates (Erickson 1982, Kolenosky and Strathearn 1987, Lindzey 1987, Rolley 1987, Chilelli et al. 1996). The question arises as to whether harvest statistics and harvest composition are reasonable approximations of changes in demographic performance (e.g., survival) and population abundance over time.

Of all demographic estimates, wildlife managers are most interested in monitoring animal abundance because annual changes in abundance measure the net balance among births, immigrants, deaths, and emigrants (BIDE), and indicate whether there is a surplus that can be sustainably harvested from year to year. Because a complete census is never possible, abundance must be estimated using appropriate methods that can account for imperfect detection and even multiple counting of individuals. Indeed, a number of approaches have been proposed for estimating cougar abundance and associated densities (Van Dyke et al. 1986, Smallwood and Fitzhugh 1995, Choate et al. 2006), but all have logistic limitations and statistical assumptions that are difficult to meet in a field setting.

When abundance becomes too difficult to accurately estimate, attention is sometimes transferred to the BIDE vital rates that determine abundance to monitor population trends rather than abundance per se. Immigration and emigration may play a large role in the change of male cougar abundance (Robinson et al. 2008), but in the female-limiting component of the population attention should be focused on reproductive success and survival (Lambert et al. 2006). Regardless of whether the focus is on the male or female component, cause-specific mortality analyses can provide deeper insight into the factors underlying management-relevant changes in survival and population dynamics (e.g., hunting vs. vehicle collisions).

The Utah Division of Wildlife Resources (UDWR) currently uses harvest rate, percent females in the harvest, and number of cougars treed per day to set the following years harvest quotas (Utah Cougar Advisory Group 2011). The cougars treed per day can be thought of a catch-per-unit-effort estimator (Choate et al. 2006). Although there was no significant relationship between cougars treed/day and the size of 2 cougar populations monitored for 6 years (Choate et al. 2006), the UDWR incorporates this index in their formula to determine harvest levels. We calculated estimates of key demographic parameters from 2 cougar populations that were intensively monitored in Utah for 17 years, and compared these estimates to harvest statistics provided by the UDWR over the length of the study period. Cougars in the Oquirrh-Stansbury cougar management unit (OSCMU) were primarily exposed to non-hunting anthropogenic sources of mortality and cougars in the Monroe cougar management unit (MCMU) were mostly influenced by hunting mortality. Our objective was to assess the correlations between currently used harvest statistics and independently derived population parameters within the OSCMU and MCMU.

STUDY AREA

We examined cougar populations on the OSCMU and MCMU, located in the Great Basin and Colorado Plateau ecoregions, respectively, in Utah. Mountain ranges in these ecoregions were surrounded by desert basins and formed a basin and range landscape. Annual precipitation ranged from 60 cm to 120 cm in the higher elevations to 15–20 cm in the desert basin regions with most of the precipitation arriving as snow in January and February (Moller and Gillies 2008). The Oquirrh-Traverse Mountains were dominated by Gambel oak (*Quercus gambelii*), sagebrush (*Artemisia* spp.), and Utah juniper (*Juniperus osteosperma*), whereas Monroe Mountain was dominated by pinyon (*Pinus edulis*)-juniper (*Juniperus* spp.) woodlands.

The OSCMU was located in north-central Utah on the eastern edge of the Great Basin (40.5°N, 112.2°W). The Oquirrh Mountains measured >950 km^2, but the study area was focused on a 500-km^2 area encompassing the northeastern slope on properties owned and managed by the Utah Army National Guard (Camp Williams) and the Kennecott Utah Copper Corporation. The site was bounded on the north by the Great Salt Lake and on the east by the Salt Lake Valley. Approximately, 55% of the study area was under the jurisdiction of the Bureau of Land Management (BLM), with the remainder held by individuals, grazing associations, mining companies, and the military. The study area was situated within the larger OSCMU, but both properties (Camp Williams and Kennecott) were closed to the public and cougar hunting was prohibited. Although radio-collared cougars leaving those properties were legally protected within the management unit, they were susceptible to poaching, depredation control, trapping, and road kill. Thus, this population was considered to be semi-protected.

Monroe Mountain comprised part of the Sevier Plateau in south-central Utah (38.5°N, 112°W). The study area measured approximately 1,300 km^2, and formed the central part of the Fishlake National Forest. Additional landholders included the BLM, the State, and various private interests. The study area was within the MCMU, where cougars were managed for sustainable hunting opportunities. Other carnivores present included bobcats (*Lynx rufus*) and coyotes (*Canis latrans*), which were both subject to trapping pressure. Resource use included livestock grazing (cattle, sheep), logging, fossil fuel exploration, and off highway vehicle recreation (e.g., all terrain vehicles). Stoner et al. (2006) provide a more detailed description of the study areas.

METHODS

Cougar Harvest in Utah

Nearly all cougars harvested in Utah are taken with the aid of dogs (Utah Cougar Advisory Group 2011). An individual hunter is restricted to holding either a limited entry permit or a harvest objective permit per season, and must wait 3 years to reapply once they acquire a limited-entry permit. The bag limit is 1 cougar/season, and kittens and females accompanied by young are generally protected from harvest. Currently, the cougar hunting season runs from late November through late May on both limited entry and most harvest objective units. Some units are open year-round and some have earlier or later opening dates. Pursuit (chase or no-kill) seasons provide additional recreational opportunities over most of the state. The pursuit season generally follows the hunting season, but specific units have year-round pursuit and a few units are closed to pursuit (Utah Cougar Advisory Group 2011).

We used information covering 1996–2012 that was published in the most recent Utah Cougar Annual Report (Utah Division of Wildlife Resources 2012), which collated information for a number of harvest and pursuit statistics used by UDWR managers from the OSCMU and MCMU; reporting of each cougar harvested is legally mandated. We first focused on the 3 indices used to monitor cougar population trends and guide management in Utah: percent females in harvest, number of cougars treed per day, and number of cougars harvested annually. We examined additional harvest indicators that were specific to each sex (i.e., annual no. harvested males, % of males in the harvest) and harvest indicators that pertained to age (i.e., proportion of cougars that were $\geq$6 years of age in the harvest, the mean age of harvested animals each year). Finally, we examined statistics related directly to harvest regulations (i.e., % of hunting permits filled each year, no. sport-harvested cougars, no. harvest permits allotted, including all limited entry, conservation, and conventional permits; Utah Division of Wildlife Resources 2012).

Field Methods

From January 1996 to June 2012, we conducted capture efforts during winter (Dec to Apr). We pursued cougars with trained hounds, and then immobilized each cougar with a combination of ketamine hydrochloride (10 mg/kg) and xylazine hydrochloride (2 mg/kg; Fort Dodge Animal Health, Fort Dodge, IA) following recommendations in Kreeger (1996). We sexed, weighed, measured, ear tattooed, and microchipped (AVID, Norco, CA) each individual. For aging the animal, we extracted a vestigial premolar (P2) for aging with cementum annuli, a field estimate of age using gum-line recession (Laundré et al. 2000), and tooth wear (Ashman et al. 1983). We fitted all adult (>24 months) and sub-adult (12–24 months) cougars with a very high frequency (VHF) radio-collar (Advanced Telemetry Systems, Isanti, MN) or a global positioning system (GPS) collar (i.e., Televilt Simplex, Lindesberg, Sweden; LoTek 4400S, Newmarket, Ontario, Canada). We located cougars with a VHF collar twice a month with aerial or ground telemetry (Mech 1983); we attempted to acquire locations of cougars with a GPS collar every 3 hours. We marked kittens (0–12 months) that were too small to wear a radio-collar with a microchip (AVID) and tattooed their ears with a unique identification number. We released all animals at the capture site. For each population, data collection was based on radio-telemetry information collected between 1 January 1996 and 30 June 2012. Animal capture and handling procedures were conducted in accordance with Utah State University Institutional Animal Care and Use Committee standards (approval no. 937-R).

The Utah cougar hunting season commenced in mid-November and continued to the end of May each year. However, most of the harvest occurred during a 4-month period when snow was on the ground (Dec to Mar). We used individual locations within the MCMU collected after 1 March 1996, directly after the harvest season, so we would not split a harvest season across an analysis year and to maximize use of available data (the first individuals were marked in Jan 1996); similarly, the study began in the OSCMU on the 1 March 1997.

The fate of most marked individuals was known with the exception of 11 cases for which we could not ascertain an emigration or death status. We ascertained emigration status and radio-collar failures for 35 and 47 individuals in the QSCMU and the MCMU, respectively (Table 1). Kittens that did not survive to age 1 were not included in the analyses because their fates were dependent on the fate of their mothers. However, kittens that survived to their first birthday and remained in the unit where they were initially marked were included in the analyses; through left-truncation, we included such individuals from age 1 onward in all analyses.

We determined the causes of mortality through visual inspection and necropsy of carcasses (Stoner et al. 2006). When we could not determine cause of death in the field, we submitted the carcass to the Utah Veterinary Diagnostics Lab (Logan, Utah) for a detailed necropsy. Precision of mortality dates varied: with GPS-collared and hunter-harvested animal mortality, dates were known to within 1 day, whereas we estimated dates for animals wearing conventional VHF radio-collars using the midpoint between the last live signal and the detection date of the first mortality signal (+/− 15 days).

Demographic Analyses

Classical survival models used in human demography (Kleinbaum and Klein 2005) are appropriate for estimating survival trajectories when individuals are followed from entrance into the study until death (Murray et al. 2010, Aubry et al. 2011, Sandercock et al. 2011). Various extensions to the non-parametric Kaplan–Meier (Kaplan and Meier 1958) estimator, such as the Cox Proportional Hazard model (CPH; Cox 1972), further allow identification of the measurable (i.e., observed) covariates associated with patterns in survival trajectories. We used semi-parametric CPH models because they do not require assumptions about the shape of the underlying mortality hazard (the force of mortality) over life. Rather, each covariate within the model is assumed to act multiplicatively (i.e., proportionally) on the baseline mortality hazard at each time step (Bradburn et al. 2003): $h_i(t) = h_0(t)^{*}\exp(\beta_i X_i)$ such as where h_0 refers to the baseline hazard (i.e., the hazard's value when all covariate values are null), X denotes a vector of

Table 1. Sex- and location-specific deaths by cause of mortality for radio-collared cougars in the Oquirrh-Stansbury Cougar Management Unit (OSCMU), 1997–2012, and in the Monroe Cougar Management Unit (MCMU), 1996–2012, Utah, USA.

	OSCMU						MCMU					
	Total		Females		Males		Total		Females		Males	
Mortality cause	*n*	% of total mortality	*n*	% of total mortality	*n*	% of total mortality	*n*	% of total mortality	*n*	% of total mortality	*n*	% of total mortality
1 Hunting	16	32.0	5	17.2	11	52.4	72	67.9	28	53.8	44	81.5
2 Poaching	1	2.0	1	3.4	0	0.0	6	5.7	4	7.7	2	3.7
3 Depredation control	1	2.0	0	0.0	1	4.8	7	6.6	5	9.6	2	3.0
4 Road kill	3	6.0	3	10.3	0	0.0	0	0.0	0	0.0	0	0.0
5 Capture mortality	1	2.0	1	3.4	0	0.0	4	3.8	3	5.8	1	1.8
6 Intra-specific strife	11	22.0	6	20.7	5	23.8	12	11.3	8	15.4	4	7.4
7 Predation attempt	5	10.0	3	10.3	2	9.5	3	2.8	2	3.8	1	1.8
8 Injury, starvation	12	24.0	10	34.5	2	9.5	2	1.9	2	3.5	0	0.0
Total mortality	50		29		21		106		52		54	
Anthropogenic (1–5)	22	44.0	10	34.5	12	57.1	89	83.9	40	76.9	49	90.7
Harvest (1)	16	32.0	5	17.2	11	52.4	72	67.9	28	53.8	44	81.5
Natural only (6–8)	28	56.0	19	65.5	9	42.9	17	16.0	12	23.1	5	9.3

covariates such as $X = (X_1, X_2, \ldots X_i)$, and t denotes time (in our case, time elapsed since marking; Murray and Patterson 2006). We conducted all analyses in R (version 2.15.0, Development Core Team 2012).

Standard survival estimators consider the elapsed time from some origin until the occurrence of death or failure. If $\geq$1 type of end point is of interest, these end points are called competing risks (Geskus 2011). With radio-telemetry data, a competing risk analysis can be used to attain unbiased estimates of cause-specific mortality, whereas standard tabular presentations of percentage representations for cause-of-death data are inherently biased (Heisey and Patterson 2006) but can nevertheless be useful to visualize the cause of death data. Because specific causes of mortality might be more reliable indicators of harvest statistics used to guide cougar management, we considered 2 dichotomies in mortality estimates. We estimated annual cause-specific mortality at each study area for human harvest versus all other causes of death, or all anthropogenic causes of mortality (i.e., harvest, poaching, depredation control, road kill, capture-related mortality) versus natural mortality agents (i.e., intra-specific strife, injury during predation attempt) using the R package wild1 (Sargeant 2011, Wolfe et al. 2015). For the purpose of this assessment, we were specifically interested in estimating annual mortality from hunting exclusively (i.e., the harvest rate $\hat{h}_t$) because it should be most closely linked to harvest statistics if such relationships exist.

We used a minimum abundance index or population estimate for each management unit that included the number of adults and independent sub-adults (i.e., no longer with their mother) based on all captures, radio-telemetry, tracking, and mortality data (Logan and Sweanor 2001, Choate et al. 2006, Cooley et al. 2009). We also calculated corresponding densities based on the size of each unit (adult and independent sub-adult cougars per 100 km^2).

We used Spearman's rank correlation coefficient (r) to examine the relationships between the harvest indices collected by the UDWR and the independently derived demographic rates (Zar 1999). Correlation coefficients range from -1 (i.e., perfect negative correlation) to $+1$ (i.e., perfect positive correlation), where a correlation of 0 indicates there is no relationship between the 2 variables. We used the standard error of a correlation coefficient to determine the confidence intervals around a true correlation of 0, and t-tests to test the null hypothesis that the true correlation was 0 (Zar 1999). For each analysis, we reported the correlation coefficient and associated P-value and considered correlation coefficients with P-values $\leq$0.10 significant.

RESULTS

Overall, demographic analyses were based on 235 marked individual cougars (MCMU: $n = 148$, 66 M and 82 F, 37 sub-adults and 111 adults; OSCMU: $n = 87$, 32 M and 55 F, 24 sub-adults and 63 adults). Seventeen individuals died of natural mortality and 89 of anthropogenic causes in MCMU. In the OSCMU, 28 individuals died of natural death versus 22 of anthropogenic causes (Table 1). In the MCMU, 72 individuals were harvested and 34 individuals died of non-harvest mortality (i.e., all other causes of death). Within the OSCMU, 16 individuals were harvested and 34 individuals died of other causes (Table 1). An additional 82 cougars were right-censored because they were still alive at the end of the study or because they emigrated from the management unit (47 in MCMU and 35 in OSCMU; i.e., the data they provided while on the study area was used until they emigrated out of the study area).

We calculated an abundance index akin to a minimum population abundance estimate for each unit (Fig. 1). In the OSCMU, this index fluctuated between 10 and 20 adults and independent subadult cougars over time, with a corresponding density that ranged from 2 to 4 adult and independent subadult cougars/100 km^2 (Fig. 1). In the MCMU, this index ranged from 10 to 40 adult and independent subadults, for a corresponding density of 1 to 3.5 adult and independent subadult cougars/100 km^2 (Fig. 1).

Unit-Specific Demographic Estimates and Harvest Statistics

Annual survival fluctuated over time in the OSCMU (Fig. 2A) and MCMU (Fig. 2B). Notably, in 1999 and 2012

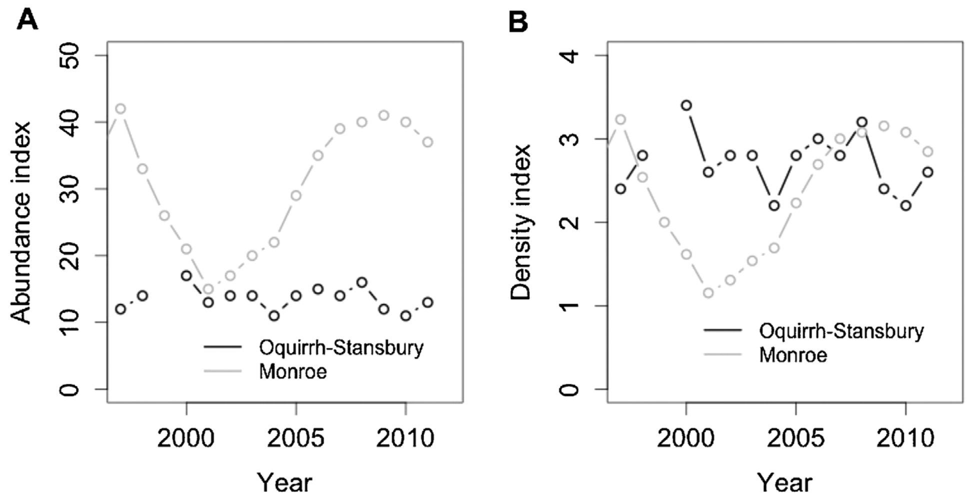

Figure 1. Changes in A) cougar abundance and B) associated density index (cougars/100 km^2), for adult and independent subadult cougars on the Oquirrh-Stansbury (1997–2012) and the Monroe (1996–2012) study areas, in Utah, USA.

annual survival in the MCMU was low (Fig. 2B). Male survival was consistently lower than female survival in both units, and survival was higher in the OSCMU compared to MCMU (Fig. 2).

In the OSCMU, the primary cause of death in males was harvest (Table 1, Fig. 3), and natural causes (injury, starvation) in females (Table 1). Intra-specific strife was also an important influence of overall mortality, equally distributed between females and males (Table 1). Individuals between ages 2 and 6 primarily died from harvest mortality or other sources of anthropogenic mortality (e.g., car collision, Wildlife Services removals). For individuals that died of non-harvest mortality, females died at a later age on average than males (Wolfe et al. 2015). Over the span of the MCMU, 67% of all individuals that died were harvested (Table 1, Fig. 3). All age-classes were subjected to harvest and non-harvest causes of mortality, and more individuals died between 2 and 4 years of age compared to any other age class.

Generally, in the OSCMU we observed a decrease in harvest indices over time. In the MCMU, however, we observed an increase in harvest indices over the last few years of the study. Specifically, increases were observed in the total harvest and in the percentage of harvest permits filled since 2006, along with an increase in the percentage of cougars harvested that were >6 years old and in the number of females harvested since 2009. The number of cougars treed/day (i.e., pursuit statistic) and mean age at harvest fluctuated over time with an increase in the pursuit statistic and harvest pressure since 2004 in the MCMU.

Correlation of Demographic Estimates and Harvest

We found significant correlations between several harvest statistics and demographic estimates for the OSCMU (Table 2) and MCMU (Table 3). In the OSCMU, we found the percent of permits filled and the minimum abundance index were positively correlated (Fig. 4A, Table 2). Further, the percent of individuals in the harvest

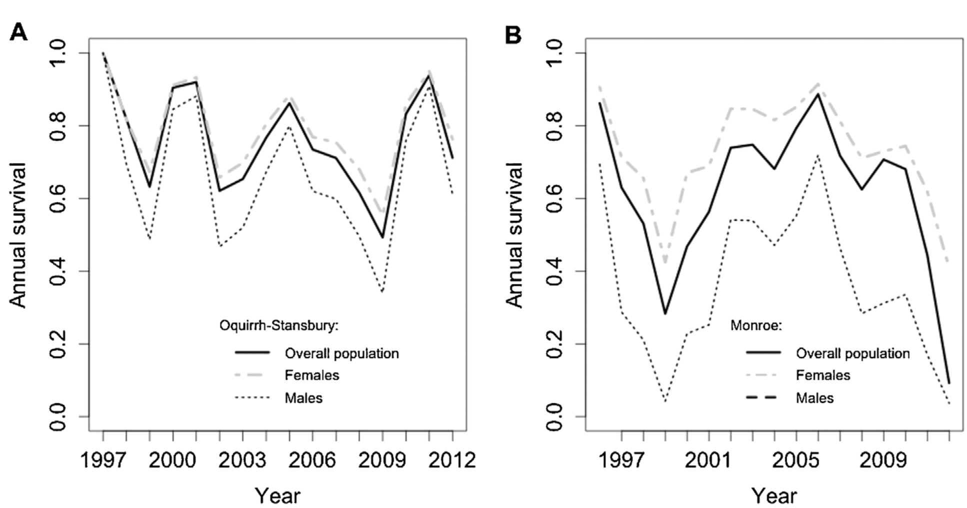

Figure 2. Changes in overall and sex-specific annual survival for radio-collared cougars in the A) Oquirrh-Stansbury and B) Monroe study areas in Utah, USA from 1997 to 2012 and 1996 to 2012, respectively.

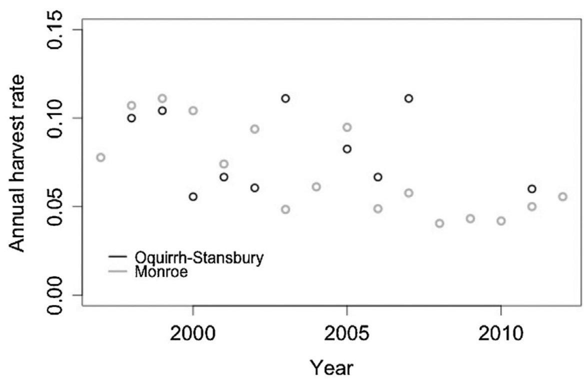

Figure 3. Changes in annual harvest mortality estimates over time in the Oquirrh-Stansbury and Monroe study areas Utah, USA from 1997 to 2012 and 1996 to 2012, respectively.

>6 years old was positively correlated with annual survival, annual male survival, and annual female survival (Fig. 4B–D, Table 2). In the MCMU, which experienced greater hunting pressure, overall annual harvest mortality was principally influenced by male annual harvest mortality (Fig. 5A, Table 3). We also observed a negative relationship between the annual number of females in the harvest and annual survival (Fig. 5B, Table 3). Additionally, we found a negative correlation between the annual proportion of females in the harvest and annual survival (Fig. 5F, Table 3). Further, percentage of permits filled each year was positively correlated with overall annual survival, annual male survival, and annual female survival (Fig. 5, Table 3). We detected a positive relationship between the number of cougars treed/day and the annual abundance index (Fig. 5G, Table 3), suggesting that pursuit success increased with the number of cougars on the unit.

DISCUSSION

Monitoring survival and determining the abundance of large carnivores is a daunting task for many wildlife agencies. Being able to use indirect measures of abundance to monitor changes in population size and survival (i.e., harvest) has routinely been used for large carnivores and cougars in particular, for several decades (Beausoleil et al. 2008, Whittaker and Wolfe 2011). However, knowing the relationships between these indirect measures or harvest indices and actual demographic parameters such as survival and population abundance requires long-term data collected with consistent field methodologies.

Even though intense harvest in the MCMU was a potential concern for sustainable management of cougars in this region, cougar densities assessed from the marked population indicated that densities rebounded and have been maintained at 3 adult cougars/100 km^2 over the last few years (Fig. 1). Immigration was a factor that we were not able to quantify, but the age structure indicated that an influx of cougars since 2006 has likely compensated for increased removal of cougar residents through hunting. Additional data on cougar movement in and out of the study area would be needed to quantify this influx, and the role immigration plays in maintaining stable dynamics (Sweanor et al. 2000, Robinson et al. 2008, Cooley et al. 2009). Abundance estimates obtained from the results of genetic mark-recapture procedures (Long et al. 2008, Kelly et al. 2012), and more sophisticated analytical methods such as dead recovery multi-state analysis (Koons et al. 2014) could help improve abundance estimates in the future. However, the question of whether a density of 3 adult cougars/100 km^2 is the target density that state wildlife agencies should manage for remains unresolved.

Densities ranged from 2 to 4 adult and independent subadult cougars/100 km^2 in the OSCMU and 1 to 3.5 adult and subadult cougars/100 km^2 in the MCMU (Fig. 1). According to the 2009–2021 Utah Cougar Management Plan (Utah Cougar Advisory Group 2011), high quality habitat was assigned a density range of 2.5–3.9 adult and subadult cougars/100 km^2, medium quality habitat was 1.7–2.5 adult and subadult cougars cougars/100 km^2, and low quality habitat was 0.26–0.52 adult and subadult cougars cougars/100 km^2. According to these standards, the OSCMU and MCMU cougar populations would be classed as high quality habitat. Because cougars have large home ranges, these numbers would be valid in locations where cougar home ranges are not constrained by human development and encroachment. This is not the case in the OSCMU, and might not hold true in the MCMU either.

Table 2. Correlations matrix between demographic parameters and harvest statistics in the Oquirrh-Stansbury Cougar Management Unit, 1997–2012, Utah, USA. Significant correlations ($P < 0.1$) are indicated with an asterisk.

		Harvest statistics							
Demographic parameter		**Sport harvest**	**Male sport harvest**	**Female sport harvest**	**% permits filled**	**% harvest >6 years**	**% females harvested**	**No. cougars treed/day**	**Mean age of harvest**
Annual survival	*r*	0.192	0.052	0.329	0.063	0.552*	0.313	−0.093	0.267
	P	0.475	0.847	0.213	0.816	0.026*	0.237	0.742	0.318
Annual male	*r*	0.131			0.013	0.546*	0.307	−0.123	0.286
survival	*P*	0.627			0.961	0.028*	0.248	0.663	0.282
Annual female	*r*	0.132			0.029	0.550*	0.293	−0.099	0.268
survival	*P*	0.625			0.913	0.027*	0.271	0.726	0.315
Annual	*r*	0.218	0.284	0.104	0.600*	−0.199	−0.337	0.260	−0.358
abundance index	*P*	0.453	0.325	0.723	0.023*	0.496	0.238	0.390	0.209
Annual harvest	*r*	−0.435	−0.393	−0.396	−0.433	−0.441	−0.002	0.062	−0.460
mortality	*P*	0.209	0.261	0.258	0.211	0.202	0.996	0.864	0.181

Table 3. Correlations matrix between demographic parameters and harvest statistics in the Monroe Cougar Management Unit, 1996–2012, Utah, USA. Significant correlations ($P < 0.1$) are indicated with an asterisk.

		Harvest statistics							
Demographic parameter		**Sport harvest**	**Male sport harvest**	**Female sport harvest**	**% permits filled**	**% harvest >6 years**	**% females harvested**	**No. cougars treed/day**	**Mean age of harvest**
Annual survival	*r*	−0.237	0.035	−0.419*	0.630*	0.034	−0.453*	0.058	0.056
	P	0.359	0.893	0.094*	0.009*	0.896	0.067*	0.836	0.831
Annual male survival	*r*	−0.275			0.659*	−0.065	−0.370	−0.193	−0.050
	P	0.275			0.050*	0.804	0.144	0.490	0.849
Annual female survival	*r*	−0.262			0.679*	0.030	−0.374	−0.131	0.041
	P	0.310			0.004*	0.908	0.139	0.641	0.875
Annual abundance index	*r*	0.308	0.249	0.248	−0.013	0.038	0.017	0.747*	0.149
	P	0.246	0.353	0.353	0.961	0.888	0.951	0.002*	0.581
Annual harvest mortality	*r*	0.370	0.463*	0.119	−0.393	−0.040	−0.046	−0.355	−0.289
	P	0.144	0.061*	0.648	0.132	0.880	0.861	0.193	0.260

Specifically, dispersing cougars are potentially exposed to car collisions and Wildlife Services removal. Also, demographic stochasticity alone could lead to small populations of cougars in both locations. We suggest that the UDWR consider re-examining their density and habitat quality indices for future cougar management, and the size of management units for a species whose populations are predominantly regulated by source-sink dynamics (Robinson et al. 2008, Cooley et al. 2009).

The most intuitive finding of our analysis was the positive correlation between the percentage of permits filled and the minimum abundance index in the OSCMU. This was a fairly simple relationship indicating that hunters were more successful when cougars were more abundant. The fraction of females in the harvest is arguably the statistic most widely used by managers to monitor changes in cougar populations (Cooley et al. 2011). However, our analysis revealed no significant correlation between this metric and either annual female survival or annual abundance in the OSCMU, possibly because this index combines a variable fraction of non-reproductive sub-adult females with adult females. Anderson and Lindzey (2005) noted that the sex ratio of harvested cougars alone is of limited value in identifying population change, but when combined with age structure, both provide a more reliable index to population change. This was substantiated by our findings that at least for the OSCMU population, the percent of the harvest >6 years was positively correlated with annual female survival. However, this metric generally served as a proxy for the age structure of the population and was likely indicative of a population that has experienced several years of high survival and a greater proportion of more fecund females in the population.

In the MCMU, overall annual harvest mortality was principally influenced by male annual harvest mortality, suggesting that males were more heavily targeted than females in the MCMU. We further observed a positive correlation between the percentage of permits filled and annual survival overall but also independently for both female

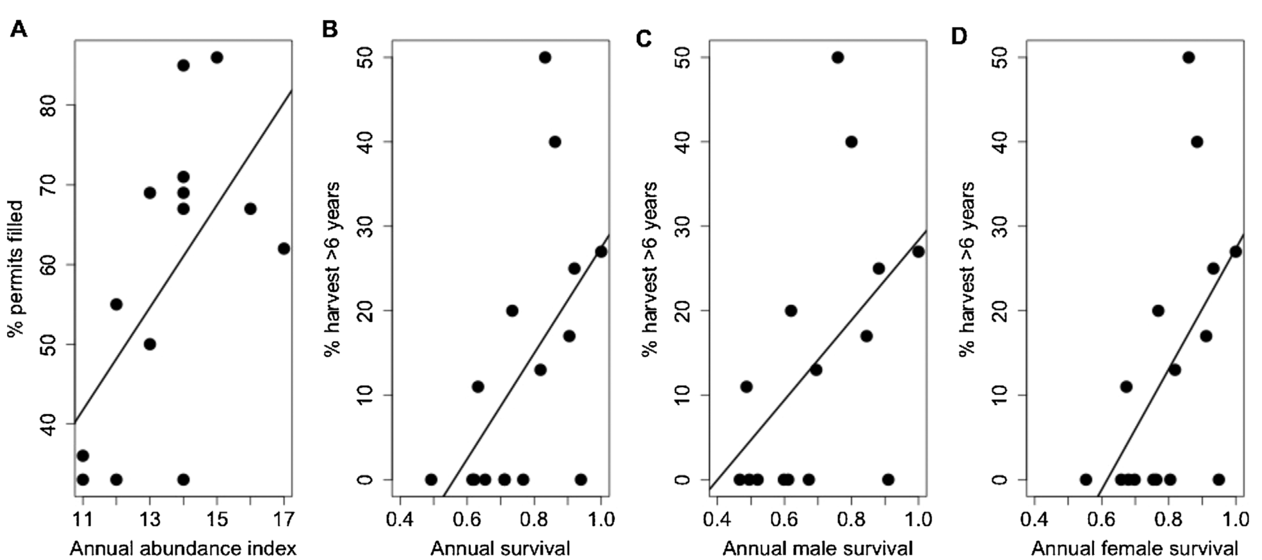

Figure 4. Significant correlations between A) % permits filled and annual abundance, B) % of harvested cougars >6 years old and overall annual survival, C) % of harvested cougars >6 years old and annual male survival, and D) % of harvested cougars >6 years old and annual female survival, for the Oquirrh-Stansbury Cougar Management Unit, 1997–2012, Utah, USA.

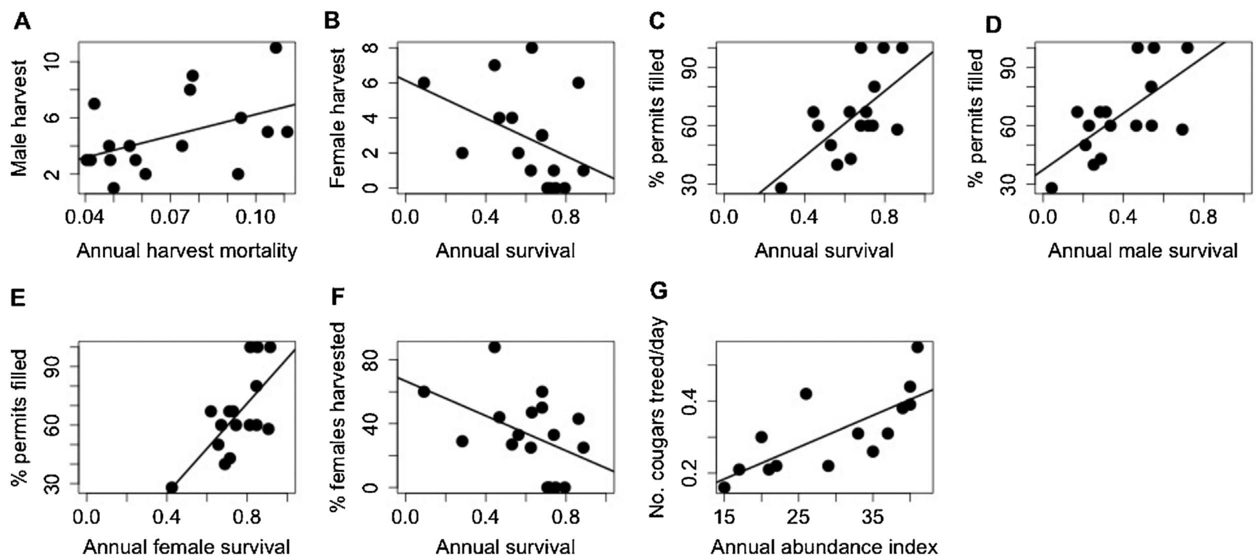

Figure 5. Significant correlations between A) male harvest rate and annual harvest mortality, B) female harvest and annual survival, C) % permits filled and overall annual survival, D) % permits filled and annual male survival, E) % permits filled and annual female survival, F) % females in the harvest and annual survival, and G) no. cougars treed/day and annual abundance for the Monroe Cougar Management Unit, 1996–2012, Utah, USA.

and male survival. This relationship indicates that hunters were more successful when annual cougar survival was high for the population as a whole, but also for females and males separately. The number of females harvested and the fraction of females in the harvest were negatively correlated with annual survival, suggesting that in this management unit, both statistics are relevant and their use is justified as the most widely used harvest index to monitor changes in cougar populations (Cooley et al. 2011). One of the more surprising results was the strong positive relationship between the number of cougars treed per day during the pursuit-season and the index of minimum annual cougar abundance on the MCMU. This index was arguably independent from harvest data because it is derived from the success of non-lethal pursuit permits. Choate et al. (2006) reported a weak ($P = 0.13$) correlation from the same unit that was derived in the same manner but for a much shorter time span (6 years). As discussed by Whittaker and Wolfe (2011), this pursuit index is a catch-per-unit-effort estimator, and although easily obtained, this index is subject to several assumptions including demographic and geographic independence and constant catchability throughout the period of data collection. The latter assumption may be unrealistic because it implies that cougars do not learn to avoid capture. Despite these limitations, the relatively low cost of obtaining this index via phone surveys of sportsmen warrants further investigation and refinement.

MANAGEMENT IMPLICATIONS

Using harvest statistics that are already commonly collected from hunters in the state of Utah to determine harvest quotas for cougars was justified by our analyses. Specifically, the total number of females harvested and the fraction of females in the harvest were negatively correlated with annual survival; managers are right to pay particular attention to these harvest statistics for monitoring cougar populations. In the MCMU, the percentage of permits filled was also a good proxy to changes in annual survival, annual female survival, and annual male survival. The highest correlation between cougars treed/day and the annual abundance of cougars suggests that pursuit indices may be an informative metric for wildlife managers to determine cougar population trends in intensely harvested management units. These harvest statistics may be suitable for cougar management units that have a similar hunting management regime as MCMU, with hunting being the predominant source of mortality.

In the OSCMU, the percentage of cougars in the harvest >6 years of age was correlated to overall annual survival, annual female, and male survival making them useful for monitoring changes in the demographics of cougar management units where harvest is not the only dominant cause of death (Wolfe et al. 2015). In such units, the percentage of permits filled tracked changes in annual cougar abundance, suggesting that this metric is a good indicator of population abundance in units that are not under intense harvest pressure.

Ideally, managers should also keep track of change in demographic rates, specifically survival and abundance, in key harvest management units that display contrasting harvest and mortality regimes. Our results illustrate the value of long-term data collection and suggest the possibility of expanding the scope of such comparisons to additional management units. Because the OSCMU and MCMU were subjected to contrasting mortality regimes (Wolfe et al. 2015), our results could be expanded to additional management units that share either the OSCMU or the MCMU characteristics. Ultimately, we suggest this analytical framework be extended to other harvested carnivore species for which harvest indices are available. When demographic information is available for certain harvest management units, correlations between harvest indices and demographic rates can be used to assess which harvest indices are better proxies to changes in survival, abundance, and population dynamics.

ACKNOWLEDGMENTS

Logistical support was provided by the United States Forest Service, Fish Lake National Forest, and the United States Department of Agriculture, Wildlife Services, National Wildlife Research Center. This work relied to a great extent on the dedication of outstanding houndsmen (C. Mecham, M. Mecham, B. Bateman) and pilots (C. Shaffer, C. Hunt, and S. Biggs). D. L. Mitchell and C. Hendrix also contributed field assistance, and R. T. Skirpstunas conducted necropsies at the Utah Veterinary Diagnostic Lab. We are also grateful to K. D. Bunnell, A. J. Neville, and K. Rasmussen for advice and technical support. We are thankful to D. N. Koons for comments on earlier versions of the manuscript. Principal funding was provided by the Utah Division of Wildlife Resources, Kennecott Utah Copper Division of the Rio Tinto Mining Company, and the Utah National Guard.

LITERATURE CITED

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

Anderson, C. R., F. Lindzey, K. H. Knopff, M. G. Jalkotzy, and M. S. Boyce. 2010. Cougar management in North America. Pages 41–54 *in* M. Hornocker and S. Negri, editors. Cougar ecology and conservation. University of Chicago Press, Chicago, Illinois, 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.

Aubry, L. M., E., Cam, D. N. Koons, J.-Y. Monnat, and S. Pavard. 2011. Drivers of age-specific survival in a long-lived seabird: contributions of observed and hidden sources of heterogeneity. Journal of Animal Ecology 80:375–383.

Beausoleil, R. A., D. Dawn, D. A. Martorello, and C. P. Morgan. 2008. Cougar management protocols: a survey of wildlife agencies in North America. Pages 204–242 *in* D. Toweill, S. Nadeau, and D. Smith, editors. Proceedings of the 9th Mountain Lion Workshop, Idaho Game and Fish Department, Boise, USA.

Bradburn, M. G., T. G. Clark, S. B. Love, and D. G. Altman. 2003. Survival analysis Part II: Multivariate data analysis: an introduction to concepts and methods. British Journal of Cancer 89:431–436.

Chilelli, M. E., B. Griffith, and D. J. Harrison. 1996. Interstate comparisons of river otter harvest data. Wildlife Society Bulletin 24:238–246.

Choate, D. M., M. L. Wolfe, and D. C. Stoner. 2006. Evaluation of cougar population estimators in Utah. Wildlife Society Bulletin 34:782–799.

Cooley, H. S., K. D. Bunnell, D. C. Stoner, and M. L. Wolfe. 2011. Population management: cougar hunting. Pages 111–134 *in* J. A. Jenks, editor. Managing cougars in North America. Berryman Institute, Utah State University, Logan, Utah, USA.

Cooley, H. S., R. B. Weilgus, G. M. Koehler, H. S. Robinson, and B. T. Maletzke. 2009. Does hunting regulate cougar populations? A test of the compensatory mortality hypothesis. Ecology 90:2913–2921.

Cox, D. R. 1972. Regression models and life-tables. Journal of the Royal Statistical Society B Series 34:187–220.

Erickson, D. W. 1982. Estimating and using furbearer harvest information. Pages 53–65 *in* G. C. Sanderson, editor. Midwest furbearer management. Proceedings of 43rd Midwest Fish and Wildlife Conference, Wichita, Kansas, USA.

Funston, P. J., R. J. Groom, and P. A. Lindsey. 2013. Insights into the management of large carnivores for profitable wildlife-based land uses in African savannas. PloS One 8(3):e59044.

Gese, E. M. 2001. Monitoring of terrestrial carnivore populations. Pages 373–396 *in* J. L. Gittleman, S. M. Funk, D. Macdonald, and R. K. Wayne, editors. Carnivore conservation. Cambridge University Press, Cambridge, United Kingdom.

Geskus, R. B. 2011. Cause-specific cumulative incidence estimation and the fine and gray model under both left truncation and right censoring. Biometrics 67:39–49.

Ginsberg, J. R. 2001. Setting priorities for carnivore conservation: what makes carnivores different? Pages 498–523 *in* J. L. Gittleman, S. M. Funk, D. Macdonald, and R. K. Wayne, editors. Carnivore conservation. Cambridge University Press, Cambridge, United Kingdom.

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

Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. Journal of the American Statistical Association 53:457–481.

Keefover-Ring, W. J. 2005. Mountain lions, myths, and media: a critical reevaluation of The Beast in the Garden. Environmental Law 35:1083–1095.

Kelly, M. J., J. Betsch, C. Wultsch, B. Mesa, and L. S. Mills. 2012. Noninvasive sampling of carnivores. Pages 47–69 *in* L. Boitani and R. A. Powell, editors. Carnivore ecology and conservation: a handbook of techniques. Oxford University Press, Oxford, United Kingdom.

Kleinbaum, D. G., and M. Klein. 2005. Survival analysis: a self-learning approach, second edition. Springer, New York, New York, USA.

Kolenosky, G. B., and S. M. Strathearn. 1987. Black bear. Pages 444–454 *in* M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, editors. Wildlife furbearer management and conservation in North American. Ontario Ministry of Natural Resources, Toronto, Canada.

Koons D. N., R. F. Rockwell, and L. M. Aubry. 2014. Effects of exploitation on an overabundant species: the lesser snow goose predicament. Journal of Animal Ecology 83:365–374.

Kreeger, T. J. 1996. Handbook of wildlife chemical immobilization. Wildlife Pharmaceuticals Inc., Fort Collins, Colorado, USA.

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

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

Lindzey, F. 1987. Mountain lion. Pages 657–668 *in* M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, editors. Wildlife furbearer management and conservation in North American. Ontario Ministry of Natural Resources, Toronto, Canada.

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

Long, R. A., P. MacKay, W. J. Zielinski, and J. C. Ray, editors. 2008. Noninvasive survey methods for carnivores. Island Press, Washington, D.C., USA.

Loveridge, A. J., S. W. Wang, L. G. Frank, and J. Seidensticker. 2010. People and wild felids: conservation of cats and management of conflicts. Pages 161–195 *in* D. W. Macdonald and A. J. Loveridge, editors. Biology and conservation of wild felids. Oxford University Press, Oxford, United Kingdom.

Mech, L. D. 1983. Handbook of animal radio-tracking. University of Minnesota Press, Minneapolis, USA.

Moller, A. L., and R. R. Gillies. 2008. Utah climate. Second edition. Utah Climate Center Utah State University Research Foundation, Logan, USA.

Murray, D. L., and B. R. Patterson. 2006. Wildlife survival estimation: recent advances and future directions. Journal of Wildlife Management 70:1499–1503.

Murray, D. L., D. W. Smith, E. E. Bangs, C. Mack, J. K. Oakleaf, J. Fontaine, D. Boyd, M. Jiminez, C. Niemeyer, T. J. Meier, D. Stahler, J. Holyan, and V. J. Asher. 2010. Death from anthropogenic causes is partially compensatory in recovering wolf populations. Biological Conservation 143:2514–2524.

Pollock, K. H., J. D. Nichols, and K. U. Karanth. 2012. Estimating demographic parameters. Pages 169–187 *in* L. Boitani and R. A. Powell,

editors. Carnivore ecology and conservation: a handbook of techniques. Oxford University Press, Oxford, United Kingdom.
R Development Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Robinson, H. S., R. B. Weilgus, H. S. Cooley, and S. W. Cooley. 2008. Sink populations in carnivore management: cougar demography and immigration in a hunted population. Ecological Applications 18:1028–1037.
Rolley, R. R. 1987. Bobcat. Pages 672–681 *in* M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, editors. Wildlife furbearer management and conservation in North American. Ontario Ministry of Natural Resources, Toronto, Canada.
Sandercock, B. K., E. B. Nilsen, H. Brøseth, and H. C. Pedersen. 2011. Is hunting mortality additive or compensatory to natural mortality? Effects of experimental harvest on the survival and cause-specific mortality of willow ptarmigan. Journal of Animal Ecology 80:244–258.
Sargeant, G. A. 2011. Wild1: R tools for wildlife research and management. R package version 2.15.0. Geological Survey Northern Prairie Wildlife Research Center, Jamestown, North Dakota, USA.
Sillero-Zubiri, C., and M. K. Laurenson. 2001. Interactions between carnivores and local communities: conflict or co-existence? Pages 282–312 *in* J. L. Gittleman, S. M. Funk, D. Macdonald, and R. K. Wayne, editors. Carnivore conservation. Cambridge University Press, Cambridge, United Kingdom.
Smallwood, K. S., and E. L. Fitzhugh. 1995. A track count for estimating mountain lion *Felis concolor californica* population trend. Biological Conservation 71:251–259.
Stoner, D. C., M. L. Wolfe, and D. M. Choate. 2006. Cougar exploitation levels in Utah: implications for demographic structure, population recovery, and metapopulation dynamics. Journal of Wildlife Management 70:1588–1600.
Sweanor, L. L., K. A. Logan, and M. G. Hornocker. 2000. Cougar dispersal patterns, metapopulation dynamics, and conservation. Conservation Biology 14:798–808.
Treves, A., and K. U. Karanth. 2003. Human-carnivore conflict and perspectives on carnivore management world-wide. Conservation Biology 17:1491–1499.
Utah Cougar Advisory Group. 2011. Utah Cougar Management Plan V.2.1. Utah Division of Wildlife Resources, Salt Lake City, USA.
Utah Division of Wildlife Resources. 2012. Utah Cougar Annual Report. Utah Division of Wildlife Resources, Salt Lake City, USA.
Van Dyke, F. G., R. H. Brocke, and H. G. Shaw. 1986. Use of road track counts as indices of mountain lion presence. Journal of Wildlife Management 50:102–109.
Whittaker, D. and M. L. Wolfe. 2011. Assessing cougar populations. Pages 71–110 *in* J. A. Jenks, editor. Managing cougars in North America. Berryman Institute Utah State University, Logan, USA.
Wolfe, M. L., D. N. Koons, D. C. Stoner, P. Terletzky, E. M. Gese, D. M. Choate, and L. M. Aubry. 2015. Is anthropogenic cougar mortality compensated by changes in natural mortality? Insight from long-term studies. Biological Conservation 182:187–196.
Zar, J. H. 1999. Biostatistical analysis, fourth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

Associate Editor: Barbara Zimmermann.