# Numerical and Demographic Responses of Pumas to Changes in Prey Abundance: Testing Current Predictions

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ABSTRACT Information on factors affecting population size of pumas (Puma concolor) can be important because their principal prey over most of the western United States are valued big game species (e.g., mule deer [Odocoileus hemionus], elk [Cervus elaphus], and bighorn sheep [Ovis canadensis]). Based on the hypothesis that puma numbers are limited by their food supply, puma populations should track changes in prey abundance by growing exponentially with increases in prey and by declining with a lag response when prey decreases. Additional predictions proposed by researchers are that body mass of pumas, female productivity, kitten survival, and adult survival should decrease after a prey decline. We used a 15-year database from a hunted population of pumas in southern Idaho and northwestern Utah to test these predictions. During the 15-year time span of the database, a major decline in mule deer abundance occurred. Estimates of puma numbers and demographic characteristics came from intensive capture and radiocollaring efforts. We calculated kitten and adult survival with MICROMORT software. We found that adult puma numbers increased exponentially at r=0.07 during a period of increasing mule deer numbers. Four years after the mule deer abundance declined, puma numbers decreased at a rate of r = -0.06. Body mass of female pumas was lower after the decline in puma numbers (42.6  $\pm$  SE = 1.2 kg, n = 40 vs. 40.1  $\pm$  0.64 kg, n = 34, t = 5.06, P = 0.045). Kitten survival was less after the decline in deer abundance (0.573  $\pm$  0.016, n = 30 vs. 0.856  $\pm$  0.015, n = 25, Z = 2.40, P < 0.01). Survival of resident females was significantly less after the decline in puma numbers (0.783  $\pm$  0.03 vs. 0.929  $\pm$  0.019, U=55.0, P=0.009). Female productivity did not differ before or after the decline in deer abundance. Our results supported the majority of the predictions concerning the impact of changing deer abundance, which supported the hypothesis that the abundance of mule deer limited our population of pumas. (JOURNAL OF WILDLIFE MANAGEMENT 71(2):345-355; 2007)

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Information on factors affecting population size of predators is important because predation impacts on prey species relate to changes in their densities (Logan and Sweanor 2001). For large predators such as pumas (*Puma concolor*), this information is important because their principal prey over most of the western United States are valued big game species (e.g., mule deer, [*Odocoileus hemionus*], elk [*Cervus elaphus*], and bighorn sheep [*Ovis canadensis*]). The impact of pumas on these species is debatable (Ballard et al. 2001, Cougar Management Guidelines Working Group [CMGWG] 2005) and basic information on factors that affect population changes of pumas over time would help resolve this controversy.

Hornocker (1970) and Seidensticker et al. (1973) originally proposed that territorial behavior in pumas resulted in a land tenure system, which regulated resident puma numbers below that set by prey abundance. Recently Pierce et al. (2000) and Logan and Sweanor (2001) tested and rejected the land tenure hypothesis and concluded that puma numbers are ultimately limited by food supply. Under this hypothesis, puma populations should mimic changes in the relative abundance of their primary prey (e.g., mule deer).

Relative to increasing prey abundance, Lindzey et al. (1994) reported a weak positive relationship between deer pellet group indices and puma numbers. Logan and Sweanor (2001, fig. 10.1) reported an exponential increase in puma

numbers during which their models projected increasing mule deer numbers. However, for 5 years prior to the Logan and Sweanor (2001) study, hunters removed an average 11 adult pumas per year. It is unclear if the increases in puma numbers in the New Mexico, USA, study resulted from increases in prey densities or a release of the puma population from this hunting pressure (Lindzey et al. 1992, Logan and Sweanor 2001, Anderson and Lindzey 2005).

When faced with prey reductions, populations of many large predators decline, usually following a lag time (e.g., Todd and Keith 1983, Boertje and Stephenson 1992, Mowat et al. 1996). Logan and Sweanor (2001) proposed this should also occur in pumas and further predicted that the lag in their response should be approximately 4 years. Based on literature for other predators, Logan and Sweanor (2001) also predicted a series of specific demographic changes that should occur in a puma population and eventually contribute to their decline:

- 1) The physical condition of pumas should decline.
- 2) Female reproductive output should decline.
- 3) Kittens should have reduced survival to independence.
- 4) Adults should have reduced survival and death from starvation should occur.
- 5) There should be higher emigration of subadult females.

Although the models of Logan and Sweanor (2001) projected a 40% decline in mule numbers for the last 3 years of their study, the puma population continued to increase.

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Figure 1. Location of the puma study area in southern Idaho and northwestern Utah, USA. The total study area included the Raft River Mountains in wildlife management Unit 1 of Utah and game management Units 55 and 57 of Idaho. We also indicated the locations of other management units in Idaho where Idaho Fish and Game personnel conducted winter deer surveys from 1992–2004.

Logan and Sweanor (2001) also found little evidence to support the 5 predicted demographic changes. They concluded that their study terminated too soon to adequately test their predictions (Logan and Sweanor 2001).

An additional factor we need to consider is the impact of human harvest of pumas on their response to prey population change. As puma populations in the West are hunted, it is important to evaluate the impact of long-term harvest on any potential numerical response of pumas to dynamics of their prey base. In most past studies, human harvest of pumas was low or did not occur over most of the study (Hornocker 1970, Lindzey et al. 1992, Logan and Sweanor 2001). Consequently, we did not find any data relative to impacts of long-term annual harvest of pumas over varying deer abundance.

From 1985–2002, we studied a hunted population of pumas in southern Idaho–northwestern Utah, USA (Fig. 1). During this time, the population experienced low (10%) to high (48%) harvest rates. In 1992–1993, mule deer populations over most of the West experienced a major decline (Ballard et al. 2001). Prior to this period, deer numbers were increasing from a previous low period in the late 1960s to early 1970s (Unsworth et al. 1999, Ballard et al. 2001). Thus, over the course of our study we were able to monitor the response of a hunted population of pumas to an increasing and then rapidly decreasing prey abundance.

We used this long-term dataset over changing harvest pressure and prey abundance to test the predictions that 1) puma numbers should increase exponentially with increasing deer abundance, and 2) puma numbers should decline when faced with a reduction in deer abundance. We further analyzed the impact that puma harvest might have on the responses of pumas to changing prey abundance. Finally, we tested the 5 predictions made by Logan and Sweanor (2001) relative to expected demographic changes.

## **STUDY AREA**

The overall study area was in southern Idaho and northwestern Utah (Fig. 1). The Idaho portion of the study area was in Idaho Department of Fish and Game (IDFG) game management units 55 and 57 in Cassia County, Idaho. The Utah portion was in the extreme northwestern corner of Utah Division of Wildlife Resources (UDWR) game management unit 1 in Box Elder County, Utah (Fig. 1). We chose this area because it represented the type of mountain physiognomy and habitat structure characteristic of this region. The total area of 2,400 km<sup>2</sup> contained approximately 1,700 km<sup>2</sup> of puma habitat within 5 small, semi-isolated mountain ranges (65-760 km<sup>2</sup>) with elevations of 1,830-3,151 m. Mule deer were the principal prey of pumas, with only a remnant (<50) elk population. Other species pumas occasionally consumed during the study period included coyotes (Canis latrans), bobcats (Lynx rufus), and porcupines (Erethizon dorsatum).

Mountain ranges consisted of open and forested habitat patches that varied in size. Forested patches contained various mixes of Douglas fir (*Pseudotsuga menziesii*), subalpine fir (*Abies lasiocarpa*), juniper (*Juniperus osteosperma* and *J. scopulorum*), pinyon pine (*Pinus edulis*), quaking aspen (*Populus tremuloides*), and curl-leaf mountain mahogany (*Cercocarpus ledifolius*). Dominant shrubs in open areas included big sagebrush (*Artemisia tridentata*), gray rabbitbrush (*Chrysothamnus nauseosus*), bitterbrush (*Purshia tridentata*), and buffaloberry (*Shepherdia rotundifolia*). The climate was hot and dry in the summers (20–35° C) and cold and windy in the winters ( $-25-4^\circ$  C). Humidity rarely exceeded 40%, and precipitation was sporadic with an annual average of 30 cm.

## **METHODS**

To verify if relative mule deer abundance in our study area followed the regional patterns reported in the literature (Unsworth et al. 1999, Ballard et al. 2001), we obtained estimates of relative deer abundance from IDFG reports, which provided data on deer harvests and winter sightability surveys in the Idaho portion of our area (Hurley and Unsworth 2000, Hurley and Zager 2004). We did not have these data for the Utah portion of our study area so we used the Idaho data as representative of trends for the overall area. Because we were primarily interested in whether the deer population was increasing, stable, or declining, we considered relative indices of change to be sufficient. Game management units 55 and 57 in the Idaho portion of our study area were permit-only hunts. Although the number of permits issued varied annually (Fig. 2), the number of permits issued each year was relatively constant from 1981-1993 (2,150-2,185 permits). Idaho Department of Fish and Game personnel annually obtained estimates of hunter



**Figure 2.** Deer population trends (1970–2004) based on Idaho Fish and Game winter surveys at 8 sites in and around the study area and on the relative changes in harvest levels from the units 55 and 57 in the study area. We included the number of deer hunting permits issued per year in units 55 and 57 as a comparison with actual harvest levels. Included are the annual population trends of pumas in the study area over the 15 years of the study. We present all data relative to the percent maximum value recorded for each category.

success via check stations and telephone surveys (Steinert et al. 1994, Unsworth et al. 2002). Thus, we also used hunter success as an index of relative deer abundance (Lindzey et al. 1994, Marshal et al. 2002). Starting in 1992, IDFG personnel established 8 trend survey areas within the Idaho portion of the study area and surrounding management units (Fig. 1). Each March from 1992-2004, trained IDFG personnel conducted aerial sightability surveys with a Bell 47 helicopter in these trend areas. These surveys followed the protocol established by Unsworth et al. (1994) and the IDFG use these results to track deer abundance trends. The results of such trend surveys are reliable in tracking relative changes in deer abundance (Freddy et al. 2004). We used the results of these surveys to estimate relative deer abundance for 1992-2004. To compare the 2 methods, we expressed annual estimates of hunter success and survey results as percentages of the maximum value for each [(annual estimate/max. estimate)  $\times$  100], with the maximum value being 100%.

To test the predictions about puma demographics, we estimated the number, age and sex structure, births, mortalities, causes of death, survival, and dispersal of pumas in our study area. Data came from intensive field efforts to capture pumas and locate puma tracks from November through February of each year. When we found fresh tracks, we attempted to capture these animals with trained dogs. Once dogs cornered a puma in a tree, we tranquilized the animal with a mixture of ketamine hydrochloride (9 mg/kg) and xylazine hydrochloride (1.5 mg/kg). We attached a radiocollar to each animal and estimated its age at first capture with formulas for standard body measurements (Laundré and Hernández 2002) or gum-line recession (Laundré et al. 2000). We then administered an intravenous injection of the xylazine antagonist yohimbine and stayed

with the animals until they recovered sufficiently to navigate. In addition to our capture efforts, we collected and verified information about other pumas in the area from houndsmen, whom we knew from experience to be reliable, and also reviewed annual mandatory harvest reports for the area. Through intensive summer telemetry (Blum 2003) we monitored the movements, dispersal, and mortality of collared pumas.

We compiled a population chart similar to that used by Hornocker (1970) and Logan and Sweanor (2001). We placed the first point of the timeline for each animal in the month of their first capture. If we were able to estimate the age of the animal, we extended the line to the left up to its birth month. We extended the line to the right until the individual either dispersed from the area, died, or until the last month we knew it to be alive in the study area. By counting the number of lines that crossed the beginning of each study year (Nov–Feb) we were able to estimate the minimal number of pumas present in the study area at that time. Researchers showed this level and type of analysis to be a reliable method for determining puma numbers in an area (Logan and Sweanor 2001, CMGWG 2005).

We identified 4 social and age classes. Resident males were adult males >20 months old with an affinity to an area for at least 2 months. Resident females were adult females with an affinity to an area or that eventually reproduced. Dependent kittens were young born in the area up to the time they became independent of their mothers. Transients were immigrants and independent young of the area until they either dispersed or became residents (Lindzey et al. 1994).

We used data on puma numbers to test whether the puma population in our study increased exponentially (positive exponential rate of increase, r; Caughley 1978) over a period of estimated increasing deer abundance. We then tested the prediction that puma numbers declined, with a lag response, in response to declines in deer abundance. To test if pumas responded exponentially to increases in deer abundance, we followed the method of Logan and Sweanor (2001) for calculating the observed exponential rate of increase (r). We regressed the natural log of the annually estimated number of adult pumas against the number of years of the study. The slope of the regression line is considered an estimate of r(Caughley 1978). For the time period of decreasing deer abundance we used the annual estimated number of resident pumas to test if the puma population declined and if this decline exhibited a lag time relative to the decline in deer abundance.

To evaluate the impact of human harvest on the numerical response of pumas, we compiled UDWR and IDFG harvest records for our study area. Over the study period, UDWR regulated the human harvest of pumas in Utah portion of our study area by permit. Under this system, UDWR issued a fixed number of permits via a lottery. The number of permits each year varied from 5 to 8 for the Utah portion of the study area (UDWR, unpublished data). The harvest season normally was from December–January to mid-June. In the Idaho portion of our study area, puma harvest was

unlimited for the first 3 years of the study. From 1989–1990 to the end of the study there was a female harvest quota wherein the season closed after the harvest of a fixed number of females (Laundré and Clark 2003). The number of females in the quota ranged from 2 to 9 (Laundré and Clark 2003). The harvest season normally was from September to the end of February or March. In both states, harvest reports were mandatory.

We also compared the body mass of adult pumas captured before and after the deer decline. Similarly, we compared the number of litters born per year, the number of kittens per litter, and the percentage of litters in the population between the predecline and postdecline years. To test the prediction that reductions in deer abundance would affect kitten survival to independence, we used MICROMORT (Heisey and Fuller 1985). In this analysis we were interested in the survival rate of kittens from birth to age of independence rather than annual survival rates. Thus we pooled individuals of a given cohort of interest (e.g., all F kittens over the total study period) and entered them together at the beginning of the time interval (i.e., birth). We found average age to independence in our study to be  $16.1 \pm 0.26$ months (n = 56) so we used an interval length of 490 days. We conducted separate analyses for: 1) all kittens, 2) just females, and 3) just males for the total study period and for the periods before and after the decline in deer abundance. As we were only interested in the impact of reduced deer abundance, we disregarded kittens that died from human causes or infanticide. We tested for differences between cohorts with the Z statistic for a normal approximation, which we then compared with critical values of the *t* statistic for large sample sizes (Bangs et al. 1989, DeYoung 1989, Zar 1999).

To test whether survival of adult pumas changed with deer abundance, we also used MICROMORT to estimate annual survival rates and compared survival rates before and after the decline in deer. Our interval length was 365 days and the span length was the number of years of the study in which we had sufficient data (see Results). We used a staggered entry, entering animals as they appeared in the study based on capture dates. Because our intensive survey and trapping efforts sometimes extended into May with late snowfalls, we ran our intervals from 1 June to 31 May. We left and right censored animals as appropriate. We used the MICROMORT software to facilitate comparison with earlier studies that used the same software (Lindzey et al. 1994, Logan and Sweanor 2001). Regarding the prediction of increased dispersal of female offspring, we compared the number of female offspring who dispersed out of the study area before and after the mule deer decline.

To test the demographic predictions statistically we divided the study period between the pre- and postdecline periods in deer numbers (1985–1992 and 1993–2002). We compared the various measurements between these time periods with a *t*-test design or the Mann–Whitney Rank Sum (U) nonparametric equivalent if the data failed the requirements for parametric tests (Zar 1999). We conducted

all statistical tests with Sigmastat© software (Systat Software, Inc., Point Richmond, CA). We transformed all percent data with the arc-sin square root transformation before performing statistical tests. We set our rejection level at  $P \leq 0.05$  and we reported all means as  $\pm$  standard error.

## RESULTS

### Deer Population Trends over the Study Period

From 1981–1986 deer hunter success varied from 45%– 60% of the maximum success rate (Fig. 2). In 1987 hunter success increased to almost the highest recorded and remained high up to the fall of 1992 (Fig. 2). In 1993 IDFG issued the same number of permits but hunter success declined to the previously low level of the early 1980s (Fig. 2). The trend survey data for 1992 and 1993 corroborated the harvest success with the highest estimate being in 1992 and a subsequent decline of  $56.8 \pm 12.2\%$  (n = 4) in 1993. Trend survey and hunter success estimates fluctuated slightly after 1993 but remained low through 2004.

Predictions 1 and 2: Numerical Response of Adult Puma Numbers to Increasing and Decreasing Deer Abundance Over the 17 years of the study, we captured 147 pumas ranging in age from <1 month to 5 years old at first capture. We recaptured 51 of these animals from 2 to 6 times over the study period. During this time, we verified the harvest of 53 uncollared animals from our study area. Within the first 5 years of the study we verified the presence of 1-4 animals per year via their tracks or information from hunters. We captured many of these animals the following years. From 1987-1988 to 1989-1990 the number of animals we handled was low (10.0-17.9%) and we based our estimates of puma numbers primarily on harvest reports, track sightings, and back dating the timeline from subsequent years. From the winter of 1990-1991 to 2001-2002 we marked an average of 72% (range 36-85%) of the total number of animals we believed to be present on the study area. We marked a mean of 88% (range 62-100%) of the resident females. We had sufficient information from our captures and the other sources to begin estimating the number of pumas present in our study area starting with the winter of 1987-1988 (15 yr). However, we limited our estimates of demographic characteristics needed to test predictions for the 12 years (1990-1991 to 2001-2002) in which we had a majority of the resident females marked.

The annual estimates of the total population varied considerably between 1987–1988 and 1996–1997 but eventually increased from a low of 28 animals in 1989–1990 to a high of 47 animals in 1996–1997 (Fig. 3). In 1997–1998, the population declined to 26 animals and remained around 35 animals to the end of the study. When we distinguished different sex, age, and social status criteria, we also saw no pattern in the change in the number of resident males, which averaged  $4.8 \pm 0.24$  males per year (Table 1). Numbers of resident females ranged from 9–11 individuals the first 3 years of the study but then gradually increased to 22 individuals by 1996–1997 (Fig. 3). This represented a 120.0% increase over the average number the



Figure 3. Annual estimates of the total puma population and of resident adult females over the 15 years (1987–2002) of the study in Idaho and Utah, USA.

first 3 years. The number of resident females declined the following year (1997–1998). By the last 4 years of the study, female numbers returned to levels similar to those at the beginning of the study (13.0  $\pm$  0.89 animals/yr; Fig. 3).

The regression line of the natural log of estimated resident animals against the first 8 years of the study fit well  $(r^2 = 0.79_{adj.}, P < 0.001;$  Fig. 4). The slope of the regression line and the estimate of r was 0.07 (Fig. 4). Thus, the resident puma population grew at an exponential growth rate over the first 8 years. This growth rate included the first 3 years after mule deer numbers declined in 1992–1993 (Fig. 2). The adult puma population apparently declined after 1996–1997. This decline occurred 4 years after the reduction of mule deer numbers. The regression of the natural log of the population estimates over the last 7 years of the study indicated the puma population declined at a rate of r = -0.060 but the regression only explained 14% of the variation in the data (Fig. 4). The poor fit was

mainly because of increases in resident puma numbers the last 2 years of the study (Fig. 4). When we regressed only the first 4 years of the decline, the regression explained 78% of the variation and the estimated rate of decrease was -0.182.

## Prediction 3: Adult Body Mass Should Be Less after the Decline of Deer Numbers

We had body mass estimates for only 6 adult male pumas between 1985 and 1992–1993 and 28 adult males between 1993–1994 and the end of the study in 2001–2002. Body masses of males captured up to 1992–1993 did not differ from animals caught during subsequent winters (55.9  $\pm$  2.2 kg vs. 52.5  $\pm$  1.4 kg, P = 0.23). As the number of resident animals began to decline after 1996–1997, we also compared body mass of males caught from the beginning of the study to 1996–1997, with males caught after that winter. Male body mass of animals caught from 1985 to 1996–1997 was slightly greater than those after 1996–1997 but the difference was not significant (54.9  $\pm$  1.7 kg, n = 18 vs. 51.1  $\pm$ 1.8 kg, n = 16, P = 0.14).

We also found no difference in female body mass between animals captured up to 1992–1993 and after that time (41.2  $\pm$  3.9, n = 6 vs. 39.8  $\pm$  0.7, n = 60, P = 0.53). Average female puma body mass after the 1996–1997 decline in pumas was significantly less than before (40.1  $\pm$  0.64 kg, n= 36 vs. 42.6  $\pm$  1.2 kg, n = 40, t = 5.06, P = 0.045), but the average difference was only 2.5 kg.

#### Prediction 4: Reproductive Output Should Be Less after the Deer Decline

We verified the presence of 61 litters (148 kittens) during 15 years of the study. Forty-eight (79%) of the 61 litters were from collared females. Of the 48 litters, we captured all the kittens present for 34 litters and  $\leq 1$  kitten for 5 other litters. Average age of kittens at first capture for the 39 litters was 4.7  $\pm$  3.7 months (range: 0.2–12 months). For the remaining 9 litters of collared females, we verified their

Table 1. Estimated minimum number of pumas in the Idaho-Utah study area each winter (Nov-Feb) of the 1987-2002 study.<sup>a</sup>

		М		F		Kittens		Transients	
Yr	Total	No.	%	No.	%	No.	%	No.	%
1987–1988	30	5	16.7	10	33.3	10	33.3	5	16.7
1988-1989	37	4	10.8	11	29.7	15	40.5	7	18.9
1989-1990	28	4	14.3	9	32.1	11	39.3	4	14.3
1990-1991	36	5	13.9	13	36.1	15	41.7	3	8.3
1991-1992	44	4	9.1	13	29.5	22	50.0	5	11.4
1992-1993	34	4	11.8	14	41.2	7	20.6	9	26.5
1993-1994	37	7	18.9	13	35.1	14	37.8	3	8.1
1994-1995	44	6	13.6	17	38.6	14	31.8	7	15.9
1995-1996	44	6	13.6	21	47.7	13	29.5	4	9.1
1996-1997	47	5	10.6	22	46.8	17	36.2	3	6.4
1997-1998	26	4	15.4	14	53.8	2	7.7	6	23.1
1998-1999	35	5	14.3	12	34.3	13	37.1	5	14.3
1999-2000	34	4	11.8	11	32.4	15	44.1	4	11.8
2000-2001	35	4	11.4	16	45.7	10	28.6	5	14.3
2001-2002	35	5	14.3	12	34.3	14	40.0	4	11.4

<sup>a</sup> We derived the estimates from intensive capture efforts each winter, from harvest records of local wildlife agencies, and from reports of puma hunters. For each yr, we also give the no. of individuals of each social class. Percentage of each social class was of the total no.



**Figure 4.** Estimates of rate of increase (r) for years of increasing and decreasing puma numbers over 1987–2002 and for the first 4 years (1996–2000) of the declining puma population in the Idaho–Utah, USA, study area. The rate of increase is the slope of the regression line of the natural log of puma numbers against the years of the study with the first year designated as zero.

presence, but did not capture the kittens. We confirmed the presence of the other 13 litters and the number of kittens per litter based on tracks and harvest records.

Average number of litters born per year over the 15 years of the study was  $4.1 \pm 0.48$  litters per year. The average number of litters born per year up to 1992–1993 was  $3.8 \pm 0.73$  (n = 5) and did not differ from the average for the subsequent years ( $4.2 \pm 0.65$  litters/yr, n = 10, P = 0.71). Average litter size for the 61 litters was  $2.4 \pm 0.08$  kittens. The number of kittens per litter before 1992–1993 did not differ from the number of kittens per litter after 1992–1993 ( $2.4 \pm 0.15$  kittens/litter, n = 20 vs.  $2.4 \pm 0.10$  kittens/ litter, n = 42, P = 0.76).

The number of kittens present per year varied from 2 in 1997–1998 to 22 in 1991–1992 (Table 1). Kittens comprised an average of  $34.4 \pm 2.6\%$  of the population (range 7.1–48.9%; Table 1). However, their proportion in the population declined in 1992–1993 and remained significantly lower ( $42.9 \pm 2.4\%$ , n = 4 vs.  $31.3 \pm 3.4\%$ , n = 10, U = 46.0, P = 0.028) during the rest of the study.

#### Prediction 5: The Survival of Kittens to Dispersal Age Should Be Less after the Deer Decline

Of the 39 litters with marked kittens, 27 litters had some or all the kittens reach independence (56 kittens, 32 M and 24 F). For 82 kittens, we were able to calculate survival to independence, which was  $0.72 \pm 0.005$ . Average survival to independence did not differ significantly by sex (M:  $0.726 \pm 0.011$ , n = 37 vs. F:  $0.775 \pm 0.011$ , n = 45, P > 0.50). Survival of all kittens born before the decline in deer abundance ( $0.856 \pm 0.015$ , n = 25) was significantly higher than the kittens born during the 3 years after the decline ( $0.573 \pm 0.016$ , n = 30, Z = 2.40, P < 0.01). Survival to independence before the deer decline was significantly higher for female kittens ( $0.892 \pm 0.03$ , n = 10 vs.  $0.616 \pm 0.04$ , n = 14, Z = 1.66, P = 0.046) and male kittens

 $(0.907 \pm 0.03, n = 11 \text{ vs. } 0.625 \pm 0.04, n = 14, Z = 1.80, P = 0.03).$ 

# Prediction 6: Adult Survival Rates Should Decline after a Reduction in Deer Abundance

From 1990-1991 to 2001-2002, a minimum of 34 different resident males inhabited our study area. The number of resident males ranged from 4–7 animals per year (4.8  $\pm$  0.24 M/yr) and comprised an average of 13.4  $\pm$  0.65 % of the population (Table 1). We collared 14 (41.2%) of these animals. Average estimated age at first capture was 4.2  $\pm$ 0.36 years. Of the other 20 unmarked animals, hunters harvested 13 and most were probably in their first year of residency because they replaced resident males killed the year before. Many of these animals we knew to be present via tracks, but hunters harvested them before we could capture them. Hunters also harvested 5 of the 14 collared animals, 4 of them within weeks of their capture. Of the remaining 9 collared males, we found 2 dead, 5 disappeared after 2 or more years of residency, and 2 were still residents at the end of the study. Residency time for the 14 collared males averaged 1.9  $\pm$  0.24 years with the maximum residency of 4 years. Because male mortality from hunting was so high and we had so few males collared, we did not have sufficient data to conduct a MICROMORT analysis of male survival rates.

We estimated a minimum of 51 resident females within our study area from 1990-1991 to 2001-2002. We collared 38 (74.5%) of these females. The number of resident females in the study area varied annually from 9-22 (Table 1; Fig. 3) and comprised from 29.5%-53.8% of the population (38.1  $\pm$  1.9 %). Average age at first capture for the 38 collared females was 22.7  $\pm$  3.1 months. We captured 28 (73.7%) of these females as kittens (13 individuals) or at the beginning of their residency (approx. 20 months old). We detected the presence of 11 other females based on harvest reports and 2 more based on tracks. We followed 33 of the collared females from their first year of residency to their last; average residency was 4.6  $\pm$  0.49 years (range: 1-9 yr). Twelve of these 33 females maintained their residency for 7 years or more. From 1990-1991 to the end of the study, the average age of known resident females varied from 2.7 to 5.8 years. The oldest female in our study reached 11 years of age and we had 14 females that lived to be 7 years or older.

Estimated annual survival rates of adult females ranged from 1.0 to 0.700 over the study and averaged 0.856  $\pm$  0.028 (n = 12). The annual adult female survival rate before 1996–1997 was 0.929  $\pm$  0.019 (n = 6), which was significantly higher (U = 55.0, P = 0.009) than the rate 0.783  $\pm$  0.030 (n = 6) found after that time.

#### Prediction 7: Female Dispersal Should Be Higher after the Deer Decline

The number of transients per year present on the study area varied from 2 to 9 animals and averaged  $4.9 \pm 0.44$  animals per year (Table 1). Transients comprised an average of 13.1  $\pm$  1.7% of the population (range: 6.7–28.6%) with 47.6% of them being young collared animals dispersing from their

Table 2. Number of harvestable pumas (residents, transients, and kittens >1.0 yr), total harvest, harvest of resident males, resident females, and transients over the 15 years (1987–2002) of the study in southern Idaho and northwestern Utah.

		Total		М		F		$\mathbf{F}^{\mathbf{e}}$		Transient	
Yr	Harvestable	No. <sup>a</sup>	% <sup>b</sup>	No. <sup>c</sup>	% <sup>d</sup>	No. <sup>c</sup>	% <sup>d</sup>	No.	% <sup>d</sup>	No. <sup>c</sup>	% <sup>d</sup>
1987–1988	20	2	10.0	0	0.0	2	20.0	0	0.0	0	0.0
1988-1989	22	6	27.3	1	25.0	1	9.1	0	0.0	4	57.1
1989-1990	17	4	23.5	3	75.0	0	0.0	0	0.0	1	25.0
1990-1991	21	9	42.9	3	60.0	3	23.1	0	0.0	3	100.0
1991-1992	27	4	14.8	1	25.0	1	7.7	0	0.0	2	40.0
1992-1993	32	7	21.9	1	25.0	2	14.3	0	0.0	4	44.4
1993-1994	23	5	21.7	3	42.9	1	7.7	0	0.0	1	33.3
1994-1995	32	6	18.7	1	16.7	2	11.8	0	0.0	3	42.9
1995-1996	35	7	20.0	3	50.0	1	4.8	1	4.8	3	75.0
1996-1997	33	6	18.2	3	60.0	3	13.6	7	31.8	0	0.0
1997-1998	24	5	20.8	0	0.0	5	35.7	0	0.0	0	0.0
1998-1999	22	6	27.3	1	20.0	2	16.7	0	0.0	3	60.0
1999-2000	28	3	10.7	0	0.0	1	9.1	1	9.1	2	50.0
2000-2001	25	7	28.0	1	25.0	3	18.7	0	0.0	3	60.0
2001-2002	21	10	47.6	2	40.0	4	33.3	0	0.0	4	100.0

<sup>a</sup> Total no. of animals harvested.

<sup>b</sup> Percentage animals harvested were of the total harvestable population.

<sup>c</sup> Total no. of animals harvested of the respective social group.

<sup>d</sup> Percentage animals harvested or died were of the no. of individuals in the respective group (see Table 1).

<sup>e</sup> The no. of resident F that either died or disappeared within a given yr.

natal home range. Of the 31 male kittens known to reach independence, hunters harvested 6 within the study area shortly after they separated from their mothers. All but one of the other 25 males dispersed to areas outside the study area with a maximum known distance of 550 km (Laundré and Hernández 2003). Three of the 23 female kittens to reach independence dispersed from the study area, whereas all the rest became resident animals. All 3 of these individuals reached independence and dispersed after 1992–1993.

#### The Level of Hunting and Other Causes of Mortality

Over the 15 years of our study, hunters harvested 87 pumas. Of these animals, 34 (39.1%) were pumas we collared. Annual harvest ranged from 2 to 10 animals and averaged  $5.8 \pm 0.54$  individuals per year (Table 2). Of the 87 harvested animals, 33 (37.9%) were transients (27 M and 6 F), 24 (27.6%) resident males, and 30 (34.4%) resident females. Only 6 of the 24 resident males harvested were ones we marked. Annual harvest of resident females varied from 0 to 5 and averaged  $2.0 \pm 0.32$  individuals per year (Table 2). The harvested percentage of the total harvestable population  $(\geq 1.0 \text{ yr}; \text{Lindzey et al. 1992})$  varied from 10%-47.6% with an overall average for the 15 years of 23.6  $\pm$  2.7% (Table 2). The harvest of resident males averaged  $31.0 \pm 6.0\%$ (range: 0-75%) of the resident male population (Table 2). For resident females, the harvest averaged  $15.0 \pm 2.8\%$ (range 0-35.7%) of the population (Table 2). For the transient population, the harvest averaged 45.8  $\pm$  8.2% (range 0-100%; Table 2).

In addition to human harvest, 4 resident females died and 5 disappeared and we presumed that they died (Table 2). One individual died or disappeared in 1995–1996 and 7 in 1996–1997, 3 and 4 years after the deer decline. Three of the 4 residents that died in 1996–1997 were residents for 2, 5, and 6 years. The other was a young female in her first year of residency. The other 5 animals were residents for 2–7 years ( $\bar{x} = 4.7 \pm 0.84$  yr). For 1995–1996 and 1996–1997, the combined harvest and nonharvest losses for resident females represented 9.5% and 45.5% of their population segments (Table 2).

### DISCUSSION

Although the number of hunters, weather conditions, and other variables can influence deer hunter success (Unsworth et al. 2002), hunter numbers per year were constant over our period of interest. Weather conditions perhaps contributed to minor fluctuations in success we noted from 1981 to 1986. However, the major increase in hunter success we saw in 1987 can best be explained by an increase in deer numbers. This was also the same year Lindzey et al. (1994) recorded a substantial increase in hunter success in southern Utah, which corresponded to an increase in pellet survey results. Both these results correspond to increasing trends in most of the West (Unsworth et al. 1999, Ballard et al. 2001). Consequently, we concluded that the deer population in our study area began increasing substantially from the beginning of our study in 1985. The concurrence of the hunter success data and the trends survey results from our area also supported our conclusion that deer numbers remained high until 1992, declined dramatically in 1993, and remained low during the rest of our study.

# Numerical Response of Pumas to Changing Deer Abundance

Our results supported the prediction that pumas will respond exponentially to increases in deer abundance. Our estimated rate of increase of r = 0.07 during the growth phase of the puma population compares with the 0.04–0.08 rate Logan and Sweanor (2001) calculated for an expanding

hunted population in Alberta (Ross and Jalkotzy 1992). However, both estimates are lower than the estimates of 0.11–0.21 found by Logan and Sweanor (2001) for the expanding puma population in New Mexico. This difference is perhaps because there was no hunting of the puma population during the study in New Mexico and it was recovering from a previous severe reduction at the time of an increasing deer population (Logan and Sweanor 2001). Logan and Sweanor's (2001) estimate of an exponential rate of increase of r = 0.28 for the puma subpopulation that they experimentally reduced supports this supposition.

Relative to declining prey abundance, our resident puma population continued to increase even after the deer population declined in 1992–1993. However, the puma population did peak in 1995–1996 and began to decline 4 years after the decline in deer abundance. The population decline was quite rapid (r = -0.182) the first 3 years, but then puma numbers stabilized over the last 3 years of the study, indicating that the puma population adjusted to the lower deer abundance. Thus, our results supported the prediction that a puma population would track prey declines with a 4-year lag response (Logan and Sweanor 2001).

#### Impact of Harvest on Puma Population Changes

The mean annual harvest rate over the study period was 5.8 individuals per year. This rate is equivalent to  $23.6 \pm 2.7\%$  of the harvestable population (Lindzey et al. 1992) and is higher than found in northern Idaho ( $11 \pm 2.1\%$ , n = 4, our calculations; Hornocker 1970), Wyoming (0% and 15%, Logan et al. 1986), and Alberta ( $8.2 \pm 4.3$ , n = 6; Ross and Jalkotzy 1992). In contrast, our average rate was similar to the simulated one-year 27% harvest rate of the harvestable animals of a protected population in southern Utah (Lindzey et al. 1992). Our maximum harvest rate of 47.6% (Table 2) was close to the 53% simulated one-year harvest of a protected population in New Mexico (Logan and Sweanor 2001). Thus, in comparison to other harvest levels, ours were moderate to high.

Over the study period, the major source of mortality we recorded for harvestable males was from hunting. We recorded only one male death due to starvation, which occurred after the deer decline. The harvest rate for resident males averaged  $36.6 \pm 7.2\%$  (range 0–75.0%; Table 2). This harvest rate was significantly higher than the  $8.7 \pm 2.8\%$  mortality rate that Logan and Sweanor (2001) reported for their nonhunted population (t = 3.43, df =15, P = 0.004). As a result, we considered much of the harvest of resident males in our study as additive rather than compensatory. As population biologists rarely consider adult males to be important to population growth, whether the level of harvest is additive or compensatory should have little effect on the population's numerical response to increasing deer abundance.

During the 9 years of population growth, harvest by humans was the only source of mortality for resident females and averaged  $10.8 \pm 2.4\%$  (range: 0–23.1%, Table 2). In southern Utah, the average annual mortality rate was 17.8 ± 8.4% for the 5 years when there was no harvest (Lindzey et al. 1988). For the nonhunted population in New Mexico, the average annual mortality rate for resident females was  $17.6 \pm 5.1\%$ , n = 8 (Logan and Sweanor 2001). In a oneway analysis of variance, we found no differences between the female harvest rate in our study and the mortality rates in these 2 nonhunted populations (P = 0.50). Because mortality rates of resident females from nonhunting causes equaled ours from hunting, we suggest that during the time period of increasing puma numbers, the moderate to high hunting mortality on this social group was primarily compensatory. The number of females drives population growth and if the mortality from hunting was compensatory, we further suggest that the harvest levels of resident females in our study did not affect population growth beyond what would occur without hunting.

For the impact of the harvest on the decline in puma numbers, we found the average total harvest rates before and after the decline did not differ (25.4  $\pm$  5.1%, n = 6 vs. 22.3  $\pm$  3.1%, n = 9, P = 0.59). However, for resident females, the percentage harvest rate before the decline in the population (10.8  $\pm$  2.4%, n = 9) was significantly lower (t = 2.22, P = 0.045) than after the decline (21.2  $\pm$  4.0 %, n =6). Yet, in the year before the decline (1996-1997) the harvest rate of females, which would affect the number of females the following year, was only 13.6%. Based on the results of Lindzey et al. (1988) and Logan and Sweanor (2001), this level of harvest would be compensatory under most circumstances. The disappearances (deaths or dispersals) and deaths from nonhunting sources of 31.8% of the resident females differed for that year. This was well above the average natural mortality rates Lindzey et al. (1988) and Logan and Sweanor (2001) reported and exceeded the harvest rates for the previous 9 years. This additional high loss of resident females at a time when survival of female kittens to independence was low resulted in a net loss of 8 resident females the next year (Table 1). Thus, it was this high loss of resident females mainly from nonharvest causes that initiated the decline in the puma population. A 35.7% loss from the harvest the next year followed the high loss of resident females in 1996-1997 (Table 2). It might be expected that this high loss rate, be it additive or compensatory, should drive the population down further. However, it resulted in a net loss of only 2 resident females (Table 1). Evidently, once the puma population size adjusted to the lower deer abundance, it again became resilient to occasionally high harvest rates, as noted in the studies of Lindzey et al. (1992) and Logan and Sweanor (2001). However, puma harvests in much of the West rose from around 1,500 or fewer animals per year prior to 1992 to almost 3,500 animals per year in 1997 and remain around 3,200 animals per year (Keefover-Ring 2005). This raises concern about the sustainability of puma populations because we do not know what the impact of chronically high harvest rates will be on puma populations, especially after they declined. Such high harvest rates might cause the collapse of the metapopulation structure needed to maintain

these populations and put puma populations at risk on a wide geographic scale (Sweanor et al. 2000).

In conclusion, the increases in natural mortality at a time when recruitment was reduced primarily drove the decline of pumas 4 years after the reduction in deer abundance. In our study, the low harvest rate during the critical first year of the decline seemed to have a limited role.

## Demographics of Puma Response to a Declining Deer Population

We found support for the prediction that the physical condition of pumas should decline with declining prey abundance. However, we found that body mass did not begin to decline until after the puma population declined. This indicates that adult males and females are somewhat resilient to the initial declines in prey abundance but as prey numbers remain low, they will eventually be affected.

Because of the declines in physical condition, survival rates of female pumas in our study, as predicted, were lower after the deer decline. Part of this lower survival was from slightly higher harvest rates of females after 1998. However, in the year of the puma decline (1996-1997), the greatest portion of the MICROMORT-estimated mortality was from resident females dying from causes other than hunting (19.9% vs. 10.0%). As predicted by Logan and Sweanor (2001), these deaths, likely from starvation, and the disappearances of other established residents from the population occurred after the decline in deer numbers. Hemker et al. (1984) and Lindzey et al. (1988) also recorded several deaths of adult pumas unrelated to hunting or conflicts with other pumas during their 1978-1986 studies. They attributed at least 2 of these to starvation. If, as the regional data and data from our study indicate, deer populations were low during most of this time, these data support the prediction that low prey abundance can lead to mortalities from starvation. In contrast, Hornocker (1970), under conditions of increasing prey abundance, did not find any deaths that might be attributed to starvation. Spreadbury et al. (1996) and Ross and Jalkotzy (1992), who studied pumas in the late 1980s when regional prey abundance was increasing, also did not record any deaths from starvation. Likewise, during the 8-year study in New Mexico under increasing deer numbers, only 2 of 19 deaths of adult females were from unknown causes unrelated to intraspecific strife or disease (Logan and Sweanor 2001). These data further support the prediction that reduced prey abundance will result in pumas starving, especially resident females.

A logical prediction based on a reduction in physical condition of females is that they should have a reduced reproductive output. However, we found no difference in the number of litters born per year or in litter sizes for pumas before and after the deer decline in our area. Our results coincide with those of Logan and Sweanor (2001), who also found no reduction in fecundity rates in their study. Thus, these results refuted the prediction that females will respond to prey declines with decreased productivity.

Although females may not reduce the number of kittens born, it is still possible that reduced deer numbers could



**Figure 5.** Annual population trends of pumas from various studies in western United States and Canada expressed as percentage of the maximum number of pumas recorded within a study. We plotted the values relative to the years in which the investigators conducted the studies.

affect kitten survival. Our finding that kitten survival to independence declined within the first year of the decline in mule deer supports this prediction. Consequently kitten survival to independence in our study appeared to be highly sensitive to declines in prey abundance, which reduced recruitment at a time of high mortality of resident females.

Lastly, relative to higher emigration by subadult females, we recorded the only 3 dispersals of females from our study area after the decline in deer abundance. These results are limited but they do support the prediction that limited food will cause more female offspring to disperse from natal areas.

The demographic changes we documented support the scenario presented by Logan and Sweanor (2001) in how a puma population should respond to a declining food supply. First kitten survival is affected because of the females' reduced hunting efficiency. As the scarcity in prey continues, the physical condition of females declines and starvation results. The combined reduction in kitten survival and recruitment and survival of adults then leads to a decline in the resident female population. All these results then, support the hypothesis proposed by Pierce et al. (2000) and Logan and Sweanor (2001) that pumas are limited primarily by their food supply, even in hunted populations. The overall result is that puma abundance exhibits cycles, which are linked to changes in prey abundance (Lindzey et al. 1988, Logan and Sweanor 2001). These cycles seem to coincide closely in time over large geographical areas (Fig. 5). Peaks seem to occur approximately every 10 years (Fig. 5) and at least the last 2 cycles corresponded to cycles in deer abundance (Unsworth et al. 1999, Ballard et al. 2001).

## MANAGEMENT IMPLICATIONS

The evidence that puma populations cycle over time is of importance to the management of a sustainable harvest of pumas. During the increasing phase of a cycle, our data and other published studies indicate that a harvest rate of approximately 20% of harvestable individuals is likely compensatory and puma populations can withstand this rate and occasional higher harvests (Lindzey et al. 1992, Logan and Sweanor 2001). Nevertheless, even when our population declined, an average harvest rate of 25% of the harvestable population did not produce further declines in the population. These results suggest that harvest goals set at approximately 20% of the harvestable population, when the population is >20 individuals, should not negatively affect puma populations in the long term.

Most of the replacement of resident females in our study came from local reproduction. This underscores the importance in providing some protection to resident females. Our data demonstrated that an average 10%harvest of resident females did not prevent our population from increasing and an average of about 20% after the decline did not reduce the population further. These results suggest a reasonable harvest goal for a population of >10 females should be around 15-20% of resident females.

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## LITERATURE CITED

- Anderson, C. R., Jr., and F. G. Lindzey. 2005. Experimental evaluation of population trend and harvest composition in a Wyoming cougar population. Wildlife Society Bulletin 33:179–188.
- Ballard, W. B., D. Lutz, T. W. Keegan, L. H. Carpenter, and J. C. deVos, Jr. 2001. Deer-predator relationships: a review of recent North American studies with emphasis on mule and black-tailed deer. Wildlife Society Bulletin 29:99–115.
- Bangs, E. E., T. N. Bailey, and M. F. Portner. 1989. Survival rates of adult female moose on the Kenai Peninsula, Alaska. Journal of Wildlife Management 53:557–563.
- Blum, S. 2003. Habitat use by mountain lions (*Puma concolor*) in the Northern Great Basin. Thesis, Idaho State University, Pocatello, USA.
- Boertje, R. D., and R. O. Stephenson. 1992. Effects of ungulate availability on wolf reproductive potential in Alaska. Canadian Journal of Zoology 70:2441–2443.

- Caughley, G. 1978. Analysis of vertebrate populations. John Wiley and Sons, New York, New York, USA.
- Cougar Management Guidelines Working Group [CMGWG]. 2005. Cougar Management Guidelines. First edition. WildFutures, Bainbridge Island, Washington, USA.
- DeYoung, C. A. 1989. Mortality of adult male white-tailed deer in south Texas. Journal of Wildlife Management 53:513–518.
- Freddy, D. J., G. C. White, M. C. Kneeland, R. H. Kahn, J. W. Unsworth, W. J. deVergie, V. K. Graham, J. H. Ellenberger, and C. H. Wagner. 2004. How many mule deer are there? Challenges of credibility in Colorado. Wildlife Society Bulletin 32:916–927.
- Heisey, D. M., and T. K. Fuller. 1985. Evaluation of survival and causespecific mortality rates using telemetry data. Journal of Wildlife Management 49:668–674.
- Hemker, T. P., F. G. Lindzey, and B. B. Ackerman. 1984. Population characteristics and movement patterns of cougars in Southern Utah. Journal of Wildlife Management 48:1275–1284.
- Hornocker, M. G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. Wildlife Monograph 21.
- Hurley, M., and J. W. Unsworth. 2000. Southeast mule deer ecology. Idaho Department of Fish and Game, Federal Aid in Wildlife Restoration Job Progress Report, Project W-160-R-27, Boise, USA.
- Hurley, M., and P. Zager. 2004. Southeast mule deer ecology. Idaho Department of Fish and Game, Federal Aid in Wildlife Restoration Job Progress Report, Project W-160-R-31, Boise, USA.
- Keefover-Ring, W. 2005. State of pumas in the West: Heading towards overkill? Page 213 in R. A. Beausoleil and D. A. Martorello, editors. Proceedings 8th Mountain Lion Workshop. Washington Department of Fish and Wildlife, 17–19 May 2005, Olympia, Washington, USA.
- Laundré, J. W., and T. W. Clark. 2003. Managing puma hunting in the western United States: through a metapopulation approach. Animal Conservation 6:159–170.
- Laundré, J. W., and L. Hernández. 2002. Growth curve models and age estimation of young cougars in the Northern Great Basin. Journal of Wildlife Management 66:849–858.
- Laundré, J. W., and L. Hernández. 2003. Factors affecting dispersal in young male pumas. Pages 151–160 in S. A. Becker, D. D. Bjornlie, F. G. Lindzey, and D. S. Moody, editors. Proceedings of the Seventh Mountain Lion Workshop. Wyoming Game and Fish Department, 15–17 May 2003, Lander, USA.
- Laundré, J. W., L. Hernández, D. Streubel, and K. Altendorf. and C. López González. 2000. Aging mountain lions using gum-line recession. Wildlife Society Bulletin 28:963–966.
- Lindzey, F. G., B. B. Ackerman, D. Barnhurst, and T. P. Hemker. 1988. Survival rates of mountain lions in southern Utah. Journal of Wildlife Management 52:664–667.
- Lindzey, F. G., W. D. Van Sickle, B. B. Ackerman, D. Barnhurst, T. P. Hemker, and S. P. Laing. 1994. Cougar population dynamics in southern Utah. Journal of Wildlife Management 58:619–624.
- Lindzey, F. G., W. D. Van Sickle, S. P. Laing, and C. S. Mecham. 1992. Cougar population response to manipulation in Southern Utah. Wildlife Society Bulletin 20:224–227.
- Logan, K. A., L. L. Irwin, and R. Skinner. 1986. Characteristics of a hunted mountain lion population in Wyoming. Journal of Wildlife Management 50:648–654.
- Logan, K. A., and L. L. Sweanor. 2001. Desert puma evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington, D.C., USA.
- Marshal, J. P., P. R. Krausman, V. C. Bleich, W. B. Ballard, and J. S. McKeever. 2002. Rainfall, el Niño, and dynamics of mule deer in the Sonoran desert, California. Journal of Wildlife Management 66:1283–1289.
- Mowat, G., B. G. Slough, and S. Boutin. 1996. Lynx recruitment during a snowshoe hare population peak and decline in southwest Yukon. Journal of Wildlife Management 60:441–452.
- Pierce, B. M., V. C. Bleich, and R. T. Bowyer. 2000. Social organization of mountain lions: does a land-tenure system regulate population size? Ecology 81:1533–1543.
- Ross, P. I., and M. G. Jalkotzy. 1992. Characteristics of a hunted population of cougars in southwestern Alberta. Journal of Wildlife Management 56:417–426.
- Seidensticker, IV, J. C., M. G. Hornocker, W. V. Wiles, and J. P. Messick.

1973. Mountain lion social organization in the Idaho Primitive Area. Wildlife Monographs 35.

- Spreadbury, B. R., K. Musil, J. Musil, C. Kaisner, and J. Kovak. 1996. Cougar population characteristics in southeastern British Columbia. Journal of Wildlife Management 60:962–969.
- Steinert, S. F., H. D. Riffel, and G. C. White. 1994. Comparisons of big game harvest estimates from check station and telephone surveys. Journal of Wildlife Management 58:355–340.
- Sweanor, L. L., K. A. Logan, and M. G. Hornocker. 2000. Cougar dispersal patterns, metapopulation dynamics, and conservation. Conservation Biology 14:798–808.
- Todd, A. W., and L. B. Keith. 1983. Coyote demography during a snowshoe hare decline in Alberta. Journal of Wildlife Management 47: 394–404.
- Unsworth, J. W., N. F. Johnson, L. J. Nelson, and H. M. Miyasaki. 2002. Estimating mule deer harvest in southwestern Idaho. Wildlife Society Bulletin 30:487–491.
- Unsworth, J. W., F. A. Leban, D. J. Leptich, E. O. Garton, and P. Zager. 1994. Aerial survey: user's manual and practical tips for designing and conducting aerial big game surveys. Idaho Department of Fish and Game, Boise, USA.
- Unsworth, J. W., D. F. Pac, G. C. White, and R. M. Bartmann. 1999. Mule deer survival in Colorado, Idaho, and Montana. Journal of Wildlife Management 63:315–326.
- Zar, J. H. 1999. Biostatistical analysis. Fourth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

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