Impact of puma predation on the decline and recovery of a mule deer population in southeastern Idaho

J.W. Laundré, L. Hernández, and S.G. Clark

Abstract: We modeled the impact of puma (*Puma concolor* (L., 1771)) predation on the decline and recovery of mule deer (*Odocoileus hemionus* (Rafinesque, 1817)) in southern Idaho based on estimates of puma numbers, predation rates of pumas, and reproductive variables of deer. Deer populations peaked in 1992–1993, then declined more than 55% and remained low for the next 11 years. Puma numbers peaked 4–6 years after deer populations peaked but then declined to original levels. Estimated puma predation on the deer population before and after the decline was 2.2%–3.3% and 3.1%–5.8%, respectively. At high puma densities (>3 pumas/100 km^2), predation by pumas delayed deer recovery by 2–3 years. Percent winter mortality of fawns (r^2 = 0.62, P < 0.001) and adult female deer (r^2 = 0.68, P < 0.001) correlated positively with December–January snowfall. Incorporation of winter snowfall amounts in the model produced a pattern of deer population change matching estimated changes based on field survey data. We conclude that pumas probably were a minor factor in the decline of the deer population in our area and did not suppress deer recovery. We propose that winter snowfall was the primary ultimate and proximate factor in the deer decline and suppression of their recovery.

Résumé : Nous avons modélisé l'impact de la prédation par les pumas (*Puma concolor* (L., 1771)) sur le déclin et la récupération des cerfs-mulets (*Odocoileus hemionus* (Rafinesque, 1817)) dans le sud de l'Idaho d'après les estimations de densité des pumas, les taux de prédation des pumas et les paramètres reproductifs des cerfs. Les populations de cerfs ont atteint un sommet en 1992–1993, puis ont décliné de >55 % et sont demeurées basses pendant les 11 années suivantes. Les populations de pumas ont atteint un sommet 4–6 ans après le maximum des populations de cerfs, puis elles sont revenues à leur densité d'origine. La prédation des pumas sur la population de cerfs avant et après le déclin est estimée à respectivement 2,2 % – 3,3 % et 3,1 % – 5,8 %. Aux fortes densités de pumas (>3 pumas/100 km^2), la prédation par les pumas retarde la récupération des cerfs de 2–3 ans. Il y a une corrélation positive entre le pourcentage de mortalité des faons (r^2 = 0,62, P < 0,001) et des femelles adultes (r^2 = 0,68, P < 0,001) en hiver et les précipitations de neige en décembre–janvier. L'incorporation dans le modèle des quantités de précipitations de neige de l'hiver génère un patron de variations dans les populations de cerfs qui correspond aux changements observés dans les données d'inventaire de terrain. En conclusion, il semble que les pumas aient été un facteur relativement peu important dans le déclin des populations de cerfs dans notre région et qu'ils n'aient pas empêché la récupération des cerfs. Nous pensons que les précipitations de neige en hiver sont le principal facteur ultime et immédiat du déclin des cerfs et de la suppression de leur récupération.

[Traduit par la Rédaction]

Introduction

Pumas (*Puma concolor* (L., 1771)) are currently the only large predator in most of western North America, and their role in ecosystem processes has been the subject of much debate (e.g., Clark et al. 2005). Many conservationists view pumas as essential ecosystem elements, even as a keystone or umbrella species (Kellert and Smith 2000; Laundré and Clark 2003). Hunters see them both as valued game animals and as competitors for limited supplies of large ungulate game such as elk (*Cervus elaphus* L., 1758) and mule deer (*Odocoileus hemionus* (Rafinesque, 1817)) (Hansen 1992; Barness 1998; Deurbrouck and Miller 2001). Ranchers view them as predators on livestock (Shaw 1977), while the general public considers them a valuable symbol of nature but also a threat to human life (Beier 1991, 1992; Deurbrouck and Miller 2001). Reflecting these conflicting views is the continuing debate about the role of pumas in the dynamics of prey populations, principally mule deer (Ballard et al. 2001; Logan and Sweanor 2001).

The decline of mule deer populations in many areas of the West in the early 1990s added urgency to this debate (Ballard et al. 2001). Deer populations declined in 1992–1993, and as of 2004 many had yet to recuperate fully (Hurley and Unsworth 2000; Ballard et al. 2001; Idaho Department of Fish and Game 2004). Many people contend that this is the result of increasing puma populations over most of the West (Logan et al. 2003). Yet, the few studies that have

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been done have yielded equivocal results about the impacts of pumas on ungulate populations and no clear evidence exists to support the contention that puma populations have increased. Thus, the controversy has continued and has renewed attempts to assess the effect of predation generally and by pumas specifically on deer populations.

The most recent such assessment was an extensive review by Ballard et al. (2001) of literature on mule deer populations. Unfortunately, these authors were unable to clarify the role of predation by coyotes (*Canis latrans* Say, 1823) and pumas in mule deer population dynamics and supported Connolly's (1978) original observation that the role of predators seemed to depend on which studies were examined. Ballard et al. (2001) did find evidence that predation effects were usually minimal when deer populations were considered high. However, though not implicated in major declines of deer, predation may suppress deer numbers and prevent a timely recovery after such declines (Sinclair 1991; Ballard et al. 2001). This hypothesis, however, has not been adequately tested, primarily because of the lack of studies of the impacts of pumas on deer. Of the 17 studies cited by Ballard et al. (2001) in their review, only 3 investigated the impact of pumas on deer (Logan et al. 1996; Bleich and Taylor 1998; Unsworth et al. 1999). Of these, only 1 monitored puma numbers annually in conjunction with their analysis (Logan et al. 1996; Logan and Sweanor 2001). In addition to the New Mexico study (Logan and Sweanor 2001), only 1 other study, from central Idaho, incorporated annual data on both puma and deer population dynamics (Hornocker 1970).

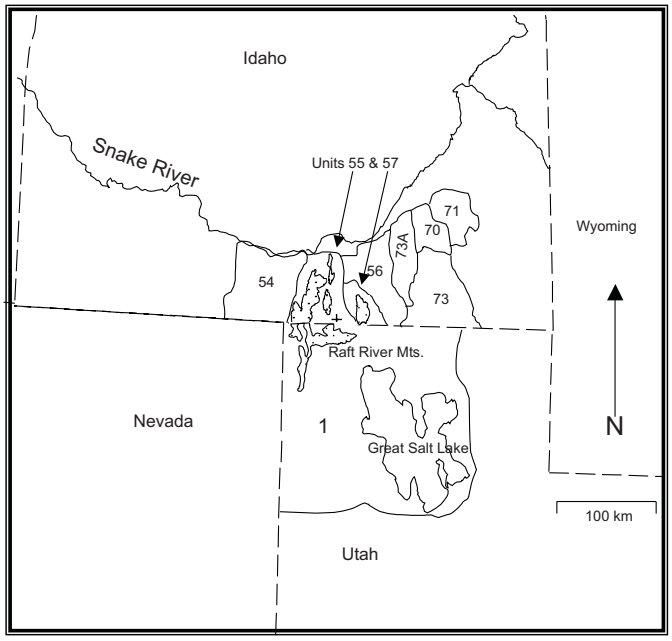
In central Idaho, Hornocker (1970) found that deer populations increased even though he recorded some of the highest numbers of pumas found in the area. Consequently, Hornocker (1970) concluded that pumas were not capable of preventing deer population growth in his study area. In the New Mexico study, Logan and Sweanor (2001) also found increasing deer numbers at the same time that puma numbers were increasing. In the last years of their study, deer numbers declined and they concluded that puma predation was the major proximate cause "driving the deer population downward" (Logan and Sweanor 2001, p. 333). However, they noted that even the 7-year time span of their data was not sufficient to document causative factors affecting puma and deer numbers (Logan and Sweanor 2001).

An additional problem with all the studies of puma predation on deer is the failure to consider the effects of weather (particularly heavy snowfall or drought) on deer populations. Although weather is often mentioned and even implicated in the changes seen in deer populations (Anthony 1976), it is rarely incorporated directly in analyses of the data or in projections of models (Unsworth et al. 1999; Ballard et al. 2001; Logan and Sweanor 2001).

Thus, to date, results of the few studies that exist are equivocal, and the hypothesis that pumas can limit deer numbers when they are low has not been adequately tested. Also, no attempt has been made to test the hypothesis that weather conditions can suppress the recovery of deer populations after a major decline.

From 1985 to 2002 we studied a population of pumas in southern Idaho and northwestern Utah. Over 15 years of the study we were able to estimate the minimum number of pumas in the area (Laundré et al. 2007). During this period, the mule deer population in the region, including our study area, was extremely high but experienced a major decline in 1992–1993 (Hurley and Unsworth 2000). There is also accurate meteorological data available for the area. Thus, we had the three necessary data sets to test the following hypotheses. First, puma predation was the proximate cause of the deer decline in our area. Second, after the deer population declined, the puma population kept the deer population from recovering. Third, weather effects, primarily winter snowfall amounts, contributed to the deer decline and were a causative factor in preventing the recovery of the deer population.

Fig. 1. Location of study area in southern Idaho and northwestern Utah. The total study area included the Raft River Mountains in wildlife management unit 1 of Utah, but the data for determining recovery time for the mule deer (*Odocoileus hemionus*) population included only the Idaho portion of the study area (game management units 55 and 57). The locations of other management units in the region are also indicated.



Methods

Study area

The data on pumas came from our long-term study of a hunted population in southern Idaho and northwestern Utah. The study area was located in Idaho Department of Fish and Game (IDFG) game management units 55 and 57 of Cassia County, Idaho, and the extreme northwestern corner of Utah Division of Wildlife Resources game management unit 1 in Box Elder County, Utah, USA (Fig. 1). The total area of 2800 km^2 contained approximately 1700 km^2 of puma habitat (940 km^2 in Idaho) within five small, isolated mountain ranges with elevations of 1830–3151 m. The majority (>80%) of the mountainous lands are administered by the US Forest Service and US Bureau of Land Management (J.W. Laundré, unpublished data). Mountain ranges were fragmented into open and forested habitat patches that var-

ied in size. Forested patches consisted of various mixes of Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), juniper (*Juniperus osteosperma* (Torr.) Little and *J. scopulorum* Sarg.), pinyon pine (*Pinus edulis* Engelm.), quaking aspen (*Populus tremuloides* Michx.), and curl-leaf mountain mahogany (*Cercocarpus ledifolius* Nutt.). Dominant shrubs in open areas included big sagebrush (*Artemisia tridentata* Nutt.), gray rabbitbrush (*Chrysothamnus nauseosus* (Pallas ex Pursh.) Britt.), bitterbrush (*Purshia tridentata* (Pursh.) DC), and buffaloberry (*Shepherdia rotundifolia* Parry). Although there was some human development in the area over the 16 years of the study, little habitat change occurred on the US Forest Service land (J.W. Laundré, personal observations). Climate was characterized by hot, dry summers (20–35 °C) and cold, windy winters (–25 to –4 °C). Humidity rarely exceeded 40%, and precipitation was sporadic, averaging 30 cm annually. With only a remnant (<50) elk population in the area, mule deer were the principal prey species of pumas. Other prey species used occasionally by pumas during the study period included coyotes, bobcats (*Lynx rufus* (Schreber, 1777)), and porcupines (*Erethizon dorsatum* L., 1758).

Modelling

To calculate recovery time for the deer population under puma predation in our study area we used a spreadsheet-based deterministic model as outlined by the Cougar Management Guidelines Working Group (CMGWG 2005). We used this type of model because it is considered more robust and realistic for site-specific data than more general theoretical "canned" models (CMGWG 2005). We restricted our analysis to 1993–2004, following the reported decline in deer numbers in the winter of 1992–1993.

Model input data

For pumas, we obtained data directly from our intensive field efforts conducted annually from November through February to locate puma tracks and capture pumas. We radio-collared all pumas captured and monitored their fate over the course of the study. Previously we published details of our capture efforts and how we estimated the number of pumas in the study area (Laundré et al. 2007). This type of intensive field effort is recognized as the most reliable method for estimating puma numbers and population structure (CMGWG 2005).

For mule deer, we used data from IDFG survey reports for our study area and from published studies on regional deer herds. Estimates of relative deer numbers were based on aerial sightability surveys made by trained IDFG personnel each March from 1992 to 2004 with a Bell 47 helicopter in designated trend areas within established winter ranges in our study area and surrounding management units. These surveys were conducted according to the protocol established by Unsworth et al. (1994). Because these survey data were available only for Idaho, we restricted our model to the Idaho portion (units 55 and 57; 940 km^2) of the study area. Fawn to doe and buck to doe ratios were obtained from winter deer herd composition surveys conducted in late December and early January by IDFG personnel (Idaho Department of Fish and Game 2001, 2004).

To estimate annual fawn production, we used the average pregnancy rate of 84.8% ± 8.2% (n = 283) for yearling and adult does reported for our area by IDFG personnel (Hurley and Unsworth 2000). These data were based on blood serum samples collected from 1998 to 2000 in various management units near our study area (units 54, 56, 71, and 73A). We multiplied this rate by an average June fawn-at-heel to doe ratio of 1.67 ± 0.04 (n = 5 years), estimated by IDFG personnel from 1998 to 2002 by ground observations of females with fawns (Hurley and Zager 2004). These data came from hunting unit 56, which is adjacent to our study area (Fig. 1). We then multiplied this per-doe birth rate by the estimated number of adult females in our model population in the spring of each year to obtain annual fawn production estimates.

To estimate annual predation rates by pumas, we multiplied the number of deer consumed annually per puma for each of four social classes (males, females, females with kittens, and transients; Laundré 2005) by our estimate of the number of pumas in each social class (Laundré et al. 2007) and then summed the four values (Table 1). Annual deer consumption per social group for our study area, based on energetic needs and a mixed diet of fawns to adults, was calculated previously (Laundré 2005). We estimated the proportion of male and female deer killed based on the sex ratio of 120 deer we found killed by radio-collared pumas during our intensive field effort (67.0% female vs. 33.0% male; J.W. Laundré, unpublished data). We obtained estimates of harvests by human hunters from IDFG reports (Idaho Department of Fish and Game 2001, 2004). Units 55 and 57 are controlled hunt areas where specific numbers of hunter permits are issued each year. IDFG estimates hunter success based on information obtained from roadside check stations and phone surveys, which have been shown to be reliable estimators of success (Steinert et al. 1994; Unsworth et al. 2002). For each year, we subtracted an additional 5% from the model population for "other" causes of mortality (Hurley and Unsworth 2000). This percentage was based on IDFG estimates of cause-specific mortality of adult radio-collared does from 1998 to 2000 for units 56 and 73A, near our study area (Hurley and Unsworth (2000). Annual mortality rates from all causes except puma predation and malnutrition (primarily a cause of mortality in winter) averaged 3.0% ± 1.8% (range 0%–11.3%). Because of the large standard error of this estimate, we decided to use a "worst-case" value of 5.0% rather than the average.

To calculate fawn mortality for the first 6 months of life, we compiled the fawn to doe ratios for unit 56 from the December–January 1998–2002 aerial composition surveys (Hurley and Zager 2004). By December, the average fawn to doe ratio for this unit was 61.8 ± 3.8 fawns/100 does (n = 5 years) (Hurley and Zager 2004). We then subtracted this ratio from the June fawn-at-heel to 100 does ratio and then divided the difference by the June ratio to estimate summer to early winter mortality. The 5-year average was 64.1% ± 2.4% (range = 60.5%–73.8%). To calculate the number of fawns surviving to December for 1998–2002, we multiplied the estimate of survival (100% – percent mortality) for a given year by fawn production for that year. For the years prior to 1998 (1993–1997) and after 2002 (2003–2005), we multiplied the estimated fawn production by the average survival rate of 35.9% (100% – 64.1%). Once we had esti-

Table 1. Puma (*Puma concolor*) numbers and annual predation levels in the Idaho portion of the study area for 1987–1988 to 2001–2002.

					No. of deer killed/year by pumas	
Year	Resident males	Resident females/no	Resident females/yes	Transients	Est. pop.	+50%
1987–1988	4	5	3	2	310	465
1988–1989	3	6	3	4	344	516
1989–1990	3	2	7	0	384	576
1990–1991	3	6	2	1	246	369
1991–1992	2	6	3	3	305	457
1992–1993	3	8	1	9	392	587
1993–1994	5	5	4	2	369	553
1994–1995	4	5	5	3	408	612
1995–1996	2	10	4	5	443	664
1996–1997	2	7	5	2	380	570
1997–1998	3	8	1	5	314	471
1998–1999	3	6	2	1	246	369
1999–2000	2	3	4	3	300	450
2000–2001	2	9	2	2	291	436
2001–2002	4	2	5	1	325	487

Note: The number of mule deer (*Odocoileus hemionus*) killed per puma was 19.4/year for males and transients, 14.9/year for females without kittens (females/no), and 39.6/year for females with kittens (females/yes) and was based on data from Laundré (2005). The first estimate of puma predation is based on our estimated population (Est. pop.) of pumas and the last predation calculation is based on 50% more pumas in each category.

mated the number of fawns surviving to December, we divided this number into males and females based on a reported 50:50 sex ratio for our area (Hurley and Unsworth 2000).

Overwinter mortality estimates

There were no data available on annual overwinter survival rates of deer from our study area. However, data were available from a long-term (15 years) study in western Colorado with conditions similar to those in our area. Unsworth et al. (1999) found that survival rates in Colorado did not differ from those in two other study areas, including one in southern Idaho. Thus, we assumed we could apply their findings to our study area. Minimal January–March mortality rates for mild winters with minimal snow cover were 25% for fawns and 0.0% for does (Unsworth et al. 1999). Although minimal adult doe mortality was 0.0%, it is unlikely that no adult does would die during mild winters over the 12 years we ran the model, so we used a base 5% mortality rate to again provide a "worst-case" scenario. Adult male mortality was assumed to be 5% higher (10%) than doe mortality based on data from the long-term study of Logan and Sweanor (2001).

To incorporate the possible effect of increasing winter snow levels on recovery rates of deer, we first regressed annual estimates of overwinter (January–March) mortality rates for fawns and does for the long-term study in western Colorado (Unsworth et al. 1999) against snow depths reported for the area (http://www.wrcc.dri.edu/climsum). Unsworth et al. (1999, p. 320) reported only overall annual survival rates for does. To estimate mortality resulting only from winter conditions, primarily malnutrition, we subtracted mortality due to other causes, including predation by pumas, from the mortality rates (1 – survival) reported by Unsworth et al. (1999). The mortality rate from other causes, 8.6% (SE = 2.0, n = 6), is from the study of Hurley and Unsworth (2000) for management units 56 and 73A, near our study area, from 1998 to 2000. For fawns, Unsworth et al. (1999) reported overwinter mortality rates, which included predation, from January through May, so we used these estimates directly. We regressed these estimated winter mortality rates for does and fawns against total winter and December–January snowfall (cm) to determine which might best explain the variability in mortality rates. The resulting best-fit regression equations were then used to estimate annual winter mortality rates for fawns and does in our area based on local snowfall amounts (http://www.wrcc.dri.edu/climsum). Adult male mortality rates were again 5% higher than those estimated for females. Annual values for each parameter we used in the model for winter effects are in Table 2.

Running the model

To begin our modeling we first had to estimate the number of deer in our study area at the beginning of the recovery period in spring of 1993. As most deer populations in the state were at a long-time high in 1992 before the 1992–1993 decline (Hurley and Unsworth 2000), we estimated deer numbers for the study area at this time by multiplying the size of our study area (940 km^2) by an estimated maximum density (no./km^2) of deer for our region. High density estimates from other areas in the West for mule deer ranged from 29 to 70 deer/km^2 (Ballard et al. 2001). It is possible that densities in our study area were within this range (Hurley and Unsworth 2000), but because the sightability survey data were designed to provide only relative changes in deer numbers, no density estimates were available. Consequently, we decided to use a conservative estimate of 20 deer/km^2 or 18 800 deer in the fall of 1992.

After estimating the deer population in our area for 1992, we decreased the estimate to reflect declines in deer numbers

Table 2. Model inputs used for the modeling of winter effects on mule deer recovery.

Year	Pregnancy rate (%)	Snow depth (cm)	Fawn mort., winter (%)	Fawn mort., summer (%)	Doe mort., winter (%)	Doe mort., summer (%)
1992–1993	84.8	85.7	80.6	na	12.2	na
1993–1994	84.8	5.6	25.1	64.1	0.0	5
1994–1995	84.8	18.7	34.1	64.1	0.3	5
1995–1996	84.8	53.2	58.1	64.1	6.5	5
1996–1997	84.8	75.0	73.2	64.1	10.4	5
1997–1998	84.8	11.2	29.0	64.1	0.0	5
1998–1999	84.8	34.8	45.3	60.5	3.2	5
1999–2000	84.8	30.7	42.5	61.4	2.6	5
2000–2001	84.8	38.1	47.6	73.8	3.8	5
2001–2002	84.8	67.6	68.0	61.7	9.0	5
2002–2003	84.8	5.1	24.7	64.0	0.0	5
2003–2004	84.8	77.8	75.1	64.1	10.8	5
2004–2005	84.8	78.4	74.4	64.1	11.0	5

Note: The pregnancy rate is the average calculated by Hurley and Unsworth (2000). Snow depths are for December–January in Burley, Idaho; data are from the Western Regional Climate Center (http://www.wrcc.dri.edu/climsum). Fawn and doe winter mortality rates (mort.) are estimated from the regression equations derived from Unsworth et al. (1999). Summer fawn mortality rates for 1998 to 2002 are from Hurley and Unsworth (2000) for southeastern Idaho. For the remaining years we used the average rate for 1998–2002 from Hurley and Unsworth (2000). The summer doe mortality rate is the average of data from 1998 to 2002 reported by Hurley and Unsworth (2000) for annual mortality of adult does from all causes except pumas and malnutrition. Male mortality rates were 5.0% higher than female mortality rates.

in the winter of 1992–1993 for our region (Hurley and Unsworth 2000; Hurley and Zager 2004). Based on trend survey results from various units in and around our study area, the average decline was 56.9% ± 12.2%, n = 4, range = 21.7%–78.1% (Idaho Department of Fish and Game 2001). To provide a worst-case scenario, we reduced the 1992 estimate by 60%, to 7520 animals. This revised estimate represented the starting population of deer in spring 1993, the beginning of the recovery period. This number of deer was divided into females and males based on the 25:100 buck to doe ratio estimated by IDFG for the area (Idaho Department of Fish and Game 2001).

Once we had estimated the spring 1993 deer population size, we subtracted our estimates of deer killed by pumas from this starting population to account for losses of animals during the year to pumas. We then calculated the estimated fawn production. Then, we subtracted the human harvest of deer, divided by sex, for our study area (units 55 and 57; Idaho Department of Fish and Game 2001) and the June to December fawn mortality estimates. This gave us the pre-winter deer population estimate.

To test the effects of puma predation on the recovery of the deer population without confounding winter weather effects, we initially assumed mild winter conditions and minimal mortality rates of 25% for fawns, 5% for does, and 10% for bucks. We subtracted winter losses from the December population estimate to obtain the spring population size for the subsequent year. When calculating fawn production for subsequent years, we did not include doe fawns in the reproductive base.

We repeated this process for each year to determine the annual growth in the deer population and the number of years needed for the population to recover to pre-1993 levels under mild winter conditions. We calculated recovery time for three scenarios of puma numbers: the estimated number of pumas, 50% fewer pumas, and 50% more pumas. The scenario of 50% fewer pumas provided us with an analysis of how control of puma numbers might help recovery. We added the scenario of a higher puma population to provide a "worst-case" estimate of recovery time.

To incorporate the possible effect of winter snow levels on recovery rates of deer, we estimated winter mortality for each year based on the regression equations developed from the Colorado study (Unsworth et al. 1999) and snowfall (cm) in our area. We then incorporated the estimated winter mortality rates into the model for the three puma population scenarios.

After calculating the yearly changes in deer numbers based on our model inputs for puma predation and winter conditions (Tables 1 and 2), we compared the model estimates of percent change/year in deer numbers and estimated numbers of deer/year with actual field data collected by the IDFG. This comparison helped us evaluate how well our model performed. We calculated percent change/year in deer numbers for both the model output and the trend surveys by dividing a given year's estimate by the previous year's estimate and multiplying by 100. For the trend survey data of IDFG, our estimate was the average of eight different management units, including unit 55 of our study area. To compare estimated numbers of deer/year, we first needed to estimate the number of deer based on trend surveys. To do this, we first estimated the post-decline deer population in fall 1993 by multiplying the average percent (56.9% ± 12.2%) decline we calculated from the trend surveys for units in our region (Idaho Department of Fish and Game 2001) by the estimated high deer population (18 800) in 1992. After this year, we increased or decreased the number of deer by the average percent change (+ or –) we calculated from the survey data collected by IDFG personnel.

We conducted all statistical tests with SigmaStat® software (Systat Software Inc., Richmond, California, USA). We used parametric tests or their nonparametric equivalents if the data failed the requirements for parametric tests. Specific tests used are indicated. We report all means with standard error.

Fig. 2. (*a*) Annual population trends of pumas (*Puma concolor*) in the study area over 15 years (Laundré et al. 2007). Mule deer (*Odocoileus hemionus*) population trends based on IDFG winter surveys at eight sites in and around the study area and on the relative changes in harvest levels from units 55 and 57 in the study area are also presented. The number of deer hunting permits issued per year in units 55 and 57 is included for comparison with actual harvest levels. All data are presented as a percentage of the maximum value recorded for each category. (*b*) Relative changes in annual snowfall for the weather station located in Burley, Idaho, approximately 30 km north of the study site.

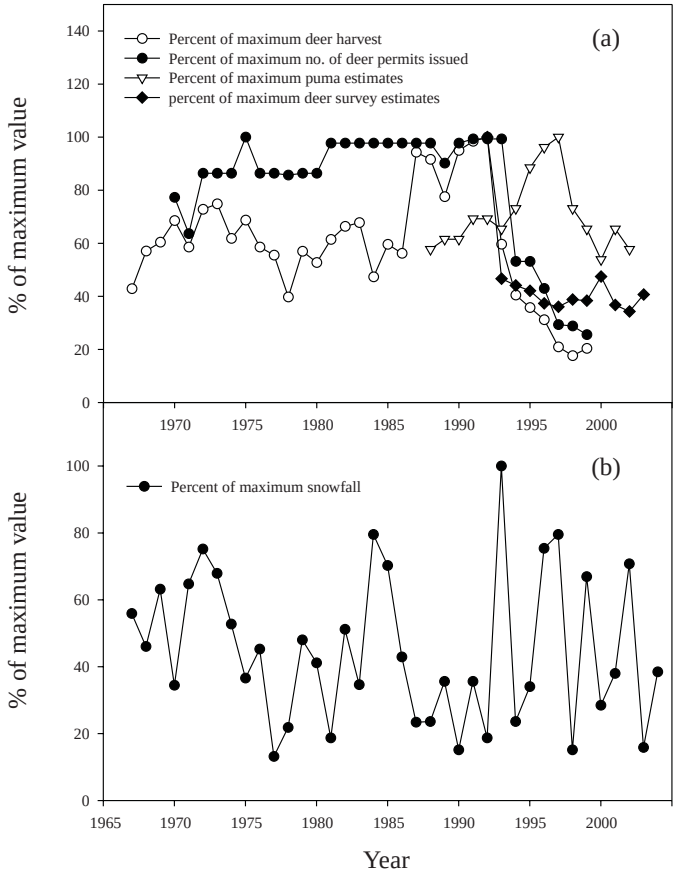
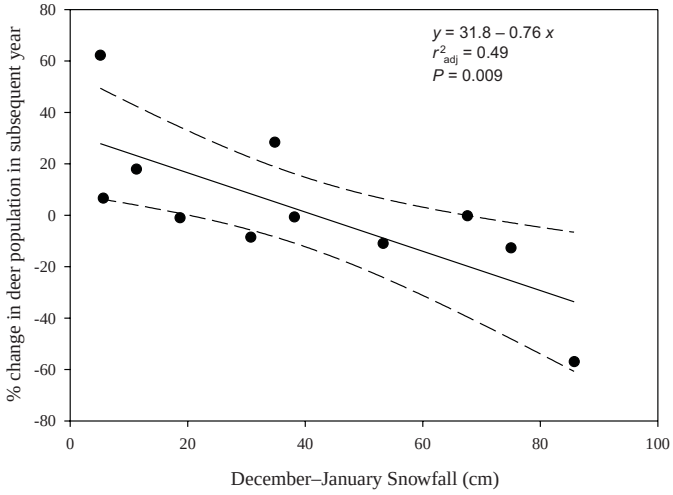


Fig. 3. Regression of the annual percent change in deer numbers, based on IDFG surveys, against the amount of snowfall recorded for December–January of the previous year. The relationship was significant at the $P = 0.009$ level with $r^2_{adj} = 0.49$.



Results

Population and weather trends

For our study area, we had estimates of the number of adult resident males and females, kittens, and transient pumas for 1987–1988 to 2001–2002 (Laundré et al. 2007). The number of resident animals varied over the 15 years, peaking in 1996–1997 and then declining back to original levels by the end of the study (Fig. 2*a*).

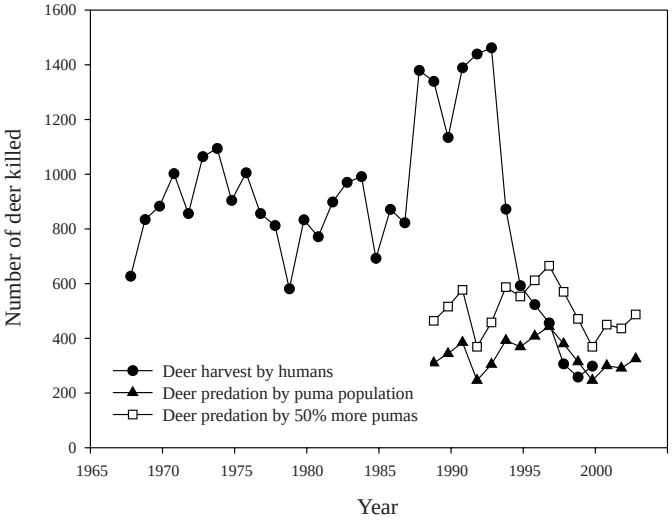
For mule deer, trend survey data were available only from 1994–1995 to 2003–2004 for one area in unit 55 of our study area and three other areas in nearby units 54 and 56 (Fig. 1; Idaho Department of Fish and Game 2001, 2004). However, we did find trend survey data for 1992–1993 to 2003–2004 for four areas in three surrounding units (71, 73, and 73A; Fig. 1). In all these units, the deer population estimate was highest in 1992–1993 and declined an average of 56.8% ± 12.2% the subsequent year (Fig. 2*a*). Based on harvest reports for our study area (units 55 and 57), human harvests of deer during the 6 years prior to the 1992–1993 population peak were the highest on record since 1966 (Fig. 2*a*). Permit numbers were similar from 1980 up to and including fall 1993 (Fig. 2*a*). However, in the fall of 1993 the harvest declined by 40.3% (Fig. 2*a*). Thus, based on these harvest data, it is assumed that the deer population in our study area declined to a degree similar to that in other units. After the deer decline in 1992–1993, trend survey estimates for the region varied annually, with the percent change in annual estimates between years varying from –10.9% to 31.3%.

We obtained snowfall data for the winter seasons (≈October–February) for the years of the study (1986–2005) for the town of Burley, Idaho, 30 km north of the study area (http://www.wrcc.dri.edu/climsum). Local snowfall was substantially below normal from 1986 to the winter of 1991–1992. In the winter of 1992–1993 the area reported the highest snowfall in 43 years (Fig. 2*b*). After 1992–1993, snowfall varied greatly (Fig. 2*b*). When we regressed the amount of snow received in December–January against the percent change in regional deer survey estimates the following year, we found a significant negative relationship (Fig. 3).

Impact of pumas on the pre-decline deer population and estimated recovery time for deer

The number of adult and independent pumas in the Idaho portion of the study area varied from 12 to 21 (Table 1). Based on the energetic requirements of each puma social class (Laundré 2005), we calculated that at our estimated population levels pumas would kill a minimum of 246 deer in 1991 and a maximum of 443 deer in 1996 (Table 1). For the 50% higher puma population, the lowest number of deer killed would be 369 and the highest would be 664 (Table 1). Assuming a maximum density of 20 deer/km^2, we estimated the number of deer in the 940 km^2 study area in fall 1992 to be 18 800. Assuming an approximate 60% decline in deer numbers in 1992–1993, the estimated population in the study area in the spring of 1993 would have been 7520 animals (6010 females and 1510 males). For the pre-decline

Fig. 4. Comparison of the annual number of deer harvested by humans and pumas within the study area. The estimates for humans are based on telephone surveys by IDFG personnel and the estimates for pumas are calculated from estimated puma numbers plus per-animal energetics calculations (Laundré 2005). The two estimates for pumas are derived for the estimated number of pumas in the study area and for a population 50% higher than estimated.



deer population of 18 800 animals in 1992, the calculated puma harvests of deer for the estimated and 50% higher puma populations were 2.2% and 3.3% of the deer population (Fig. 4). In contrast, the human harvest was 7.8% (Fig. 4), or 3.5 and 2.4 times higher than the estimated kill by pumas. After the decline in 1992–1993, the estimated kill by pumas approximately equaled the reduced human harvest (Fig. 4) and ranged from 3.1% to 5.8% of the estimated remaining deer population. The 50% higher puma population would have killed more deer than humans did (4.7% to 8.7% of the deer population; Fig. 4).

Under predation by the estimated puma population and mild winter conditions, the deer population would have increased by 4.1% in the first year after the decline, would have exceeded 10% growth in 5 of the 11 years, and would have been close to recovery by fall 2004 (Fig. 5*a*). For a puma population 50% higher than estimated, the deer population would have grown by 1.4% the first year and more than 10% in 3 of the 11 years but would not have approached recovery until the fall of 2005 (Fig. 5*a*). For the 50% reduced puma population, the deer population would have approached recovery by fall 2003. In all cases, recovery was slowed in 2001 by an unusually high (73.8%) summer fawn mortality rate.

When we compared annual deer population growth rates for the three puma population scenarios with actual growth rates estimated from IDFG trend surveys in eight areas of unit 55 and five surrounding units, we found that in all three cases deer populations were capable of growth at rates comparable to or higher than observed rates (8%–40%/year; Idaho Department of Fish and Game 2001, 2004). However, deer populations rarely achieved these rates and exhibited declines in 6 of the 10 years (Fig. 5*a*).

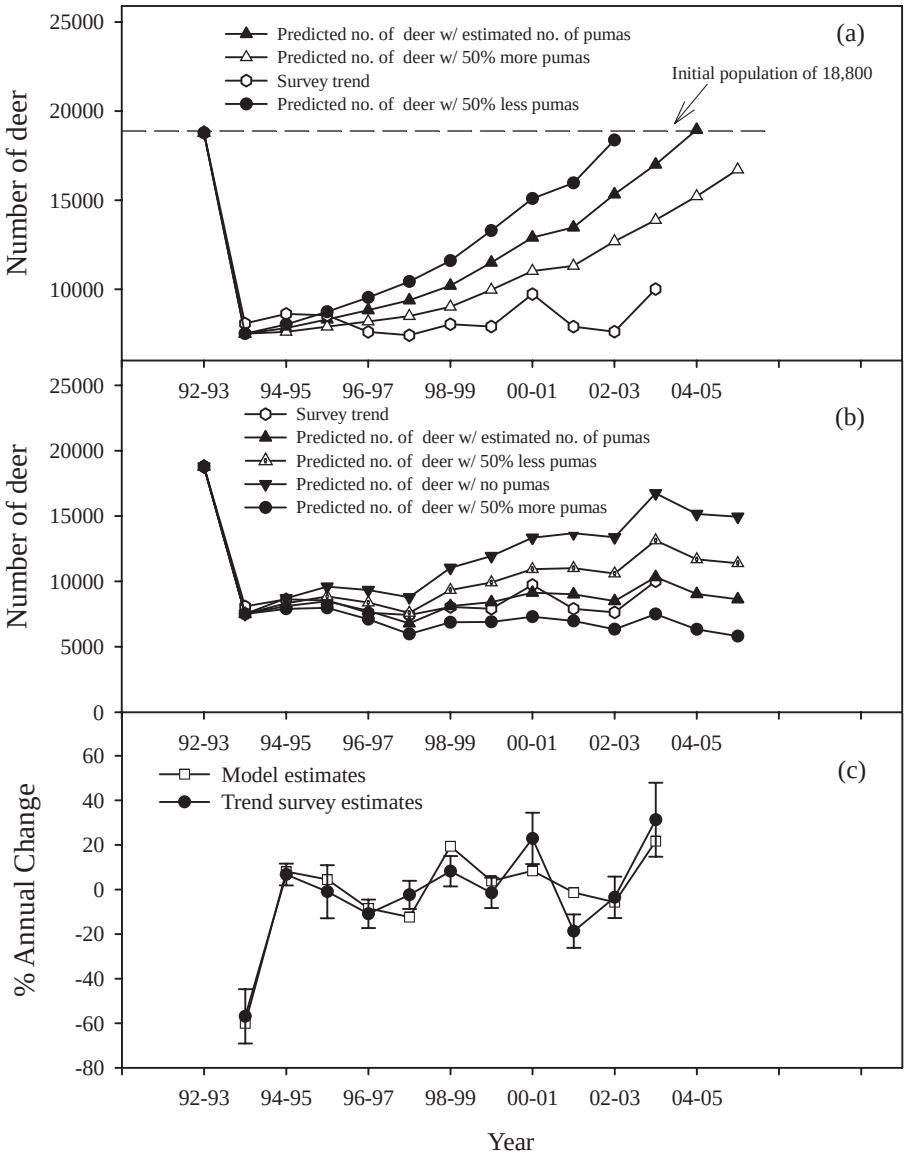
Winter fawn and doe mortality rates from the study in Colorado regressed against snow levels yielded a significant and positive relationship, with the strongest relationship observed between mortality rates and the amount of snow received in December and January (Fig. 6). Based on the regression equations derived from these analyses and December–January snow amount for our study area, fawn mortality rates would have ranged from 25.1% in 1993–1994 to 80.4% in 1992–1993 (Table 2). Doe mortality would have ranged from 0.0% in 1993–1994 and 1997–1998 to 12.1% in 1992–1993 (Table 2). When we incorporated these estimates into the calculations based on the estimated number of pumas, deer populations increased modestly the first 2 years after the 1992–1993 decline but then decreased over the winters of 1996–1997 and 1997–1998 (Fig. 5*b*). Deer numbers recuperated in 1998–1999 and gradually increased thereafter but stabilized in 2001–2002 (Fig. 5*b*). In 2002–2003, deer populations were projected to increase by 21.7% for the model with the estimated puma population and by 18.2% for the model with 50% more pumas (Fig. 5*b*). However, over the next 2 years, these models predicted overall declines of 17.1% and 23.6%, respectively (Fig. 5*c*). Therefore, the only difference in results between the model with the estimated puma population and the model with 50% more pumas was the overall number of deer (Fig. 5*b*). When compared with the estimated changes in deer numbers based on trend surveys, both models patterned the increases and decreases closely. The magnitude of change predicted by the model with the estimated number of pumas also closely matched the survey-based estimates for most years (Fig. 5*b*).

Comparing the percent annual change in deer numbers between the model with the estimated number of pumas and the trend survey data, we found close agreement in population trends in 8 of the 10 years (Fig. 5*c*). The magnitude of model-predicted changes was within 1 standard error of the trend survey estimates for 6 of the 10 years and within 2 standard errors of the trend survey estimates for 9 of the 10 years.

We ran the model with a 50% reduced population of pumas to determine how effective predator control would be in overcoming the impact of winter snow conditions on deer populations. In the first 2 years after the deer decline, this scenario predicted modest increases in deer numbers (Fig. 5*b*). However, during the next 2 years, this scenario predicted declines in deer numbers even though puma predation had been reduced significantly (Fig. 5*b*). Over the next 4 years, the population was again predicted to grow but did not increase in the following year. By the fall of 2002, the deer population was estimated to be only 27.1% higher than estimated with puma predation and had recovered to only 69.9% of the original population. Also, the population was projected to decline in 2004 and 2005.

We also ran the most extreme scenario, elimination of all pumas, to see whether the deer population would recover faster. Even elimination of all pumas did not prevent the deer population from declining during some years (Fig. 5*b*). By the fall of 2003, the population had recovered to 89.1% of the original population but was predicted to decline by 10.7% by 2005 (Fig. 5*b*). Thus, totally eliminating puma predation failed to prevent the deer population from declining substantially at times and did not result in full recovery, even after 11 years.

Fig. 5. (*a*) Estimated deer recovery patterns assuming a 60% deer population decline and three puma population levels (estimated, 50% higher than estimated, and 50% lower than estimated). (*b*) Estimated trajectories of deer population changes based on a 60% deer decline and winter fawn, doe, and buck mortality rates for the estimated puma population level, a 50% higher than estimated population, a 50% lower than estimated population, and completely eliminated puma predation. Included in (*a*) and (*b*) are the estimated changes in deer numbers based on the annual field surveys conducted by the IDFG in eight areas in and around our study area. (*c*) Estimated percent annual change in deer numbers based on a population model using estimated puma numbers and based on field data collected during IDFG aerial surveys.



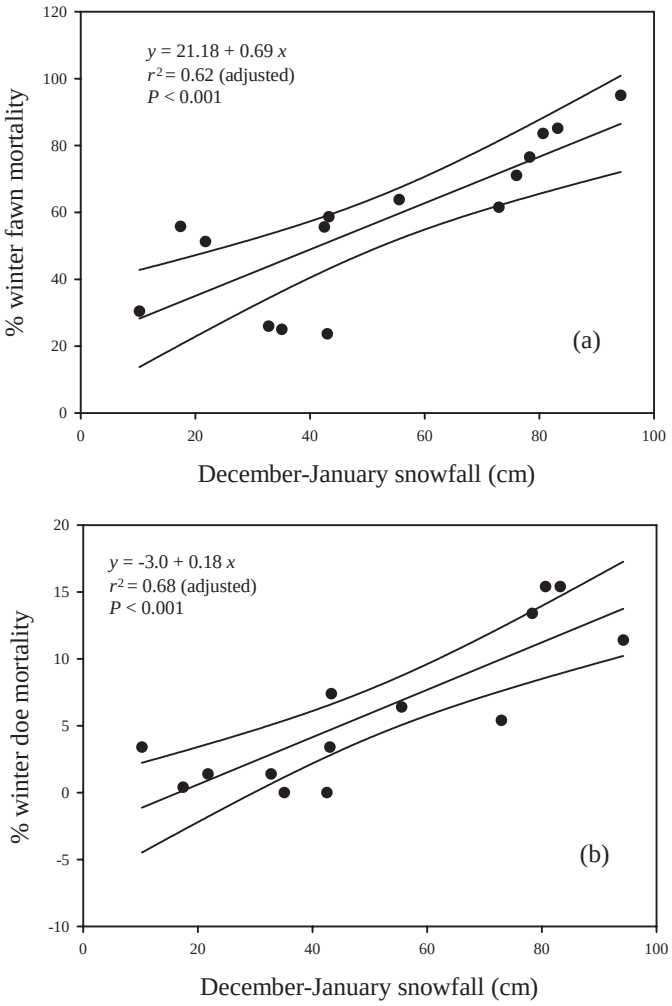
Discussion

Quality of the data used for the model and analysis used

In the use of any model, it is important to consider the quality of the input data. The puma population estimates came from our long-term intensive radiotelemetry effort (Laundré et al. 2007). This type of effort is recognized by the Cougar Management Guidelines Working Group (CMGWG 2005) as the "gold standard" for estimating the number of pumas within an area. In analyzing our field data we used established and extensive accounting methods (Logan and Sweanor 2001; Laundré et al. 2007) to insure our annual estimates of puma numbers were as accurate as possible. For our estimates of predation rates by pumas, we used our recently published data on puma energetics for our study area (Laundré 2005).

Almost all of the data on deer biology and population estimates were gathered in our study area or surrounding management units by experienced deer biologists of the Idaho Department of Fish and Game. These researchers used widely accepted and tested field methods to estimate population trends (Unsworth et al. 1994; Unsworth et al. 2002; Freddy et al. 2004). The estimates of pregnancy rates, fawn to doe and buck to doe ratios, etc., were collected under strict field protocols. Estimates of mortality rates of does and fawns were based on the widely accepted method of monitoring the fates of radio-collared individuals. The only data we did not have available for our study area or nearby

Fig. 6. Regression relationship between winter fawn (*a*) and doe (*b*) mortality rates and December–January snowfall for a study area in western Colorado (data from Unsworth et al. 1999).



areas were the estimates of winter mortality of does and fawns relative to snowfall amounts. These data were reported in the literature (Unsworth et al. 1999) and did not differ over three widely distributed study areas (western Colorado, southwestern Idaho, and southcentral Montana; Unsworth et al. 1999). We chose to use the data set from Colorado because it was the longest data set and because the weather conditions, especially winter snowfall, and habitat characteristics in our study area were more similar to those in Colorado than to those in southwestern Idaho.

In our calculations of deer recovery patterns, we used a simple deterministic spreadsheet model (CMGWG 2005) because we had site-specific annual estimates over the period of interest for many of the model parameters (Tables 1 and 2). Other parameters we used had relatively low variances, justifying the use of average values. Such a modeling approach is recommended by the Cougar Management Guidelines Working Group (CMGWG 2005) over the use of more sophisticated "canned" population models that use more generalized input values that may or may not apply to a specific area.

Once we were assured the input values were reliable, we had to determine whether the output values were realistic. To do this, we compared them with independently estimated values based on field data from the model area. Hurley and Unsworth (2000) estimated winter fawn mortality rates for units 56 and 73A (Fig. 1) to be 38% and 50% for 1998, 41% and 52% for 1999, and 17% and 53% for 2000. Our regression estimates for these 3 years were 45.3%, 42.5%, and 47.6%, respectively (Table 2). For adult does, the winter mortality estimates of Hurley and Unsworth (2000) were 1.9% and 11.3% for 1998, 0% and 3.3% for 1999, and 0% and 3.6% for 2000. Our regression estimates for these 3 years were 3.2%, 2.5%, and 3.8%, respectively (Table 2). Thus, our estimated winter mortality rates were within the ranges reported by Hurley and Unsworth (2000). In a 5-year study of mule deer survival in southern Idaho from 1992 to 1993, Bishop et al. (2005) reported winter mortality rates for does and fawns from three study areas. We conducted a paired-*t* comparison of their five average annual estimates of winter mortality rates of fawns and does (Bishop et al. 2005; Table 2) with our model-predicted estimates for the same years (Table 2). There was no significant difference between their estimates and ours for either fawns ($t = 0.76$, $P = 0.49$, df = 4) or does ($t = 1.7$, $P = 0.16$, df = 4). Consequently, the winter mortality estimates we used based on our regression analysis seem to be comparable to field estimates from our area as well as other areas of Idaho.

Relative to predicted predation rates of pumas on mule deer, Hurley and Unsworth (2000) provided mortality rates of adult does due to pumas for 1998–2000. For the two management units (56 and 73A), they found puma predation rates of 3.8% and 5.6% for 1998, 13.5% and 3.3% for 1999, and 1.8% and 5.4% for 2000. In our model, estimated puma predation rates on female deer for the same years were 4.6%, 3.2%, and 3.7%, respectively. Again, our estimates of puma predation rates on female deer were within the ranges reported by Hurley and Unsworth (2000). In addition to the concordance of our puma predation rates with field data from our area, our 12-year mean total predation rate (males and females) of 4.0% ± 0.31% (range = 2.8%–5.7%) is comparable to that reported for deer in Yellowstone National Park (Murphy 1998), west Texas (Lawrence et al. 2004), and southwestern Idaho (Bishop et al. 2005). Thus, our model predation rates generated from estimated numbers of pumas (Laundré et al. 2007) and energetic calculations (Laundré 2005) seem to be comparable to field-derived values.

The last test is to determine how realistic the model incorporating winter mortality was in predicting percent annual change in deer numbers and in estimating potential deer population numbers. Here again, we found concordance with independent field estimates (Figs. 5*b*, 5*c*). Not only did our model predict similar directions of population change (increase or decrease) as field data but in most cases it predicted similar magnitudes of change (Fig. 5*c*). Because of the concurrence of our input and output data with independent field estimates, we concluded our model outputs were biologically reasonable.

Impact of pumas on deer population decline

Given that our model seems biologically reasonable, what does it tell us about the impact of puma predation and weather effects on the decline and recovery of the deer herd

in our study area? First, our results did not support the hypothesis that puma predation was a major (driving) factor in the decline of mule deer in our area. The estimated kill of deer by pumas (estimated population) in the year before the decline (1992) was 27% of the harvest by humans (392 vs. 1462; Fig. 4). If we assume a pre-decline population of 18 800 deer, the estimated maximum puma harvest (50% higher puma population) of 587 deer (Table 1) represents only 3.1% of the population. Also, the numbers of deer killed by pumas and humans were relatively constant for 6 years before the decline and there was no notable impact on deer numbers. Even if we overestimated deer numbers at the peak by 8000 (a peak population of 10 800; 11.5 deer/km^2), puma harvest would represent only 5.4% of the deer population. As mentioned, our model-estimated puma predation rate of 3%–5% agrees with that reported for deer in Yellowstone National Park by Murphy (1998), who also concluded that pumas were not impacting deer populations. Thus, we conclude that puma predation was not a causative factor in the decline of the deer population in our area.

The concurrence of high human deer harvests and periods of low snowfall in our study area (Fig. 2) supports the suggestion that increases of deer are primarily the result of mild winter conditions (Ballard et al. 2001). The start of the increase in human deer harvest in 1987 leading to the peak harvest and peak population estimates in 1991–1992 was coupled with the start of a 6-year period of low snowfall. Conversely, the major decline in deer numbers in our area was coupled with the greatest winter snowfall in 43 years. Thus, we conclude that the decline in deer numbers in our area, and likely in most northern areas, was the result of heavy winter snowfall.

Impact of puma predation on the recovery of the deer population

Although the data do not support the hypothesis that pumas were a major factor in the decline of deer, the puma population in our area peaked while deer were at their lowest level (Fig. 2*a*). Thus, pumas would have their maximum impact on deer when deer populations are low (Ballard et al. 2001). Additionally, the increase in deer populations began at about the same time puma populations were declining or were at their lowest level. This may indicate that the reduction in puma numbers was "releasing" deer from predation pressure. However, these interpretations of the data still do not provide conclusive proof that pumas were suppressing deer recovery (Ballard et al. 2001).

Our model results demonstrated that with mild winters, a deer population under predation by pumas can recover from a 60% decline within 10 years, achieving more than 60% recovery within 6 years. Increasing puma numbers delayed the deer population recovery by only 1 year, and the deer population still recovered to over 50% 6 years after the decline (Fig. 5*a*). The predicted recovery of deer without winter mortality would have been more rapid except that summer fawn mortality during 2000 was high (73.8%; Table 2). This high fawn mortality coincided with one of the driest summers (June–September) in the previous 30 years (rainfall 0.88 cm vs. average = 4.6 ± 0.58 cm; http://www.wrcc.dri.edu/climsum).

The addition of winter mortality to the deer population model changed the population trajectory from steady recovery to the actual field-documented lack of recovery. However, even under this scenario, both the model and the field data demonstrated that when December–January snowfall was less than 30 cm, deer populations were capable of high growth rates even in the presence of pumas (Fig. 5*b*). All this supports the hypothesis that winter snow depth has a major role in mule deer population recovery in our area.

When we reduced puma predation or totally removed it from the model, we found a minimal impact on the deer population in the first 5 years, only marginal increases of the population by 2002, and the same predicted declines in 2004–2005 (Fig. 5*b*). These results imply that eliminating or greatly reducing puma predation might help deer populations grow modestly in years of below-average snowfall (as in the winter of 1997–1998, for example, when December–January snowfall for the study area was only 10 cm). However, such effects of predator reduction are quickly negated by average or above-average snowfall.

In conclusion, our study findings support those of others showing that pumas rarely cause the major declines in deer populations that are characteristic of this species (Ballard et al. 2001). These major declines in northern areas are more likely caused by overriding weather patterns (heavy snowfall). However, more importantly, our study provides the first results showing that pumas do not substantially suppress deer populations when deer have been reduced to low numbers primarily because of weather factors. Adverse weather — in our case, snowfall — during the recovery period was the critical factor that determined whether deer numbers increased or decreased. We have demonstrated that in our study area deer populations can and do recover rapidly after such declines, even in the presence of puma predation, if weather conditions are favorable.

We have also demonstrated that state wildlife agencies can possibly predict the impact of winter snowfall on subsequent deer numbers in our area via the regression equations we have provided. By providing the ability to apply local results on a larger regional scale (Bleich and Taylor 1998; Unsworth et al. 1999), these formulas could be valuable predictive tools for most of the northwestern states, where winter precipitation is primarily in the form of snow. However, such predictions would first need to be tested adequately in other areas.

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