

Stochastic predation events and population persistence in bighorn sheep

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Many studies have reported temporal changes in the relative importance of density-dependence and environmental stochasticity in affecting population growth rates, but they typically assume that the predominant factor limiting growth remains constant over long periods of time. Stochastic switches in limiting factors that persist for multiple time-steps have received little attention, but most wild populations may periodically experience such switches. Here, we consider the dynamics of three populations of individually marked bighorn sheep (*Ovis canadensis*) monitored for 24–28 years. Each population experienced one or two distinct cougar (*Puma concolor*) predation events leading to population declines. The onset and duration of predation events were stochastic and consistent with predation by specialist individuals. A realistic Markov chain model confirms that predation by specialist cougars can cause extinction of isolated populations. We suggest that such processes may be common. In such cases, predator–prey equilibria may only occur at large geographical and temporal scales, and are unlikely with increasing habitat fragmentation.

Keywords: stochasticity; predator–prey; individual differences; limiting factors; population dynamics; population viability analysis

1. INTRODUCTION

The conservation of biodiversity relies increasingly on our knowledge of the dynamics of small populations, particularly for large animals (Morris & Doak 2002). Much previous work stressed the importance of stochastic factors for such populations (Morris & Doak 2002; Lande *et al.* 2003). Stochasticity is typically incorporated into the population models by drawing numbers from a specified distribution and using them to determine parameter values for each time-step. Substantial work has focused on catastrophes, where the specified distribution is highly skewed by a few extreme values (Reed *et al.* 2003). There has been limited research on the dynamical consequences of shifts in the factor limiting population growth in stochastic models, although the role of stochastic factors in switching dynamics between deterministic limiting factors has been explored (Rohani *et al.* 2002; Coulson *et al.* 2004). Small populations may be particularly susceptible to unpredictable shifts in limiting factor (Coulson *et al.* 2001b), with substantial dynamical consequences.

Our current understanding of the demography and dynamics of large vertebrates relies heavily on a few

long-term studies of marked individuals, often in populations without large predators (Gaillard *et al.* 2000). These studies have seldom considered the demographic and dynamic consequences of predation (but see Peterson *et al.* (1998)). Predation is thought to be a major determinant of the demography and population dynamics of small mammals (Graham & Lambin 2002), but in ungulates its role on population dynamics is the subject of much debate (Boutin 1992; Messier 1994; Sinclair *et al.* 2003). Most studies of predator–prey relationships in ungulates were based on large-scale surveys and total counts that cannot reveal the susceptibility to predation of different sex–age classes. Given the importance of sex–age structure on ungulate population dynamics (Coulson *et al.* 2001a), low resolution on the mortality caused by predators limits our understanding of the role of predation. Predation can be sustained over the long term by populations of temperate cervids over large areas (Messier 1994). For many African ungulates, predation is the most common cause of death (Sinclair *et al.* 2003), but little attention has been paid to the possible role of stochastic predation by individual specialist predators on the dynamics of small populations of ungulates.

As habitat fragmentation leads to many species persisting only in small isolated populations, the potential impact of specialist predators on population persistence is substantial (Vazquez-Dominguez *et al.* 2004). A classic example is the eradication of the Stephen's Island wren (*Xenicus lyalli*) by a single domestic cat (Greenway 1967).

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Table 1. Models compared to assess the effects of cougar predation on bighorn sheep survival.

model no.	notation	biological interpretation
1	ϕ_c	the baseline model with four age groups for females and three for males (yearlings, 2–7 years, 8–13 years and, for females, over 13 years). Survival is assumed to be constant all years for all sex–age classes
2	$\phi_{c \times q}$	the baseline model with a different survival for each age class in the years with and without cougar predation. Allows different effects of cougar predation on all age classes
3	ϕ_{c+q}	same as model 2, but forcing the same effect of predation on survival of all age classes. Assumes that age and predation effects are additive
4	$\phi_1 \phi_{2q}$	same as model 2, but with different survival probabilities for old males and for old and very old females. Assumes that predation affects only the survival of older sheep
5	$\phi_{1+q} \phi_{2q}$	same as model 2, but with a similar effect of predation on the survival of yearlings and prime-aged adults, and a different effect of predation on the survival of old males and of old and very old females

Predation by specialist killer whales (*Orcinus orca*) may lead to extirpation of sea otters (*Enhydra lutris*; Williams *et al.* 2004). Many ungulates exist as small, discrete populations that are demographically isolated by habitat fragmentation and female philopatry (Festa-Bianchet 1991). These populations may be unable to support predators: predation on fragmented populations of caribou, for example, can lead to extirpation within a decade (Kinley & Apps 2001). We present evidence that cougar (*Puma concolor*) predation on bighorn sheep (*Ovis canadensis*) occurs unpredictably, possibly as the result of individual specialization. When predation events occur, they dominate population dynamics.

2. STUDY AREAS AND METHODS

We studied three populations of bighorn sheep: Ram Mountain and Sheep River in Alberta, Canada and National Bison Range (NBR) in Montana, USA. Cougars occurred in all three areas. Over 95% of bighorn sheep were individually recognizable and their age was known (Hogg 1988; Jorgenson *et al.* 1993). By monitoring three fully marked populations over 80 population-years, we quantified the impact of predation on different vital rates and assessed directly its effect on population growth.

At Sheep River, most cougars were equipped with radio collars in 1983–1995, and records of their kills were obtained. In 1983–1992, the home ranges of 2–4 cougars overlapped the sheep winter range but they killed less than one bighorn a year (Ross & Jalkotzy 1992). In 1993–1995, two radiocollared cougars began preying on bighorn sheep. One 10-year-old female who previously fed mostly on deer (*Odocoileus* spp.) switched to killing almost exclusively sheep. Her home range, that had overlapped the bighorn winter range since her birth, shrank to include exclusively the areas used by sheep (Ross *et al.* 1997). The predation episode ended with this cougar's death in 1995.

We identified all other episodes of elevated predation using the following field evidence: (i) recovery of cougar kills, easily recognized because the hair is stripped and remains are buried (Rezendes 1992); (ii) observation of attacks and stalking (Pelletier *et al.* in press); (iii) abrupt disappearance of animals that were in good condition and routinely observed; and (iv) increased wariness, agitation and location shifts by bighorn. Thus, episodes were defined by increase in a specific form of mortality and associated behaviours. Low cougar predation years were identified by the relative absence of

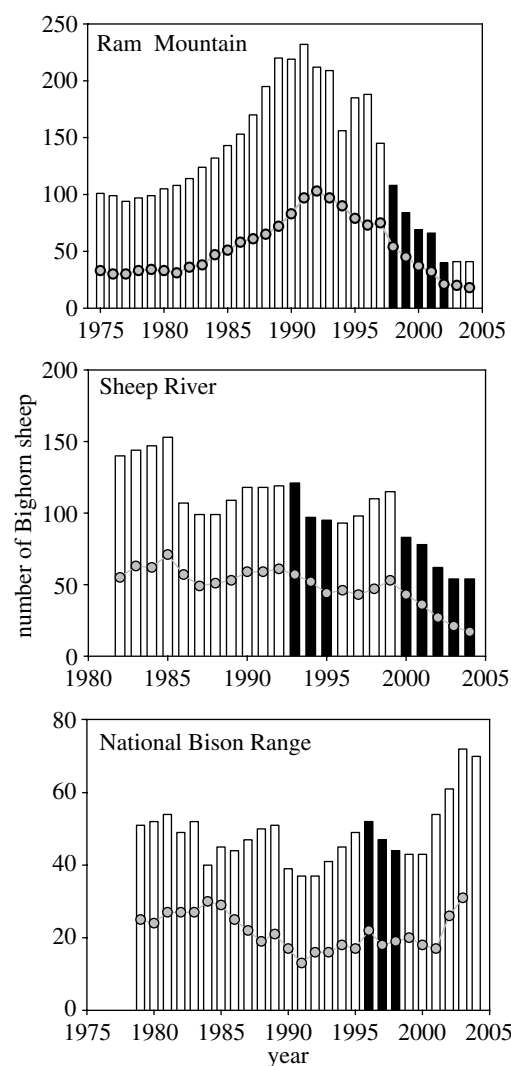


Figure 1. Number of adult ewes (circles) and total numbers of bighorn sheep at (a) Ram Mountain (1975–2004), (b) Sheep River (1981–2004) and (c) National Bison Range (1979–2004). Filled bars indicate years of cougar predation episodes.

(i)–(iv) and evidence (tracks, sightings and, periodically, radio telemetry) of continued cougar presence in the study areas. For example, five adult females and five kittens were resident in the NBR in 1999–2000 (Choates in preparation), yet only two bighorns were judged to be killed by cougars in 2000 and annual survival of weaned lambs and adult bighorn during 1999 and 2000 was 93 and 91%.

Table 2. Survival estimates for bighorn sheep of different sex-age classes in years with and without cougar predation in three populations.

population	sex	age	survival (s.e.)		decline in survival rate ^a
			no predation	predation	
<i>Ram Mountain</i>					
	both	lambs	0.531 (0.048)	0.203 (0.043)	0.238
	male	yearling	0.839 (0.024)	0.698 (0.060)	0.141
		2-7 years	0.853 (0.014)	0.720 (0.047)	0.133
		8 years +	0.710 (0.062)	0.521 (0.070)	0.189
	female	yearling	0.823 (0.023)	0.721 (0.049)	0.102
		2-7 years	0.941 (0.007)	0.899 (0.020)	0.042
		8-13 years	0.834 (0.022)	0.737 (0.036)	0.097
		13 years +	0.782 (0.561)	0.447 (0.925)	0.335
<i>Sheep River</i>					
	both	lambs	0.407 (0.036)	0.210 (0.062)	0.197
	male	yearling	0.757 (0.045)	0.826 (0.066)	-0.069
		2-7 years	0.860 (0.025)	0.850 (0.028)	0.010
		8 years +	0.867 (0.089)	0.598 (0.090)	0.269
	female	yearling	0.907 (0.023)	0.765 (0.049)	0.142
		2-7 years	0.920 (0.014)	0.792 (0.027)	0.128
		8-13 years	0.893 (0.026)	0.735 (0.043)	0.158
		13 years +	0.738 (0.100)	0.484 (0.013)	0.254
<i>National Bison Range</i>					
	both	lambs	0.391 (0.056)	0.277 (0.063)	0.114
	male	yearling	0.949 (0.026)	0.882 (0.060)	0.067
		2-7 years	0.964 (0.010)	0.914 (0.028)	0.050
		8 years +	0.811 (0.038)	0.632 (0.087)	0.179
	females	yearling	0.939 (0.027)	0.891 (0.050)	0.048
		2-7 years	0.933 (0.014)	0.880 (0.035)	0.053
		8-13 years	0.723 (0.043)	0.580 (0.095)	0.143
		13 years +	0.333 (0.272)	0.210 (0.211)	0.123

^a Increase in mortality in years of cougar predation compared to other years.

We calculated bighorn sheep vital rates in years with and without cougar predation from accurate information on marked known-age individuals. Population density had strong effects on age of primiparity and lamb survival at Ram Mountain (Jorgenson *et al.* 1993; Portier *et al.* 1998), and the population was declining at the onset of cougar predation. For that population we only considered 'declining' years, from 1992 to 2003 because we knew of no cougar predation during the increase phase. All years were included for Sheep River and Bison Range.

To estimate survival of yearlings and adults, we used recent capture-mark-recapture (CMR) methods (Lebreton *et al.* 1992). Bighorn survival is adequately represented by four age classes for females and three for males (Jorgenson *et al.* 1997). We compared this baseline model with four models assuming different effects of predation (table 1). We used Akaike Information Criterion (AIC) to select the best models (Burnham & Anderson 2002). When the difference between competing models was greater than 2 we retained the model with the lowest AIC, otherwise we selected the model with fewer parameters (see Festa-Bianchet *et al.* (2003) for more details on CMR modelling of bighorn sheep).

Using data from Ram Mountain, we constructed an age-structured stochastic matrix model to simulate the consequences of changes in the frequency and duration of predation episodes (see electronic supplementary material). Analyses of age-specific survival and recruitment data supported the inclusions of population density in the previous year in survival (assessed with logistic regressions in the CMR

framework; Lebreton *et al.* 1992) and recruitment rates (including age of primiparity and lamb survival to one year assessed using logistic regressions) in predation-free years, giving a long-term population growth of 0. Density-dependence was not detected in predation years and the long-term growth rate was negative.

3. RESULTS

Our long-term studies clearly indicate that stochastic predation episodes led to a switch in limiting factor. In most years we recorded no cougar predation on bighorns (figure 1), but each population experienced at least one episode of elevated predation. During all predation episodes, survival was reduced for all sex-age classes (table 2) except for Sheep River rams, whose winter range was outside the home range of the sheep-killing cougars during the first episode (Ross *et al.* 1997) and apparently outside it during the second. All predation episodes were associated with population declines (table 3).

Onset of predation was unrelated to sheep density (figure 1). At Ram Mountain, predation started during a density-dependent population decline (Jorgenson *et al.* 1993; Portier *et al.* 1998). In contrast, the Bison Range episode interrupted an upward trend and both Sheep River episodes occurred during periods with no clear population trend. Predation episodes lasted between 3 and 5 years. The first episode at Sheep River was mostly attributable to one female that killed almost exclusively sheep during three winters (Ross *et al.* 1997). The sudden

Table 3. Annual population growth of bighorn sheep calculated from time-series of population sizes in the presence and absence of cougar predation.

population	period	predation	mean annual growth rate (w)
Ram Mountain	1975–1997	no	1.017
Sheep River	1982–1993	no	0.987 ^a
Sheep River	1986–1993	no	1.012 ^b
Sheep River	1996–1999	no	1.073
National Bison Range	1979–1996	no	1.001
<i>mean</i>			1.012
Ram Mountain	1997–2002	yes	0.789
Sheep River	1993–1996	yes	0.916
Sheep River	1999–2003	yes	0.828
National Bison Range	1996–1999	yes	0.939
<i>mean</i>			0.868

^a Includes 1985–1986, when population decline was caused by pneumonia epizootic.

^b Overlaps with other periods; not included in the calculation of mean.

onset and cessation of all other episodes is consistent with a pattern of specialization by individual predators, ending with the death or emigration of the specialist.

Years of predation were associated with declines in adult survival, and older animals may have been more vulnerable than prime-aged ones (tables 2 and 4). Models including additive or interactive (i.e. increased predation on older ewes) effects of predation and age were retained in all cases. Anecdotal information suggested that cougars often ambushed the lead (and typically older) ewe as sheep travelled along traditional trails. Model 3 including effects of predation and age is additive on a logit scale; therefore, the increase in mortality in years of predation is proportional to mortality in years without predation. Because older ewes experience high mortality through senescence, their relative increase in mortality in years of predation was greater than for prime-aged adult ewes, even according to model 3.

Could stochastic episodes of cougar predation cause the extirpation of bighorn populations? A stochastic, age- and sex-structured Markov chain model constructed for Ram Mountain (the population with the most data) adequately and qualitatively captured bighorn sheep dynamics as suggested by comparisons of simulated and observed time-series (figure 2a). Modelling suggested that the level of predation seen at Ram Mountain would lead to a greater than 50% probability of extinction within 100 years if predation episodes lasting on average 3.5 years (the mean duration of observed episodes) occurred once per decade (figure 2b). We observed four predation episodes during 80 population-years of monitoring, or one every 20 years.

Assuming an upper limit to the number of sheep one cougar will kill in a year, the probability of extirpation under predation will be linearly and negatively related to

Table 4. Model selection for the effects of cougar predation on bighorn sheep adult and yearling survival by sex in the three study areas. (Selected models are indicated in bold. See table 1 for a biological interpretation of models 1–5.)

study area	sex	model no.	number of parameters	AIC
Ram Mountain	male	1	4	1159.695
		2	7	1154.421
		3	5	1151.214
		4	5	1157.159
		5	6	1152.766
Ram Mountain	female	1	5	1488.845
		2	9	1479.236
		3	6	1476.679
		4	7	1475.781
		5	6	1481.471
Sheep River	male	1	4	569.902
		2	7	571.535
		3	5	571.707
		4	6	570.252
		5	5	568.295
Sheep River	female	1	5	661.012
		2	9	638.439
		3	6	635.240
		4	7	636.347
		5	6	660.546
Bison Range	male	1	5	277.549
		2	7	274.807
		3	6	274.034
		4	6	272.926
		5	6	276.034
Bison Range	female	1	6	361.828
		2	9	364.787
		3	7	360.890
		4	6	361.828
		5	6	360.890

population size. Thus, about 125 sheep would be required to obtain 95% probability of persistence if on average predation occurred every 20 years and lasted 3.5 years. Many bighorn populations number fewer than 125 sheep and could not sustain this level of predation. A greater frequency of predation events would increase the chances of extirpation (figure 2c). Drastic population declines during most predation episodes support our predictions: in the last year of predation at Ram Mountain, 15 of 36 adult and yearling ewes disappeared; during the second predation episode at Sheep River, adult ewes declined from 44 to 15 in 4 years.

4. DISCUSSION

How can cougar predation have such dramatic impacts on bighorn populations? Cervids are the main prey of cougars in North America (Ross *et al.* 1997), and to prey on bighorn sheep, cougars would require very different hunting techniques. Predation on bighorn sheep is risky: at Sheep River one cougar fell to its death while attacking a lamb (Ross *et al.* 1997). Cougars that learn the very predictable space-use patterns of bighorn sheep, however, become highly successful at preying on this species (Wehausen 1996; Ernest *et al.* 2002; Rosas-Rosas *et al.* 2003; Rominger *et al.* 2004). We could not determine if each predation episode was due to a single individual specialist, but clearly

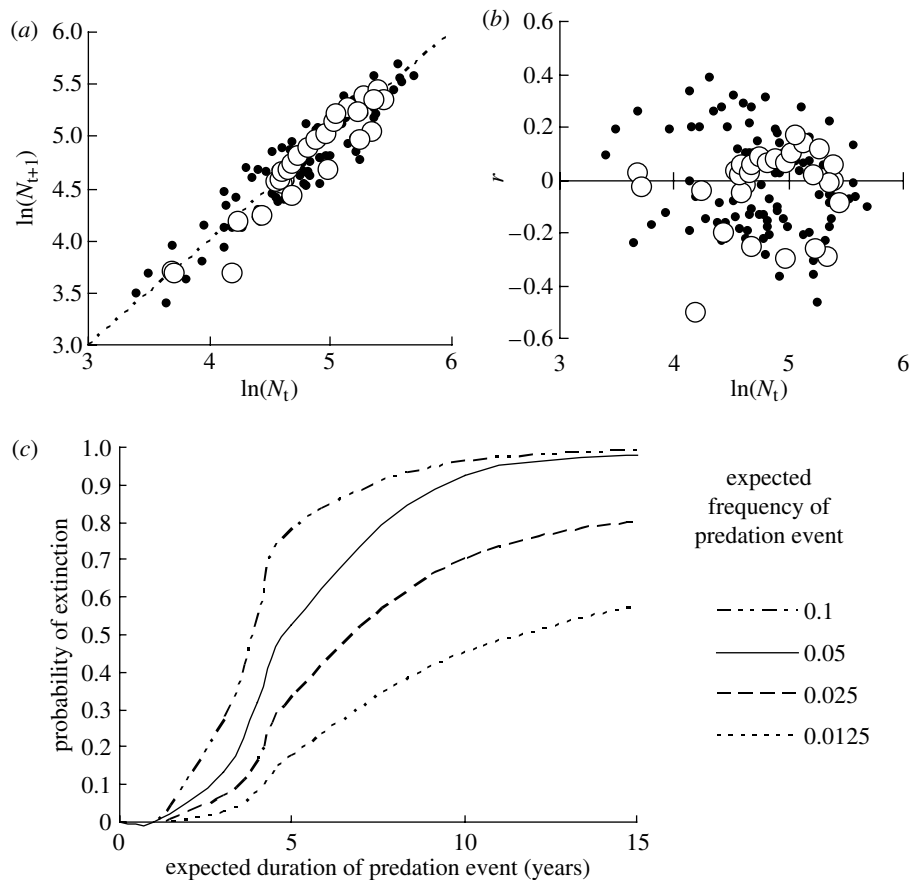


Figure 2. (a) Plot of the natural log of population size in one year against the natural log of population size in the previous year for data from the Ram Mountain population (open symbols) and from one simulation of 100 years (solid symbols). The simulated data included a probability of predation commencing of 0.1 and an expected duration of 3.5 years. (b) Plot of population growth, r , against logged population size using the same data as in (a). The model captured the essential features of the population dynamics. (c) Probability of extinction as a function of the probability of a predation episode commencing in any one year and of its expected duration.

cougar predation on sheep did not simply involve opportunistic killings while searching for other prey. Once they started preying on bighorns, cougars concentrated on this species. Cougars and bighorns coexisted for decades in all study areas without any evidence that cougar predation affected sheep population dynamics. Yet, during 12% of years at Bison Range, 16% at Ram Mountain and 36% at Sheep River, cougar predation was the overriding factor affecting bighorn numbers. Because of the availability of alternative prey, predation on bighorn sheep could continue until the last individual is eaten, as reported with other species that are not typical cougar prey (Switzer *et al.* 1997; Kinley & Apps 2001). In addition, high predation over consecutive years generates a positive autocorrelation in mortality rates, leading to a more negative impact on population growth rate than if years of high predation were not consecutive (Pike *et al.* 2004).

The impact of specialist predators on small populations of prey is important, yet unpredictable (Bonsall & Hastings 2004). An opportunistic predator may begin the process, or changes in the availability of other prey species may be involved. No previous study has accurately quantified the demographic impacts of stochastic predation. We were able to fill this gap because we monitored for a minimum of 25 years three populations of bighorn sheep where we knew the sex and exact age of each individual.

The apparent unsustainability of cougar predation on bighorn sheep raises questions about the ecological

relationship between these two species and underlines the importance of very long time-scales to understand population dynamics and evolution of life histories in large mammals. There is no clear evidence that cougar numbers have increased over the past 20 years. On the other hand, mule deer have generally declined while white-tailed deer have increased in much of western North America (Robinson *et al.* 2002). Other ecological changes could affect the relationship between bighorns and cougars, such as increased forest cover (providing visual cover for ambush) and changes in the abundance of wolves (*Canis lupus*), whose ecological relationships with cougars are unclear (Husseman *et al.* 2003). Owing to the very patchy distribution of bighorn sheep, very few cougars have sheep within their home range, compared to those that overlap with deer. Probably, most cougars learn to hunt deer rather than sheep, possibly explaining why in most years we found no evidence of cougar predation. Bighorn sheep antipredator behaviour appears effective against coursing predators such as wolves, but may not be as effective against ambush predators such as cougars (Festa-Bianchet 1991).

Because it is impossible to accurately predict when a population will go extinct, the use of population viability analyses as a management tool has received criticism (Coulson *et al.* 2001b). Population viability analysis, however, can be useful to compare the performance of contrasting management strategies, rather than the exact

consequences of one strategy. Our simulation shows that the cougar predation we quantified in three studies can lead to extinction of small bighorn populations. An increase in the frequency and length of cougar predation events will increase the probability of extinction via the combined effect of heightened mortality and demographic stochasticity in small populations.

If cougar predation regularly led to the extirpation of local populations of bighorn sheep, then metapopulation dynamics involving local extinctions and recolonizations may become important, but because bighorn ewes are extremely philopatric (Festa-Bianchet 1991), those processes would require a very long time-scale. Regardless of the ecological or behavioural processes that lead to them, stochastic episodes of elevated predation can have severe negative effects on small populations and may be unsustainable over the long term (Williams *et al.* 2004). We documented that switches to predation as the limiting factor occur surprisingly frequently in bighorn sheep populations. Multiple processes are associated with declines and extinction of small populations including human-induced and genetic effects (Coltman *et al.* 2003; Spielman *et al.* 2004). We identified a previously unsuspected process that can further threaten the persistence of isolated populations.

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