

LETTER

Predator-driven component Allee effects in a wild ungulate

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Abstract

Negative density dependence is an important driver of population dynamics of large vertebrates. Allee effects (positive density dependence), however, can affect small populations. Allee effects can be generated by predation and recent research has revealed potentially important indirect effects of predation on population dynamics. For wild populations, however, quantification of both Allee effects and indirect effects of predation remains scarce. We monitored for 27 years a bighorn sheep (*Ovis canadensis*) population that declined dramatically as episodes of cougar (*Puma concolor*) predation depressed survival. Predation led to a positive relationship between lamb survival and population size below a threshold, and to an overall positive relationship between yearling and adult ewe survival and population size. During years of high predation, lambs also suffer mortality through reduced growth, contributing a third of the total impact of predation on lamb survival. There was no positive association between population growth and population size, probably because growth was affected by several factors other than predation, including disease. Our results support the contention that predator-driven component Allee effects may exacerbate the effects of other environmental drivers and increase the risk of extinction of small populations.

Keywords

Allee effect, bighorn sheep, population dynamics, predation, risk effect, ungulate.

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INTRODUCTION

Understanding how birth and death rates vary with population density is crucial to predict changes in population size, identify factors affecting those changes and ultimately conserve wild populations. The theory of population regulation assumes negative density-dependent growth (Sinclair & Pech 1996), with empirical support from many wild populations (Brook & Bradshaw 2006). Under some circumstances, however, low density can reduce population growth (Allee *et al.* 1949). Positive density dependence is known as the ‘Allee effect’ (Allee 1931). A formal definition was proposed by Stephens *et al.* (1999) as ‘any component of an individuals’ fitness positively correlated to population density or size’. They also suggested differentiating between component Allee effect on individual fitness components and demographic Allee effect on population growth. Despite their theoretical importance (Dennis 1989, 2002; Moller & Legendre 2001), few studies have documented either component or demographic Allee effects in the wild (Kuussaari *et al.* 1998; Angulo *et al.* 2007).

Predators that exploit multiple prey species are particularly likely to generate Allee effects, because their persistence is independent of that of secondary prey species (Angulo *et al.* 2007). These predators may show a Type II functional response, leading to positive density-dependent prey survival up to a critical threshold (Gascoigne & Lipcius 2004). For example, small populations of caribou (*Rangifer tarandus*) are unlikely to persist when habitat alterations allow an increase in other ungulates and predators, with greater per capita risk

of predation especially if average caribou group size declines at low density (McLellan *et al.* 2010). Predator-driven Allee effects can originate from reduced cooperative anti-predator behaviours (Courchamp *et al.* 1999), reduced foraging to increase vigilance and avoidance of areas with high risk of predation (Creel *et al.* 2009).

Allee effects depend on the total demographic impact of predators. Predators kill some individuals, but recent research suggests that they may also have indirect demographic effects on prey by affecting their foraging behaviour (Le Roux *et al.* 2009), habitat use (Fortin *et al.* 2005) and stress hormone levels (Creel *et al.* 2009). The indirect effects of predation may exacerbate predator-driven Allee effects through reduced body growth and reproductive success. No study, however, has quantified both direct and indirect effects of predation on prey fitness. We used 27 years of detailed monitoring of a bighorn sheep (*Ovis canadensis*) population that experienced episodes of intense cougar (*Puma concolor*) predation to quantify the impacts of direct and indirect effects of predation on fitness components and population growth. The combined direct and indirect effects of predation led to components Allee effects.

MATERIAL AND METHODS

Animals and population

Since 1981, we monitored a bighorn population wintering in the Sheep River Provincial Park (50°40′ N, 114 35′ W), Alberta (Festa-Bianchet

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1986). Lambs aged 4–6 months were captured by chemical immobilization (Festa-Bianchet & Jorgenson 1985) and marked with ear tags. Since 1985, all resident ewes have been individually marked. From 1982 to 2005, we measured chest circumference of 189 males and 211 female lambs born to 130 ewes. Body mass was measured on 73 lambs. The length of the time series varies between analyses because weather data were not available for the last 4 years of the study.

In spring, visual observation of the udder was used to score females as lactating or not. Mother–offspring links were assessed by repeated observations of a suckling lamb. Survival was monitored through repeated censuses. *Lamb survival to weaning* was the proportion of lactating ewes still accompanied by a lamb in late September. *Lamb winter survival* was the survival of marked lambs from September to May. Between 1982 and 2007, we marked 77% of 616 lambs that survived to weaning. *Yearling recruitment* was the ratio of yearlings to adult ewes in March. *Population size* was the number of resident sheep each year in March. As > 95% of the sheep were marked and resighting probability was near 1.0 (Jorgenson *et al.* 1997; Loison *et al.* 1999), population counts were accurate.

Cougar predation

Almost all cougars in the study area were radio-collared from 1985 to 1997 and monitored weekly. They typically preyed on cervids (Ross & Jalkotzy 1992) and in most years there was no known predation on sheep. Occasionally, however, single cougars specialize on sheep (Ross *et al.* 1997; Festa-Bianchet *et al.* 2006). The first episode of predation involved a radio-collared cougar. Similar patterns of cougar predation have been reported for several other bighorn sheep populations (Wehausen 1996; Rominger *et al.* 2004; Festa-Bianchet *et al.* 2006). After 1997, we classified years of high cougar predation based on: (1) recovery of cougar kills, easily recognized because the hair is stripped and remains are buried; (2) direct observation of predation attempts; (3) abrupt increase in disappearance rates (see Festa-Bianchet *et al.* 2006 for more details). Based on these criteria, we determined that the population experienced three episodes of high cougar predation: 1993–1995, 2000–2004 (Festa-Bianchet *et al.* 2006) and 2007–2008. We coded years with low predation as '0' and years of high predation as '1'.

Environmental conditions

To quantify the effects of predation on survival and growth while controlling for other changes in the environment, we accounted for variation in primary productivity and climate.

Vegetation

We quantified net primary productivity through the Normalized Difference Vegetation Index (NDVI) (Pettorelli *et al.* 2005). We used values provided by the Global Inventory Modelling and Mapping Studies (GIMMS), with a pixel size of 64 km² and records on the 1st and the 15th day of each month. To evaluate vegetation phenology in spring, we used the average NDVI maximum increase of three 8 × 8 km pixels for which data were available from 1982 to 2007 (Pettorelli *et al.* 2005) and that covered most of the study area. The maximum increase is the steepest slope between two consecutive NDVI values from March to July and is negatively correlated with lamb growth (Pettorelli *et al.* 2007).

Climate

Weather data were collected from the High River meteorological station of Environment Canada, 40 km SW of the study area. This station was closed in 2006; we do not have weather data after that date. We investigated how lamb survival to weaning responded to changes of average temperature (°C) and total precipitation (mm) in spring (March 1–June 30) preceding birth of each cohort. To model the effect of weather on lamb winter survival, we used the Pacific Decadal Oscillation (PDO) as a large-scale climatic index (Ezard *et al.* 2009) obtained from the Joint Institute for the Study of the Atmosphere and Ocean website (<http://jisao.washington.edu>). We used winter PDO while females were gestating, calculated as the average of monthly values from December to April, to evaluate the effect of winter harshness on lamb size and survival.

Statistical analyses

Survival and population growth rate

We explored the relationship between lamb survival to weaning and population size using a broken stick regression model implemented in R version 2.8.1 (R Development Core Team 2010). We fitted nine models with thresholds increasing by five from 70 to 110 individuals. Based on Akaike information criterion (AIC) values (Burnham & Anderson 2002), the threshold was between 80 and 100 sheep with a peak at 90 (Tables S1 and S2). We fitted a linear regression between yearling recruitment in March and population size a year earlier, and between population growth rate (defined as $w = N_{t+1}/N_t$) and population size.

Lamb size and winter survival

The strong correlation between lamb chest circumference and mass after log-transformation ($r = 0.90$, $P < 0.001$) suggests that chest circumference is a good proxy of mass (Pelletier *et al.* 2005). We therefore used chest circumference instead of mass because we had a larger sample size. We adjusted chest circumference to mean capture date (October 9) with a sex-specific linear regression. We assessed the influence of cougar predation, chest circumference, sex and their interactions on overwinter lamb survival with a generalized linear mixed effects model (using a binomial error structure with a logit link function) including mother identity and year as random factors (see Table S3 for model selection). We then examined the effects of NDVI, climate, population size (linear and quadratic) and predation on chest circumference. As we measured several lambs from the same mother, lamb size was analysed using a linear mixed effects model including maternal identity and year as random factors (Pinheiro & Bates 2000). Models also included maternal age as a quadratic function and lamb sex. We tested for an interaction between lamb sex and population size because male ungulates are more susceptible than females to density effects (Gaillard *et al.* 2000) (see Table S4 for details on model selection).

Modelling was performed using AIC values and AIC weights to select the best model. AIC were calculated from models fitted using maximum likelihood, whereas model estimation used restricted maximum likelihood, as recommended by Wood (2006). When the AIC differed by < 2, we retained the model with fewer parameters (Burnham & Anderson 2002). All statistical analyses were conducted using R version 2.8.1. The 'lme4' package (version 0.999375–28) was used to fit mixed effects models (Bates *et al.* 2008).

Ewe survival

We used capture–mark–recapture modelling to obtain unbiased estimates of age- and time-specific survival (Lebreton *et al.* 1992) of bighorn ewes. We used as baseline the four age-class model [yearly survival of yearlings, prime-aged (from 2 to 8 years of age), old (8–13 years) and senescent (older than 13 years)] females that provided the best fit in previous analyses (Table 1) (Festa-Bianchet *et al.* 2003; Gaillard *et al.* 2004). We then fitted models including additive and interactive effects of cougar predation and population size on age-class specific survival and selected the best model based on minimum AIC (Burnham & Anderson 2002). All calculations used M-SURGE (Choquet *et al.* 2004).

RESULTS

In the early 1980s, the population exceeded 150 individuals (Fig. 1a). It was reduced to *c.* 100 by pneumonia in 1985–1986 (Festa-Bianchet 1988a), then declined during three episodes of cougar predation (Festa-Bianchet *et al.* 2006). Over 27 years, the population showed little evidence of negative density dependence. On the contrary, below a threshold of *c.* 80–100 sheep, lamb survival to weaning increased with population size (Fig. 1b; Tables S1 and S2). Yearling recruitment in March decreased dramatically from 73% in the 3 years with the highest population size to 13% in the 3 years with the lowest (Fig. 1c), indicating a strong Allee effect over the range of population sizes monitored. We did not find negative density dependence in population growth (Fig. 1d), even though the population ranged from 39 to 152 sheep. Instead, the population declined in 5 of 8 years with fewer than 90 sheep and is now at its lowest level in over 55 years (Wishart 1958), having declined during 7 of the last 10 years (Fig. 1a).

Lamb winter survival decreased in years of high predation and increased with lamb size (Table 2a). There was no interaction between lamb size and cougar predation affecting survival, confirming that predation was not size-selective (Ross *et al.* 1997). Average lamb chest circumference in autumn was 2.1 cm smaller in years with high predation (Table 2b), suggesting an indirect effect of predation on lamb growth. We therefore decomposed the effect of cougars on lamb winter survival into a direct effect through predation and a likely indirect effect through reduced growth. We reasoned that lambs would have been larger without predation. We estimated the indirect effect by calculating predicted survival after adding 2.1 cm of chest circumference to each lamb in years of high predation. For an average-sized female lamb, the indirect effect accounted for just under a third of the decrease in survival (–8%), leaving two-thirds that appeared directly due to predation (–20%; Fig. 2).

Cougar predation decreased survival of all ewe age classes (Tables 1 and 3). Overall, adult ewe survival showed an Allee effect, increasing

Table 1 Capture–mark–recapture estimates of bighorn ewe survival in years with and without high cougar predation, Sheep River, Alberta, 1982–2008

Age class (years)	Survival	
	Low cougar predation (SE)	High cougar predation (SE)
Yearling	0.901 (0.022)	0.778 (0.044)
Adult (2–7)	0.925 (0.010)	0.826 (0.022)
Old (8–13)	0.887 (0.018)	0.752 (0.032)
Senescent (13+)	0.735 (0.050)	0.517 (0.065)

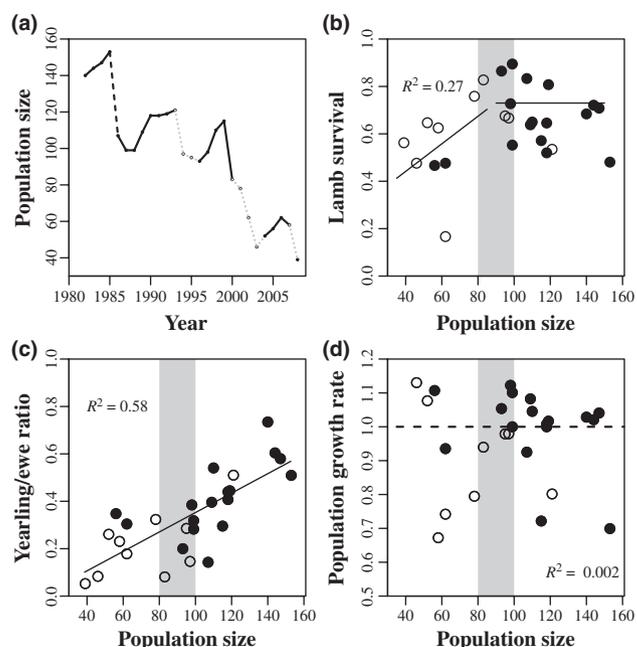


Figure 1 Population dynamics of Bighorn sheep at Sheep River, Canada. (a) Number of bighorn sheep in March, 1981–2008. The dashed line indicates a decline due to a pneumonia epizootic, dotted grey lines link years with high cougar predation. (b) Lamb survival to weaning, (c) yearling recruitment and (d) population growth rate as a function of population size. The dashed line indicate stable population growth ($w = 1$). Below this line the population declined. In panels b–d: open circles represent years with high cougar predation, black circles years with low predation. The grey zone represents the range in threshold population size suggested by our analyses (see Tables S1 and S2).

with population size with a slope of 0.890 (95% CI 0.138–1.643) on a logit scale. The positive correlation, however, disappeared when years were categorized by presence or absence of cougar predation (Table 3) suggesting that at low density cougar predation was the most important driver affecting ewe survival.

DISCUSSION

We suggest that the component Allee effects documented here were mainly caused by predation episodes whose occurrence was density-independent, as reported in other populations (Festa-Bianchet *et al.* 2006). The impact of predation episodes on population dynamics, however, showed positive density dependence. As the population declined, the proportion removed by specialist cougars increased, reducing ewe survival and leading to positive density dependence in recruitment (Fig. 1b,c). Our data also suggested an effect of predation on lamb growth. The smaller size of lambs in mid-October could not be due to predation on larger lambs, as cougars do not select sheep based on size (Ross *et al.* 1997) and most predation occurred after October (Ross *et al.* 1997). The Sheep River winter range provides high-quality forage (Festa-Bianchet 1988b), but in years of high predation, most sheep wintered in the mountains to the west, with lower productivity and deeper snow (Pelletier *et al.* 2006). When at Sheep River, sheep spent more time moving to avoid cougars (Pelletier *et al.* 2006), possibly reducing foraging efficiency and increasing stress (Creel *et al.* 2007; Creel & Christianson 2008). Smaller size in years of high predation would have lowered lamb winter survival by *c.* 8%. Lower lamb survival to weaning with

Table 2 Estimates from (a) generalized mixed effect model of lamb overwinter survival and (b) linear mixed effect models for chest circumference of lambs adjusted to October 9, for bighorn sheep at Sheep River, Canada, 1982–2008

Variables	Estimate	Standard error
(a) Lamb winter survival ($n = 424$ lambs born to 137 ewes)		
Intercept	-8.755	2.532
Sex (female)	0.237	0.251
Maternal age	-0.140	0.167
Maternal age ²	0.010	0.010
Cougar predation*	-1.179	0.467
Population size	-0.009	0.009
NDVI	-0.5923	5.537
Chest circumference	0.145	0.029
(b) Lamb chest circumference† ($n = 400$ lambs born to 130 ewes)		
Intercept	86.596	4.855
Lamb sex (female)	-7.583	2.263
Maternal age	2.017	0.285
Maternal age ²	-0.115	0.017
Cougar predation*	-2.059	0.903
Population size	-0.061	0.021
Spring precipitation	-0.009	0.005
Mean spring temperature	-1.087	0.379
Lamb sex (female) × population size	0.049	0.021

NDVI, Normalized Difference Vegetation Index.

Mother identity and year were included as random effects in both models. Details on model selection are in Tables S3 and S4.

*Years with high cougar predation.

†1982–2005.

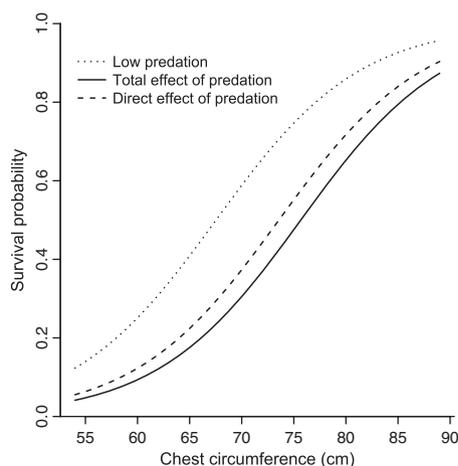


Figure 2 Direct and indirect effects of predation on winter lamb survival at Sheep River, Canada. The three curves are predicted from general mixed effects models on winter lamb survival (see Table S4), with mother identity and year as random effects. The effect of size and predation is shown for female lamb but the same effect was observed for males.

decreasing population size (Fig. 1b) may also be partly an indirect effect of predation, as ewes stressed by predation risk may reduce reproductive effort. In Yellowstone, physiological changes in elk (*Cervus canadensis*) associated with wolf (*Canis lupus*) predation may reduce calf recruitment through increased stress and female movement rates (Creel *et al.* 2007, 2009). Low lamb survival and positive density dependence prevented our study population from recovering after it declined below a threshold of $c. 90$ individuals (Fig. 1b).

Table 3 Model selection of between-year variation of age-specific survival of bighorn ewes at Sheep River, Canada

Model	Parameters	AIC	Δ AIC	AICw
(1) Y + P + O + V + cougar	6	1012.939	0	0.6068
(2) Y + P + O + V + cougar + density	7	1014.369	1.430	0.2969
(3) (Y + P + O + V) × cougar	9	1017.019	4.080	0.0789
(4) (Y + P + O) × cougar + V	8	1020.972	7.333	0.0155
(5) (Y + P) × cougar + O + V	7	1024.500	11.561	0.0019
(6) Y + P + O + V + density	6	1036.356	23.417	0.0000
(7) Y × cougar + P + O + V	6	1036.416	23.477	0.0000
(8) Y + P + O + V	5	<i>1043.447</i>	<i>30.508</i>	<i>0.0000</i>
(9) (Y + P + O + V) × density	8	1046.863	33.924	0.0000
(10) Age (full age-specific model)	19	1050.520	37.581	0.0000

Y, yearlings; P, prime age adults aged 2–8 years; O, old adults, 8–13 years; V, very old, 13 and older. The selected model (1) is in bold and the best age model (8) in italic. Models are ranked from the most to the least likely to be the best among those fitted. Including either the effects of cougar predation [model (1)] or of density [model (6)] provides a better fit than the simple age-class model [model (8)]. When accounting for both cougar and density effects, only the effect of predation on age-specific survival remains.

Positive density dependence was evident over the entire observed range of population size for yearling recruitment in March (Fig. 1c) and for adult ewe survival. We suggest that the component Allee effects we report were shaped mainly by predation, because we accounted for other possible confounding effects of environmental factors such as vegetation productivity and climate.

Despite evident Allee effects on recruitment (Fig. 1b,c) and on adult female survival, during our study the population did not provide statistical support for a demographic Allee effect (Fig. 1d), but declined in most years with fewer than 90 sheep. Reasons why ‘component’ Allee effects (affecting a single vital rate, see Courchamp *et al.* 1999) may not produce a ‘demographic’ Allee effect (positive density-dependent population growth) have been discussed (Gascoigne & Lipcius 2004; Kramer *et al.* 2009). Lack of statistical relationship between population growth and population size in the presence of strong component Allee effects, however, is not an argument against increased risk of extinction. Statistical relationships that only exist below a threshold are not easily detected (Gregory *et al.* 2010). A population that went extinct in 1 year would add one datum to the analysis: little statistical power but substantial biological significance. There was no compensation in any other vital rate as no parameter showed negative density dependence. A few immigrants (0–3 a year) during the last 10 years of the study also affected the growth rate of the population. For example, immigration of just two ewes in 2003 increased the population by 4.5%. Finally, at very low density most sheep remained in high-elevation sites much of the winter (Pelletier *et al.* 2006), apparently to avoid cougar predation. That may partly explain the lack of a demographic Allee effect. Avoidance of the traditional winter range in 2005–2008 might have allowed positive population growth rates despite the very low population size.

Our long-term research has major implications for our understanding of vertebrate population dynamics. We provide empirical support that fear of predation can substantially reduce prey fitness (Creel *et al.* 2007, 2009). More importantly, we provide a direct empirical quantification of component Allee effects on lamb survival to weaning, lamb winter survival and adult female survival. These effects

potentially threaten the persistence of a population of long-lived vertebrates. As cougars mostly prey on cervids (Ross & Jalkotzy 1992), they do not depend on the bighorn sheep population (Festa-Bianchet et al. 2006). In a context of global environmental changes, more wildlife populations will be driven to very low numbers. It is essential to understand how component and demographic Allee effects may affect wild populations, to assess how human-driven changes may affect their ability to persist.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 Model selection for broken stick regression comparing bighorn lamb survival to October and population size at Sheep River, Alberta.

Table S2 Summary statistics for broken stick regression model comparing bighorn lamb survival to October and population size at Sheep River, Alberta, with a threshold at 90 sheep.

Table S3 Model selection by the Akaike information criterion (AIC) for overwinter lamb survival ($n = 413$) at Sheep River, Alberta, 1982–2005.

Table S4 Model selection by the Akaike information criterion (AIC) for the lamb chest circumference ($n = 400$) in autumn at Sheep River, Alberta, 1982–2005.

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