



Incorporating preferential prey selection and stochastic predation into population viability analysis for rare prey species



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ABSTRACT

There is increasing evidence that predation can cause the decline and extinction of small populations of prey, and that stochastic predation resulting from variation in prey selection by individual predators can have significant consequences for population persistence. Modelling approaches that ignore variation in prey selection exhibited by individual predators may inaccurately predict the effect of predation on prey populations, especially over longer time scales. We assess the impacts of variation in prey selection by building PVA models for endangered huemul deer *Hippocamelus bisulcus* that sequentially include and exclude observed stochasticity in predation among individual pumas *Puma concolor*. Our results indicated that huemul are at risk of extinction in all scenarios modelled, although the immediacy of this risk differed based on model structure and time period considered. Specifically, modelling predation as a random effect based on an interrupted Poisson process rather than as a directional and continuous change in survival rates, resulted in significantly longer estimates of time to extinction independent of the assumed intensity of predation. Our results highlight the importance of determining whether specialist predators are driving predation on rare prey, and when they are, incorporating said stochastic predation when attempting to predict persistence probabilities of rare prey using PVA models. Since results of PVA models are commonly used to develop conservation strategies, we advocate for the inclusion of stochastic predation in future PVA models where warranted to more accurately inform strategies for the conservation of rare prey and their predators.

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1. Introduction

Population viability analysis (PVA) is a modelling tool used to quantitatively evaluate the status of species or populations and to assess factors affecting the probability of their persistence (Shaffer, 1981; Beissinger and McCullough, 2002). Accurate prediction of population persistence requires, at a minimum, estimates of vital rates – such as age-specific survival and fertility rates – from the system of interest as well as a measure of the uncertainty associated with these estimates (Coulson et al., 2001; Reed et al., 2002). A mechanistic understanding of the factors causing population declines is also critically important (Caughley, 1994). Without such an understanding, it is impossible to make reliable predictions about population persistence in spatially and temporally variable

environments (Morris and Doak, 2002). Comparing outcomes of different modelling scenarios that incorporate likely causes for suppressed vital rates and associated stochasticity has been particularly effective in helping stakeholders prioritize conservation management (Bekessy et al., 2009; Pe'er et al., 2013).

For many large herbivores, predation is a major cause of mortality (e.g. Sinclair et al., 2003) and predation has increasingly been identified as the proximate cause for observed declines of many ungulates in North America, including common species with large populations such as elk *Cervus elaphus* (White and Garrott, 2005) and mule deer *Odocoileus hemionus* (Forrester and Wittmer, 2013), but also endangered species with small populations such as non-migratory woodland caribou *Rangifer tarandus caribou* (Wittmer et al., 2005) and bighorn sheep *Ovis canadensis* (Festa-Bianchet et al., 2006; Johnson et al., 2013). Because our current understanding of predator–prey dynamics is largely based on models in which all predators are assumed to exhibit the same “mean”

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foraging strategies across a range of prey densities (Holling, 1959), models used to understand predator–prey interactions generally do not explore possible effects due to differences in prey selection among individual predators (e.g. Fryxell et al., 2007; McLellan et al., 2010). This is a concern, since recent research suggests that, while a predator species as a whole may indeed forage on a wide range of prey species (Sinclair et al., 2003), many populations consist of individual predators that exhibit preferences for different prey species (Estes et al., 2003; Woo et al., 2008; Elbroch and Wittmer, 2013). Modelling approaches ignoring the presence of such specialists within a population may inaccurately predict the effect of predation on prey populations (Pettorelli et al., 2011). Furthermore, variation in prey selection exhibited by predators in multi-prey systems may result in sporadic, intense bouts of stochastic predation on rare prey. In these cases, stochastic predation is driven by the presence of individuals that select for the rare prey more than expected based on their availability (Festa-Bianchet et al., 2006; Elbroch and Wittmer, 2013).

Here we assess the importance of incorporating uncertainty in the overall impact or intensity of predation and stochasticity in prey selection by individual predators when attempting to predict the population dynamics and persistence probability of their prey. We utilized data on a population of endangered huemul *Hippocamelus bisulcus* (Jimenez et al., 2008) from Chilean Patagonia that suggested that the dynamics of these deer might be negatively affected by predation in the form of “apparent competition” (Holt, 1977) where most of the observed mortality of huemul >1 year of age was attributed to a few specialist pumas *Puma concolor* that preferentially preyed upon huemul in the area (Elbroch and Wittmer, 2013; Wittmer et al., 2013a,b). We compared outcomes of seven alternative stochastic population models. Our first model used age-specific estimates of female huemul survival based on data from marked individuals that experienced little adult mortality from predation (Corti et al., 2010). Our second and third models were based on survival estimates for the same population observed during periods of increased predation from pumas and evaluated possible effects of compensatory (i.e. predation did not change the overall mortality rate of huemul) and additive (i.e. predation increased the overall mortality rate of huemul) predation of female huemul >1 year old by pumas (Wittmer et al., 2013a). Given that pumas are solitary ambush predators that opportunistically select prey of any health where structural complexity (e.g. slope, vegetation) provide them an advantage (Huselman et al., 2003; Atwood et al., 2007), exploring consequences of possible additive predation seemed particularly important. Our fourth and fifth models were the same as our second and third, respectively, with the addition of individual variation in prey selection. For these last two models we adopted a theoretical framework based on an interrupted Poisson process (IPP) (Beyer and Nielsen, 1996) that enabled us to incorporate observed variation in prey preferences among individual pumas (Elbroch and Wittmer, 2013) and suspected temporal stochasticity in these predation events into models predicting the probability of persistence of huemul. Finally, we compared outcomes from models incorporating individual variation in prey selection based on IPP against predictions from models based on intermediate predation rates in two additional scenarios. We simulated all scenarios over both short (i.e. 20 year) and long (i.e. 200 year) time frames. Our approach allowed us to determine if estimates of population persistence were substantially altered by uncertainty in the overall impact of predation as well as by inclusion of individual variation in prey preferences and stochasticity in observed predation events, and to assess whether this knowledge should influence recommendations for future management strategies aimed at conserving rare prey.

2. Materials and methods

2.1. Study area

Data to initialize models were drawn from studies conducted in central Chilean Patagonia. The area consisted of approximately 2650 km² of public (Lago Cochrane National Reserve (LCNR) 69 km²; Lago Jeinimeni National Reserve (LJNR) 1611 km²) and private lands (Estancia Valle Chacabuco 810 km²), which together are currently being converted into the future Patagonia National Park (PNP). The primary purpose of the PNP is the protection of the local huemul population (Conservación Patagónica, 2013), which accounts for approximately 10% of all remaining huemul in Chile (Wittmer et al., 2013a). Research on the effect of predation on huemul focused on a 1200 km² area immediately north of Lago Cochrane (W 47.8000°, S-72.0000°, Fig. 1) and encompassed most of the known distribution of huemul in the PNP (Corti et al., 2010; Wittmer et al., 2013a). Other characteristics of the study area such as terrain, land cover and climate have been described elsewhere (Corti et al., 2010; Elbroch and Wittmer, 2012).

2.2. Huemul abundance and vital rates

Attempts to enumerate the local huemul population have been largely restricted to the small LCNR (Fig. 1). Inside the LCNR, population surveys have been conducted since 1991, with more accurate estimates made from 2005 onwards when individuals were marked or distinguished based on individual characteristics (Corti et al., 2010; Wittmer et al., 2010). Outside the LCNR, periodic population surveys were conducted to map huemul occurrence on the landscape and estimate their abundance. Overall, population estimates suggest that there are currently approximately 120 huemul in the entire PNP (Wittmer et al., 2013a).

Age-specific estimates of vital rates (Table 1), including survival based on encounter histories of marked individuals, were first provided by Corti et al. (2010) with fawn survival estimates subsequently updated by Wittmer et al. (2013a) based on 2 additional years of data. Survival estimates that more accurately reflected observed high predation rates of adult female huemul >1 year old from pumas became available when puma foraging ecology was studied with the help of Argos-GPS collars (Elbroch and Wittmer, 2012, 2013). From 2008 to 2010, a total of 9 pumas were monitored intensively as part of a study of puma diets; kills of 433 prey, including 7 huemul, were documented during this period (Elbroch and Wittmer, 2013). Huemul only constituted 1.3% of total biomass killed by pumas, and, more importantly, only a small subset of pumas that overlapped the distribution of huemul (2 of 6) actually preyed on them. When combined with information from collared huemul, Wittmer et al. (2013a) provided adjusted age-specific survival estimates based on the assumption that puma predation was either compensatory or additive (Table 1). Adjusted survival estimates for huemul >1 year old were significantly lower than previously thought due to the observed 5.45-fold increase in predation from pumas between the 2005–08 (Corti et al., 2010) and 2008–10 periods (Elbroch and Wittmer, 2013; Wittmer et al., 2013a). The increase in puma predation appeared linked to management changes on the Estancia Valle Chacabuco associated with the establishment of the future PNP (Wittmer et al., 2013a). In particular, elevated predation rates from pumas were likely a consequence of both reductions in prey availability following the removal of >30,000 domestic sheep over a 3-year period and simultaneous cessation of efforts to control pumas.

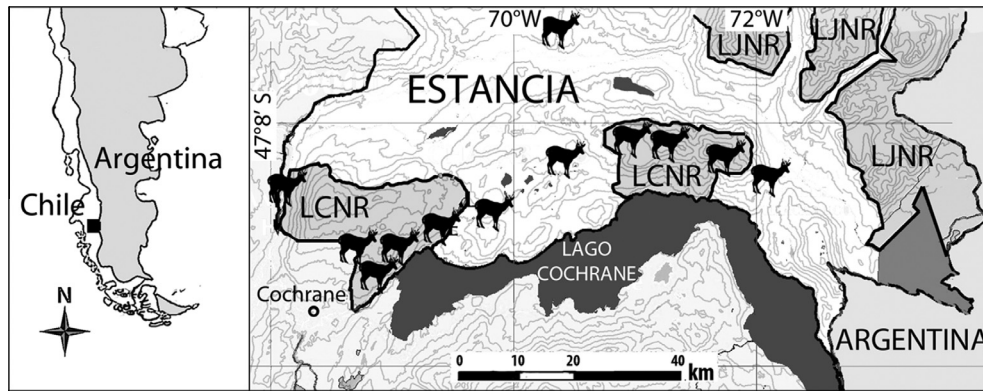


Fig. 1. Distribution of the huemul population in the future Patagonia National Park. Each deer symbol represents approximately 10 individuals.

Table 1
Model parameters (mean [\pm standard deviation]) used to determine population dynamics of huemul in the Lago Cochrane area. The survival rate standard deviations are based on variances corrected for sampling error.

Parameter	Corti et al. (2010): data until 2008	Compensatory puma predation ^a	Additive puma predation ^a
Fertility (adults \geq 3 years)	0.72 [\pm 0.20]	0.72 [\pm 0.20]	0.72 [\pm 0.20]
<i>Survival</i>			
0–1 year (fawns) ^b	0.18 [\pm 0.19]	0.18 [\pm 0.19]	0.18 [\pm 0.19]
1–2 years (yearlings)	0.88 [\pm 0.10]	0.78 [\pm 0.10]	0.70 [\pm 0.10]
2–3 years (juveniles)	0.91 [\pm 0.05]	0.84 [\pm 0.05]	0.78 [\pm 0.05]
\geq 3 years (adults)	0.94 [\pm 0.05]	0.89 [\pm 0.05]	0.85 [\pm 0.05]

^a From Wittmer et al. (2013a).

^b Updated fawn survival estimates using data until 2010 (from Wittmer et al. (2013a)).

2.3. PVA model and sampling error correction

We constructed an age-structured, female-only matrix population model assuming annual birth-pulse reproduction (Tuljapurkar and Caswell, 1997) and a maximum age of 15 years for adult huemul (Smith-Flueck, 2000). Age-specific parameter estimates for survival and fertility predict population parameters in November (pre-breeding) just before the birthing season, as well as for decreased survival through compensatory and additive puma predation (Table 1). In all models huemul are reproductively active from their third birthday onwards (Corti et al., 2010). Data on mean survival rates and associated within-year variances [from Corti et al. (2010) and Wittmer et al. (2013a)] were used to account for sampling error in the variance estimates of the survival rates following White (2000). All modelling and analysis were performed using R v2.15.3 (R Development Core Team, 2013). Code for implementing White's (2000) method for accounting for sampling error was based on Matlab examples in Morris and Doak (2002).

2.4. Estimating uncertainty in vital rates

In order to reflect uncertainty in survival and fertility estimates the matrix model re-sampled a set of parameter values for each of the 1000 model iterations for both vital rates from a beta and log-normal distribution, respectively (Morris and Doak, 2002). These distributions were produced using the *rbeta* (stats v2.15.3 R package) and *lnorms* (popbio v2.4 R package) functions (*mn*, *sdev*), where *mn* and *sdev* relate to the estimate and standard deviation of the vital rate respectively. At the end of each model run the predicted finite rate of increase (λ) at time $t = 20$ or 200 years was determined as $\lambda = \left(\frac{N_t}{N_0}\right)^{\frac{1}{t}}$, resulting in 1000 repeated measurements for each model scenario from which we constructed 95% confidence intervals based on the bootstrap percentile method (Efron and Tibshirani, 1993).

2.5. Initial population sizes

Wittmer et al. (2013a) reported an approximate huemul population size of 120 individuals within the PNP. For all scenarios, we assumed a sex ratio of 50:50 for determining the initial number of females; thus the initial population size for all scenarios was 60 females. We assumed a sex ratio of 50:50 despite data suggesting a potential biased sex ratio with approx. 60% females (Corti et al., 2010) since available estimates were limited to a small area with almost no predation from pumas; there is no indication that the bias extended over the entire distribution of huemul in the PNP. Our estimate of the initial number of females was nevertheless likely optimistic since the total population estimate of 120 individuals presented in Wittmer et al. (2013a) also included an unknown number of fawns just short of transitioning to the yearling category. We distributed the number of starting individuals among age classes from 1 to 15 years old following the stable-stage distribution calculated from the scenario-specific survival and fertility estimates, leaving age class 0 years empty at the start of each model iteration.

2.6. Scenarios assuming constant vital rates

In our first scenario (S1), we used survival and fertility rates for huemul >1 year old published by Corti et al. (2010) combined with the more accurate estimates of fawn survival published in Wittmer et al. (2013a). In the following two scenarios (S2, S3), we used the survival rates of female huemul >1 year old adjusted for observed compensatory (S2) and additive (S3) predation following changes in predator–prey management on the Estancia Valle Chacabuco reported in Wittmer et al. (2013a). For all three initial model scenarios we used variances corrected for sampling error (Table 1). Each model scenario was run for 20 (short-term) and 200 (long-term) year periods.

2.7. Scenarios with stochastic puma predation

In our subsequent models (S4, S5), we investigated the effects of stochastic puma predation on population growth and persistence of huemul in the study area. In the first of these two models (S4) we used survival estimates of huemul >1 year old published in Corti et al. (2010) and updated survival estimates of the same age classes under the compensatory predation scenario (Table 1). In contrast to the initial three scenarios, vital rates were allowed to change following an IPP process (Beyer and Nielsen, 1996), where the inter-arrival times (time between predation events) as well as the lag periods (duration of predation events) were drawn from separate exponential distributions with higher exponential rates resulting in lower inter-arrival times. The rate defining the exponential distribution of inter-arrival times of predation events was the product of the estimated population size at the beginning of each simulation year and a base rate, which was calculated from observations of puma predation on huemul in the field by Elbroch and Wittmer (2012). Elbroch and Wittmer (2012) presented data showing that over a total of 915 days six pumas monitored with GPS-Argos collars in the PNP overlapped with a cumulative sum of 197 huemul. During the observation period two out of the six pumas killed huemul (Elbroch and Wittmer, 2013), resulting in individual pumas killing huemul for every 915 days of observation and 98.5 potential huemul available, or a base rate for a puma turning to hunting huemul of 0.004 per huemul per year. Such a base rate corresponded to a 7%, 45% and 70% chance of predation occurring within a huemul population of 10, 100 and 200 individuals, respectively, within a given simulation year. The occurrence of predation events, defined as the time period of increased predation on huemul by a specialist puma, in the simulation was marked by switching survival rates of huemul >1 year old from those published by Corti et al. (2010) to the compensatory predation rates (Table 1) for a duration defined by an exponential distribution of rate 0.285. This value corresponds to an average length of 3.5 years observed by Festa-Bianchet et al. (2006) for the duration of puma predation episodes on bighorn sheep *Ovis canadensis* populations in Canada that resulted in a decrease in bighorn sheep survival rates. Scenario (S5) differed from the previous stochastic predation scenario only in that it used additive instead of compensatory predation rates (Table 1). Model scenarios were again run for 20- and 200-year periods.

2.8. Scenarios with averaged vital rates from stochastic predation models

Since survival rates under the stochastic predation scenarios based on IPP (S4, S5) essentially alternated between low and high predation years (and thus values from the initial scenarios S1 versus S2 or S3), we further assessed the effect of stochasticity in predation by comparing model outcomes to scenarios assuming intermediate, static survival rates. For these two scenarios (S6, S7) we estimated averages of survival rates used in scenarios S4 and S5 from both the 20- and 200-year period models (Table 2),

but reverted model structure back to the static scenario used in S1 to S3.

3. Results

Predicted average estimates of λ based on our most optimistic model (S1 = survival estimates based on values when negligible mortality of huemul >1 year of age from puma predation was observed) were either slightly above (20-year time frame) or slightly below (200-year time frame) 1, with 95% confidence intervals for both time frames overlapping 1 (Fig. 2). Associated extinction probabilities under this scenario predicted a 0.11 probability of the huemul population in the PNP becoming extinct over the next 200 years (Table 3). Our models assuming elevated and constant predation from pumas on huemul >1 year of age (S2 = compensatory mortality, S3 = additive mortality) returned average values for λ of less than 1.0 for both short and long time frames (Fig. 2), and, with the exception of the 20-year predictions for S2 (95% CI slightly overlap 1), predicted significant population declines. Associated extinction probabilities predicted huemul becoming extinct in the PNP within 128 (S2) or 60 (S3) years (Table 3). While the 95% confidence intervals of predicted λ s for all 3 initial model scenarios overlap each other for the 20-year time frames, none of the confidence intervals for the 200-year time frames overlap (Fig. 2).

When we incorporated stochasticity in foraging strategies among individual predators into our PVA models (S4, S5) model outcomes consistently predicted increases in average λ s independent of the assumed effect and thus severity of predation (S2, S3) and the time frames we considered (Fig. 2). For the 200-year time frames, estimates of λ were significantly higher when compared to scenarios assuming constant predation from pumas (95% CI do not overlap). While both models assuming stochastic predation continue to predict high extinction risks for huemul in the PNP, quasi-extinction probabilities no longer converged to 1 (Table 3). Under both the compensatory and additive scenario assuming stochasticity in predation (S4, S5), predicted λ s showed some overlap in confidence intervals with predictions based on values when negligible mortality of huemul >1 year of age from puma predation was observed (S1). When 'averaged' vital rates from stochastic predation scenarios (S4, S5) were used in 'static' models (S6, S7), predicted values for λ s were slightly lower but not significantly different (95% CI do overlap) (Fig. 2) resulting in essentially identical estimates of extinction probabilities (Table 3).

Significant population declines over the next 20 years were predicted by all models based on survival estimates of huemul >1 year of age following observed increases in mortalities from pumas after implementation of management changes associated with the establishment of the PNP (Table 4). Magnitudes of predicted declines of female huemul over the next 20 years under these scenarios range from 35% to 78%, with models assuming additive effects of predation (S3, S5) predicting the most severe population declines (78% and 62% respectively). Predicted remaining population sizes under the 'static' predation scenarios (S6, S7) were

Table 2

Fertility and survival rate values (\pm standard deviations) used in scenarios 6 and 7 (Fig. 2); survival rate values have been averaged from scenarios 4 (stochastic compensatory predation) and 5 (stochastic additive predation) respectively over a 20- and 200-year simulation period.

Parameter	Scenario 6		Scenario 7	
	20	200	20	200
Fertility (adults \geq 3 years)	0.72 \pm [0.20]	0.72 \pm [0.20]	0.72 \pm [0.20]	0.72 \pm [0.20]
Survival				
0–1 year (fawns)	0.18 \pm [0.19]	0.18 \pm [0.19]	0.18 \pm [0.19]	0.18 \pm [0.19]
1–2 years (yearlings)	0.81 \pm [0.12]	0.85 \pm [0.11]	0.77 \pm [0.14]	0.85 \pm [0.12]
2–3 years (juveniles)	0.87 \pm [0.06]	0.89 \pm [0.06]	0.83 \pm [0.08]	0.89 \pm [0.07]
\geq 3 years (adults)	0.91 \pm [0.06]	0.93 \pm [0.05]	0.89 \pm [0.07]	0.92 \pm [0.06]

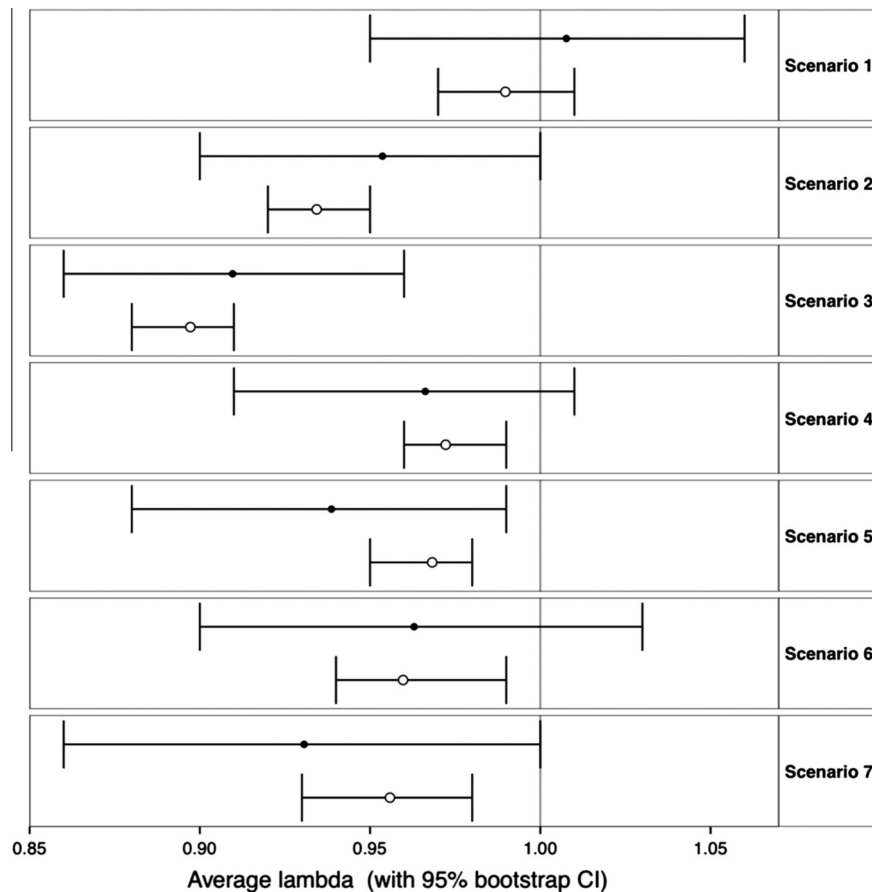


Fig. 2. Average values (with 95% bootstrap percentile confidence intervals) for lambda for each of the seven scenarios determined over a simulation period of 20 (closed circle) or 200 (open circle) years and 1000 iterations: scenario 1 = Corti et al. (2010) with negligible predation from pumas; scenario 2 = following increased predation described in (Wittmer et al., 2013a) where predation is assumed to be compensatory; scenario 3 = as scenario 2 but with predation assumed to be additive; scenario 4 = predation assumed to be stochastic using data described in Elbroch and Wittmer (2013) and compensatory; scenario 5 = predation assumed to be stochastic using data described in Elbroch and Wittmer (2013) and additive; scenario 6 = using average vital rates and variances calculated from scenario 4, but without stochastic predation; scenario 7 = as scenario 6, but using average vital rates from scenario 5.

Table 3

Year in which the probability of quasi-extinction (threshold of ≤ 1 female remaining in population) converges to 1; the results for the different scenarios are based on 1000 simulation runs; * = did not converge to a cumulative quasi-extinction probability of 1 over a 200 year simulation period, average cumulative quasi-extinction probability for year 200 shown in parentheses.

Scenario	Estimated year of reaching probability = 1 of quasi-extinction	Lower 95% confidence interval (years)	Upper 95% confidence interval (years)
1	(0.107)*	(0.000)	(0.725)
2	128	91	128
3	60	47	60
4	(0.831)*	(0.081)	(1.000)
5	(0.874)*	(0.210)	(1.000)
6	(0.836)*	(0.095)	(1.000)
7	(0.880)*	(0.230)	(1.000)

substantially higher compared to outcomes based on ‘stochastic’ predation scenarios (S4, S5), albeit with larger degrees of uncertainty (Table 4).

4. Discussion

With increasing evidence for stochastic predation (Festa-Bianchet et al., 2006; Elbroch and Wittmer, 2013) and population level consequences from individual specialist predators on rare prey species (Williams et al., 2004; Wittmer et al., 2013a), dynamical modelling approaches capable of predicting outcomes of spatial and temporal variation in foraging strategies among individual predators are becoming increasingly relevant (Pettorelli et al.,

2011). Modelling the viability of huemul in the future PNP under different predation scenarios produced three important results. First, models accounting for stochastic variation in individual foraging strategies predicted significantly different estimates of λ s and extinction probabilities for huemul when compared to static scenarios based on mean predation rates. Second, our results emphasize that the efficacy of conservation management interventions can be enhanced by consideration of models that appropriately incorporate both uncertainty in the overall impact or intensity of predation and the foraging strategies of individual predators. Third, estimated λ s based on data following recent conservation management in the PNP (i.e., the removal of domestic sheep) predicted pronounced population declines and high extinction probabilities for huemul independent of model uncertainties.

Table 4

Expected number of female huemul remaining in the Patagonia National Park after 20 years; results based on initial population of 60 females separated for the seven different model scenarios repeated over 1000 simulation runs.

Scenario	Average number of female huemul (SD) remaining after 20-year period	Average percent change (%)
1	77 (44)	+28
2	30 (17)	–50
3	13 (8)	–78
4	39 (22)	–35
5	23 (14)	–62
6	56 (50)	–7
7	55 (50)	–8

Modelling predation as a random process rather than as a directional and continuous change in survival rates of huemul resulted in significantly higher estimates of λ and thus reduced estimates of extinction probability over longer time frames. These model outcomes suggest that short, periodic bouts of intense predation from individual specialists have less negative effects on small prey populations than sustained, widespread predation and associated low survival rates. Differences in predicted λ s and associated extinction probabilities largely disappeared when we compared outcomes from models that included stochasticity in predation (S4, S5) with ‘static’ models based on average survival rates from the aforementioned stochastic scenarios (S6, S7). However, while λ s estimated based on ‘static’ predation models were only slightly lower than those estimated based on our ‘stochastic’ predation scenarios, the estimated number of remaining females at the end of our 20-year predictions were substantially higher under ‘static’ models. Together these results highlight the importance of incorporating stochasticity in predation as a result of different foraging strategies among individual predators in any attempt to predict dynamics and persistence probabilities of rare prey.

We also suggest that the modelling framework based on interrupted Poisson processes (IPP) (Beyer and Nielsen, 1996) that we applied to stochasticity in predation captured observed variation in predation well and consequently resulted in less biased estimates of population persistence when compared to scenarios that did not incorporate stochastic predation. Predator–prey models based on IPPs have been developed to model predator encounters with patchy prey but have so far primarily been applied to marine systems. Although IPP models are not routinely used to incorporate temporal and spatial variation in predation, the data necessary to parameterize such models are relatively easy to collect in terrestrial systems. For example, inter-arrival times (time between predation events) as well as lag periods (duration of predation events) can easily be estimated from data collected from individual predators fitted with GPS collars. Combined with data on the spatial distribution of prey and specialist predators, sufficient information should be available for many species to incorporate stochastic predation into predator–prey models for terrestrial systems.

Discrepancies in model predictions highlighted the difficulty in conclusively determining the effect of predation on huemul in the PNP. Future research will need to resolve whether only a small number of individual pumas continue to kill huemul (Elbroch and Wittmer, 2013), the duration of predation bouts if these individuals are allowed to persist in the population, and whether mortality from puma predation is additive or compensatory for huemul (Wittmer et al., 2013a). The best approach to resolving these questions would be to reinstate intensive monitoring efforts of pumas and huemul in the PNP together with active system manipulation within an adaptive management framework (Wittmer et al., 2014). System manipulation should focus on quantifying benefits associated

with the removal of pumas known to kill adult huemul in greater numbers given their availability (i.e., huemul specialists) rather than widespread puma control. In addition, monitoring at kill sites should include assessments of bone marrow of huemul to assess the role of body condition in the unsustainable predation rates currently observed (see McLellan et al., 2012 for an example involving woodland caribou) given that previous data suggested that at least some huemul killed by pumas were in poor physical condition (Elbroch and Wittmer, 2013). However, outcomes from baseline models based on vital rates when negligible puma predation occurred indicate that solely addressing predation from pumas will be insufficient to achieve significant population growth of huemul. Thus control efforts of specific, huemul specialist pumas is not necessarily the solution, or would need to be accompanied by other management options.

Unlike other ungulates, such as mule deer (Forrester and Wittmer, 2013), huemul cannot increase their reproductive output and thereby compensate for high adult mortality rates. Previous research has indicated that survival estimates of huemul fawns in the PNP are suppressed by high predation by culpeo foxes *Lycalopex culpaeus*, and that fawn survival rates are too low to compensate for observed high adult mortalities (Wittmer et al., 2013a). We thus recommend that any conservation measures to increase the probability of huemul persistence should include an assessment of the culpeo fox population in the PNP, including the potential role abundant, exotic hares *Lepus europeus* play in subsidizing and inflating the fox population. Further research exploring fox predation on huemul fawns is also needed. Simultaneous reductions of specialist pumas and foxes in areas where they overlap with huemul may subsequently prove the best strategy to ensure huemul persistence in the PNP. Alternatively, future research may reveal that increasing fawn survivorship through fox reductions will be sufficient.

Overall, however, outcomes from all model scenarios consistently predicted population declines independent of the uncertainty surrounding the influence and severity of predation. Approximately 10% of the total number of huemul remaining in Chile are thus at risk of becoming extinct within the next 200 years. These predictions suggest that huemul in the future PNP are a conservation-reliant species (*sensu* Scott et al., 2010) and will require active management for the foreseeable future. Results from previous studies suggest that huemul in other parts of their distribution in Chile can respond quickly to management that addresses major limiting factors (Briceño et al., 2013). However, reductions in huemul survivorship following management associated with the establishment of the PNP, namely the abrupt removal of >30,000 domestic sheep together with increases in predators following the simultaneous discontinuation of control efforts, appear to have increased rather than reduced extinction probabilities for this population of huemul (see also Elbroch and Wittmer, 2013; Wittmer et al., 2013a). Our results thus call to question past and current management and suggest careful consideration is required to determine how best to proceed to increase the probability of huemul persistence in the PNP (see above and also Wittmer et al., 2013b, 2014). Since our results also highlight the potential for dramatic declines over the next 20 years, immediate action is required to mitigate any risk that the PNP population of huemul will decline to thresholds below which recovery is unlikely.

Conserving rare prey species affected by predation is difficult (Wittmer et al., 2013b), and culling native predators even to protect native species is controversial (Orians et al., 1997). Given predicted rates of decline of huemul, however, predator control may offer the only opportunity to prevent extinction of huemul in the future PNP. The most important task is to now communicate outcomes of our PVA to stakeholders so that appropriate management can be implemented (Pe'er et al., 2013).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2014.02.003>.

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