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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.

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 (Husseman 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 km^2 of public (Lago Cochrane National Reserve (LCNR) 69 km^2; Lago Jeinimeni National Reserve (LJNR) 1611 km^2) and private lands (Estancia Valle Chacabuco 810 km^2), 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 Patagonica, 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 km^2 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.