How to effectively manage invasive predators to protect their native prey

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ABSTRACT

Invasive predators can have substantial effects on their native prey and often there is a need for rapid action to quell this impact. Conservation action is often employed on behalf of the native prey by means of predator removal or birth control. The decision to employ such actions is often based on the outcome of a population viability analysis (PVA) or similar method aimed at reducing the predator population. These models typically focus on one species and ignore the effects of that species' interaction with others. Thus, there is inherently a disconnect between what is being managed (the predator population) and the desired outcome of the management (the persistence of a prey population). We built stage-based, stochastic matrix models of an invasive generalist predator and its native prey and coupled these using a functional response. We generated management recommendations based on the number of times the prey population persisted, and considered a range of life history types for predators and prey. We compared the results of our model to those generated by a traditional elasticity analysis commonly used in PVA. Recommendations from our model disagreed with those made by traditional elasticity most often when considering management of short-lived predators, and showed complete agreement between methods when considering long-lived predators. We illustrate that traditional PVA approaches to managing predators for the benefit of prey can provide inefficient control recommendations. Our coupled predator–prey model provides a flexible yet comprehensive approach to exploring management actions designed to benefit native prey species, including the option of 'do nothing'.

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1. Introduction

Invasive predators have pernicious effects on their prey often driving native species to extinction, especially on oceanic islands and island continents (Blackburn et al., 2004; Salo et al., 2007; Kovacs et al., 2012). Conservation actions on behalf of the native prey often involve the employment of predator management measures such as lethal removal or birth control (Whitehead et al., 2008). Such measures can be controversial for ethical or legal reasons, and are nearly always expensive to mount (Boertje et al., 2010). For example, Busch and Cullen (2009) showed that the average cost of producing one additional yellow-eyed penguin (*Megadyptes antipodes*) nest through intensive predator management was $68,600 NZD ($56,214 USD). Given these constraints, ideally managers would possess a level of certainty on the efficacy of their management actions. A standard tool in this context is a population viability analysis (PVA) centered on the invasive predator, where the goal is to identify how to efficiently drive their total numbers down through time (Harding et al., 2001). However, a central limitation to such PVAs is the failure to explicitly model the response of the native prey population to the control of the predator (Sabo, 2008). Here we extend standard PVA models to include the response of a native prey population to invasive predator control. In so doing, we highlight when standard single-population PVAs fail to identify the most effective and efficient tactic for increasing the probability of native prey persistence.

Invasive predators can have rapid and lasting effects on their prey and, through this interaction, alter the ecosystem that they invade. For example, Savidge (1987) documented the swift extinction of native birds and reptiles caused by the brown tree snake (*Boiga irregularis*) after its introduction to Guam in the 1940s. The loss of these native prey species has led to fundamental shifts in ecological processes (Mortensen et al., 2008). The resultant efforts to control brown tree snakes have been epic but successful only to the extent that the snake has not yet invaded other susceptible islands (Rödder and Lötters, 2010). Experiences such as this one argue strongly for a rapid management response to the incursion of an invasive predator (Kaiser and Burnett, 2010). However, quick action can lead to employment of improper strategies and the waste of resources if done without pausing long enough to gain some fundamental insights into the predator–prey dynamics that prevail in each situation (Keedwell et al., 2002; Whitehead et al., 2008; Chadès et al., 2012).

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An established and quick approach to evaluating predator management options is to use mathematical models such a PVA (e.g., Harding et al., 2001). PVA has been extensively used to predict probabilities of extinction, compare and rank management strategies for at-risk species, and has been shown to do so accurately (Crouse et al., 1987; Doak, 1995; Bustamante, 1998; Brook et al., 2000; McCarthy et al., 2003). PVA uses a population projection matrix consisting of vital rates to detail the life history of the target species. A subsequent elasticity analysis of the matrix elements compares the response of the finite rate of population increase (λ) to a proportional change in each element of the vital rate matrix (de Kroon et al., 1986). The vital rate with the highest elasticity value is then targeted for management with the goal to increase (Crouse et al., 1987) or decrease (Gauthier and Brault, 1998; Harding et al., 2001) λ of the target species. Elasticity values may also be ranked to produce a suite of effective management options recognizing that the most effective option may not be the most feasible for legal, ethical, logistical, or financial reasons, and that the rankings should reflect this (Citta and Mills, 1999; Harding et al., 2001; Baxter et al., 2006; Verboom et al., 2007; Reed et al., 2009).

Most often PVA is restricted to considering a single species, ignoring the effects of the interactions this species may have with others (Glen and Dickman, 2005). Many factors will contribute to the dynamics of a population under management consideration, creating a situation where it is desirable to directly manage the interactions themselves rather than one species in this interaction (Vucetich and Creel, 1999). Despite this intuitive insight, Sabo (2008) found that such an approach to PVA was very rare only occurring in 19 of 378 published PVAs he reviewed. Only three of those 19 PVAs modeled the interaction explicitly. Sabo (2008) also showed that the predictive value of a single-species PVA was poor for a prey population when the interaction with its predator is not explicitly considered. Sabo (2008) argued that the performance of such models could be markedly improved by explicitly modeling both the predator and prey populations, linked by their interaction.

Following this advice, we built a stage-based, stochastic matrix model for an invasive generalist predator and its rare native prey, and coupled these matrices using a type III predator–prey functional response. We chose a type III functional response because we model a generalist predator and its effects on rare prey. This functional response allows the predator to switch to another prey as the prey becomes difficult to find, or to accelerate its feeding on the rare prey as the population of the prey increases. This relationship is in contrast to a type II functional response where at low prey densities the number of prey consumed has a linear relationship with the abundance of prey (Holling, 1959). Such functional responses may be quite suitable for other predator–prey dynamics, which is a topic we come back to below.

We generated recommendations for controlling the invasive predator using an elasticity analysis on just the predator matrix, thus mimicking standard previously published PVA approaches to predator management problems. We also generated management recommendations from our coupled predator–prey matrix model, where the interaction is explicitly considered. We note when the recommendations from the coupled model disagreed with those produced using only predator elasticities (Fig. 1). We also noted how often a predator control measure allowed the prey population to persist through the time frame of our model. We considered this number an index of the effectiveness of an adopted predator management strategy, and it gave us another metric to use in evaluating the usefulness of our coupled predator–prey matrix model.

2. Methods

2.1. Coupled predator–prey model

In order to evaluate a range of possible predator–prey scenarios, we generated data to simulate vital rates for three different predator populations reflecting three different life histories: a long-lived predator, moderate-lived predator (average life span between that of a short-lived and a long-lived species), and a short-lived predator. We matched these predators with a range of prey life histories; a long-lived prey, moderate-lived prey, and short-lived prey. Each species (predator or prey) consisted of three life stages: newborn (from birth to the juvenile stage), juveniles (from the end of the newborn stage until sexual maturity) and adults (post-sexual maturity). We used stage-based rather than age-based models to accommodate species with life stages lasting longer than one time-step. Thus, each species was represented by a 3X3 matrix of vital rates where the rates in each cell were chosen from a range of values that reflect each life history type (Table 1). A is the vital rate matrix for the prey (N) and predator (C) populations so that

$$
\Lambda_N = \begin{matrix} 0 & 0 & F_N \\ S_{N_{NB}} & 0 & 0 \\ 0 & S_{N_J} & S_{N_A} \end{matrix}
$$

$$
\Lambda_C = \begin{matrix} 0 & 0 & F_C \\ S_{C_{NB}} & 0 & 0 \\ 0 & S_{C_J} & S_{C_A} \end{matrix} \tag{1}
$$

where $F_{i \in N,C}$ is fecundity, and $S_{i \in NNB,NJ,NA,CNB,CJ,CA}$ is survival of the relevant stage class.

The vital rates for each life history type fall within reported ranges from empirical studies of birds, mammals, and reptiles (Heppell, 1998; Simons et al., 2000; Jouventin and Dobson, 2002; Gardali et al., 2003; Gaillard and Yoccoz, 2003). The choice of these ranges ensured that expected life-history tradeoffs among vital rates were maintained for each predator and prey type. Thus, for example, a long–lived predator cannot simultaneously have relatively high fecundity since these vital rates are negatively correlated in such life histories (Stearns, 1989).

Each matrix was allowed to project forward one time-step so that

$$
\overline{N}_{(t+1)} = \Lambda_N \times \overline{N}_t
$$
$$
\overline{C}_{(t+1)} = \Lambda_C \times \overline{C}_t \tag{2}
$$

where $\overline{N}$ and $\overline{C}$ are population vectors representing the numbers of prey (N) and predators (C) in each stage at time t. N, the total prey population size is calculated by adding the number prey in each stage class that remain after interacting with the predator and C, the total predator population size, is the total number of predators at a given time step. We allowed our model to continue for $t = 10$ time steps, which for most vertebrate predator–prey systems would equal 10 years. We chose this time frame to reflect the likely time window for managing the invasive predator as, once detected, quick action to manage the invader is crucial to minimizing the damage it may cause (Lockwood et al., 2013). Thus, our model reflects this time horizon and the associated population dynamics.

We chose to illustrate the use of our model using the effects of a newly established terrestrial vertebrate predator population on its prey, and as such we set the initial total population size of the predator at a low value (50) and at an age distribution that is adult-heavy and not stable in all realizations. Terrestrial vertebrates are most often introduced as non-natives either as purposeful releases (e.g., biocontrol releases on mongooses) or as accidental escapees from ships or airplanes (e.g., rats on islands).