

available at www.sciencedirect.comjournal homepage: www.elsevier.com/locate/biocon

Population viability and species interactions: Life outside the single-species vacuum

John L. Sabo

School of Life Sciences, Arizona State University, P.O. Box 874501, Tempe AZ 85287-4501, United States

ARTICLE INFO

Article history:

Received 22 November 2006

Received in revised form

19 September 2007

Accepted 8 October 2007

Keywords:

Species interaction

Population viability analysis

Predation

Competition

Disease

Mutualism

Time-series

ABSTRACT

Population viability analysis (PVA) has become a widely used set of tools for evaluating relative extinction risk and prioritizing management options among imperiled populations. While PVA is a widely sanctioned tool in conservation biology, the field of population viability is in its infancy with respect to species interactions. In this paper, I review available methods for evaluating extinction risk when species interactions contribute significantly to population viability. This review includes an evaluation of six broad categories of species interactions (predation, disease, competition, mutualism, parasitism and host-parasitoid interactions) in population viability analysis, with a particular focus on predation as a case study. I first evaluated how often species interactions are considered when PVA is applied to population data from imperiled species. I identified 378 articles in commonly cited conservation journals, of which 24 attempted a viability analysis for populations threatened by interactions with other species. Most of these PVA's treat a putative species interaction as a constant source of mortality rather than a coupled, dynamic population process. Second, I reviewed the literature to identify the availability of time-series of abundance data for two interacting species in which at least one species was threatened or endangered. Adequate time-series data were available for both species comprising an interacting pair in only 9 out of 407 papers reviewed. Third, I used a stochastic, fully stage-structured predator prey model to create time-series data (vital rates and projection matrices) in order to quantify the efficacy of two matrix-based, single-species PVA approaches. Simple single-species PVAs confound stochastic variation with population cycles induced by species interactions (in this case predation). As a result these models provide conservatively biased forecasts of viability. Unfortunately, the data needed to construct more complex PVA's with feedback and multi-species stochasticity are rarely collected. I close with a discussion of key advances needed to “escape the population vacuum” in a move toward more realistic estimates of extinction risk.

© 2007 Published by Elsevier Ltd.

1. Introduction

In recent years, population viability analysis (PVA), has become a widely applied set of techniques for evaluating relative extinction risk and prioritizing management options among imperiled populations (Doak et al., 1994; Gerber and

VanBlaricom, 2001; Morris and Doak, 2002; Pascual et al., 1997; Soule, 1990). PVAs come in a variety of forms (Morris and Doak, 2002); in this paper I rely on one particular form of PVA, a stage-structured demographic approach applied to data describing the vital rates of a species of concern. The development of population viability analyses (PVA) is required

E-mail address: John.L.Sabo@asu.edu

0006-3207/\$ - see front matter © 2007 Published by Elsevier Ltd.

doi:10.1016/j.biocon.2007.10.002

for IUCN Species Survival Plans developed for threatened and endangered species (IUCN, 1994). In addition, PVA is increasingly being used in the US to fulfill the Endangered Species Act requirement that recovery plans include “objective, measurable criteria which, when met, would result in a determination... that the species be removed from the List” (16 U.S.C. § 1533(f)(1)(B)(ii); Gerber and Hatch, 2002). At the same time, PVA has been criticized for its limited ability to incorporate uncertainty (Fieberg and Ellner, 2000; Ludwig, 1999; Taylor, 1995) and a lack of biological realism (Beissinger, 1995; Dennis, 2002; Ellner et al., 2002; Engen and Saether, 1998; Foley, 1994; Fox and Kendall, 2002; Kendall and Fox, 2002; Lande, 1993; Zeng et al., 1998; Sabo and Gerber, 2007). Here I focus on the latter criticism and discuss the implications of species interactions for forecasting risk of threatened populations using PVA.

A central tenet of the US Endangered Species Act is to protect individual species as a surrogate for the conservation of ecological communities (16 U.S.C. § 1533). Ironically, single-species approaches to conservation have rarely provided umbrella protection for whole communities (Andelman and Fagan, 2000), and these approaches have almost always ignored communities when analyzing the risk faced by the flagship species. While PVA is now widely accepted as a general tool in conservation biology, the field of population viability is faced with the philosophical dilemma of embracing or ignoring the realism and complexity of interactions in ecological communities (Sabo and Gerber, 2007; Holmes et al., 2007). Specifically, most PVA models have borrowed exclusively from single-species fisheries and wildlife models, ignoring the direct and indirect effects of species interactions on the dynamics of the focal population (Caughley, 1996). Recent validation exercises suggest that simple state-space models can capture enough detail from a time-series to predict population fate (e.g., the risk of population declines) without knowing the true population process generating the data (e.g., Holmes et al., 2007). Thus, though rich sets of observed population dynamics may be driven by for example, the delayed effects of predation (Royama, 1981; Hanski et al., 1993; Turchin et al., 1999; Turchin and Hanski, 2001), these causes of dynamics may not be necessary for forecasting the focal population’s risk of decline (i.e., quasi-extinction). The degree to which this conclusion applies to other single-species PVAs is less known. Stage- or age-based matrix models are commonly applied in PVA and form the backbone for many canned PVA packages. These models often include copious detail about the population of interest. For example, in a three-stage model, we must estimate a minimum of six transition probabilities and the six corresponding uncertainties. Very few of these models consider species interactions, for example predation in birth or death functions. More surprising, there have been very few attempts to even quantify the degree to which a species interaction is even included (explicitly or not) in a PVA.

In this paper, I review and synthesize methods for evaluating extinction risk when species interactions contribute significantly to population viability. This review includes an evaluation of six broad categories of species interactions (predation, disease, competition, mutualism, parasitism and host-parasitoid interactions) in population viability analysis, with a particular focus on predation as a case study. Specifi-

cally, I examine three questions: (1) How often are species interactions explicitly incorporated into viability models?, (2) For introduced species as a case study, what types of data are needed to predict population viability in the face of species interactions and how often are these data collected? I focus here on time-series of abundance data and models that characterize viability using this type of data (Dennis et al., 1991; Holmes, 2001). Finally, I use a stochastic, three-stage predator–prey model to simulate population data (vital rates and projection matrices) for prey populations threatened by non-native predators. I then use these data to quantify the efficacy of two very commonly used matrix-based, single-species PVA models at estimating quasi-extinction risk in the face of cycles induced by the predator–prey interaction.

2. Methods

2.1. How often do PVA’s explicitly include species interactions?

I used the Web of Knowledge (Thomson ISI, New York) to search for abstracts containing the search phrases “population viability analysis”, “extinction risk”, “sensitivity analysis” and “elasticity analysis” and one of six common species interactions (predation, competition, disease, mutualism, parasitism and “parasitoid”). This search was carried out in three of the most commonly cited conservation journals (Conservation Biology, Ecological Applications and Biological Conservation) from 1955 to present. This search yielded 378 articles of which 24 attempted a viability analysis. I then classified these 24 studies as *implicit*, *stationary* or *dynamic*, according to the way species interactions were incorporated into the analysis.

Implicit species interactions drew conclusions about species interactions without including the species interaction explicitly in the analysis. This category includes papers that report one of many types of PVA on the target species but only speculated about the putative benefits of reducing the impact of one or more species interactions (i.e., increasing λ). *Stationary* species interactions included perturbations to demographic schedules corresponding to hypothesized impacts of species interactions. These papers directly analyzed the effects of a particular species interaction by conducting simulation experiments in which these effects were altered by changing model parameters. The most basic approach was standard demographic sensitivity analysis in which mortality rates of the native species were reduced to simulate the reduction of effects from heterospecifics. I called this approach a stationary PVA because the effects of the heterospecific are assumed to be the same among years, not varying as a function of the abundance of the population of the other species. Finally, *dynamic* species interactions included varying degrees of dynamic feedback between species. Here, dynamics of heterospecific populations were directly embedded in the PVA model.

2.2. How frequently do empirical studies report abundance for both introduced and native species?

In reviewing papers that conducted PVA on species engaged in a species interaction, it became apparent that many of

these studies lacked careful data describing the ‘non-focal’ species (i.e., the predator of a threatened prey species). Specifically, though datasets abound for threatened and endangered species (Fagan et al., 2001), few studies monitor the abundance of species that may cause declines in abundance as closely. Thus, I conducted a second literature search to identify the availability of time-series of abundance data for two interacting species in which at least one species was threatened or endangered. I focus on introduced species as an important category of species interactions, and used the search terms “non-native”, “introduced”, “exotic”, “invasive”, “threatened” and “endangered” searching the same journals identified as above. This search produced a library of 407 abstracts. I searched all papers in this library for time-series data on introduced and native species. Studies that did not estimate abundance for either species (0 years) and those that compared abundance of a threatened species during one year in habitats with and without a second species (1 year) were pooled into one category. Papers with only 2 years of abundance estimates were typically studies that employed “Before–After” designs in which the second species (usually a predator) was removed and abundance was compared between years. All other studies were classified as having data for one or both species and grouped in 3-year categories (e.g., 3–5, 6–8, etc.).

2.3. How do single-species PVA models perform in the face of predator–prey cycles?

Introduced predators are a globally significant threat to native prey populations (Mack et al., 2000; Myers et al., 2000), especially on island ecosystems (Atkinson, 2001; Towns and Ballantine, 1993; Towns and Broome, 2003). Curiously there are no general techniques available to forecasting extinction risk for prey populations threatened by non-native predators (Table 1). The most commonly used approach in PVA adjusts prey survival rates by some fraction of empirically estimated predation to simulate population growth rates (λ) of the native prey species under predator control. This exercise is done primarily in the context of matrix-based demographic models. With this approach one can evaluate the effect of reducing predation related mortality rates (simulating predator harvest) on the population trend of the native prey population. This “stationary” approach often (but not always) includes stochasticity but assumes that the effects of predation are stationary and included via the survival rate of the prey. In this way, these models ignore important dynamic feedbacks between abundance of predators and prey. A more mechanistic “dynamic” approach (Sinclair et al., 1998) relies on 2-species models that include important feedbacks between predator and prey abundance levels, but does not include environmental stochasticity. Clearly, some combination of these features—feedback between predator and prey abundance and stochasticity—is desirable for effective multi-species PVA’s.

2.3.1. The PVA models tested

I explored the consistency of two simple *single-species* PVA models at forecasting risk for an endangered prey species when the vital rates of this prey species were influenced by

predation. The two PVA models tested here are both stationary projection matrix models as neither includes any feedback between predator abundance and prey vital rates. These PVA models differ in that one ignores stochasticity, while the other includes stochasticity by drawing vital rates randomly from estimated distributions of these parameters. I call these two PVA models the static projection matrix (or ‘StaPM’) and the stochastic vital rate (or ‘StoVR’) models, respectively to differentiate between the way stochastic variation in vital rates is incorporated in each. These models are described in detail elsewhere (Morris and Doak, 2002; Sabo and Gerber, 2007). Briefly, the StaPM approach involves the construction of a single projection matrix-based on point estimates of stage-specific survival and fecundity to estimate a time specific overall growth rate, λ_t . This value of λ_t is then used to project the current population into the future or in a sensitivity or elasticity analysis (Crouse et al., 1987; Wisdom et al., 2000; Morris and Doak, 2002) to quantify the best way to change λ_t via managing a particular vital rate. For example, if adult survival has the highest elasticity, then protecting adults from predation by non-native species may be the best recourse for recovering the population (i.e., achieving and maintaining $\lambda_t > 1$, where growing populations are characterized by $\lambda_t > 1$ and declining population are characterized by $\lambda_t < 1$).

In contrast to the StaPM, the StoVR uses empirically measured statistical distributions of each vital rate to generate random projection matrices when forecasting future population dynamics. Statistical distributions of vital rates are based on a minimum of five (and often more) point estimates of each rate (Morris and Doak, 2002). One then draws random survival rates from a beta distribution (based on transformations of the mean and variance of this vital rate) and fecundities from a log-normal distribution, calculates λ_t , and then uses this value of λ_t to project the population (to $t + 1$). With adequate replication (i.e., 1000 Monte Carlo runs) one can then generate a distribution of relevant extinction metrics including the probability of reaching a threshold abundance level (extinction or quasi-extinction).

2.3.2. Generating the data via a predator–prey model

I generated time-series of vital rates and abundances for a prey species interacting with a predator via a stochastic, fully stage-structured and fully dynamic matrix model. Though simpler models (e.g., Ives, 1995; Abrams, 2002; Sabo, 2005) would suffice for generating time-series of abundance data, only a fully stage-structured, two species model is capable of generating both abundance and vital rate data at each time step and vital rates are the data required by the StaPM and StoVR PVA approaches. The predator prey model I used is described in detail elsewhere (Barbeau and Caswell, 1999; Sabo and Gerber, 2007). Briefly, the model followed the general form,

$$\mathbf{N}(t + 1) = \mathbf{A}_N^{(t)} * \mathbf{N}(t) \quad (1a)$$

$$\mathbf{C}(t + 1) = \mathbf{A}_C^{(t)} * \mathbf{C}(t) \quad (1b)$$

where $\mathbf{N}(t)$ and $\mathbf{C}(t)$ are vectors of abundances of prey (N) and predators (C) at time t , in each of three stages and $\mathbf{A}_N^{(t)}$ and $\mathbf{A}_C^{(t)}$ are population projection matrices for prey and predators, respectively in year t . In these matrices, I incorporated density

Table 1 – Examples of metrics for risk assessment methods that include species interactions, found during literature search for articles assessing effects of non-native predators on the viability of native prey species as a general category of multi-species viability studies

Approach	# Species directly observed	Type of inference	Type of response measured	Data quantity (yrs)	Considers stochasticity	Retrospective vs. predictive	Examples from the literature
<i>Empirical and experimental studies</i>							
Presence/absence	1	Circumstantial short term	Change in abundance	1	No	Retrospective	1
Diet analysis	2	Circumstantial short term	Change in mortality	1–2	No	Retrospective	2
Experimental removal (with control)	2	Strong short term	Change in mortality & abundance	1–8	No	Retrospective	3
Range expansion	2	Circumstantial long term	Change in distribution	Decades	No	Retrospective	4
Approach	# Species directly modelled	Type of prediction	Type of data required	Data required (yrs)	Include stochasticity	Retrospective vs. predictive	Examples
<i>Analytical forecast methods</i>							
Bioenergetics	1	Mortality	Diet analysis, temperature	1	Yes ^a	Predictive	5
Stability analysis of Lotka-Volterra	1	Deterministic growth rate	Mortality to predation, prey population abundance	5+	No	Predictive	6
Stationary-elasticity	1	Deterministic growth rate	Prey vital rates, Mortality to predation	1	No	Predictive	7
Stationary-projection	1	Probability of persistence	Prey vital rates (mean and variance), mortality to predation	3 ^b	Yes	Predictive	8
Dynamic uncoupled	1	Probability of persistence	Prey: growth rate (mean and variance), mortality rate, carrying capacity; Predator: index of abundance ^{d,e}	3 ^b	Yes for 1 species	Predictive	9 ^c
Dynamic coupled	2	Probability of persistence	Prey: growth rate (mean and variance), mortality rate, carrying capacity; Predator: conversion and metabolic efficiencies (mean and variance) ^e	Unknown but $\gg 8^{b,e}$	Yes for both species	Predictive	10
References are as follows: (1) Alvarez-Castaneda and Ortega-Rubio (2003), Burbidge and Manly (2002), Massaro and Blair (2003), Wilson et al. (1998); (2) Risbey et al. (1999); (3) Banks et al. (2004), Kinnear et al. (1998), Nordstrom et al. (2003); (4) Phillips et al. (2003), Wootton (1987); (5) Kitchell et al. (1997), Ruzycski et al. (2003); (6) Courchamp and Sugihara (1999), Sinclair et al. (1998); (7) Basse et al. (1999), Doak et al. (1994), Elliott (1996), Harding et al. (2001); (8) Forsys and Humphrey (1999), Kelly and Durant (2000), Li and Li (1998); (9) Vucetich et al. (1997); (10) Ives et al. (2003).							
a Approximated by seasonal periodicity in temperature.							
b Morris and Doak (2002).							
c Vucetich et al. modelled predator–prey dynamics of wild dogs on the Serengeti plains with explicit predator (dog) dynamics but prey dynamics represented by an uncoupled forcing function approximating prey fluctuations driven by periodicity in rainfall.							
d Environmental periodicity scaled to the abundance of a predator could be accomplished for example for introduced fox populations dependent on secondary introduced prey populations such as <i>Peromyscus</i> which are well known to cycle periodically with environmental fluctuations in temperature or rainfall.							
e Alternatively, these parameters could be estimated with extensive time-series of abundance for both predator and prey species. These models are only beginning to be developed Ives et al. (2003).							

dependence in prey fecundity (as $u[\mathbf{N}(t)]$), environmental stochasticity in mortality for both species (as $\varepsilon_N^{(t)}$ or $\varepsilon_C^{(t)}$), and a prey-dependent Type II functional response (as $v_i[\mathbf{N}(t), \mathbf{C}(t)]$ or $w_i[\mathbf{N}(t), \mathbf{C}(t)]$, for prey and predators, respectively) viz:

$$\mathbf{A}_N = \begin{bmatrix} f_1 * u[\mathbf{N}(t)] & f_2 * u[\mathbf{N}(t)] & f_3 * u[\mathbf{N}(t)] \\ \min\{1, (1 - v_1[\mathbf{N}(t), \mathbf{C}(t)] + \varepsilon_N^{(t)})\} & 0 & 0 \\ 0 & \min\{1, (1 - v_2[\mathbf{N}(t), \mathbf{C}(t)] + \varepsilon_N^{(t)})\} & \min\{1, (1 - v_3[\mathbf{N}(t), \mathbf{C}(t)] + \varepsilon_N^{(t)})\} \end{bmatrix} \quad (2a)$$

$$\mathbf{A}_C = \begin{bmatrix} F_1 * w_1[\mathbf{N}(t), \mathbf{C}(t)] & F_2 * w_2[\mathbf{N}(t), \mathbf{C}(t)] & F_3 * w_3[\mathbf{N}(t), \mathbf{C}(t)] \\ \min\{1, (1 - (m_1 * w_1[\mathbf{N}(t), \mathbf{C}(t)] + \varepsilon_C^{(t)}))\} & 0 & 0 \\ 0 & \min\{1, (1 - (m_2 * w_2[\mathbf{N}(t), \mathbf{C}(t)] + \varepsilon_C^{(t)}))\} & S_{C3} \end{bmatrix} \quad (2b)$$

where f_i and F_j are the maximum fertilities of the prey of stage i and the predator of stage j , respectively, m_j is the stage-specific density-independent mortality rate of the predator and S_{C3} is the fixed survivorship of the third stage-class of the predator. Details about the implementation of the functional response, prey density dependence, prey dependence of the predator and stochasticity can be found in Sabo and Gerber (2007).

2.3.3. Overview of model behavior

The predator–prey model described above (Eqs. (1) & (2)) exhibits a wide variety of behavior, ranging from stationary (but stochastic) fluctuations about a deterministic equilibrium to limit cycles (amplified by stochasticity) to chaos (Sabo and Gerber, 2007). Transitions between these behaviors are achieved simply by changing the encounter rate of predators in the third stage-class with prey of all stage-classes (in $v_i[\mathbf{N}(t), \mathbf{C}(t)]$ and $w_i[\mathbf{N}(t), \mathbf{C}(t)]$). This encounter rate increases with the predator’s body radius (following Barbeau and Caswell, 1999). Larger predators cover more area searching for prey, have higher encounter rates and thus higher kill rates of prey. Higher kill rates translate into instability of the deterministic prey dynamics (see Sabo and Gerber, 2007). This instability (recorded as cycles or chaos) could possibly be confounded with additional variation brought on by environmental stochasticity in simple single-species PVA models because these PVA models do not anticipate any oscillations in prey dynamics driven by predators. Here I evaluate this claim for 2 commonly used PVAs in the context of introduced predators. Specifically, I evaluate how well the StaPM and StoVR PVA models estimate risk when confronted with increasing amounts of instability driven solely by the predator–prey interaction (e.g., not by stochasticity). I do this by testing the efficacy of each PVA model across a range of encounter rates, and thus deterministic variability in prey abundance using the same parameters for the simulation model as in a similar analysis of count-based PVA techniques (see parameter set with low stochastic variation in Sabo and Gerber, 2007). This deterministic variability is measured from simulated time-series with no stochastic variation in either prey or predator survival as the coefficient of variation (CV) of prey abundance (hereafter, the ‘coefficient of intrinsically derived variance’, as in Sabo and Gerber, 2007).

2.3.4. Cross-validation routine

Cross-validation approaches have been used to evaluate PVA efficacy in a variety of other contexts (Meir and Fagan, 2000; Holmes and Fagan, 2002; Sabo et al., 2004) Here I outline the

basic steps to cross validating a PVA with simulated data. First, I create the data necessary for PVA with a simulation model (Eqs. (1) & (2), above). In this paper I simulate 30 years of projection matrices (following Sabo and Gerber, 2007). I use the first 15 years of data to parameterize the 2 PVA models analyzed here—StaPM and StoVR. For the StaPM model—which requires only a single projection matrix-based on a minimum of 2 years of observations—I use one of the first 15 projection matrices to estimate parameters for the PVA. In this case, estimation is simply extracting the projection matrix from the simulated time-series of vital rates. Estimated parameters are then used to forecast the population fifteen years into the future. Because a single projection matrix may not be representative of the longer (15-year) trend, I use averages of all elements over the first 15 years of data to construct the single projection matrix. This approach to implementing the StaPM is actually much more rigorous than the way this PVA is implemented in many of the studies reviewed in the literature surveys presented above.

To estimate the parameters for the StoVR PVA model, I generate means and variances of each element in the projection matrix (3 survivals, 3 fecundities) using the first 15 years of data and then project the population 15 years into the future by drawing random elements from statistical distributions based on these means and variances. I assumed log-normal variability for fecundity values and beta-distributed survivals (Morris and Doak, 2002).

In each case (StaPM and StoVR) the variability in the performance of estimated single-species models was determined by repeating the validation process described above for 1000 randomly generated realizations from the full predator–prey model. This is done for each of 8 values of the body radius of stage-3 predators. Increasing body radius of this stage-class of predators leads to increasing deterministic variation in prey abundance (e.g., cycling, Sabo and Gerber, 2007). These simulated realizations are then used to parameterize PVA models and seed the PVA projections with an initial abundance level. Thus for each simulated realization, I estimate the parameters (as StaPM or StoVR) and then project the population 1000 times (once more) from the abundance level at year 16 (N_{16}) of the original realization to N_{30} . Using these 1000 PVA runs I then quantify ‘predicted’ levels of extinction risk. In addition to these 1000 PVA projections (using estimated parameters), I also project the population 15 years

into the future from N_{16} using the base model (Eqs. (1) & (2)) and parameters (again 1000 times). Using these 1000 control runs I then quantify ‘observed’ levels of extinction risk faced by the same simulated prey populations.

I quantified observed extinction risk as the probability of the population declining below 80% of its initial abundance (i.e., $0.2 * N_{16}$) in either real or PVA projections. P_{80} is one of two quasi-extinction metrics used by the IUCN for classifying species as threatened and endangered on the Red List. Here I quantify both the accuracy and the precision of each PVA at predicting P_{80} as the mean and 97.5 and 2.5 percentile values (e.g., 95% confidence interval) for error in PVA estimates of P_{80} . I estimate error as the deviation between predicted and observed P_{80} such that negative values indicate overly-optimistic error and positive values indicate conservative error. I then plot the mean and 95% interval of error against the coefficient of intrinsically derived variance (following Sabo and Gerber, 2007) in prey abundance to test the efficacy of StaPM and StoVR at estimating P_{80} when confronted with increasing amounts of deterministic variation induced by predators. As a control I measured the accuracy and precision of StaPM and StoVR on a dataset generated by parameter values in which prey species experienced no deterministic variation at all (coefficient of intrinsically derived variance = 0). In this way I test the prediction that error (bias and imprecision) is negligible when prey population trajectories exhibit little deterministic variability but increases with increasing values for the coefficient of intrinsically derived variance (a measure of deterministic oscillations).

3. Results

3.1. How often do PVA models incorporate species interactions?

Only 24 of 378 papers in the first search applied PVA to conservation problems in which a species interaction was implicated in the decline of the target species (Fig. 1). Only 19 of these case studies include species interactions explicitly in the PVA (Fig. 1, Table 1). Many papers in the “implicit” category do not actually include the species interaction in the PVA (i.e., as a source of controllable mortality in a matrix-based PVA), but rather simply mention species interactions as an important variable. The majority (ca. 63%) of case studies were “stationary”, applying matrix-based approaches that do not include important feedbacks between the 2 species. Only 3 papers report dynamic PVA’s where the species interaction is modeled explicitly. These include dynamic models for predation and disease (Vucetich et al., 1997), competition and disease (Vucetich and Creel, 1999), and disease (Haydon et al., 2002).

3.2. How often do conservation efforts quantify abundance levels of both the target prey species and the non-native predator?

I categorized case studies based on modeling approach, type of inference, data requirements and data availability (Table 1). Time-series data were available for both species in only 9 of 407 papers (Fig. 2a). More studies (19) reported time-series data for one of two interacting species, and many of the more

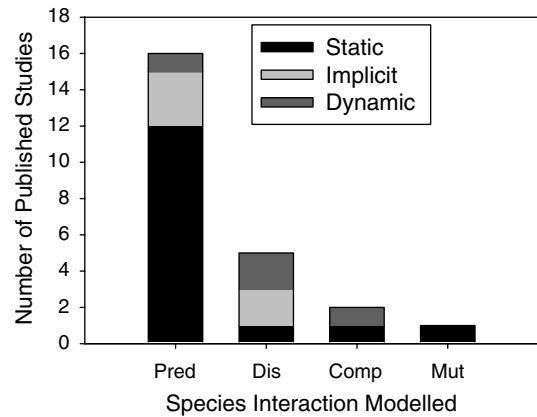


Fig. 1 – Articles retrieved from a broad ISI search from three commonly cited conservation journals (*Biological Conservation*, *Conservation Biology* and *Ecological Applications*) containing the key words “extinction risk”, “Population Viability Analysis”, “Elasticity Analysis” or “sensitivity analysis” and one of six species interactions (Predation, Competition, Disease, Mutualism, Parasitism and Parasitoid). The initial search retrieved 387 articles of which 24 attempted a viability analysis. I found no PVA’s concerning parasites or parasitoids. I then classified these 24 studies according to the way species interactions were incorporated into the analysis. “Implicit” species interactions drew conclusions about species interactions without including the species interaction explicitly in the analysis; “Stationary” species interactions included perturbations to demographic schedules corresponding to hypothesized impacts of species interactions, and “Dynamic” species interactions included varying degrees of dynamic feedback between species.

extensive datasets were for single-species (Fig. 2b). A majority of studies (15 of 19 single-species time-series, Fig. 2b) do not monitor the introduced species, but only monitor the native species. Only 6 studies included time-series for both species spanning more than 8 years.

3.3. How well do matrix-based, single-species PVAs perform when predicting risk for prey interacting with predators?

True risk of an 80% decline in 15 years (P_{80}), ranged from 0–35% and increased with increasing deterministic variation caused by the predator–prey interaction (Fig. 3). Thus the risk levels faced by prey populations in this analysis range from undetectable to moderate. The two matrix-based (single-species) approaches to PVA I analyzed here both provide accurate (zero bias) and precise (narrow 95% CI) estimates of true risk when deterministic variation is not present in prey time-series (Fig. 4, abscissa). This provides a convenient control demonstrating that these two models are capable of predicting low risk when deterministic variation is low.

In contrast to the robust performance of these two single-species PVA approaches when deterministic variation is low, both over-estimate quasi-extinction risk (i.e., $\hat{P}_{80} - P_{80} > 0$)

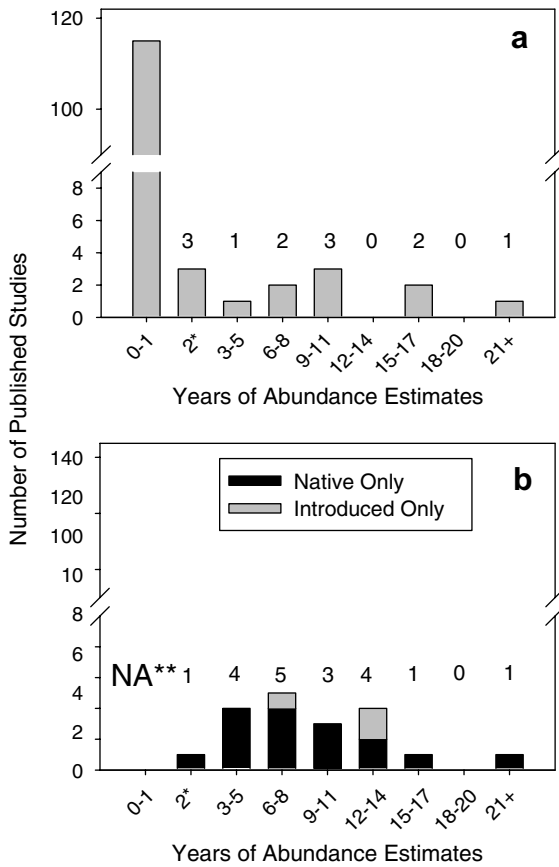


Fig. 2 – Articles retrieved from an ISI search for abstracts from 3 conservation journals (as in Fig. 1) with the key words “endangered”, “threatened” and “non-native”, “introduced”, “exotic” or “invasive”. These search terms yielded 407 articles. Time-series data (here >2 yr) were available for both species in 9 papers (a) and for only one of two interacting species in 18 papers (b). Papers with only 2 years of abundance estimates were typically studies that employed “Before–After” designs (*). All papers with less than 2 year of data (for one or both species) are plotted in (a) and indicated as “NA” in (b).

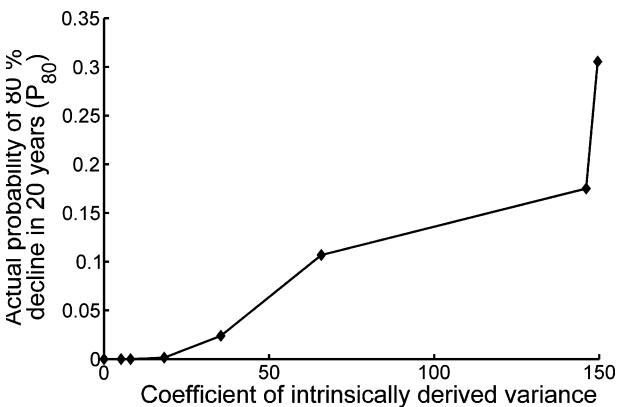


Fig. 3 – Observed levels of quasi-extinction risk for prey populations threatened by a predator. Figure shows the true probability of an 80% decline in abundance (P_{80}) observed over 15 years of prey population data as a function of the coefficient of intrinsically derived variance in prey abundance.

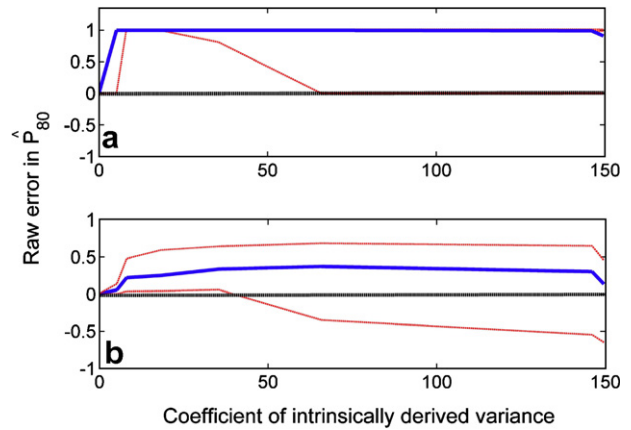


Fig. 4 – Raw error, or bias, in estimated probabilities of an 80% decline (estimated–observed P_{80}) for two matrix-based, single-species PVA models, a static projection model (a) and a stochastic vital rate model (b). Median (solid, black line) and 95% confidence interval (dotted, thin gray lines) values of error are plotted for 1000 replicate population realizations. Perfect predictions would have median and 95% CI values of zero (dotted, thick horizontal line). Positive error indicates over-estimation of risk, or conservative forecasts. Negative error indicates under-estimation of risk, or overly-optimistic forecasts.

when the coefficient of intrinsically derived variance is greater than zero. Bias increases and precision decreases with increasing magnitude of deterministic variation (as indexed by the coefficient of intrinsically derived variance, Fig. 4) for both PVA models. The static projection matrix PVA (StaPM) forecasts certain quasi-extinction ($\hat{P}_{80} = 1$) across a broad range of values for true risk. By contrast, the stochastic vital rate approach (StoVR) yielded less biased, but still conservative estimates of P_{80} (Fig. 4). This PVA model consistently over-estimated P_{80} by 10% or more (95% CI spanning 50% under- and over-estimates of true risk).

4. Discussion

Threatened and endangered species do not exist in a vacuum, isolated from interactions with predators, competitors and diseases. Introduced predators provide a salient example of the importance of species interactions in managing declining populations. Here I quantify how rarely PVA models include species interactions. Less than 7% (24 of 378) of all records examined here incorporated species interactions into a PVA framework (Fig. 1). When species interactions are included in a PVA, they are usually treated as a stationary source of mortality within the context of a stationary projection matrix (Fig. 1). Moreover, one of the most commonly applied PVA approaches, a single-species matrix model, grossly over-estimates quasi-extinction risk as measured by a probability of an 80% decline in abundance, or P_{80} (Fig. 3). Finally, and most unfortunately, many published studies of endangered species threatened by a species interaction likely have inadequate data to parameterize even the most simple single-species PVA models, much less approaches capable of analyzing the

persistence of populations within a community framework (e.g., multivariate autoregressive models, Table 1).

4.1. Cycles, noise and the efficacy of single-species PVA in multi-species settings

In this paper I find that species interactions are typically portrayed as a non-dynamic source of mortality in the context of matrix-based PVA models like the StoVR (stationary mortality) and StaPM (static mortality). The results from the subsequent cross-validation of these PVA models illustrate just how wrong this practice can be when the dynamics of the species interaction cause variation in vital rates of the target species as in predator–prey cycles. Both the static and stochastic matrix-based PVAs overestimate quasi-extinction probabilities (positive bias on average in Fig. 4). Moreover, precision (inversely proportional to span of 95% CI) is quite low for both models even with only slight deterministic variation brought on by the predator–prey interaction.

The cause of bias in these two models as a result of predator–prey oscillations is different for each PVA model. In the case of the static projection matrix model (StaPM), the forecast is binary ($\hat{P} = 0, 1$). Thus, when the average vital rates across the 16 year fitting interval produce an annualized growth rate of $\lambda \leq 0.904$ (i.e., $\lambda \sim e^{(\ln(n)/w)}$, where n is the proportion of initial abundance, here 0.2 for an 80% decline, and w is the forecasting interval, here 16 years) the forecast is for quasi-extinction, and where $\lambda > 0.904$ the forecast is for quasi-persistence. In practice, the StaPM model is applied to a single set of vital rates, not an average of 16 estimates of each rate as in this paper. Thus, overestimation of risk by StaPM in my analysis may result from under-estimation of λ when using vital rates averaged across a long time period. However, when parameterized with a single set of vital rates, performance of the StaPM model is likely more variable. For example, forecasts would be gloomy with the descending limb of a predator–prey oscillation and overly-optimistic during the rising limb of the predator–prey oscillation. In summary, StaPM models overestimate risk because both stochastic and deterministic (predator–prey driven) fluctuations are interpreted as true trend (population increase or decline) producing the observed binary forecast distribution (Fig. 4).

In contrast to the StaPM model, over-estimation of risk by the StoVR model owes more to its inability to differentiate between predator–prey oscillations and noise driven by variation in the environment. Incorporation of stochasticity in this PVA model reduces bias and increases precision of estimates of P_{80} relative to the StaPM as expected (Fig. 4). However, deterministic variation still leads to considerable bias and much lower precision of StoVR estimates of P_{80} when compared to a control (no deterministic variation). This bias and imprecision owes most likely to misattribution of predator–prey oscillations to stochastic environmental variation (e.g., as in Holmes et al., 2007). When predator–prey oscillations are treated as environmental stochasticity, risk estimates are inflated over the true values.

These results—that single-species models, and the parameters estimated by these single-species models fail to tell the future accurately enough to predict extinction—highlight a need to clarify which single-species measurements provide

good indicators of viability given the reality of multi-species communities. Several recent studies provide insights along these lines.

First, the common state variables and parameters employed by PVA—initial population size & environmental stochasticity—may not always provide relevant guidance to predicting extinction risk when intrinsic (deterministic) variability is stronger than noise. For example, Belovsky et al. (1999) found that initial population size of laboratory reared populations of brine shrimp (*Artemia franciscana*) provided very little explanatory power for predicting ultimate extinctions of these populations. These authors also found that environmental stochasticity gave less insight into extinction than did the proximity of the population to carrying capacity and thus, the propensity to exhibit deterministic cycles via strong density dependent feedbacks. Cycles were more strongly associated with extinction than noise. This problem would be less of a concern if PVA models were able to differentiate between cycles and noise, and thus use the appropriate measure of stochastic variation when projecting future populations (see Section 4.4).

Finally, noise and cycles are not necessarily independent (Turchin et al., 1999). Stochastic variation can either dampen or exacerbate deterministic oscillations (Ives, 1995; Sabo, 2005). More importantly, the interaction between noise and non-linearities (as in a predator prey interaction) can have counterintuitive effects on the average population size. For example, long term environmental change may have less noticeable effects on average population size of populations that cycle, versus those that are more stable (Ives, 1995). Similarly, the effects of deteriorating environmental conditions (e.g., habitat loss) on the abundance of predators may lag behind the onset of this deterioration due to compensatory responses of resource populations and non-linear responses of consumers to these resources (Abrams, 2002). Thus, the impacts of environmental change should be harder to predict for populations that either interact non-linearly with other species and/or exhibit oscillations as a result of these non-linearities.

4.2. Measuring efficacy: real vs. simulated data

The accuracy of PVA has received a good deal of attention, and been quantified under a variety of relevant conservation scenarios over the last decade. For example, Brook et al. (2000) used datasets from real populations of imperiled species to quantify bias in PVA predictions made by five commonly used PVA packages, many of which employ models like the StaPM and StoVR used in this manuscript. To do this, Brook et al. analyzed 21 real datasets (dividing them in half for parameterization and validation as in this paper), and then compared PVA model estimates of probabilities of decline (0–100%) to the fraction of the 21 real populations that actually declined to that abundance level. The authors observed that predicted probabilities were very similar to the observed fraction of declines, leading to the conclusion that all five PVA packages provide unbiased risk assessments. Interestingly, 4 out the 5 PVA packages tested by Brook et al. yield overestimates of risk (i.e., predict higher probabilities of decline than observed in the real data) with bias on the order of 10–15%, and bias (positive and negative) increases with

increasing levels of true risk (e.g., Fig. 1 in Brook et al. (2000)). Both of these observations are consistent with the results of the current study. Specifically, I observed over-estimation of risk (or positive bias) though bias was slightly higher on average (~15–30% for the StoVR model), and an increase in bias with an increase in true risk.

The similarities between the (Brook et al., 2000) results and the current study may be mere coincidence, and thus point to a need for understanding the complementary of validation exercises on real and simulated population data. Simulation analyses offer some advantages over validation exercises based on real data. First, power is much higher—here I simulate 1000's of populations under a wide range of representative population dynamics and validate PVA predictions using a second set of 1000's of projected populations based on estimated parameters. Second, simulated data offer the advantage of measuring precision which cannot be measured when validating PVA with a single real population realization. By contrast, the disadvantage of simulated datasets is that the data are not real, but derived from a drastically over-simplified model of population dynamics. Future work should attempt to identify how these two approaches might be used together to more adequately understand the efficacy of viability models.

4.3. Bridging the data gap between community-level data and conservation

Data for a single threatened population are typically sparse without additional data demands at the community level. My results suggest that most studies of endangered populations threatened by a non-native species rely on less than 8 years of data to draw conclusions about how to best recover the focal species. Data for the pest species are rare and commonly even less copious than those for the target species. The lack of data describing pest species population parameters is problematic for at least 3 reasons: (1) as more sophisticated time-series methods evolve (MAR, and other approaches), there will not be data available to make them useful, (2) inference would be strengthened by more long term patterns to corroborate short term results from experiments, and (3) in real world conservation settings abundance data for non-native species can inform adaptive management programs for threatened native populations in cases where eradication of non-natives is implausible (Sabo, 2005). Thus, initiating long-term monitoring programs for both introduced predators and native prey is not only important for future modeling work, but also for making informed conservation decisions regarding the conservation of imperiled populations.

4.4. Escaping the single-species vacuum—will it be necessary?

In this paper I demonstrate that two very mechanistic single-species PVA models perform poorly at predicting extinction risk for a population interacting with predators. These models are mechanistic in that they accurately portray the stage structure of the prey population; however both models ignore mechanism at the community level—a strong predator–prey interaction. There are two potential solutions the lack of bio-

logical realism at the community level—embracing species interactions through a more detailed and biologically realistic model, or seeking less mechanistic yet adequately predictive descriptions of single-species population data.

There are a variety of statistical tools that population biologists currently use to reveal the cause of complex behavior in single-species time-series (e.g., Royama, 1981). Many of these tools fully embrace the notion that species interactions—usually 'predation' interpreted broadly to include host-parasitoid interactions—can contribute significantly to prey population cycles. For example, Kendall et al. (1999) identify a variety of time-series 'probes' that one can use to characterize the nature of variability in time-series of abundance data. These probes include, the period, amplitude and order of population oscillations and the chaotic nature of these oscillations as indexed by the Lyapunov exponent. The order of the series tells us if the dynamics are related directly to density (e.g., self regulation at lag 0, or direct density dependence) or to density at various lags in time, or delayed-density dependence. Many of the best examples of predator induced cycles in prey dynamics involve delayed density dependence (Hanski et al., 1993; Turchin et al., 1999; Turchin and Hanski, 2001). In contrast to most PVAs, these tools are typically used to understand the mechanisms responsible for observed dynamics, not to forecast future dynamics.

Despite focus of time-series methods on identifying mechanisms underlying population dynamics, there is a rich set of time-series tools waiting to be applied to forecasting population abundance, even in complex communities. For example, multivariate autoregressive (MAR) models constitute one promising avenue for estimating risk for single-species using multi-species community time-series data. Here one analyzes time-series of abundance for a suite of sympatric populations of interacting species to estimate the community matrix (i.e., coefficients describing interaction strength) and environmental stochasticity (Ives et al., 2003). This approach has the strength of providing an estimate of community-wide stability. This approach could also be used to simulate future time-series for the entire community and quantify quasi-extinction probabilities for a target species embedded within the community.

Alternatively, a simpler approach may be to side-step community dynamics altogether—especially since long time-series for whole communities are much less common than those for single-species. For example, linear Gaussian state-space approaches to time-series analysis allow now for flexible handling of time-series plagued by observation error (Holmes, 2004; Holmes et al., 2007) and density dependence (Dennis et al., 2006). These state-space models offer a big improvement over previous single-species PVA models, providing low bias/high precision alternatives to specifying multi-species models. The simplest versions of these models (CSEG, sensu Holmes et al., 2007) estimate three parameters that describe patterns in the observed data—the trend or 'process', noise in this process and non-process noise. In the context of species interactions that cause cycles in the dynamics of the target species, CSEG models attribute these cycles to non-process noise, and thus, use a less biased estimate of process noise (environmental stochasticity) to generate predictions of quasi-extinction probabilities. The advantage of

the state-space approach is that only a single-species' time-series is required. Thus given the findings that community time-series are rare in conservation settings (especially invasions), CSEG's and their allies (e.g., Gompertz model in Dennis et al., 2006) may be the only approach warranted until more time-series data are available for entire communities (Holmes et al., 2007).

Acknowledgements

I thank P. Abrams, L. Gerber, P. Kareiva, K. With and four anonymous reviewers for comments, ideas and comments on previous versions of this paper.

REFERENCES

- Abrams, P.A., 2002. Will small population sizes warn us of impending extinctions? *American Naturalist* 160, 293–305.
- Alvarez-Castaneda, S.T., Ortega-Rubio, A., 2003. Current status of rodents on islands in the Gulf of California. *Biological Conservation* 109, 157–163.
- Andelman, S.J., Fagan, W.F., 2000. Umbrellas and flagships: efficient conservation surrogates or expensive mistakes? *Proceedings of the National Academy of Sciences of the United States of America* 97, 5954–5959.
- Atkinson, I.A.E., 2001. Introduced mammals and models for restoration. *Biological Conservation* 99, 81–96.
- Banks, P.B., Norrdahl, K., Nordstrom, M., Korpimaki, E., 2004. Dynamic impacts of feral mink predation on vole metapopulations in the outer archipelago of the Baltic Sea. *Oikos* 105, 79–88.
- Barbeau, M.A., Caswell, H., 1999. A matrix model for short-term dynamics of seeded populations of sea scallops. *Ecological Applications* 9, 266–287.
- Basse, B., McLennan, J.A., Wake, G.C., 1999. Analysis of the impact of stoats, *Mustela erminea*, on northern brown kiwi, *Apteryx mantelli*, in New Zealand. *Wildlife Research* 26, 227–237.
- Beissinger, S.R., 1995. Modeling extinction in periodic environments – everglades water levels and snail kite population viability. *Ecological Applications* 5, 618–631.
- Belovsky, G.E., Mellison, C., Larson, C., Van Zandt, P.A., 1999. Experimental studies of extinction dynamics. *Science* 286, 1175–1177.
- Brook, B.W., O'Grady, J.J., Chapman, A.P., Burgman, M.A., Akçakaya, H.R., Frankham, R., 2000. Predictive accuracy of population viability analysis in conservation biology. *Nature* 404, 385–387.
- Burbidge, A.A., Manly, B.F.J., 2002. Mammal extinctions on Australian islands: causes and conservation implications. *Journal of Biogeography* 29, 465–473.
- Caughley, G.A.G., 1996. *Conservation Biology in Theory and Practice*. Blackwell Science, Cambridge.
- Courchamp, F., Sugihara, G., 1999. Modeling the biological control of an alien predator to protect island species from extinction. *Ecological Applications* 9, 112–123.
- Crouse, D.T., Crowder, L.B., Caswell, H., 1987. A stage-based population-model for loggerhead sea-turtles and implications for conservation. *Ecology* 68, 1412–1423.
- Dennis, B., 2002. Allee effects in stochastic populations. *Oikos* 96, 389–401.
- Dennis, B., Munholland, P.L., Scott, J.M., 1991. Estimation of growth and extinction parameters for endangered species. *Ecological Monographs* 61, 115–143.
- Dennis, B., Ponciano, J.M., Lele, S.R., Taper, M.L., Staples, D.F., 2006. Estimating density dependence, process noise, and observation error. *Ecological Monographs* 76, 323–341.
- Doak, D., Kareiva, P., Klepetka, B., 1994. Modeling population viability for the desert tortoise in the Western Mojave Desert. *Ecological Applications* 4, 446–460.
- Elliott, G.P., 1996. Mohua and stoats: a population viability analysis. *New Zealand Journal of Zoology* 23, 239–247.
- Ellner, S.P., Fieberg, J., Ludwig, D., Wilcox, C., 2002. Precision of population viability analysis. *Conservation Biology* 16, 258–261.
- Engen, S., Saether, B.E., 1998. Stochastic population models: some concepts, definitions and results. *Oikos* 83, 345–352.
- Fagan, W.F., Meir, E., Prendergast, J., Folarin, A., Kareiva, P., 2001. Characterizing population vulnerability for 758 species. *Ecology Letters* 4, 132–138.
- Fieberg, J., Ellner, S.P., 2000. When is it meaningful to estimate an extinction probability? *Ecology* 81, 2040–2047.
- Foley, P., 1994. Predicting extinction times from environmental stochasticity and carrying-capacity. *Conservation Biology* 8, 124–137.
- Forys, E.A., Humphrey, S.R., 1999. Use of population viability analysis to evaluate management options for the endangered Lower Keys marsh rabbit. *Journal of Wildlife Management* 63, 251–260.
- Fox, G.A., Kendall, B.E., 2002. Demographic stochasticity and the variance reduction effect. *Ecology* 83, 1928–1934.
- Gerber, L.R., Hatch, L.T., 2002. Are I recovering? An evaluation of recovery criteria under the US Endangered Species Act. *Ecological Applications* 12, 668–673.
- Gerber, L.R., VanBlaricom, G.R., 2001. Implications of three viability models for the conservation status of the western population of Steller sea lions (*Eumetopias jubatus*). *Biological Conservation* 102, 261–269.
- Hanski, I., Turchin, P., Korpimaki, E., Henttonen, H., 1993. Population oscillations of boreal rodents: regulation by mustelid predators leads to chaos. *Nature* 364, 232–235.
- Harding, E.K., Doak, D.F., Albertson, J.D., 2001. Evaluating the effectiveness of predator control: the non-native red fox as a case study. *Conservation Biology* 15, 1114–1122.
- Haydon, D.T., Laurenson, M.K., Sillero-Zubiri, C., 2002. Integrating epidemiology into population viability analysis: Managing the risk posed by rabies and canine distemper to the Ethiopian wolf. *Conservation Biology* 16, 1372–1385.
- Holmes, E.E., 2001. Estimating risks in declining populations with poor data. *Proceedings of the National Academy of Sciences of the United States of America* 98, 5072–5077.
- Holmes, E.E., 2004. Beyond theory to application and evaluation: diffusion approximations for population viability analysis. *Ecological Applications* 14, 1272–1293.
- Holmes, E.E., Fagan, W.E., 2002. Validating population viability analysis for corrupted data sets. *Ecology* 83, 2379–2386.
- Holmes, E.E., Sabo, J.L., Viscido, S., Fagan, W.M., 2007. A statistical approach to quasi-extinction forecasting. *Ecology Letters* 10, 1182–1198.
- IUCN, 1994. *IUCN red list categories*. International Union for Conservation of Nature and Natural Resources. IUCN, Gland, Switzerland, pp. 21.
- Ives, A.R., 1995. Predicting the response of populations to environmental change. *Ecology* 76, 926–941.
- Ives, A.R., Dennis, B., Cottingham, K.L., Carpenter, S.R., 2003. Estimating community stability and ecological interactions from time-series data. *Ecological Monographs* 73, 301–330.
- Kelly, M.J., Durant, S.M., 2000. Viability of the Serengeti cheetah population. *Conservation Biology* 14, 786–797.
- Kendall, B.E., Fox, G.A., 2002. Variation among individuals and reduced demographic stochasticity. *Conservation Biology* 16, 109–116.

- Kendall, B.E., Briggs, C.J., Murdoch, W.W., Turchin, P., Ellner, S.P., McCauley, E., Nisbet, R.M., Wood, S.M., 1999. Why do populations cycle? A synthesis of statistical and mechanistic modeling approaches. *Ecology* 80, 1789–1805.
- Kinnear, J.E., Onus, M.L., Sumner, N.R., 1998. Fox control and rock-wallaby population dynamics – II. An update. *Wildlife Research* 25, 81–88.
- Kitchell, J.F., Schindler, D.E., Ogutu-Ohwayo, R., Reinhall, P.N., 1997. The Nile perch in Lake Victoria: interactions between predation and fisheries. *Ecological Applications* 7, 653–664.
- Lande, R., 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* 142, 911–927.
- Li, X.H., Li, D.M., 1998. Current state and the future of the crested ibis (*Nipponia nippon*): a case study by population viability analysis. *Ecological Research* 13, 323–333.
- Ludwig, D., 1999. Is it meaningful to estimate a probability of extinction? *Ecology* 80, 298–310.
- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M., Bazzaz, F.A., 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10, 689–710.
- Massaro, M., Blair, D., 2003. Comparison of population numbers of yellow-eyed penguins, *Megadyptes antipodes*, on Stewart Island and on adjacent cat-free islands. *New Zealand Journal of Ecology* 27, 107–113.
- Meir, E., Fagan, W.F., 2000. Will observation error and biases ruin the use of simple extinction models? *Conservation Biology* 14, 148–154.
- Morris, W.F., Doak, D.F., 2002. *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis*. Sinauer Associates Inc., Sunderland, MA, USA.
- Myers, J.H., Simberloff, D., Kuris, A.M., Carey, J.R., 2000. Eradication revisited: dealing with exotic species. *Trends in Ecology & Evolution* 15, 316–320.
- Nordstrom, M., Hogmander, J., Laine, J., Nummelin, J., Laanetu, N., Korpimäki, E., 2003. Effects of feral mink removal on seabirds, waders and passerines on small islands in the Baltic Sea. *Biological Conservation* 109, 359–368.
- Pascual, M.A., Kareiva, P., Hilborn, R., 1997. The influence of model structure on conclusions about the viability and harvesting of Serengeti wildebeest. *Conservation Biology* 11, 966–976.
- Phillips, B.L., Brown, G.P., Shine, R., 2003. Assessing the potential impact of cane toads on Australian snakes. *Conservation Biology* 17, 1738–1747.
- Risbey, D., Calver, M., Short, J., 1999. The impact of cats and foxes on the small vertebrate fauna of Heirisson Prong, Western Australia. I. Exploring potential impact using diet analysis. *Wildlife Research* 26, 621–630.
- Royama, T., 1981. Fundamental concepts and methodology for the analysis of animal population dynamics, with particular reference to univoltine species. *Ecological Monographs* 51, 473–493.
- Ruzycki, J.R., Beauchamp, D.A., Yule, D.L., 2003. Effects of introduced lake trout on native cutthroat trout in Yellowstone Lake. *Ecological Applications* 13, 23–37.
- Sabo, J.L., 2005. Stochasticity, predator–prey dynamics, and trigger harvest of nonnative predators. *Ecology* 86, 2329–2343.
- Sabo, J., Gerber, L., 2007. Predicting extinction risk in spite of predator–prey oscillations. *Ecological Applications* 17, 1543–1554.
- Sabo, J.L., Holmes, E.E., Kareiva, P., 2004. Efficacy of simple viability models in ecological risk assessment: does density dependence matter? *Ecology* 85, 328–341.
- Sinclair, A.R.E., Pech, R.P., Dickman, C.R., Hik, D., Mahon, P., Newsome, A.E., 1998. Predicting effects of predation on conservation of endangered prey. *Conservation Biology* 12, 564–575.
- Soule, M.E., 1990. *Viable Populations for Conservation*. Cambridge University Press, Cambridge, UK.
- Taylor, B.L., 1995. The reliability of using population viability analysis for risk classification of species. *Conservation Biology* 9, 551–558.
- Towns, D., Ballantine, W., 1993. Conservation and restoration of New-Zealand island ecosystems. *Trends in Ecology & Evolution* 8, 452–457.
- Towns, D., Broome, K., 2003. From small Maria to massive Campbell: forty years of rat eradications from New Zealand islands. *New Zealand Journal of Zoology* 30, 377–398.
- Turchin, P., Hanski, I., 2001. Contrasting alternative hypotheses about rodent cycles by translating them into parameterized models. *Ecology Letters* 4, 267–276.
- Turchin, P., Taylor, A.D., Reeve, J.D., 1999. Dynamical role of predators in population cycles of a forest insect: an experimental test. *Science* 285, 1068–1071.
- Vucetich, J.A., Creel, S., 1999. Ecological interactions, social organization, and extinction risk in African wild dogs. *Conservation Biology* 13, 1172–1182.
- Vucetich, J.A., Peterson, R.O., Waite, T.A., 1997. Effects of social structure and prey dynamics on extinction risk in gray wolves. *Conservation Biology* 11, 957–965.
- Wilson, P.R., Karl, B.J., Toft, R.J., Beggs, J.R., Taylor, R.H., 1998. The role of introduced predators and competitors in the decline of kaka (*Nestor meridionalis*) populations in New Zealand. *Biological Conservation* 83, 175–185.
- Wisdom, M.J., Mills, L.S., Doak, D.F., 2000. Life stage simulation analysis: estimating vital-rate effects on population growth for conservation. *Ecology* 81, 628–641.
- Wootton, J.T., 1987. Interspecific competition between introduced house finch populations and 2 associated passerine species. *Oecologia* 71, 325–331.
- Zeng, Z., Nowierski, R.M., Taper, M.L., Dennis, B., Kemp, W.P., 1998. Complex population dynamics in the real world: modeling the influence of time-varying parameters and time lags. *Ecology* 79, 2193–2209.