STOCHASTICITY, PREDATOR–PREY DYNAMICS, AND TRIGGER HARVEST OF NONNATIVE PREDATORS

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Abstract. Environmental stochasticity is one of the premier features of population models used to forecast population persistence; however, most population viability analyses ignore interactions with other species. By contrast, theory in community ecology draws from a tradition of determinism: focusing on the processes (competition, predation) that promote the coexistence of groups of species (i.e., coexistence), while generally ignoring environmental variation in these processes (process noise or environmental stochasticity). Here I considered the role of deterministic and stochastic sources of variation in a predator–prey interaction on the probability of prey population extinction. Using discrete-time stochastic versions of a classic predator–prey model I show that even low levels of predator process noise increase the probability of prey extinction. Surprisingly, predator process noise has stronger negative effects on prey persistence than stochasticity in the population growth rate of the prey species itself. This conclusion is robust across a wide range of deterministic model behaviors, suggesting that the effects of stochastic variation in predator abundance on prey persistence may be pervasive. I then applied these insights to the management of endangered prey populations threatened by a nonnative predator and examined the relative efficacy of three predator control techniques at reviving declining prey populations. These techniques included immediate eradication and reduction of predator populations through either “proportional” harvest or “trigger” harvest. Under a proportional harvest regime, a constant proportion of predators were removed each year, with little attention paid to the natural variation experienced by predator populations. By contrast, I implemented trigger harvest by reducing predator abundance to a fixed threshold abundance level only in years in which the predator exceeds this harvest threshold. Trigger harvest reduces both the relative abundance and variance of predators, whereas proportional harvest only reduces the abundance of these species. My analysis suggests that the reduction of predator variance through trigger harvest can revive declining prey populations and, in some cases, revive them more effectively than a proportional reduction of predator abundance: the default control strategy when eradication cannot be achieved.

Key words: coexistence theory; environmental stochasticity; extinction risk; introduced species; population viability; predator; prey; process error; process noise; trigger harvest.

INTRODUCTION

A central goal of community ecology is to understand the factors that promote the coexistence of species (Hutchinson 1959, Paine 1966, Tilman 1982, Menge and Sutherland 1987, Ricklefs and Schluter 1993, Rosenzweig 1995). Coexistence theory in community ecology derives in large part from a tradition of determinism. This tradition was shaken, but not abandoned, after the experimental demonstration of the “nonequilibrial” maintenance of diversity by physical disturbance in rainforest and rocky intertidal habitats (Connell 1978, Sousa 1979, 1984, Connell and Sousa 1983) and the development of a “lottery” theory for coexistence among competitors occupying coral reefs (Sale 1977, Chesson and Warner 1981). Despite the ubiquity of disturbance and other, less catastrophic sources of temporal variability in ecology (e.g., environmental stochasticity), most models of simple communities still make the blanket assumption that temporal variation in the environment has sufficiently little influence on coexistence that this source of variation can be ignored when studying
the process of interest (e.g., competition, predation, mutualism). This trend has only recently begun to change (e.g., Ives 1995, Ives and Jansen 1998, Ripa et al. 1998, Anderies and Beisner 2000, Ives et al. 2003, Kilpatrick and Ives 2003), although the approach for incorporating temporal variability into community models has been available for some time (May 1973, Nisbet and Gurney 1982).

In contrast to coexistence theory in community ecology, many theoretical models of single populations embrace the concept of temporal variability in the environment (e.g., environmental stochasticity; Mode and Jacobson 1987, Lande and Orzack 1988, Dennis et al. 1991, Lande 1993). Here, one asks not if a population persists, but with what probability? This approach is the core of modern population viability analysis and provides a rigorous statistical framework for predicting population dynamics in the face of environmental and other sources of variability (e.g., Morris and Doak 2002). The upshot of much of this work is that environmentally driven, temporal variability in the population growth process (environmental stochasticity or “process noise”) can be a much more significant determinant of population persistence than the process of population growth itself (Lande 1993). This is especially true for small populations, even those with positive growth rates (Morris and Doak 2002). Curiously, while viability analyses that incorporate process noise for single populations abound, very few of these studies have incorporated interactions with other species.

The lack of cohesion between coexistence theory in community ecology and extinction risk theory in population biology is unfortunate for three reasons. First, some species interactions are known to cause temporal variation in abundance simply as a result of the deterministic process linking the dynamics of each population (e.g., Murdoch and Oaten 1971, McCann et al. 1998, Kendall et al. 1999, Turchin et al. 2000, Krebs et al. 2001). Second, strong stochastic variation in the abundance of one species may determine variation in the abundance of other species linked by species interactions within a community. Third, interactions between stochastic and deterministic sources of variability in the population growth rates of interacting species could exacerbate the extinction risk of a focal population and, in turn, reduce the probability of coexistence of the assemblage as a whole. While much is known about deterministic sources of variability in predator–prey dynamics, less is known about the relationship between random sources of variability, the species interaction, population persistence, and thus, coexistence. These problems have very strong implications for the management of introduced species.

Here, I illustrate how predators can increase not only the deterministic, but also the stochastic variation experienced by prey populations. Specifically, I show that even low levels of variability in predator growth rates (i.e., predator process noise) can significantly increase the risk of extinction faced by prey populations. More importantly, predator process noise has a much stronger effect on prey persistence than variation experienced by the prey itself (i.e., prey process noise). This observation is consistent for parameter sets generating unstable as well as stable underlying deterministic dynamics. Finally, using the same stochastic descriptions of predator–prey dynamics I apply insights from these models to the management of nonnative predators. My analysis suggests that the reduction of predator variance can revive declining prey populations—in some cases, more effectively than reduction of predator abundance per se.

**Predator Process Noise and Prey Population Persistence**

The underlying population model analyzed consists of a discrete-time stochastic version of a very commonly studied predator–prey system. This model is well analyzed in its continuous time form (e.g., Lotka 1925, Volterra 1926, Berryman 1992). Discrete time models are most appropriately applied to populations with nonoverlapping generations, a situation that may apply to some, but not all, populations of conservation concern. However, conservation biologists and wildlife managers typically collect *annual* population data, and thus, viability models forecast the risk of these populations in discrete time, reflecting this data limitation. In an effort to maintain consistency with the realism of data available to conservation biologists I used a discrete-time version of the Lotka-Volterra model that includes process noise in the growth rates of introduced predator and native prey populations (\(e_r\) and \(e_N\), respectively):

\[
N_{t+1} = N_t \exp \left[ r_N \left( 1 - \frac{N_t}{K} \right) - \alpha I_t + e_N \right] 
\]

\[
I_{t+1} = I_t \exp (\alpha \gamma N_t - c + e_I)
\]

where \(N\) and \(I\) are the abundance of native prey and introduced predator in year \(t\), respectively, \(r_N\) and \(K\) are the intrinsic growth rate and carrying capacity of the prey species, and \(\alpha\), \(\gamma\), and \(c\) are the predator attack rate, conversion efficiency, and density-independent death rate. I included environmental stochasticity (hereafter, “process noise”) as a log-normal variate (Dennis et al. 1991) with a mean of zero and a variance of \(\sigma_e^2\):

\[
e_i \sim \text{Norm}(0, \sigma_e^2).\]

The parameter \(\sigma_e^2\) allowed me to modify the variance in annual growth rates of introduced predator and prey species. As with continuous versions of this Lotka-Volterra model, the model I used assumes that prey dynamics are density dependent in the absence of a predator (see Berryman 1992 for historical development), that consumption of prey by predators is linearly related to prey density (Holling Type I functional re-
response; Murdoch and Oaten 1971), that predators respond to the number of prey available rather than the ratio of prey to predators (following Abrams 1994), and that predator abundance declines exponentially in the absence of prey.

**Stability conditions of the deterministic process**

The dynamic behavior of the deterministic predator–prey model analyzed here (Eqs. 1 and 2), and other similar models (Beddington et al. 1975), is well known (cf. Murray 1989). Given fixed values for the efficiency of the predator described by the parameters $\gamma$ and $c$, the stability of the model can be characterized in terms of the prey carrying capacity, $K$, and the predator attack rate, $\alpha$ (Fig. 1a). When $K$ and $\alpha$ fall below threshold values, predator populations are unsustainable and go extinct (PX in Fig. 1a). Above this threshold, predators persist and the dynamics of the predator–prey interaction are characterized by either damped oscillations to a fixed-point equilibrium (FP) or oscillations of increasing amplitude from an unstable node (UN; Fig. 1a, b; see Appendix A for details).

**Persistence of prey in the face of temporal variation in the environment**

Given the variation in deterministic model dynamics with $\alpha$ and $K$, I now show how low levels of prey and predator process noise alter the probability of prey persistence for parameter sets generating fixed-point and unstable dynamics. I generated 1000 replicate time series of abundance for native prey and introduced predators over a 100-year time frame. In all cases, I used values for the parameters $\sigma_f$, $\sigma_p$, and $\alpha$ within a range corresponding to empirical estimates from endangered species (Sinclair et al. 1998, Sabo et al. 2004). Specifically, I added only very low values of process noise to the growth equations of the prey alone, predator alone, or both. The value used in all cases corresponded to the minimum from over 20 empirically determined values for this parameter from endangered populations ($\sigma_f$; Sabo et al. 2004). To measure prey population persistence, I calculated the probability of prey populations declining to a quasi-extinction threshold of 1 individual, $P_{qe}$. In the absence of process noise, prey populations never crossed this threshold over the 100-year time horizon evaluated (spiral lines in Fig. 1c–h). Not surprisingly, stochasticity in the prey growth rate increases $P_{qe}$ for prey populations (Fig. 1c, d). However, predator process noise has a much stronger negative effect on prey persistence than prey process noise (Fig. 1e, f) and very similar effects on this metric of persistence than prey and predator process noise combined (Fig. 1g, h). These conclusions are similar across model parameters that generate fixed-point and unstable deterministic dynamics, except that $P_{qe}$ is always higher in the unstable region of parameter space (compare left- and right-hand columns of Fig. 1c–h). Variability in prey abundance and thus, extinction risk (as measured by the coefficient of variation and $P_{qe}$ respectively), both increase with increasing attack rates (and decreased stability) and predator process noise (Fig. 2). Within the stable range of parameter space ($\alpha < 0.044$ in Fig. 2), $P_{qe}$ increases by 40% over a range of predator process noise values bracketing the minimum and mean empirical estimates (i.e., $\sigma_f = 0.004–0.134$; Sabo et al. 2004) and by greater than 60% over the entire range of empirically determined values for this parameter ($\sigma_f = 0.004–0.65$). Even for very weak species interactions (i.e., interaction coefficients <0.01, corresponding to the mean of empirical estimates of $\alpha$ from eight intertidal grazers; Paine 1992), risk is increased by as much as 50% across a range of plausible values for predator process noise.

**Application of Stochastic Models to the Management of Nonnative Predators**

Introduced predators have caused extinctions of native prey populations worldwide (Atkinson 1985, Case and Bolger 1991, Mack et al. 2000, Pimentel et al. 2000, 2001). Understanding how to most effectively manage these pest species has become a critical conservation focus around the globe (Simberloff 2003a, b). On small and remote oceanic island habitats, complete and immediate eradication of nonnative species has become a feasible conservation strategy (Newman 1994, Myers et al. 2000, Taylor et al. 2000, Simberloff 2003a). However, these programs have shown few signs of success for mainland habitats (Sinclair 1997), resulting in conservation programs aimed at gradual eradication by means of serial reduction in pest abundance (Courchamp et al. 1999, Atkinson 2001).

The strong and consistent effects of predator process noise on prey persistence suggest that control efforts for nonnative predators should focus on reducing variability of these pest species in order to revive declining prey populations. Here, I evaluate the efficacy of two current management actions for the control of nonnative predators: immediate eradication and gradual eradication implemented by proportional harvest. Given the significance of external sources of temporal variability in prey and predator population growth, I also compare the relative efficacy of these more common modes of control with an alternative approach: “trigger” harvest, achieved via threshold harvest of nonnative predators.

**Control of predator variance to enhance prey population persistence**

Invasions are likely to occur at abundance levels far from equilibrium, where damped or sustained oscillations in the abundance of both species could be common. Predator process noise enhances these oscillations and, in turn, the extinction risk of prey populations (Figs. 1 and 2). I hypothesized that the efficacy of “trigger” harvest as a means for enhancing prey population persistence depends strongly on variability in predator growth rates (e.g., $\sigma_f$). To test this hypothesis,
Fig. 1. Increased prey extinction mediated by environmentally driven stochasticity, or “process noise” in the predator population growth rate. Top: Analytical deterministic model dynamics. (a) Stability conditions for the deterministic predator prey model (Eqs. 1 and 2) in terms of prey carrying capacity ($K$) and predator attack rate ($\alpha$). Subscript 0 and e denote initial and equilibrium populations, respectively, of prey ($N$) and predator ($I$). All other model parameters are held constant for simplicity: $N_0 = N_e$ for $\alpha > 0$, and $N_0 = K$ for $\alpha = 0$; $I_0 = 0.8I_e$, $r = 0.5$, $\gamma = 0.1$, $c = 0.1$, where $N_e = c/(\gamma \alpha)$, and $I_e = (r/\alpha)(1 - (N_e/K))$. This system is unable to support predators at low attack rates and prey carrying capacities (PX; $I_e = 0$, $N_e = K$). Above this trivial equilibrium, dynamics are characterized by a fixed-point equilibrium for both species (FP), or oscillations of increasing amplitude from an unstable node (UN). (b) Cycles for representative fixed-point (red) and unstable (blue) parameter sets are also shown. Here, triangles represent the starting abundance for each parameter set ($N_0 = N_e$, $I_0 = 0.8I_e$). Bottom: Simulated stochastic model dynamics for three combinations of process noise (noted between panels) and either fixed-point or unstable deterministic dynamics. (c–h) Phase plane analysis showing reduced prey persistence mediated by predator stochasticity. Log–log plots show deterministic (red or blue, corresponding to FP and UN parameter sets, respectively) and 1000 replicate stochastic time series (black) of prey (abscissa) vs. predator (ordinate) abundance over 100-year time frame with (c, d) low levels of process noise in prey growth rates ($\sigma_P^2 = 0.004$; $\sigma_I^2 = 0$), (e, f) low predator process noise ($\sigma_I^2 = 0.004$; $\sigma_P^2 = 0$), or (g, h) low prey and predator process noise ($\sigma_P^2 = 0.004$; $\sigma_I^2 = 0.004$). Process noise values are the minimum estimated from empirical data (Sabo et al. 2004). In panels (c)–(h), the dashed vertical line is the quasi-extinction (qe) threshold ($N = 1$) for prey populations, and the probability of reaching this threshold, $P_{qe}$ is given in top right corner of each panel. Other model parameters are as before, except $\alpha = 0.005$ and $K = 2500$. 
I used the same predator–prey model employed above (Eqs. 1–3) to evaluate alternative management options for introduced predators with the goal of recovering native prey populations. I parameterized the model as in the previous subsection, with values within the range of empirical estimates for the process noise and attack rate of the predator (Paine 1992, Sinclair et al. 1998, Sabo et al. 2004) and then simulated the impact of a 10-year invasion of an introduced predator on a native prey population. In these simulations I assumed that prey populations had low background levels of process noise ($\sigma^2 = 0.004$) and that the initial prey abundance was at the equilibrium level in the presence of predators ($N_0 = N_e$). Predators invaded prey communities at 80% of their equilibrium abundance level ($I_0 = I_e$) during the first year and at 10% of this level in subsequent invasion years (years 2–10). Initial densities were set intentionally near equilibrium levels (i.e., rather than at $K$ for prey and at a lower invasion abundance for predators) to standardize initial conditions, and thus, the amplitude of deterministically driven variation in abundance caused by departures from these equilibrium values.

At the end of this “invasion period,” I implemented one of three management actions over a management horizon of thirty years (years 11–40): (1) immediate eradication, (2) proportional harvest, and (3) trigger harvest. For each management action and a control (“no action”), I generated 1000 replicate sets of 40-year time series of predator and prey abundance. Immediate eradication involved complete removal of all predators during year 11. I implemented proportional harvest by harvesting a constant proportion ($h$) of the predator population present in each year (i.e., $I_{\text{culled}} = (1 - h)I_e$, where $I_{\text{culled}}$ is the abundance of predators remaining after management activities during year $t$). Finally, I implemented trigger harvest by reducing the predator population to a prespecified “trigger” abundance level only in years in which predator abundance exceeded this trigger. I defined the trigger as $I_{\text{trigger}} = H I_e$, where the threshold reduction factor, $H \geq 1$. Since the initial invasion abundance of predators was proportional to this equilibrium level ($I_0 = 0.8I_e$), the threshold predator reductions applied here are also defined in terms of the invasion abundance of predators.

Two case studies: fixed-point and unstable parameter space

Predator process noise enhances variability in prey populations, suggesting that reductions in predator variance may enhance the persistence of prey populations. When predator populations were left unchecked (i.e., no management), native prey populations declined to abundance levels of <1 individual with a higher than 90% probability. This was true for the system with fixed-point (Fig. 3) and unstable (Fig. 4) deterministic dynamics. Proportional harvest reduced the risk of prey populations reaching this quasi-extinction threshold by ~20% in a fixed-point regime, but very little in an unstable regime, despite a relatively high proportional harvest level ($h = 0.25$). Immediate eradication reduced the risk of reaching the quasi-extinction threshold by as much as 40%. Surprisingly, trigger harvest of introduced predators resulted in nearly identical effects on $P_{ww}$ as complete eradication regardless of the stability of the deterministic model (Figs. 3 and 4).

In addition to the increased efficacy of trigger harvest in these two case studies, the effort expended in implementing this management regime is potentially much lower than in proportional harvest. I defined ef-

**Fig. 2.** Sensitivity analysis showing the effect of introduced predator process noise ($\sigma^2$) and attack rate ($\alpha$) on variation in the abundance of native prey populations. Contours are (a) the average coefficient of variation (COV) from 1000 realizations of all nonzero values of annual abundance for the prey population and (b) the proportion of prey population declines to a quasi-extinction threshold equivalent to one individual ($P_{ww}$). Population dynamics over the entire time series follow a simple Lotka-Volterra predator–prey model assuming a linear functional response (no predator satiation) and deterministic prey population dynamics in the absence of predators ($\sigma^2 = 0.00$). Other parameters are: $N_0 = N_e$ for $\alpha > 0$, and $N_0 = K$ for $\alpha = 0$; $I_0 = 0.8I_e$, $r = 0.5$, $y = 0.1$, $c = 0.1$, and $K = 2500$. **CONCEPTS & SYNTHESIS**
**Fig. 3.** Efficacy of introduced predator control programs for reducing the extinction risk of a native prey species with high predator and low prey process noise. Median (thick solid line) and upper and lower quartile abundances (dotted lines) of 1000 replicate time series of native prey and introduced predator (dashed–dotted line, median only) abundance are shown under four management scenarios. In all four scenarios, predators invade the system at an initial abundance \(I_0 = 0.8I_e\) of 92 individuals (year 1) and at a rate of \(\sim 9\) individuals for the remainder of the invasion period (years 2–10). Population dynamics over the entire time series follow a simple Lotka–Volterra predator–prey model assuming a linear functional response (no predator satiation), low levels of process noise in prey population dynamics \(\sigma_0 = 0.004\), moderate levels of predator process noise \(\sigma_e = 0.3\), and a low attack rate of the predator \(\alpha = 0.005\). Once established (year 11), introduced species management programs are implemented. In the no management scenario, the predator invasion is left unchecked. Under an immediate eradication scenario, all predators are removed at year 11. Proportional harvest is implemented by removing 25% of the population each year beginning in year 21. Trigger harvest is implemented by reducing the predator population to the initial invasion abundance \(I_e\) only during outbreak years when abundance exceeds this “trigger” abundance level. This abundance approximates the median or 50th percentile abundance level in 40 years across a large number of population realizations. Probabilities of quasi-extinction \(P_qe\) are measured as the probability of the native prey population declining from a pre-invasion abundance \(N_0 = N_e = 200\) to \(<1\) individual. Management effort (“Effort”), calculated as the proportion of years that management teams must implement control programs to achieve this \(P_qe\), are given for proportional and trigger harvest. For trigger harvest, effort can be approximated by predator stochasticity as the probability of abundance exceeding the median or equilibrium level over a large number of population realizations. Other parameters are: \(N_0 = N_e, I_0 = 0.8I_e, r = 0.5, \gamma = 0.1, c = 0.1,\) and \(K = 2500\). Deterministic dynamics are within the fixed-point range in Fig. 1a.

Effort as the proportion of time steps (years) in which management was implemented for proportional and trigger harvest. In proportional harvest, effort is always 1 as predators are culled by a fixed proportion, \(h\), in all years. In trigger harvest, the relative magnitudes of predator variation (stochastic and deterministic) and the threshold harvest level, \(H\), determine effort. In both case studies, proportional effort was \(<0.3\) (i.e., 9 out of 30 years). This value is roughly equivalent to the level of stochasticity experienced by predators, and thus, the probability of exceeding the median abundance level (in this case, \(H = 1I_e\)). Thus, both the relative efficacy and efficacy per unit effort is higher under trigger vs. proportional harvest.

**How Does Trigger Harvest Work?**

In the model presented above, predators affect prey population abundance through three processes: (1) the deterministic process of consumption, (2) predator abundance (influenced by both deterministic and stochastic processes), and (3) the interaction between stochastic variation in predator abundance and deterministic predator–prey oscillations. The per capita effects of consumption are manifested by the functional response \(\alpha N_t\) in Eq. 1. Individual predators kill more prey at higher attack rates, and the attack rate, in turn, contributes to the stability of the deterministic process (Fig. 2). Naturally, the number of predators in the system, \(I\), also influences prey abundance. Both deterministic and stochastic forces influence \(I\). For example, higher stochastic variation in predator growth rates translates to a higher likelihood of both predator outbreaks and crashes. Predator outbreaks have dire consequences for prey populations; predator crashes hasten predator extinction. Unfortunately, high probabilities
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Fig. 4. Efficacy of introduced predator control programs for reducing the extinction risk of a native prey species with moderate predator and prey process noise ($\sigma_p^2 = \sigma_y^2 = 0.3$). Deterministic dynamics are within the fixed-point range in Fig. 1a. All other parameters, probabilities, and effort are as in Fig. 3.

of predator decline are conditional on high outbreak probabilities as long as predators are not managed.

Finally, stochastic variation in the abundance of the predator has a profound influence on both the magnitude of predator-prey oscillations and the rate at which these oscillations approach extinction boundaries. To illustrate this phenomenon, I plotted a single time series in phase space for a representative predator-prey interaction in which the predator is left unchecked (unmanaged), or managed by either proportional or trigger harvest (Fig. 5). In all three cases, the same sequence of random variation is used for the predator (i.e., $\varepsilon_t$ is the same for each time step in all three scenarios), while prey process noise is held constant at zero. The latter is done (as in Fig. 1) to isolate the stochastic effects of predators transmitted to prey populations. Predator process noise sustains otherwise transient oscillations in the stable system; the deterministic time series reaches equilibrium, whereas the stochastic trajectory fails to converge. More importantly, predator process noise enhances the magnitude of predator and prey oscillations such that prey are more likely to decline below quasi-extinction thresholds (in the stable system) or decline to these thresholds more rapidly (in the unstable system).

Trigger harvest diminishes predator abundance in outbreak years, constraining the upper bound of predator abundance, and thus, the lower bound of prey abundance (Fig. 5). Thus, the range of possible predator abundance levels is skewed downward, resulting in a lower frequency of prey population declines to the quasi-extinction threshold (Fig. 6). This effect is not observed for proportional harvest (prey histograms similar for no management and proportional harvest, Fig. 6). Thus, trigger management effectively dampens noise-enhanced oscillations, thereby diminishing the probability of prey extinction.

Sensitivity Analyses: How Robust is Trigger Harvest?

The observation that the efficacy of all three management actions varies with the attack rate of the predator, and thus the stability of the deterministic dynamics (Figs. 3 and 4) motivates a thorough sensitivity analysis. In this section, I explore how the relative efficacy of immediate eradication, proportional harvest and trigger harvest vary with several key parameters of interest.

Relative effects of deterministic and stochastic sources of variation on efficacy

First, I ask how efficacy changes with increasing stochastic and deterministic variation. To do this, I calculated $P_{qe}$ for a variety of values for predator attack rates and predator process noise, while holding all other parameter values constant. Increasing predator attack rates augment deterministic variability (cycles) and shift deterministic dynamics from stable to unstable regions of parameter space (Fig. 1). By contrast, increasing predator process noise increases random var-
Fig. 5. Conceptual illustration of trigger management under fixed-point and unstable regimes. Trajectories of predator–prey populations are plotted in phase space for deterministic (dotted red line) and three stochastic populations. All three stochastic populations experience the same sequence of stochastic variation over a 40-year interval, but different management schemes: unmanaged (dashed gray with squares), proportional harvest (dashed black with circles), and trigger harvest (solid red with triangles). Deterministic trajectories gravitate to (in fixed-point regime) or fan out from (in unstable regime) the deterministic equilibrium point (five-pointed star). All stochastic trajectories have the same values for the first 10 time steps and then diverge (following the open six-pointed star) according to the management strategy applied. The trigger abundance level (horizontal dashed line) is plotted for convenience. Parameter values and initial conditions are as follows: $r = 0.05, 0.01$ (fixed-point and unstable regimes, respectively), $N_0 = N_e; I_0 = 0.8 I_e, K = 2000, \gamma = 0.1, c = 0.1; \sigma_\beta = 0, \sigma_\gamma = 0.059$.

Fig. 6. Frequency histograms of prey and predator abundance after 40 iterations (e.g., $t = 40$) in (top panels) fixed-point and (bottom panels) unstable regimes. Histograms show frequency (out of 2000 iterations) of abundance under no management (solid line), proportional harvest (dashed-dotted line), and trigger harvest (dotted line). Predator abundance is more frequently high (above the trigger harvest level) and prey abundance more frequently low (below $0.2 N_e$) when unmanaged or subjected to proportional harvest then when managed via trigger harvest. Parameters for fixed-point and unstable regimes are as in Fig. 5.
FIG. 7. Sensitivity analysis: predator process noise and attack rate when prey process noise is low ($\sigma_p = 0.004$). Shown is the efficacy of three introduced-predator control programs (immediate eradication [IE], proportional harvest [PH], and trigger harvest [TH]) vs. no management (NM) at reducing the extinction risk faced by native prey populations. Contours reflect the probability of the prey population declining to a quasi-extinction threshold of one individual. Contours are plotted as a function of predator process noise ($\sigma_p$), and the predator attack rate ($\alpha$). Here, the proportional harvest rate, $h$, and threshold harvest abundance, $H$, were set to 0.25 and 1, respectively. Thus, in proportional harvest, 25% of the predator population is removed at each time step (for $t > 10$), and in trigger harvest, predators are reduced to $I_e$ in years when they exceed this threshold. Other parameters are: $N_0 = N_e$ for $\alpha > 0$, and $N_0 = K$ for $\alpha = 0$; $I_0 = 0.8I_e$, $r = 0.5$, $\gamma = 0.1$, $c = 0.1$, and $K = 2500$.

In the context of predator abundance, Trigger harvest performs as well as immediate eradication across a wide range of values for these two parameters (Fig. 7). Levels of risk as indexed by $P_{qe}$ are more similar for immediate eradication and trigger harvest for most pairs of values for $\alpha$ and $\sigma_p$, whereas risk levels for proportional harvest are not much lower than when predators are left unmanaged. This is true when prey process noise is assumed to be very low ($\sigma_p = 0.004$; Fig. 7) or equivalent to predator process noise ($\sigma_p = \sigma_p = 0.3$; Fig. 8). Proportional harvest is extremely ineffective relative to other management options when the interaction is unstable ($\alpha > 0$) and predator process noise is low (i.e., compare upper left-hand corners of panels in Fig. 7). Here, small proportional reductions (e.g., $h = 0.25$) in the abundance of predators at the peak of deterministic cycles in predator abundance sustain rather than rebuff outbreaks of the predator. This effect is less pronounced when prey process noise is high (Fig. 8), as the deterministic signal of predator–prey cycles is swamped by stochastic variation in both prey and predator abundance.

I quantified the effect of deterministic variation in prey abundance on the efficacy of proportional and trigger harvest by calculating $P_{qe}$ across a range of values describing the prey carrying capacity, $K$, and predator attack rates, $\alpha$. As in Fig. 1a, this was done while holding all other parameters constant such that increases in $\alpha$ for a given value of $K$ lead to predictable increases in cycle amplitude and shifts between fixed-point and unstable regimes. Predator and prey process noise were also fixed at values consistent with the fixed-point case study ($\sigma_p = 0.004$; $\sigma_p = 0.3$; Fig. 3). Proportional harvest was much more effective within the stable range of parameter space (FP) than the unstable range of parameter values (UN). Proportional harvest reduced risk by as much as 50% when dynamics were stable, but not by more than 10% when dynamics were unstable (Fig. 9). By contrast, trigger harvest was almost exactly as effective as immediate eradication across both stable and unstable parameter space. Thus, the efficacy of trigger harvest may stem from reductions of both deterministic and stochastic sources of predator variability.

Comparison of proportional and trigger harvest across harvest intensities

The relative efficacy of proportional and trigger harvest likely hinges on the harvest level chosen (e.g., $h$ or $H$). I quantified variation in the relative efficacy of
these two management actions (as measured by reductions in $P_{qe}$) across a range of values for predator process noise and the thresholds $h$ and $H$, used in proportional and trigger harvest, respectively. This was done for two parameter sets representing fixed-point and unstable dynamics. First, I focused on efficacy in a fixed-point regime (Fig. 10). Immediate eradication (i.e., $h = 1$, $H = 0$) leads to nearly consistent 50% reductions in $P_{qe}$, except where risk is naturally low (i.e., at low levels of predator process noise). Proportional harvest yields similar results only at relatively high harvest levels ($h > 0.5$, or a 50% reduction in predator abundance in all years). Similarly, trigger harvest yields similar results to eradication at threshold harvest levels equivalent to circa three times the median abundance of predators in the system (i.e., equivalent to $3I_e$). In the unstable regime (higher predator attack rate), minimum harvest levels for effective control are diminished substantially (Fig. 11). Proportional harvest yields similar results to eradication only at proportional harvest levels of $>0.75$, whereas trigger harvest requires a threshold harvest level of 1–1.5 times the median predator abundance level, $I_e$, to achieve similar reductions in extinction risk faced by native prey populations.

**DISCUSSION**

Environmental stochasticity is well known to diminish the persistence time of single populations (Lande and Orzack 1988, Dennis et al. 1991, Lande 1993, Morris and Doak 2002). While persistence is a common metric in deterministic analyses of population models with more than one species, stochasticity is a rare feature in these analyses (see May 1973, Ripa et al. 1998, Ives et al. 2003, and Kilpatrick and Ives 2003 for exceptions). Here I show that stochasticity in the growth rate of predators increases the probability of prey extinction during the invasion of a predator. Stochasticity in the growth rate of predators enhances both interannual variability and the amplitude of oscillations in prey abundance, thereby diminishing prey population persistence (Figs. 1 and 2). Moreover, the effect of stochastic variation in the abundance of predators (predator process noise) is much stronger than stochastic variation in the abundance of prey on prey population persistence. As a result, I show that control of predator variance can, in some cases, be a more effective technique for reviving declining prey populations than control of predator abundance (Figs. 3 and 4). This result is robust across a wide range of realistic values for predator process noise, predator attack rates (Fig. 7), prey process noise (Fig. 8), and deterministic model behavior (Fig. 9). Finally, these conclusions are robust over a range of low, but achievable, threshold harvest levels for trigger harvest (Figs. 10 and 11).

**Sources of environmental stochasticity in ecological communities**

The model I analyzed here makes four assumptions about the nature of environmental stochasticity faced
by predator and prey populations. First, both predator and prey populations vary with the environment, independent of the deterministic variation caused by the predation process. Second, variation in prey growth rates is independent of variation in predator growth rates. Third, both sources of variation are modeled as multiplicative white noise (Eq. 3). And finally, I assumed that empirical estimates of process noise derived from models that assume no species interactions adequately characterize levels of environmental stochasticity faced by species engaged in such interactions.

The first of these assumptions is likely met in many natural systems. For example, the dynamics of both zooplankton (consumers) and phytoplankton (resource) in lake ecosystems are highly variable over time (Ives et al. 2003). This observation has strong implications for the application of single species population viability analysis. Stochastic variation in a focal species of conservation concern may be magnified or diluted by interactions with other species in a community, whether weak or strong. My results suggest that even weakly interacting species (e.g., interaction coefficients <0.01, the mean of eight intertidal grazers; Paine 1992) can significantly enhance the variation and extinction probability of their prey across a range of realistic levels of predator process noise.

Single-species PVA (population viability analysis) models estimate the composite effect of all possible sources of population variation on the persistence of the focal species with little concern about the sources of this variation. These sources include, but are not limited to, intrinsic variability as a result of an interaction between a population and the environment and extrinsic sources of variability resulting from interactions with species that experience environmental stochasticity as well. Future studies should aim to evaluate the degree to which variation caused by species interactions biases estimates from simple PVA models. Simple risk assessment models typically assume density independence in the focal species (e.g., Dennis et al. 1991, Holmes 2001) and are relatively robust to violations of this assumption (Sabo et al. 2004). These models may be robust to other deterministic sources of density dependence inherent in species interactions (competition and predation) as long as the variation brought on by the species interaction is consistent between the observed data used to fit the PVA and the ensuing prediction interval (Sabo et al. 2004). By contrast, significant interactions between predator process noise and the amplitude of deterministic variation (as in unstable parameter space; Fig. 1) suggest that species interactions could strongly bias forecasts from simple
Fig. 10. Sensitivity analysis: harvest level and predator process noise for a stable (FP) parameter set. Shown is the efficacy of three introduced predator control programs vs. no management (abbreviations as in Fig. 7) at reducing the extinction risk faced by native prey populations. Contours reflect the probability of the prey population declining to a quasi-extinction threshold of one individual. Contours are plotted as a function of predator process noise ($\sigma^2$), and the proportional harvest level ($h$) for proportional harvest (PH) or threshold abundance level, ($H$, in units of $I_e$) for trigger harvest (TH). For no management (NM) and immediate eradication (IE) scenarios, I show $P_{qe}$ contours in terms of the proportional harvest rate (ordinate) for comparison, even though this parameter was not used in either case, (i.e., the plot represents 11 replicate sets of 1000 simulations at the same predator process noise). Other parameters are: $\alpha_0 = 0.004$; $N_0 = N_e$ for $\alpha > 0$, and $N_0 = K$ for $\alpha = 0$; $I_0 = 0.8 I_e$, $r = 0.5$, $K = 2500$, $\alpha = 0.005$, $\gamma = 0.1$, and $c = 0.1$.

PVAs simply by causing deviations in the variation experienced by prey populations between the prediction interval and the fitting interval. These hypotheses have not been tested by thorough cross-validation studies.

The second assumption, that stochastic fluctuations in predator and prey dynamics are uncorrelated, is likely met for some, but not all, types of species interactions or communities. For example, fluctuations in the abundance of fishes are strongly non-concordant over time in some freshwater and marine systems (Grossman 1982, Grossman et al. 1982, 1985, Ross et al. 1985). Boom years for one species may be bust years for others. Weak environmental correlation among species should characterize diffuse interactions within more speciose and reticulate (sensu Polis and Strong 1996) communities. By contrast, strong correlation in the interannual abundance of interacting species should typify interactions between specialists with codependence on the same resource (competition) or on each other (predation and mutualism). Again, these predictions remain largely untested empirically.

Third, the use of white noise in these models assumes that there is no year-to-year correlation in the conditions faced by either population. Likely, the “noise” experienced by populations is colored by seasonal or decadal-scale climate variation (Cuddington and Yodzis 1999, Inchausti and Halley 2002, Akçakaya et al. 2003). The consistency of the results described here should be tested when stochastic events affecting the growth rates of prey or predators are correlated in time.

Finally, the empirical bounds used for process noise in this analysis (from Sabo et al. 2004) were derived from population viability models that assume no species interactions, and in most cases, no density dependence. PVA models that incorporate the effects of predators are not currently available. Recent advances in the development of Monte Carlo state-space likelihood methods represent a first step in this direction (e.g., De Valpine 2003). In practice, PVA models that ignore density dependence tend to overestimate true values for process noise when populations cycle (Sabo et al. 2004). Thus, the “empirical” values used here may tend to represent the high end of true values for process...
noise. This reality likely has little bearing on my results, as trigger harvest performs better when prey process noise is low (compare Figs. 5 and 6) and better across a wider range of attack rates than proportional harvest when predator process noise is low (e.g., $\sigma^2 < 0.2$; Fig. 7).

**Implementation of variance control**

Effective ecological restoration is not possible without the control or eradication of introduced species (Myers et al. 2000). Nonnative vertebrates, such as rats, cats, pigs, and fox, are globally ubiquitous (Atkinson 2001). For example, commensal rats (*Rattus* spp.) are now found on >90% of the world’s island groups (Atkinson 1985). Fortunately, introduced rodents have been effectively eradicated on >90 islands throughout the world (Towns and Broome 2003), and successful eradication programs are now being implemented globally (Taylor et al. 2000). However, in mainland ecosystems, eradication of introduced predators is usually not practical for technical and financial reasons (Atkinson 2001). The results of this analysis suggest that variance control, implemented by trigger harvest of predators, should provide a valuable management tool for recovering endangered prey populations in situations in which predators cannot be immediately eradicated.

Variance control can be achieved by setting a “trigger” abundance level, above which the predator is culled, but otherwise ignored. Most current pest control efforts can be grouped into two broad categories of abundance reduction strategies: constant effort or constant harvest strategies. In a constant effort scenario, the number of predators culled varies proportionally to the number present in a given year (i.e., predator abundance, but not variability is reduced). In a constant harvest scenario, the same number of predators is removed each year. Here, variance may be reduced, but at a much larger cost in years when predators are rare and difficult to find. Trigger harvest combines the strengths of constant effort and constant harvest strategies (lower effort and variance reduction, respectively). For example, in my analyses (Figs. 10 and 11), trigger harvest mimicked the effects of complete and immediate eradication when the harvest level was set relatively low ($H \leq 3$). Predator abundance exceeded a threshold of $I_e$ in <30%, or 9 of 30 years, on average (Figs. 3 and 4). Thus, management was necessary in less than one-third of the years included in the management interval.

Thus, my results suggest two very practical rules of thumb for the management of introduced predators that cannot be eradicated: (1) that the predator can essentially be ignored during years of low abundance ($I_i < I_e$), as long as numbers are reduced to some pre-defined threshold during outbreak years; and (2) that by harvesting only in years when predator abundance is high, conser-
vation organizations can potentially reduce management effort (and potentially costs) without sacrificing efficacy.

Potential limitations in the application of trigger harvest

The implementation of trigger harvest may prove more difficult than a constant effort (i.e., proportional harvest) management regime for at least three reasons. First, defining the critical threshold abundance level for trigger harvest may not be practical in some situations. In the best-case scenario, the threshold harvest level would be defined in terms of the median abundance level of predators (here \( I_\alpha \), Fig. 4) from time series data collected in previous monitoring efforts. The most affordable threshold (\( H = 1-3 \)) could then be determined and implemented by harvesting to the pre-determined trigger. Thus, ongoing monitoring of predator abundance would be required to know when to manage (i.e., in which years) and when to stop harvesting.

In many situations, the time or funding required for simultaneous harvest and monitoring programs may limit the feasibility of this approach to trigger harvest. Thus, a more practical way to achieve trigger harvest may be to define the trigger harvest level (e.g., \( H_L \)) in terms of a catch per unit effort (CPUE), an index with a long history as a relative abundance index in fisheries management. Harvest should be curtailed when CPUE falls below a threshold level that corresponds to a desired threshold abundance level (e.g., as estimated from a known relationship between CPUE and \( H_L \), from previous monitoring data).

Second, in the model examined in this paper, predator reductions occur before the impacts of predators on native prey populations in a given year. In other words, the models assume that managers have perfect and immediate knowledge of predator abundance and can act before predators reduce prey populations in a given year. Clearly, perfect and immediate knowledge of predator abundance is not possible in real-world management scenarios, but rather offers a best-case scenario to illustrate the potential strengths of trigger harvest in this conservation setting.

Finally, the conclusions drawn from my analyses of trigger harvest apply only to the range of parameters examined in this study. Specifically, when single predators are capable of consuming >1% of the entire prey population in a single generation (e.g., \( \alpha > 0.01 \)), eradication may be the only means for recovering the prey population. Nevertheless, these preliminary suggestions represent a starting point for understanding new strategies for managing introduced predators and highlight the potential importance of collecting abundance data for both native prey and introduced predator populations.

Acknowledgments

I am especially indebted to Leah Gerber, who helped clarify my thinking about the application of stochastic models to the management of nonnative predators. I thank Resit Akçakaya, Jordi Bascompte, Peter Baxter, Gary Belovsky, Eli Holmes, Peter Kareiva, Mick McCarthy, Carlos Melian, Hugh Possingham, Chris Wilcox and seven anonymous reviewers for comments and suggestions that improved earlier versions of this manuscript.

Literature Cited


APPENDIX