Cost-Effective Suppression and Eradication of Invasive Predators

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Abstract: *Introduced predators can have pronounced effects on naïve prey species; thus, predator control is often essential for conservation of threatened native species. Complete eradication of the predator, although desirable, may be elusive in budget-limited situations, whereas predator suppression is more feasible and may still achieve conservation goals. We used a stochastic predator–prey model based on a Lotka-Volterra system to investigate the cost-effectiveness of predator control to achieve prey conservation. We compared five control strategies: immediate eradication, removal of a constant number of predators (fixed-number control), removal of a constant proportion of predators (fixed-rate control), removal of predators that exceed a predetermined threshold (upper-trigger harvest), and removal of predators whenever their population falls below a lower predetermined threshold (lower-trigger harvest). We looked at the performance of these strategies when managers could always remove the full number of predators targeted by each strategy, subject to budget availability. Under this assumption immediate eradication reduced the threat to the prey population the most. We then examined the effect of reduced management success in meeting removal targets, assuming removal is more difficult at low predator densities. In this case there was a pronounced reduction in performance of the immediate eradication, fixed-number, and lower-trigger strategies. Although immediate eradication still yielded the highest expected minimum prey population size, upper-trigger harvest yielded the lowest probability of prey extinction and the greatest return on investment (as measured by improvement in expected minimum population size per amount spent). Upper-trigger harvest was relatively successful because it operated when predator density was highest, which is when predator removal targets can be more easily met and the effect of predators on the prey is most damaging. This suggests that controlling predators only when they are most abundant is the "best" strategy when financial resources are limited and eradication is unlikely.*

Keywords: introduced species, management efficiency, pest eradication, predator control, predator–prey model, process error, suppression of invasive species, trigger harvest

Supresión y Erradicación Rentable de Depredadores Invasores

Resumen: *Los depredadores introducidos pueden tener efectos pronunciados sobre especies presa nativas; por lo tanto, el control de depredadores a menudo es esencial para la conservación de especies nativas amenazadas. La erradicación total del depredador, aunque deseable, puede ser elusiva en situaciones de presupuestos limitados, mientras que la supresión de depredadores es más factible y puede alcanzar metas de conservación. Utilizamos un modelo estocástico de depredador-presa basado en un sistema de Lotka-Volterra para investigar la rentabilidad del control de depredadores para lograr la conservación de presas.*

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Comparamos cinco estrategias de control: erradicación inmediata, remoción de un número constante de depredadores (control de número fijo), remoción de una proporción constante de depredadores (control de tasa fija), remoción de depredadores que exceden un umbral predeterminado (cosecha proporcional superior) y remoción de depredadores cuando sus poblaciones están por debajo de un umbral predeterminado (cosecha proporcional inferior). Analizamos el funcionamiento de estas estrategias cuando los manejadores podían remover a todos los depredadores considerados por cada estrategia, en función de la disponibilidad de presupuesto. Bajo esta suposición, la erradicación inmediata redujo la amenaza a la población presa más que las otras estrategias. Posteriormente examinamos el efecto del éxito del manejo reducido en el alcance de las metas de remoción, asumiendo que la remoción es más difícil con densidades bajas de depredadores. En este caso hubo una reducción pronunciada en el funcionamiento de las estrategias de erradicación inmediata, número fijo y (cosecha proporcional inferior. Aunque la erradicación inmediata todavía generó el mayor tamaño esperado en la población mínima de presas, la cosecha proporcional superior generó la menor probabilidad de extinción de presas y el mayor retorno en la inversión (medida por el mejoramiento en el tamaño mínimo esperado de la población por cantidad gastada). La cosecha proporcional superior fue relativamente exitosa porque operó cuando la densidad de depredadores era mayor, que es cuando se pueden alcanzar las metas de remoción de depredadores más fácilmente y el efecto de los depredadores sobre las preseas es más perjudicial. Esto sugiere que el control de depredadores sólo cuando son más abundantes es la "mejor" estrategia cuando los recursos financieros son limitados y la erradicación no es factible.

Palabras Clave: control de depredadores, cosecha proporcional, eficiencia de manejo, erradicación de plagas, error de proceso, especies introducidas, modelo depredador-presa, supresión de especies invasoras

Introduction

Introduced predators are one of the major causes of the global extinction crisis (Mack et al. 2000; Atkinson 2001; Simberloff 2005). One of the primary goals of conservation biology is therefore to eradicate or control predators that threaten native prey populations.

In practice, predator management has had mixed results. Complete predator eradication can be difficult and costly on the mainland or large islands (Mack et al. 2000; Barlow & Norbury 2001), and the risk of predator recolonization places an ongoing burden on management resources (Harding et al. 2001). Attempts to eradicate an invasive species may also present political and social obstacles (Thresher & Kuris 2004), especially if the invasive species is itself a species of conservation concern. For example, adequate protection of the endangered island fox (*Urocyon littoralis*) may depend on eradication of the Golden Eagle (*Aquila chrysaetos*), itself a protected species, from the California Channel Islands (Courchamp et al. 2003). Recent eradications from islands have demonstrated that removal of invasive species can be successful even at large spatial scales (Taylor et al. 2000; Cruz et al. 2005). Nonetheless, if predators are successfully removed, depleted prey populations can remain vulnerable to extinction through the action of environmental and demographic stochasticity (Caughley 1994; Macdonald et al. 1999).

Eradication is only one of several management options (Sinclair et al. 1998; Myers et al. 2000; Hoddle 2004) and may not be necessary to sustain the viability of a native population. In situations where logistic and financial constraints make eradication infeasible, strategies that economically meet conservation objectives may focus on suppressing predator numbers rather than outright eradication (Sinclair et al. 1998; Stapp & Hayward 2002; see also Moberly et al. 2004). Recent theoretical work shows that predator suppression can allow prey persistence if both the maximum abundance and the variability of the predator are kept effectively low (Sabo 2005). Populations reduced to low densities may subsequently decline to zero under the combined action of stochasticity and the Allee effect (Liebhold & Bascompte 2003). Such insights gained from consideration of variability render stochastic pest-control models more useful than traditional deterministic models (Choquenot & Parkes 2001).

We compared the strategy of immediate eradication with four alternative control strategies with a stochastic predator–prey model. Two are simple strategies that remove either a preset amount (fixed number) or proportion (fixed rate) of the predator population, which is directly analogous to constant-catch and constant-effort harvesting in fisheries management (Getz & Haight 1989). Fixed-number control reflects when restrictive funding limits the number of predators removed by traps or hunters for example, whereas fixed-rate control reflects traps or hunters with a certain success rate or a disease agent that affects a certain proportion of the predator population. The other two strategies attempt to capitalize on fluctuations in the predator population and trigger management action when thresholds are crossed: upper-trigger harvest only removes predators over a certain density and lower-trigger harvest attempts extirpation whenever the predator density falls below a threshold level. Sabo (2005) compared two of these strategies, upper-trigger harvest and fixed-rate control, and found that upper-trigger harvest is more successful at lowering extinction probability of the prey population and is more robust to parameter changes. Sabo, however, did not incorporate the costs of management in the assessment of the best strategies.

Given the limited resources available to conservation, it is essential to consider economic aspects of conservation planning (Myers et al. 2000; Possingham et al. 2001); doing so can change the optimal strategy (Baxter et al. 2006). Because the trigger-harvest strategies are implemented less frequently in our model than fixed-rate or fixed-number control and avoid exhausting the funding amount immediately (as would the eradication strategy), they may be more economical options. We incorporated economic factors by imposing budgetary constraints on predator control in the model and assessed the results in terms of the reduction of threat to the prey species and the return on conservation investment under each strategy. By incorporating costs in this fashion, we hoped to make the approach more applicable to conservation managers. Thus, we asked the following questions: Which strategy provides the most cost-effective means for maximizing prey population viability? and (2) How do limitations on the search efficiency of the manager (hunting non-native predators) affect the relative performances of the five strategies?

Methods

Model Details

We developed the predator–prey dynamics from a stochastic discretized approximation to the Lotka–Volterra model (Sabo 2005):

$$N(t+1) = N(t)\exp\left\{r\left[1 - \frac{N(t)}{K}\right] - \alpha P(t) + z_N(t)\right\},$$

$$P(t+1) = P(t)\exp\left[\alpha\gamma N(t) - c + z_P(t)\right] - H(t),$$

where $N(t)$ is prey population at time t, r is rate of prey population increase, K is prey carrying capacity, $P(t)$ is predator population at time t, α is kill rate of one prey individual by one predator, γ is conversion rate of eaten prey to predators, and c is predator starvation rate in the absence of prey. The variable $H(t)$ is the control removal for that year (i.e., harvest), which also depends on predator density and budget available and takes place just before time $t + 1$. The process error terms, $z_X(t)$, which represent the effects of environmental variability on the prey ($X = N$) and predator ($X = P$) populations, are normal random variables with mean $-\sigma_X^2/2$ and variance σ_X^2, that is, producing, after exponentiation, lognormal random variables with mean 1 and variance $\exp(\sigma_X^2) - 1$ (Dennis et al. 1991). We did not consider demographic stochasticity, which may place small populations at further risk (Macdonald et al. 1999). The equilibrium values for an uncontrolled, deterministic system (i.e., $\sigma_N^2 = \sigma_P^2 = H[t] = 0$) are $N^* = c/\gamma\alpha$ and $P^* = r(K - N^*)/\alpha K$. We based the initial conditions on these equilibrium values, setting $N(0) = N^*$ and modeling a predator inoculum of $0.8P^*$ the first year and $0.1P^*$ yearly for the remainder of the first decade (Sabo 2005). Predator control commenced in the 11th year.

Setting Control Targets

We calculated control targets, $h(t)$, from the predator population prior to control, denoted as $\pi(t)$ (i.e., $\pi[t] = P[t]\exp\{\alpha\gamma N[t] - c + z_P[t]\}$). The control targets also depended on the control strategy invoked—fixed-number (target denoted by h_{num}), fixed-rate (h_{rate}), upper-trigger harvest (h_{upr}), lower-trigger harvest (h_{lwr}), and immediate eradication (h_{erad})—and on the available budget $B(t)$:

$$\text{fixed-number control,}\quad h_{\mathrm{num}}(t) = \min\left[x, \pi(t), \frac{B(t)}{\kappa}\right];$$

$$\text{fixed-rate control,}\quad h_{\mathrm{rate}}(t) = \min\left[v\pi(t), \frac{B(t)}{\kappa}\right];$$

$$\text{upper-trigger harvest,}\quad h_{\mathrm{upr}}(t) = \min\left\{\max\,[0, \pi(t) - u], \frac{B(t)}{\kappa}\right\};$$

$$\text{lower-trigger harvest,}\quad h_{\mathrm{lwr}}(t) = \min\left[\tau, \frac{B(t)}{\kappa}\right],\ \pi(t) \le \tau,$$

$$= 0,\ \text{otherwise,}$$

$$\text{immediate eradication,}\quad h_{\mathrm{erad}}(t) = \min\left[\pi(t), \frac{B(t)}{\kappa}\right],$$

where x is the preset fixed-number control level, v is the fixed rate of control, u is the population threshold for upper-trigger-harvest control, τ is the population threshold for lower-trigger-harvest control and κ is the per capita cost of removing predators. The amount actually spent on control in year t was then $\kappa h(t)$, and we assumed that any unspent funding would be carried forward to the following year: $B(t + 1) = B(t) - \kappa h(t)$.

Control Success

Perfect success in removing predators means that removal targets are always met ($H[t] = h[t]$ above). At low predator densities, however, managers have difficulty meeting their targets because search efficiency is reduced. We modeled this with a curve that reflected removal success increasing with predator density (also see Hone 1990). This gave

$$H(t) = \frac{\pi^\theta}{m^\theta + \pi^\theta} h(t),$$

where m is a half-saturation density (managers only meet 50% of the target $h[t]$ when $\pi[t] = m$; we used $m = 0.25P^*$), and θ describes the shape of the relationship between managers' success and predator density ($\theta = 1$

and $\theta > 1$ for saturating and sigmoidal curves, respectively). For simplicity, we assumed that managers could not spend extra money to offset this search inefficiency, but that their expenditure was fixed, prior to carrying out control, according to their yearly removal target.

Model Parameterization and Implementation

Although pest control models are often difficult to parameterize (Choquenot & Parkes 2001), data from Langham (1990) and Roemer et al. (2001) suggest attack rates of $\alpha = 0.05$ (i.e., proportion of prey killed increases with predator density as $1 - e^{-0.05P}$; see also Basse et al. 1999). We used a conversion parameter of $\gamma = 0.01$ to yield reasonable maximum rates of predator increase (2.86-fold population increase at $N = K$) and a moderately low predator mortality rate of $c = 0.2$ (a population half-life of 3.5 years). Other model parameters were as in Sabo (2005) (i.e., $r = 0.5$; $K = 2500$; $\sigma_N^2 = 0.004$; $\sigma_P^2 = 0.3$). The model gives a fixed-point equilibrium for attack rates α within $[c/\gamma K, (1 + c)/\gamma K]$, with predator extinction at lower values of α and diverging oscillatory dynamics at higher α (Sabo 2005); therefore, our default parameter set lay just within the oscillatory region ($\alpha = 0.05 > 0.048$).

We recorded the projected predator and prey populations in 1000 iterations of 40-year duration (10 years of invasion without predator control followed by 30 years of management). We set the threshold level for upper-trigger harvest to the equilibrium predator population (i.e., $u = P^*$) and the lower trigger to $\tau = P^*/2$. To make the other management strategies comparable, we simulated a population with upper-trigger harvest without budgetary constraints, and then set the levels for fixed-number (x) and fixed-rate (v) control to match the overall targets resulting from these simulations:

$$x = \frac{1}{30}\sum_{t=11}^{40} h_{\text{upper}}(t) \quad \text{and} \quad v = \sum_{t=11}^{40} h_{\text{upper}}(t) \bigg/ \sum_{t=11}^{40} \pi(t).$$

Having set the removal targets, we simulated the effect of the different strategies including budgetary constraints. We assumed that the total amount of funding was exactly enough to meet all anticipated removals and that it became available as a once-off payment at the start of management (i.e., $B[t = 11] = 30x\kappa$). We measured the vulnerability of the prey by its expected minimum population size, which is a good summary of the risks of population decline (McCarthy & Thompson 2001). We also measured returns on investment by dividing the improvement in each strategy's minimum population relative to the unmanaged situation by the total expenditure (i.e., expected increase in minimum population per currency unit spent). A preliminary sensitivity analysis showed that expected minimum population sizes were most sensitive to changes in the attack rate (α), and in the prey rate of increase (r). Changes in the predator process error σ_P^2 had much greater effect than changes in the prey process error σ_N^2 (see also Sabo 2005). Therefore, the results presented below focus on sensitivity to the values of these parameters and to trigger levels. We also assessed the effect of including a predator–prey functional response (replacing α in the predator–prey equations with $\alpha N/[k + N]$, where k is the prey density yielding 50% of the maximum predator-attack rate; Holling 1959) and examined the sensitivity of performances to changes in the available budget.

Results

Model Behavior

Under the assumption of perfect removal success, immediate eradication was the most effective strategy at increasing the expected minimum population size of prey, and fixed-number control and upper-trigger harvest (Table 1) were the next-most effective. The poorest strategy was fixed-rate control (see also Sabo 2005), which performed only slightly better than no management. The ranking of strategies was broadly the same for probability of prey extinction and expected minimum prey population size, although upper-trigger harvest yielded a lower probability of prey extinction than did fixed-number control. The performance of the fixed-number and lower-trigger strategies relies on their potential to progressively drive the predator population to extinction. Therefore, when removal of predators was difficult at low densities ("imperfect removal success"), the effectiveness of these strategies was dramatically reduced, with immediate eradication and upper-trigger harvest being the only strategies to maintain reasonable prey populations. Under the imperfect-removal scenario the immediate eradication strategy yielded the highest expected minimum population and maintained a reasonably high return on investment, but upper-trigger harvest was the best-performing strategy in terms of both reducing extinction probability and providing a high return on investment.

Model Sensitivity

We evaluated the performance of each strategy by assessing how sensitive each was to changes in parameter values and assumptions (Figs. 1–4). We concentrated on expected minimum population size as a more suitable performance measure than return on investment, given that we assumed a fixed amount of funding for management. Performance was most sensitive to changes in the rate of predator attack (α) and improved with decreasing α (because predators have less impact on the prey population; Fig. 1). The fixed-number, lower-trigger, and eradication strategies (Fig. 1b,d,e) could all more easily achieve extirpation following predator crashes, so their

Table 1. Predator-control performance* of six management strategies (no management, upper-trigger harvest, fixed-number control, fixed-rate control, lower-trigger harvest, and immediate eradication) for the default parameter set.

	Removal success					
	perfect			*imperfect*		
Management option	*expected minimum population, SD*	*probability of prey extinction*	*return on investment (mean, SD)*	*expected minimum population, SD*	*probability of prey extinction*	*return on investment (mean, SD)*
Unmanaged	34.3, 71.1	0.407	–	34.3, 71.1	0.407	–
Upper-trigger harvest	234.0, 237.0	0.121	4.6, 5.4	212.3, 218.1	0.132	4.0, 4.8
Fixed-number control	287.8, 341.7	0.138	68.5, 135.7	80.4, 147.2	0.311	1.2, 2.9
Fixed-rate control	63.0, 104.3	0.276	1.7, 3.4	59.2, 98.0	0.278	1.4, 2.5
Lower-trigger harvest	229.8, 313.2	0.181	77.7, 144.5	72.6, 145.9	0.354	1.2, 3.6
Eradication	380.2, 386.1	0.084	75.1, 137.6	225.3, 298.2	0.175	3.3, 4.8

**Performance is measured as expected minimum prey population size (calculated from the minima for the management period of 1000 runs); probability of prey extinction (proportion of runs in which prey population dropped below 1 individual); and return on investment (increase in EMP divided by total amount spent on management).*

performance also increased with increasing predator process error σ_P^2.

The performance of all five management strategies declined when removal success declined at lower predator densities (as expected; Figs. 1f-j). The performance of upper-trigger harvest and fixed-rate control strategies, however, decreased only slightly compared with perfect removal success (see also Table 1), whereas the effectiveness of lower-trigger, fixed-number, and immediate eradication strategies decreased markedly. With imperfect removal success, these three strategies had more difficulty achieving complete extirpation at low predator densities. Accordingly, their performances also became less sensitive to changes in predator process error σ_P^2 (compare Figs. 1b,d,e & 1g,i,j).

The performance of the immediate eradication strategy was relatively insensitive to changes in the amount of funding available under the perfect-removal scenario, and it remained the best strategy (Fig. 2a). Upper-trigger harvest became less effectual as the management budget

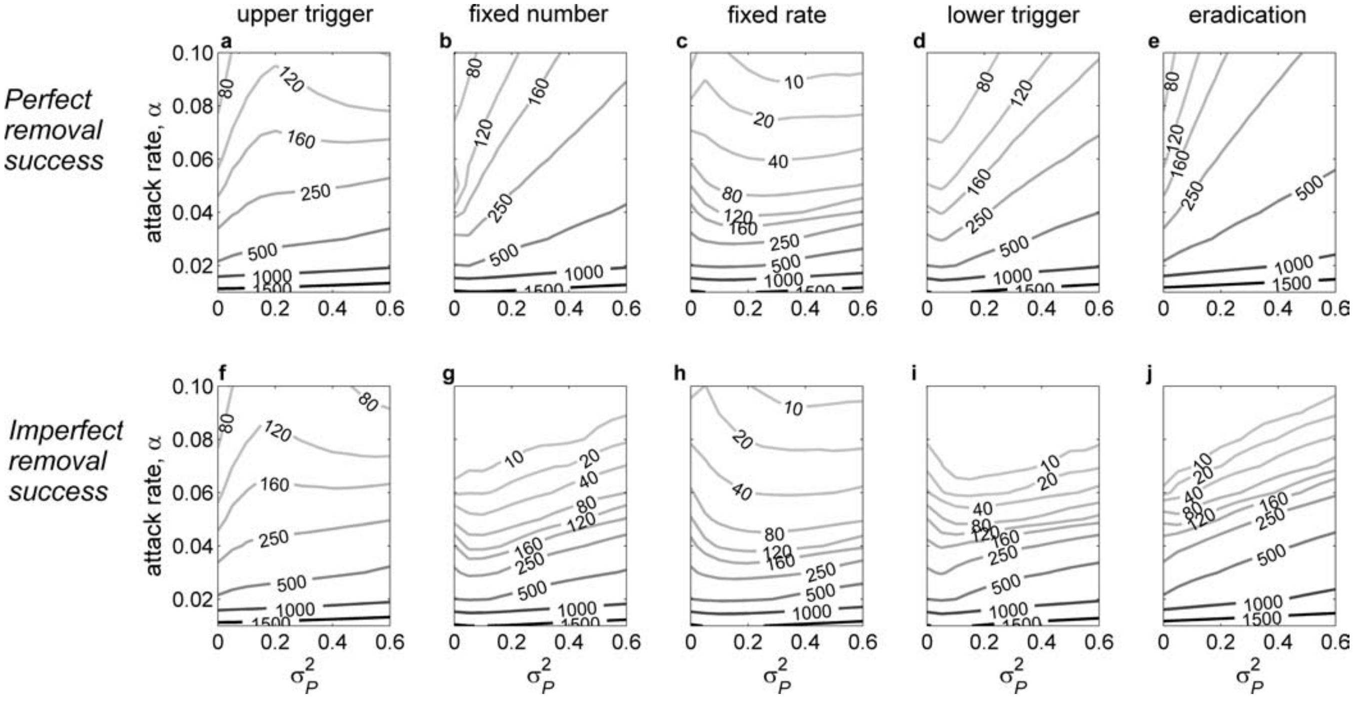


Figure 1. The sensitivity of the performance of removal strategies to changes in attack rate α and predator process error σ_P^2, assuming (a–e) perfect removal success and (f–j) imperfect removal success modeled with a Holling type-II functional response of managers to predator density. Performance is shown as expected minimum prey population size (mean of the minima for the management period of 1000 runs).

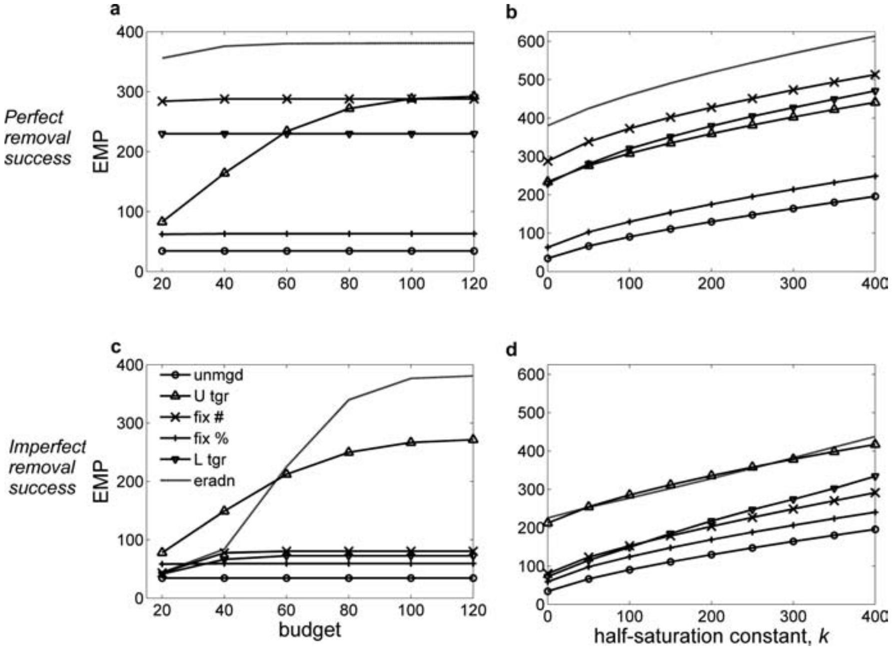


Figure 2. The sensitivity of the performance of removal strategies to (a, c) changes in allocated budget (in units of density of predators removable) and (b, d) steepness of the predator–prey functional response as indicated by the half-saturation constant k*, assuming (a, b) perfect removal success and (c, d) imperfect removal. Performance is shown as expected minimum population size (EMP; mean of the minima for the management period of 1000 runs). The removal strategies are no management (unmgd); upper-trigger harvest (U tgr); fixed-number control (fix #); fixed-rate control (fix %); lower-trigger harvest (L tgr); and immediate eradication (eradn).*

became more restrictive, due to its inability to prevent excessively high predator population densities. The other strategies were relatively insensitive to changes in funding amount. When predator removal became difficult at low densities, the performance of the immediate eradication strategy became vulnerable to low budgets (Fig. 2c) and upper-trigger harvest became a more preferable strategy. Expected minimum population size increased for all strategies and under both perfect- and imperfect-removal scenarios when a predator–prey functional response was incorporated, and it increased at higher values of the half-saturation constant *k* (which was associated with less-oscillatory dynamics). The ranking of strategies changed little as *k* increased, for both perfect- and imperfect-removal scenarios (Fig. 2b,d). Immediate eradication remained the best strategy for most strengths of functional response, although under the imperfect-removal scenario, the performance of upper-trigger harvest differed little from that of immediate eradication (Fig 2d).

Best-Performing Strategies

Assuming perfect removal success, the highest expected minimum prey-population sizes resulted from the immediate eradication strategy. When removal success was imperfect, immediate eradication was also the best-performing strategy if the predator-attack rate α or the prey population growth rate r were low (Fig. 3). At higher rates of predator attack and imperfect removal success, however, upper-trigger harvest yielded the highest expected minimum prey populations because extirpation was more difficult at low predator densities, and therefore the avoidance of very high predator densities became a better strategy. Upper-trigger harvest was also the best strategy at higher prey-population growth rates because the prey population could more easily persist in the presence of predators and extirpation was elusive at low predator densities. When the predator process error was very high, however, the eradication strategy became more successful by capitalizing on noisier dynamics to achieve extirpation.

Effect of Trigger-Level Settings

We examined the sensitivity of recommendations based on expected minimum population sizes under the imperfect-removal scenario for different upper-trigger thresholds (Fig. 4; best strategies for the default trigger settings shown in Fig. 4b). The overall pattern was quite robust to changes in the trigger level: the immediate eradication and upper-trigger harvest strategies performed best at lower and higher rates of predator attack, respectively (Figs. 4b & 4c). When the upper-trigger level was set too low, upper-trigger harvest failed to keep predator densities below the threshold and fixed-rate harvest replaced it as the best strategy (Fig. 4a).

Discussion

Our results not only show the benefit of eradication of an invasive predator but also show that when immediate eradication is elusive, an upper-trigger-based method of predator control can be more effective than alternative, more traditional, approaches (constant harvest or effort) when the conservation objective is to protect the native prey population within a constrained budget. Specifically, an immediate eradication approach was always the

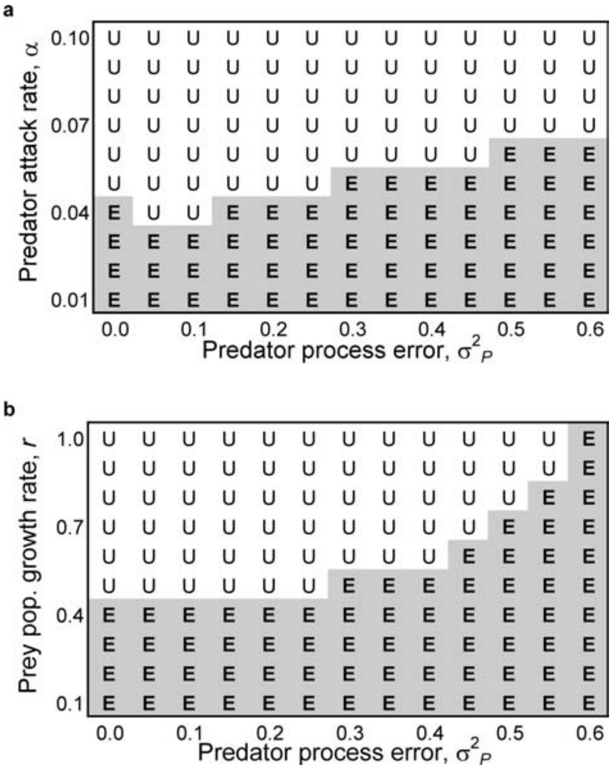
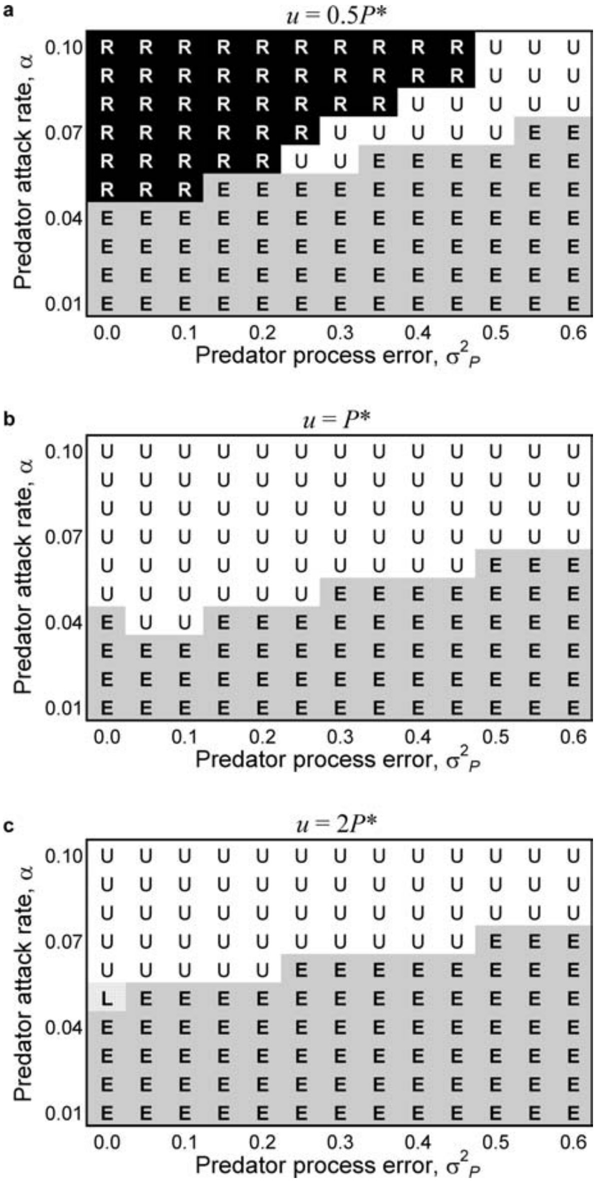


Figure 3. The management strategies that achieve the highest expected minimum prey populations assuming imperfect predator removal. Best-performing strategies are shown for combinations of values of predator process error (σ^2_{P}) with (a) predator-attack rate α and with (b) prey-population growth rate r. *The strategies are denoted as follows: E, immediate eradication; U, upper-trigger harvest.*

most effective method for conserving native prey species when the harvest of predators was "perfect" (i.e., did not decline with decreasing predator density). By contrast, when search inefficiencies at low predator densities precluded perfect removal success, an upper-trigger harvest approach often became the most effective management strategy. These results highlight the need for considering the realism of the cost and removal efficiency of control methods when evaluating the efficacy of predator control strategies.

Mechanistic Differences between Control Strategies

The five management strategies in our model differed in timing (acting immediately, continuously, or strategically) and in approach (damping population extremes or attempting extirpation). The immediate eradication strategy aimed to wipe out the predator population as soon as possible, irrespective of its size or the actual feasibility of extirpation. Fixed-number control, an ongoing strategy, did not respond directly to predator population size; it may have slowed growth of the predator population, but more important, it acted numerically to extirpate small populations. Lower-trigger harvest explicitly attempted extirpation, but only when the predator population was alread relatively small. Fixed-rate control, another continuous strategy, tracked predatory density by removing a


u = 0.5P*

u = P*

u = 2P*

Figure 4. The management strategies that achieve the highest expected minimum prey populations assuming imperfect predator removal. Best-performing strategies are shown for combinations of values of predator-attack rate α and predator process error (σ^2_{P}) for different settings of the upper-trigger level u, expressed relative to the equilibrium predator density (P). The strategies are denoted as follows: E, immediate eradication; L, lower-trigger harvest; R, fixed-rate control; U, upper-trigger harvest.*

fixed proportion annually, in effect decreasing the predator population growth rate. Upper-trigger harvest also tracked predator population size (with control implemented only when the predator population exceeded the management threshold) and operated as ceiling density dependence, where the ceiling is the upper-trigger level itself. This shared "population tracking" property resulted in the sensitivity contours for upper-trigger harvest and fixed-rate control being broadly similar and lower-trigger, fixed-number, and immediate eradication performances behaving differently, usually being somewhat more sensitive to changes in σ_P^2 (Fig. 1). The sensitivity of model output overall showed that expected performances and the "best" removal strategy could depend on the system in question and thus demonstrated the value of modeling to explore possible outcomes, especially in data-poor situations (Starfield & Bleloch 1986).

Efficiency of Trigger-Based Approaches

The immediate eradication strategy was most effective overall at increasing the expected minimum population size. Differences between the strategies' performances, however, showed how trigger-based strategies may help save valuable conservation resources. For perfect removal success, lower-trigger harvest was the most efficient (return on investment), yielding the greatest increase in minimum prey population per amount spent by timing expenditure in a more strategic fashion (Table 1). If removal targets could not always be met, the performances of all strategies declined but upper-trigger harvest was least affected and yielded the lowest probability of prey extinction and highest return on investment (Table 1; Figs. 3 & 4). These contrasts highlight a crucial step in the conservation decision-making process, namely, the formulation of a clear objective to determine how performance is measured (Shea et al. 1998; Possingham et al. 2001). For some conservation problems, it is desirable to maximize the population of concern irrespective of cost, and this may indeed be feasible in particularly high-profile and well-funded cases. In other cases a more pragmatic proposition may be to acknowledge budgetary limitations and produce the best result with the resources available.

Upper-trigger harvest performed well because it prevented extremely high predator densities, which would drastically reduce the (endangered) prey population. Successful long-term predator suppression with fixed-rate control may be elusive (Barlow & Norbury 2001); therefore, trigger-based control may offer more strategic timing of management effort (see also Choquenot & Parkes 2001). For example, intensified control prompted by a predator (stoat [*Mustela erminea*]) irruption successfully increased the breeding success of a cavity-nesting bird (O'Donnell et al. 1996). There are similarities between upper-trigger harvest and pulsed control (e.g., Basse et al. 2003), although by responding to control the highest outbreaks, upper-trigger harvest can offer a more targeted strategy and arguably, in the face of limited funding, a more realistic one. In keeping the predator population below some threshold level, dispersal of the predator to other areas may also be reduced, especially where dispersal has a density-dependent component. On the other hand, extirpation-driven strategies can be superior to upper-trigger harvest in situations where predator population crashes are more likely. Thus, noisier predator dynamics improve the performance of the fixed-number control, lower-trigger harvest, and immediate eradication strategies.

An obvious question arises when considering trigger harvest from a practical viewpoint: Does it matter where managers set the trigger levels? The overall consistency of the best strategies suggests that upper-trigger harvest performances were in fact quite robust to the actual trigger settings (Figs. 4b & 4c), so long as the trigger level was not set too low (Fig. 4a). Setting the upper-trigger level to the predator equilibrium P^* makes sense from a deterministic population dynamics perspective: as long as predator populations are kept below P^*, the prey population will tend to increase. Upper-trigger harvest lost its efficacy at very low upper-trigger levels because it was implemented too frequently, squandering its advantage of strategic timing (e.g., $u = 0.5P^*$, Fig. 4a).

Realistic Removal Targets and Upper-Trigger Harvest

The most striking outcome of our model was the reduction in performances of all strategies when removal targets were not met in full. This density-dependent removal shortfall could arise in practice for a number of reasons, such as reduced search efficiency or increased search costs with decreases in predator density. The performance reduction was particularly striking for the management options whose success depended on their ability to achieve extirpation: the fixed-number, lower-trigger, and immediate eradication strategies. The inability to extirpate populations at low densities enabled predator persistence by creating a numerical predator "refuge." Therefore, reduced removal success greatly diminished the success of these strategies across parameter space, and upper-trigger harvest often became the best strategy (Fig. 1). Reanalyzing the problem assuming that removal success increased sigmoidally with predator density (shape parameter $\theta = 4$) gave broadly similar results. The results were also generally insensitive to changes in the managers' half-saturation constant m, suggesting that any density dependence in managers' predator removal success may greatly impede the relative performance of the extirpation-reliant strategies. Irrespective of density-dependent removal, management performance may be limited more straightforwardly by budget constraints. Predator eradication was achievable if sufficient funding was available to ensure removal of all predators, even at low densities (Fig. 2a); immediate eradication was therefore the best strategy. In more budget-limited situations where removal success was imperfect, however, a suppression strategy such as upper-trigger harvest was preferable (Fig. 2c).

Caveats

To keep our findings general, we used a very general predator–prey model with many simplifying assumptions, some of which warrant further discussion. For example, we assumed that monitoring was carried out irrespective of the control strategy; therefore, we ignored monitoring costs when comparing strategies (contra Hauser et al. 2006). In reality, monitoring costs—and travel costs for monitoring, control, or both—will have different effects on the performance of the different strategies, especially for remote or island locations. Thus, the exact nature and interaction of costs may alter the efficiency of any strategy so that careful planning is necessary prior to its application.

A further simplification in our model was the adoption of a single management policy from the outset. Where immediate eradication is unlikely, combinations of different strategies may be more effective in some circumstances (Courchamp & Sugihara 1999) or management decisions that depend on a system "state" (e.g. population sizes) may be optimal. Although trigger-based strategies reflect state-dependent decision making to some extent, further insights may be gained from also including prey population size in the decision process, although there is some evidence that optimal predator control is independent of prey density (Stocker 1981). Again, the cost-effectiveness of such a flexible strategy may depend on the efficiency of monitoring the state of the system and on efficiency of control.

We used a simplified model structure to facilitate the analysis of a wide range of parameter settings and incorporation of stochasticity. For example, discrete time models are more representative of systems with nonoverlapping generations or in which densities can be considered constant between timesteps, such as systems with host-parasitoid systems; and approximating continuous-time systems with discrete-time models can generate large differences in dynamics (Gurney & Nisbet 1998; Turchin 2003). Therefore, the discrete time nature of this model may make its application more appropriate to pests with nonoverlapping generations. Our intent was to assess trade-offs between management strategies in a general sense, however, rather than to model a single system precisely. In any case care should always be taken before applying model results directly to specific situations. Nevertheless, the model could be extended to systems with overlapping generations by assuming stable age structure. May (1976) derived approximations for population-growth rates under these conditions (also see Bascompte et al. 2002).

Most of our simulations ignored the predator–prey functional response, but, when included, its effect on the relative performances of each strategy was slight (Figs 2b,d). Higher values of the half-saturation constant k stabilized the model (i.e., oscillations became more damped in the deterministic version of the model) and thus reduced the threat to the prey. Therefore, the expected minimum population size increased for all strategies (including no management) as k increased, and the ranking of strategies changed little. Immediate eradication performed best overall, but under the imperfect-removal scenario, upper-trigger harvest matched this performance (Fig. 2d). The consistency of the ranking of strategies under different strengths of the predator–prey functional response reflects the dominant role played by stochasticity in the model and emphasizes that immediate eradication and upper-trigger harvest are the best strategies to mitigate the effect of stochasticity on the prey population.

Another structural simplification was the assumption that no alternative prey species was available to the predator. The addition or removal of predators from an ecosystem can interact with existing interspecific dynamics (Kauhala et al. 1999; Roemer et al. 2002), and alternative prey species can sustain predator populations, making eradication difficult, while another prey population is decimated (Savidge 1987; Courchamp et al. 1999). If the main population dynamic role of the alternative prey species is to supplement predator population growth, however, then the relative merits of upper-trigger harvest should remain. Avoiding high predator population densities will assist in sustaining the vulnerable prey species, even in the presence of an alternative predator food source.

Summary and Recommendation

Conservation and population management can benefit from generalized rules of thumb (Sinclair & Krebs 2002). Our results suggest the following guideline. If outright eradication cannot be guaranteed—due to system dynamics, budget restrictions, or difficulty in removing the last few predators—then upper-trigger harvest is a desirable strategy, yielding the highest expected minimum prey population and the best return on investment in many circumstances.

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