

The economic value of ecological stability

Paul R. Armsworth[†] and Joan E. Roughgarden

Department of Biological Sciences, Stanford University, Stanford, CA 94305

Communicated by Kenneth J. Arrow, Stanford University, Stanford, CA, April 15, 2003 (received for review January 28, 2003)

Seemingly intangible ecosystem characteristics that preoccupy ecologists, like ecosystem stability and the responsiveness of populations to environmental variation, have quantifiable economic values. We show how to derive these values, and how their consideration should change environmental decision making. To illustrate these concepts, we use a simple reserve design model. When resource managers choose a particular landscape configuration, their decision affects both the mean abundance of species and the temporal variation in abundances. Population stability and related phenomena have economic value, because management actions affect the variance of ecosystem components. In our example, a larger reserve size is recommended when accounting for the stability of the managed ecosystem.

The dynamical stability of populations and ecosystems governs their responsiveness to fluctuating environmental conditions and determines with what reliability these natural resources provide life-sustaining services (1) to society. Population and ecosystem stability is thus a major structuring theme in ecology (2–5). An ecosystem that is only weakly stable will vary widely in response to a changing environment, but one that is more stable can be relied on to provide ecosystem services consistently. Weakly stable ecosystems will be prone to species extinctions (6) and thus could sustain less diverse biotas. Therefore, it is important that any impacts to the stability of ecosystems be considered when designing environmental management plans. However, we lack accounting frameworks that can evaluate ecosystem stability and factor it into environmental cost–benefit analyses. In this report, we develop such a framework and use it to illustrate when ecosystem stability has quantifiable economic value, and how consideration of that value should change environmental planning.

To illustrate our approach, we use a minimal model so that the ideas remain as transparent as possible. The model examines an idealized bird species that occupies a terrestrial reserve. The principles illustrated by this model are sufficiently general that they will underlie diverse management decisions ranging from marine reserve design (7) to the management of pollination services (8, 9).

General Theory

Consider an area of habitat (A with areal units chosen so that $A = 1$), part of which is to be set aside as a reserve (area R), and part of which is to be cleared for timber and then left fallow, with the proceeds from the clear-cutting invested elsewhere.[‡] Suppose the habitat contains a population of wild birds that can generate an annual revenue *in situ* (6), perhaps from ecotourism (10, 11), from a contingent or hedonic valuation of society's commitment to conservation (12), or through mitigation banking (13, 14). We assume that the birds cannot survive in cleared lands. Juveniles are born each year according to some density-dependent relationship, $f(N_t, R, a)$, where N_t is adult abundance, and parameter a describes environmental conditions. Juveniles disperse to find territories, and fraction $m(R)$ disperse into the cleared habitat where they die. Adults die each year at density-independent rate μ . The population dynamics are given by

$$N_{t+1} = f(N_t, R, a)(1 - m(R)) + (1 - \mu)N_t = g(N_t, R, a). \quad [1]$$

We restrict attention to functional forms for f and values of a for which the population has a single positive stable equilibrium, $\hat{N}(R)$, for any reserve size greater than the minimum needed to conserve it (15). The stability of the equilibrium is measured by the slope of g , $\lambda = \partial g / \partial N$. The larger the reserve, the larger and, typically, the more stable the equilibrium population.[§] Derivations can be found in the *Appendix*.

A social planner must decide what size a reserve should be. One basis for such a decision would be to maximize the total long-term economic yield both from clear-cutting and from the *in situ* value of the birds under some social discount rate, δ (16, 17). Suppose the price of timber is L per unit area clear-cut, and the annual revenue from the birds is $\pi(N_t)$. Then, the optimal reserve size satisfies

$$\delta L = \frac{\partial \pi}{\partial \hat{N}} \frac{d\hat{N}}{dR}. \quad [2]$$

By this condition, the return from clearing 1 more acre and investing the revenue elsewhere equals the return from placing that acre into the reserve and allowing a larger population of birds to flourish.

To examine the importance of stability, we extend the model to include environmental variability. We assume the number of offspring that survive to join the adult population varies in response to environmental conditions. We could model these fluctuations by perturbing population size N directly, by perturbing parameter a in f each year, or both (5).

The stochastic population dynamics are characterized by a stationary distribution in which the population fluctuates about a mean abundance \hat{N} that is set by the reserve size. The variance of population fluctuations, σ^2 , is always determined by the stability level, λ . The stability level determines how much of an initial impact the population will “remember” in subsequent years. If the perturbations are made to model parameters, then the variance is also determined by the sensitivity of the population to the environmental conditions, $\nu = \partial g / \partial a$. The environmental sensitivity of the population determines how large an impact a given fluctuation in environmental conditions has on N . Both the stability and environmental sensitivity of the population are determined by the size of the reserve.

Our condition for the optimal reserve size now becomes

$$\begin{aligned} \delta L &= \frac{d\mathcal{E}[\pi]}{dR} \\ &= \frac{\partial \mathcal{E}[\pi]}{\partial \hat{N}} \frac{d\hat{N}}{dR} + \frac{\partial \mathcal{E}[\pi]}{\partial \sigma^2} \frac{d\sigma^2}{dR} \\ &= \frac{\partial \mathcal{E}[\pi]}{\partial \hat{N}} \frac{d\hat{N}}{dR} + \frac{\partial \mathcal{E}[\pi]}{\partial \sigma^2} \left(\frac{\partial \sigma^2}{\partial \lambda} \frac{d\lambda}{dR} + \frac{\partial \sigma^2}{\partial \nu} \frac{d\nu}{dR} \right), \quad [3] \end{aligned}$$

[†]To whom correspondence should be addressed. E-mail: armsworth@stanford.edu.

[‡]Here, we examine a tradeoff between an initial liquidation of natural capital and a single sustainable use of land, but our approach could be adapted to compare alternative sustainable land uses.

[§]The equilibrium is said to be stable if $|\lambda| < 1$ and unstable if $|\lambda| > 1$. Population stability increases as $|\lambda| \rightarrow 0$, and the population becomes progressively less stable as $|\lambda|$ increases toward 1.

where ε is the expectation operator (*Appendix*), or, in words,

$$\begin{aligned}
 \left[\begin{array}{c} \text{Marginal value of} \\ \text{clearing 1 more acre} \end{array} \right] &= \left[\begin{array}{c} \text{Marginal value of} \\ \text{conserving 1 more acre} \end{array} \right] \\
 &= \left[\begin{array}{c} \text{Marginal value of} \\ \text{conserving 1 more acre} \\ \text{via increased} \\ \text{mean bird abundance} \end{array} \right] + \left[\begin{array}{c} \text{Marginal value of} \\ \text{conserving 1 more acre} \\ \text{via change in variance} \\ \text{of bird abundance} \end{array} \right] \\
 &= \left[\begin{array}{c} \text{Marginal value of} \\ \text{conserving 1 more acre} \\ \text{via increased} \\ \text{mean bird abundance} \end{array} \right] + \left[\begin{array}{c} \text{Marginal value of} \\ \text{conserving 1 more acre} \\ \text{via change in variance} \\ \text{of bird abundance} \\ \text{via increased stability} \end{array} \right] \\
 &+ \left[\begin{array}{c} \text{Marginal value of} \\ \text{conserving 1 more acre} \\ \text{via change in variance} \\ \text{of bird abundance} \\ \text{via environmental sensitivity} \end{array} \right]. \tag{4}
 \end{aligned}$$

The first term on the right-hand side of the expanded form of Eq. 3 represents the marginal expected value of adding another acre to the reserve that arises from the change to the mean population size. A similar term appears on the right-hand side of Eq. 2. However, the remaining two contributions are new and reflect the change to the variance of the population. The second term represents the marginal value of stability; it is the value from adding 1 more acre to the reserve that arises because the stability of the bird population changes and results in a change in the population variance. Likewise, the third term represents the value of the change in the environmental sensitivity of the population from conserving another acre.[†]

Economic theory that ignored environmental variation would recommend a reserve size that satisfies Eq. 2. However, in a fluctuating environment, the economically optimal reserve size is given by Eq. 3. This equation is new and different to the deterministic recommendation and often will result in larger reserves being recommended. Larger reserves are recommended because of the additional value associated with variance components like stability.

Our method contrasts with the conventional economic approach to resource management in fluctuating environments. The conventional approach would assume that managers could control natural variation and respond to future environmental conditions by shifting reserve boundaries once those conditions have been revealed in annual population counts (18–21). However, if it is excessively costly to adjust reserve boundaries each year, then an approach is required that considers an ecosystem’s intrinsic dynamics. Eq. 3 provides such an approach by accounting for the additional value offered by stable ecosystems through their reduced susceptibility to environmental variation. To obtain Eq. 3, we developed the opposing extreme of noninterventionist control to emphasize the difference between the two situations. However, we anticipate a continuum of partial control scenarios that spans the poles from perfectly responsive to unresponsive management (22, 23). The importance of maintaining stable populations will increase when traversing the continuum from responsive to unresponsive management by consideration of different ecological and institutional contexts.

An important intermediate case between the two extremes of responsive and unresponsive management arises when reserve boundaries can be shifted incrementally but unidirectionally,

because habitat destruction is irreversible. Our reserve design problem is reminiscent of Arrow and Fisher’s classic treatment of quasi-option value in such a development context (24) and of subsequent generalizations of their work (25). Our model makes clear, however, that stability and option values are distinct from one another, because, although stability value can be important here, there is no option value. There is no option value in our particular model, because the uncertainty is assumed irreducible, and the development rule is inflexible. However, in general, stability and option values will be complementary, and both will need to be considered in a full accounting framework. It would be interesting to explore any interactions between the two value sources along approach paths to long-run development equilibria.

Example

To illustrate the consequences of valuing the variance components, we specify functional forms in the model. For what follows, we assume that per capita fecundity decreases linearly with population density as resources, such as nest sites, become limiting, $f = aN(1 - N/(RK))$. Moreover, we assume that intrinsic fecundity fluctuates in response to average regional temperature by perturbing a each year. We assume that juveniles disperse smoothly over the whole area, $m = 1 - R$. We consider two *in situ* revenue functions: (i) a linear function in which there is a fixed price per bird; and (ii) a function in which each additional bird is worth progressively less, either in terms of conservation value or from tourism revenues;

$$(i) \pi = pN \quad (ii) \pi = p(1 - e^{-\alpha N}). \tag{5}$$

If the *in situ* revenue depends linearly on the population size (case i), it is optimal either to designate the entire area a reserve ($R = 1$) or to clear-cut it ($R = 0$). Which of these alternatives is preferable depends on the relative prices of birds and timber and on the discount rate. The reason that one of the two extreme solutions is optimal is that for every acre considered, either the timber value or the *in situ* value of the birds is greater, and the linearity of π ensures that the rank ordering of these values is always the same. When environmental conditions vary, the expected overall revenue is identical to the overall revenue obtained in a constant environment. Therefore, there is no economic value to stability in this case, and the optimal reserve size is unchanged when environmental variability is included. No change occurs, because the linear social objective is sensitive not to the variance in population sizes but only to the mean.

If investments in the reserve yield a diminishing return (case ii), one must first examine whether any such investment is warranted. As environmental variability is increased, the conditions that must be met for investment in the reserve to prove worthwhile become more stringent, and clear-cutting becomes an increasingly attractive option. The conditions for investment in conservation become more restrictive, because the *in situ* value of the population diminishes when it is often scarce due to natural fluctuations in abundance (Fig. 1).

Provided that some investment in the population is worthwhile, an intermediate reserve size is often optimal in the case of diminishing returns (Eq. 5, case ii) (Fig. 1). The optimal reserve size balances potential increases from the two revenue streams. So long as the bird population continues to offer a competitive investment, it is usually optimal to set aside a larger reserve in variable environments than is desirable in the special case of a constant environment (Figs. 1 and 2). In part, the increase in the optimal reserve size can be attributed to the increase in stability in larger reserves. However, stability cannot be increased in isolation, and one must account for the full suite of changes in ecosystem attributes that accompany an increase in reserve size.

[†]If N is perturbed directly, then this third term is zero.

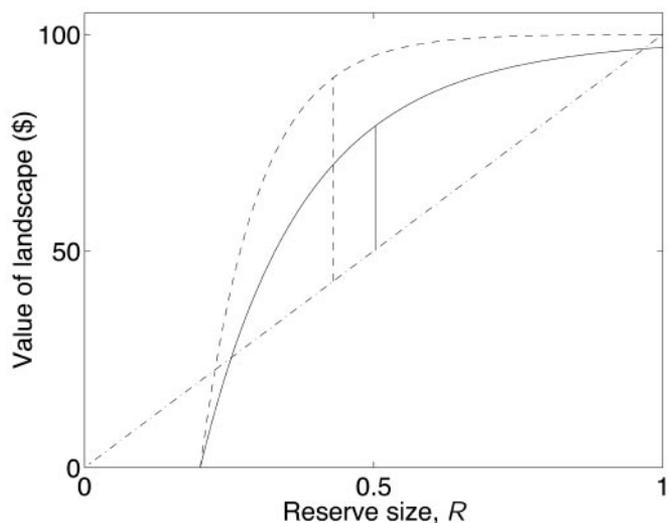


Fig. 1. Present value of *in situ* revenues (Eq. 5, case *ii*) for a constant environment (dashed curve) and opportunity cost in lost timber revenue (dot-dash line) as functions of reserve size. The optimal reserve size maximizes the difference between the revenue and the opportunity cost (vertical dashed line). In a variable environment, the expected present value of *in situ* revenues (solid curve) is less than for a constant environment, but the optimal reserve size can be greater (solid vertical line). Parameters are $[a, K, \mu, \delta, p, \alpha, L] = [0.5, 100, 0.1, 0.05, 5, 0.1, 100]$, and $CV(a) = 3$ (solid).

When choosing among particular landscape configurations, managers are choosing among different bundles of ecosystem attributes. These attributes include a mean population size, a stability level, and an associated degree of sensitivity to the environment. At the optimum, the marginal value of these attributes when summed across the entire bundle must equal the marginal value of clearing 1 more acre (Eq. 3). Optimal bundles of attributes are illustrated in Fig. 3 as the variability in the environment is increased. Note that in our particular example,

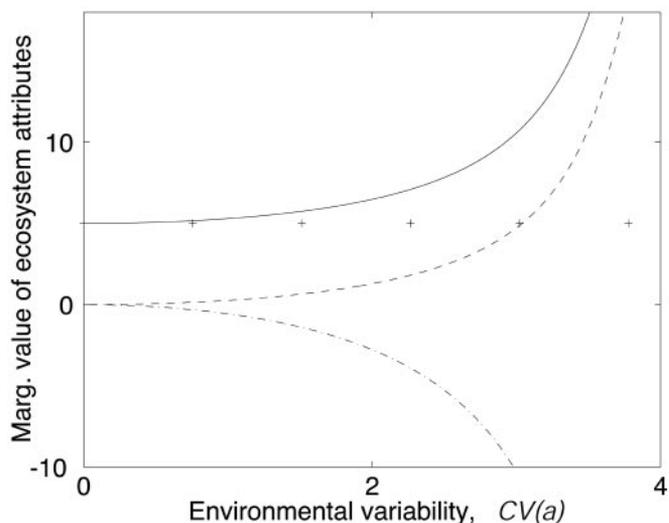


Fig. 3. Marginal values of ecosystem attributes in the optimal solution as $CV(a)$ increases to the point at which a reserve ceases to be worthwhile ($CV(a) > 3.8$). Marginal values of changes to the mean (solid curve), stability (dashed), and environmental sensitivity (dot-dash) of the population, which sum to equal the marginal value of clearing 1 more acre for timber (crosses). Case *ii* (Eq. 5), with parameters $[a, K, \mu, \delta, p, \alpha, L] = [0.5, 100, 0.1, 0.05, 5, 0.1, 100]$.

the marginal values of stability and environmental sensitivity are of opposing sign. The stability of the population increases with increasing reserve size, which enhances the value of larger reserves in fluctuating environments. However, increasing the size of the reserve exposes a larger population of birds to fluctuating climatic conditions, and thereby any particular environmental fluctuation initially induces a greater change in population size; i.e., the environmental sensitivity of the population also increases. Even when accounting for the increase in environmental sensitivity, a larger reserve size is optimal in fluctuating environments than is optimal in a constant environment, provided that we are below the threshold level of environmental variability above which no reserve is worthwhile (Fig. 2). However, the relationship between environmental variability and optimal reserve size is not monotonic, and the downturn in optimal reserve size in highly variable environments (Fig. 2) is caused by the interplay between the different ecosystem attributes.

Conclusion

The suite of ecosystem characteristics chosen with some management decision determines the quality of ecosystem services provided to society (1). For efficient decision making, managers must account for the full bundle of ecosystem attributes that are affected by any management actions. Often, economic studies have focused only on the consequences of changes to mean population size and not on additional attributes like population variances. In our example, the variance components inherit their value via the nonlinear revenue function. Alternatively, variance might be valued directly, if society prefers environmental portfolios that ensure reliable provision of ecosystem services (26). We obtain a value for stability and environmental sensitivity under an assumption of risk neutrality. Stability values could be even more important if social planners were risk averse. It would be interesting to examine the values of variance components for other ecosystem services, such as the provision of fresh water, for which there may be few readily available substitutes and for which one would need to generalize stability concepts to more complex ecosystems.

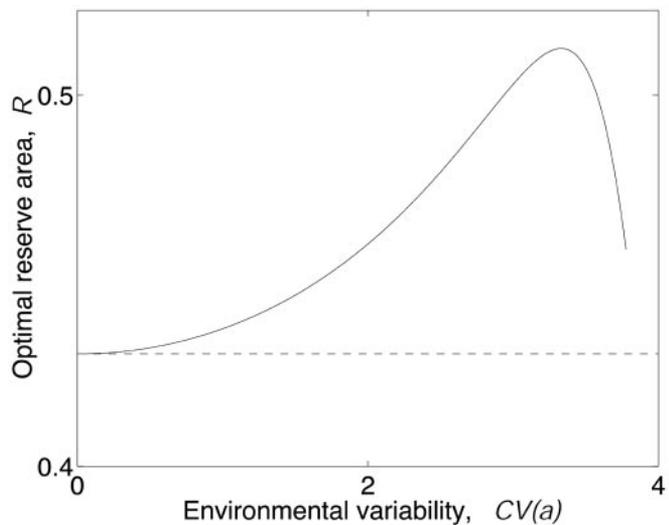


Fig. 2. Optimal reserve size as a function of environmental variability, $CV(a)$ (solid curve). The dashed line indicates the corresponding optimal reserve size in a constant environment. For modest amounts of environmental variability, larger reserves are favored in fluctuating environments. If environmental fluctuations are too violent ($CV(a) \geq 3.8$), then no reserve is optimal, and the curve jumps to zero. Case *ii* (Eq. 5), with parameters $[a, K, \mu, \delta, p, \alpha, L] = [0.5, 100, 0.1, 0.05, 5, 0.1, 100]$.

In the specific context of reserves, we argue that the impact of management actions on the variation in ecosystem components should be accounted for in reserve design. The management philosophy embodied in this approach is one of “living with” variation (7) and contrasts with an alternative tradition in natural resource management of trying to minimize and control natural variation (18). Because managers must always confront some residual natural variability, approaches that value natural variation and account for it explicitly in environmental decision making are urgently needed.

Appendix

Here we provide details of the derivations.

Deterministic Model. The deterministic dynamics are given by Eq. 1 and, by assumption, are characterized by the existence of two equilibria $N = 0$ and the solution, \hat{N} , of

$$\mu N = f(N, a, R)(1 - m).$$

The former is stable for reserve sizes below some critical threshold, and the latter is stable and positive above the threshold. The positive equilibrium is stable whenever the magnitude of eigenvalue

$$\lambda = 1 + \left. \frac{\partial f}{\partial N} \right|_{\hat{N}} (1 - m) - \mu$$

is less than 1.

The revenue from clear-cutting area $(1 - R)$ at time zero is $L(1 - R)$. The annual revenue from birds is $\pi(N_t)$. Therefore, the present value of both ecosystem services is

$$V(R) = L(1 - R) + \sum_{t=0}^{\infty} \frac{\pi(N_t)}{(1 + \delta)^{t+1}} \approx L(1 - R) + \frac{\pi(\hat{N})}{\delta},$$

where for brevity we have assumed rapid convergence to the equilibrium population size after clear-cutting. Therefore, maximizing V with the choice of R requires that Eq. 2 be satisfied.

Stochastic Model. If parameter a in f is perturbed each year, then the stochastic dynamics are

$$\begin{aligned} \hat{N} + n_{t+1} &= f(\hat{N} + n_t, a + \varepsilon_t, R)(1 - m) + (1 - \mu)(\hat{N} + n_t) \\ &= g(\hat{N} + n_t, a + \varepsilon_t, R), \end{aligned}$$

where $n_t = N_t - \hat{N}$ describes the deviation of the population size at time t from equilibrium \hat{N} . By linearizing about the equilibrium, we can approximate the dynamics with the first-order autoregressive process

$$n_{t+1} = \left. \frac{\partial g}{\partial N} \right|_{\hat{N}} n_t + \left. \frac{\partial g}{\partial a} \right|_{\hat{N}} \varepsilon_t = \lambda n_t + \nu \varepsilon_t$$

(27). If N is perturbed directly, then $\nu = 1$ in this equation. This approximation performs best in the vicinity of the equilibrium and deteriorates as perturbations from equilibrium become larger. We assume that the environmental fluctuations ε_t are independent identically distributed normal random variables, which implies that the distribution of population sizes will converge to a normal distribution with mean \hat{N} and variance

$$\sigma^2 = \frac{\nu^2 \sigma_\varepsilon^2}{1 - \lambda^2}$$

(27). For brevity, we assume that convergence to this stationary distribution occurs rapidly after clear-cutting.

By assuming rapid convergence, we focus on the long-run equilibrium outcome of development and neglect considerations of the approach path taken to this equilibrium. For local reserve design decisions, our assumption of rapid population decline after clear-cutting seems reasonable. However, when considering larger-scale environmental planning decisions and sustainability questions, it will be important to extend the current work to consider dynamics during the development process itself (25).

We assume that the objective is to maximize the expected present value from both services,

$$\begin{aligned} \mathcal{E}[V] &= \mathcal{E} \left[L(1 - R) + \sum_{t=0}^{\infty} \frac{\pi(N_t)}{(1 + \delta)^{t+1}} \right] \\ &\approx L(1 - R) + \frac{\mathcal{E}[\pi(N)]}{\delta}, \end{aligned}$$

where we have taken the expectation of a linear combination of random variables and relied on our assumption of rapid convergence. Maximizing $\mathcal{E}[V]$ with the choice of reserve size requires satisfying Eq. 3. If π is linear in N (Eq. 5, case i), then $\mathcal{E}[\pi(N)] = \pi(\mathcal{E}[N])$, and the present value of the land parcel is the same for the deterministic and stochastic environments. However, this equivalence breaks down if π depends nonlinearly on N (Eq. 5, case ii). If π is nonlinear, then the present value will depend on both the expectation and variance of the population abundance for the stochastic environment (28).

When performing the optimization, we assume that the environment varies over shorter time scales than those over which reserve design decisions are made. Specifically, we assume that managers meet to agree and legislate on a landscape plan, and that once that plan is enforced, it is difficult or expensive to reconvene the legislature to redefine reserve boundaries should more information on the bird population become available. If management were sufficiently flexible that reserve boundaries could be altered over similar time scales to those on which the environment varies, then a more sophisticated dynamic programming approach would be required (20, 25).

Example. Suppose that $f = aN(1 - N/(RK))$, $m = 1 - R$, and parameter a is perturbed. Then for a reserve of size R ,

$$\hat{N} = K \left(R - \frac{\mu}{a} \right), \quad \lambda|_{\hat{N}} = 1 - aR + \mu, \quad \text{and} \quad \nu = \frac{K\mu}{a} \left(R - \frac{\mu}{a} \right).$$

Below minimum reserve size μ/a , the population of birds goes extinct, and above it, a stable population can be maintained.

In case ii (Eq. 5), the present value of the two services in a constant environment is

$$V = \begin{cases} L(1 - R) & \text{if } R < \mu/a \\ L(1 - R) + \frac{P}{\delta} (1 - e^{-\alpha \hat{N}}) & \text{otherwise.} \end{cases}$$

A local maximum of V is given by the solution of Eq. 2,

$$R^* = \frac{1}{\alpha K} \log \frac{p\alpha K}{\delta L} + \frac{\mu}{a}.$$

For an investment in the reserve to be worthwhile, we require that $V(R^*) \geq L$ for $R^* \leq 1$ and $V(1) \geq L$ for $R^* > 1$. Provided an intermediate reserve size is optimal, then it is given by R^* , and if $R^* \geq 1$ and $V(1) > L$, then it is optimal to conserve the entire area.

When environmental conditions fluctuate, the expected present value of the land parcel is

$$\varepsilon[V] = \begin{cases} L(1 - R) & \text{if } R < \mu/a \\ L(1 - R) + \frac{p}{\delta} (1 - e^{-\alpha(\hat{N} - \alpha\sigma^2/2)}) & \text{otherwise.} \end{cases}$$

It can be seen from this expression that the overall value of a reserve decreases as environmental variability, σ_s , increases and results in an increase in σ . This finding results from the concavity of function π in case *ii*.

A local maximum of $\varepsilon[V]$ is given by the solution, R^* , of Eq. 3, which becomes

$$\delta L = p\alpha e^{-\alpha(\hat{N} - \alpha\sigma^2/2)} \left(K + \frac{a\alpha\sigma^2\lambda}{1 - \lambda^2} - \frac{\alpha\sigma^2}{R - \mu/a} \right).$$

The criterion that must be satisfied for investment in a reserve to be worthwhile is that $\varepsilon[V(R^*)] \geq L$ for $R^* \leq 1$ or $\varepsilon[V(1)] \geq$

L for $R^* > 1$. Provided that an intermediate reserve size is optimal, then it is given by R^* , or again, the extreme solution, $R = 1$, could be optimal.

The first term on the right-hand side of the above equation is the marginal value of the change to the mean population size due to an increase in reserve size; the second term is the value of the change to population stability; and the third is the value of the change to environmental sensitivity (Fig. 3, solid, dashed, and dot-dash curves, respectively). The marginal value of clearing 1 more acre appears on the left-hand side of the equation (Fig. 3, crosses).

We thank K. Arrow, W. Brock, L. Buckley, G. Daily, P. Ehrlich, P. Higgins, M. James, C. Kappel, F. Micheli, P. Munday, H. Pereira, and two anonymous reviewers for useful suggestions for improving the manuscript. P.R.A. thanks the U.K.–U.S. Fulbright Commission for support.

- Daily, G. C. (1997) *Nature's Services: Societal Dependence on Natural Ecosystems* (Island Press, Washington, DC).
- May, R. M. (1974) *Stability and Complexity in Model Ecosystems* (Princeton Univ. Press, Princeton), 2nd Ed.
- Pimm, S. L. (1991) *The Balance of Nature? Ecological Issues in the Conservation of Species and Communities* (Univ. Chicago Press, Chicago).
- Tilman, D. (1996) *Ecology* **77**, 350–363.
- Ives, A. R. & Hughes, J. B. (2002) *Am. Nat.* **159**, 388–395.
- Roughgarden, J. & Armsworth, P. R. (2001) in *Ecology: Achievement and Challenge*, eds. Press, M. C., Huntly, N. & Levin, S. (Blackwell Scientific, Oxford), pp. 337–356.
- Lauck, T., Clark, C. W., Mangel, M. & Munro, G. R. (1998) *Ecol. Appl.* **8**, S72–S78.
- Southwick, E. E. & Southwick, L., Jr. (1992) *J. Econ. Entomol.* **85**, 621–633.
- Kremen, C., Williams, N. M. & Thorp, R. W. (2002) *Proc. Natl. Acad. Sci. USA* **99**, 16812–16816.
- Munn, C. A. (1991) in *New World Parrots in Crisis*, eds. Beissinger, S. R. & Snyder, N. F. R. (Smithsonian Institution, Washington, DC), pp. 47–72.
- Bibby, C. (2002) in *Conserving Bird Biodiversity: General Principles and Their Application*, eds. Norris, K. & Pain, D. J. (Cambridge Univ. Press, Cambridge, U.K.), pp. 20–33.
- Goulder, L. H. & Kennedy, D. (1997) in *Nature's Services: Societal Dependence on Natural Ecosystems*, ed. Daily, G. C. (Island Press, Washington, DC), pp. 23–47.
- Bonnie, R. (1999) *Sci. Total Environ.* **240**, 11–19.
- Bean, M. J. & Dwyer, L. E. (2000) *Environ. Law Rev.* **30**, 10537–10556.
- Skellam, J. G. (1951) *Biometrika* **38**, 196–218.
- Armsworth, P. R. & Roughgarden, J. (2001) *Trends Ecol. Evol.* **16**, 229–234.
- Goulder, L. H. & Stavins, R. H. (2002) *Nature* **419**, 673–674.
- Reed, W. J. (1979) *J. Environ. Econ. Manage.* **6**, 350–363.
- Walters, C. J. (1986) *Adaptive Management of Renewable Resources* (Macmillan, New York).
- Clark, C. W. (1990) *Mathematical Bioeconomics: The Optimal Management of Renewable Resources* (Wiley, New York), 2nd Ed.
- Williams, B. K. (2001) *Environ. Ecol. Stat.* **8**, 269–288.
- Walters, C. J. (1978) in *Dynamic Programming and Its Applications*, ed. Puterman, M. L. (Academic, New York), pp. 233–246.
- Ludwig, D. (1980) *J. Cons. Int. Explor. Mer* **39**, 168–174.
- Arrow, K. J. & Fisher, A. C. (1974) *Quart. J. Econ.* **88**, 312–319.
- Scheinkman, J. A. & Zariphopoulou, T. (2001) *J. Econ. Theory* **96**, 180–207.
- May, R. M., Beddington, J. R., Horwood, J. W. & Shepherd, J. G. (1978) *Math. Biosci.* **42**, 219–252.
- Roughgarden, J. (1975) *Am. Nat.* **109**, 713–736.
- Ang, A. H. S. & Tang, W. H. (1975) *Probability Concepts in Engineering Planning and Design* (Wiley, New York), Vol. 1.