

# Theory for Designing Nature Reserves for Single Species

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**ABSTRACT:** We examine the question of the optimal number of reserves that should be established to maximize the persistence of a species. We assume that the mean time to extinction of a single population increases as a power of the habitat area, that there is a certain amount of habitat to be reserved, and that the aim is to determine how this habitat is most efficiently divided. The optimal configuration depends on whether the management objective is to maximize the mean time to extinction or minimize the risk of extinction. When maximizing the mean time to extinction, the optimal number of independent reserves does not depend on the amount of available habitat for the reserve system. In contrast, the risk of extinction is minimized when individual reserves are equal to the optimal patch size, making the optimal number of reserves linearly proportional to the amount of available habitat. A model that includes dispersal and correlation in the incidence of extinction demonstrates the importance of considering the relative rate at which these two factors decrease with distance between reserves. A small number of reserves is optimal when the mean time to extinction increases rapidly with habitat area or when risks of extinction are high.

**Keywords:** extinction risk, fragmentation, metapopulation, reserve design, SLOSS.

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There is ongoing analysis in the conservation literature about how to design conservation reserves to maximize benefits to biodiversity. Arguments encompass the aims of

representing a range of habitat types and different elements of biodiversity (Pressey et al. 1993; Possingham et al. 2000) through to determining the optimal spatial configuration to minimize risks of extinction (Quinn and Hastings 1987; Gilpin 1988; Burgman et al. 1993; Pressey et al. 1993; McCarthy and Lindenmayer 1999; Ovaskainen 2002). Even in the relatively simple case when all parts of the proposed reserve network are identical and the aim is to minimize the extinction risk or maximize the mean time to extinction of a single species, the optimal reserve system appears to be case-specific. The solution seems to depend on a large number of interacting factors, and general solutions are not apparent (Burgman et al. 1993).

There have been a few attempts at deriving general solutions to determine the optimal spatial arrangement of a metapopulation. Quinn and Hastings (1987) used a log-linear relationship between mean time to extinction and population size (Leigh 1981) to show that mean time to extinction of a metapopulation of equi-sized patches was maximized when the number of patches was equal to the square root of the total carrying capacity. This means that the carrying capacity of each reserve should equal the number of reserves (i.e., if total carrying capacity is 100, the optimal number of patches is 10, each with a carrying capacity of 10), which is a substantial level of fragmentation. The model of Quinn and Hastings (1987) ignored demographic stochasticity and did not include migration or spatial correlation in environmental variability. On these and other grounds, Gilpin (1988) argued that a reserve system based on the model of Quinn and Hastings (1987) may be dangerously fragmented.

The model of Quinn and Hastings (1987) is based on only one of several possible functional forms for predicting the expected time to extinction for a given carrying capacity. Other extinction models result in different conclusions. For example, Lande (1993) proposed a more general extinction model that included environmental variability, and demonstrated that mean time to extinction ( $M$ ) for a single population exposed to environmental stochasticity may be approximated by

$$M = \frac{2K^b}{\sigma^2 b^2}, \quad (1)$$

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where  $b = (2\bar{r}/\sigma^2) - 1$ ,  $\bar{r}$  is the mean growth rate,  $\sigma^2$  is the variance in growth rate, and  $K$  is the carrying capacity of the population. McCarthy (1995; see also McCarthy and Lindenmayer 1999) used this extinction model and the method of Quinn and Hastings (1987) to demonstrate that the expected time to extinction of a reserve system is maximized for small  $b$  when the number of reserves ( $n$ ) is approximately equal to

$$n^* = e^{1/b}. \quad (2)$$

In this case, the optimum number of reserves is independent of the carrying capacity of the reserve network but depends on  $b$ , a linear function of the ratio of the mean growth rate to the variance in the growth rate. As the variance in growth rate increases (i.e., as  $b$  becomes smaller), the optimal number of reserves increases.

In the model of Lande (1993), mean time to extinction is a power function of population size (or its surrogate, habitat area). Ovaskainen (2002) also used a power function to represent the relationship between reserve size and mean time to extinction but extended the analysis to include colonization of extinct reserves. A key result was that the optimal reserve configuration was primarily driven by the scaling exponents that described how changes in patch area influenced extinction, immigration, and emigration. A potential limitation of this work was a focus on deterministic analyses rather than an accounting for stochasticity that may be especially important when the number of reserves is finite.

Etienne and Heesterbeek (2000) also considered persistence of a metapopulation in the presence of dispersal, and they determined the size of reserves that maximized two different possible objectives: the time to extinction and the colonization potential of occupied patches. Ovaskainen (2002) also had the objective of maximizing the time to extinction and analyzed a second objective of maximizing the metapopulation capacity of the reserve, a quantity similar to the colonization potential used by Etienne and Heesterbeek (2000). Both Etienne and Heesterbeek (2000) and Ovaskainen (2002) found that the optimal reserve configuration depended on the chosen objective.

While it can be important to include dispersal when determining the optimal reserve size, previous studies have assumed that extinction events occur independently among patches (Etienne and Heesterbeek 2000; Ovaskainen 2002). However, if patches are close enough for colonization to occur, it is likely that extinctions will not be independent (e.g., Hof and Flather 1996). Positive correlation in the incidence of extinction will tend to counteract the benefit of increased numbers of small reserves.

Bascompte et al. (2002) determined the minimum num-

ber of patches required for a positive geometric mean growth rate in a metapopulation when every patch is identical and the patches are well connected. While their analysis examined the question of the number of necessary patches, it did not address the question of the trade-off between patch size and number. Bascompte et al. (2002) ignored the effect of density dependence, so there would be no effect of changing patch size. The question was how many equi-sized patches were necessary for persistence, rather than how big they should be.

In this article, we derive general solutions to determine the number of reserves that minimizes the risk of extinction of a metapopulation and solutions that maximize the mean time to extinction when there is a certain amount of habitat that can be reserved and dispersal does not occur. We also derive solutions to determine whether establishing two reserves is a better strategy than establishing a single reserve of the same total area. These latter solutions are obtained for the case in which there is no dispersal between the local populations and also when there is dispersal and positive correlation in the incidence of extinction.

We obtain simple expressions for the number or size of reserves that maximizes the mean time to extinction or minimizes extinction risk for reserves without dispersal or spatial correlation. While Etienne and Heesterbeek (2000) and Ovaskainen (2002) show the importance of the choice of objective, we demonstrate the unexpected result that a reserve system that maximizes the mean time to extinction does not necessarily minimize the extinction risk. We also demonstrate that a model without dispersal and spatial correlation in the incidence of extinction provides a reasonable approximation for cases that include these attributes provided that the rate of dispersal declines faster than the spatial correlation in the incidence of extinction.

## Model

The basis of our solutions is a power relationship between mean time to extinction and the area of a patch ( $A$ , as a surrogate for  $K$ , eq. [1]) that contains a single population (Lande 1993; Cook and Hanski 1995),

$$M = aA^b, \quad (3)$$

where  $a$  and  $b$  are constants. This model is supported both theoretically (Lande 1993) and empirically (Cook and Hanski 1995). Values of  $b$  appear to range commonly between 0.5 and 2.5 (Cook and Hanski 1995), although larger and smaller values may be possible.

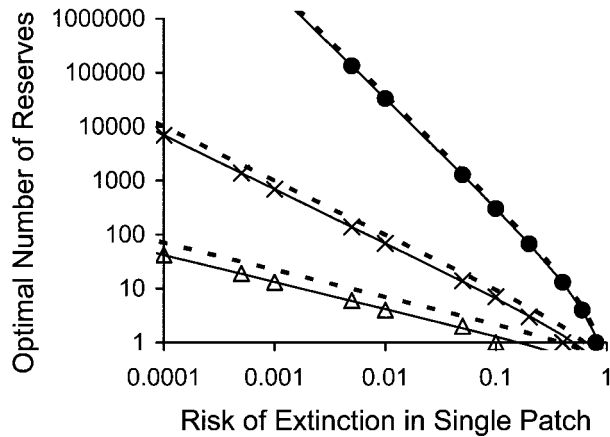


Figure 1: Optimal number of reserves in the absence of dispersal versus the risk of extinction if the total area of habitat were placed in a single reserve  $(1 - p)$  for different values of the scaling exponent:  $b = 0.5$  (circles),  $b = 1.0$  (crosses),  $b = 2.0$  (triangles). The symbols are exact solutions treating  $n$  in equation (6) as a discrete variable; the solid lines were obtained by treating  $n$  as a continuous variable (eq. [8]). The broken lines are approximations obtained by using equation (9).

*Extinction Risk*

Assuming that there is no dispersal between patches and that extinction is a Poisson process, the probability of persistence of a single reserve over time frame  $T$  can be expressed as

$$p = \exp\left(-\frac{T}{M}\right), \tag{4}$$

where  $T$  is the time frame of interest and  $M$  is given by equation (3). Using Lagrange minimization, it can be shown that the overall extinction risk is minimized when all the reserves are the same size (see the appendix in the online edition of the *American Naturalist*). We assume that there is a budget of available habitat ( $H$ ) that can be divided into  $n$  patches of equal area ( $A = H/n$ ). It follows from equations (3) and (4) that the probability of persistence of each reserve is

$$y = p^{(n^b)}, \tag{5}$$

where  $p$  is the probability of persistence if all the habitat were placed in a single reserve. Therefore, the chance of extinction of all patches, assuming they are independent, is equal to

$$f(n) = [1 - y]^n = \left\{1 - \exp\left[-\frac{T}{a} \left(\frac{n}{H}\right)^b\right]\right\}^n. \tag{6}$$

For given  $p$  and exponent  $b$ , it is then a straightforward matter to determine (numerically) the integer value of  $n$  that minimizes the risk of extinction ( $f(n)$ ; fig. 1). For example, when  $b = 1$  and  $p = 0.75$ , one finds that  $f(n)$  is minimized when  $n = 2$ .

Conditions under which two patches are better than one of the same total size may be determined by comparing the chance of both patches going extinct to the chance of the single patch going extinct. Two patches are preferred if

$$[1 - p^{(2^b)}]^2 < 1 - p,$$

which leads to the inequality

$$b < \frac{\ln\{\ln[1 - \sqrt{1 - p}]/\ln p\}}{\ln 2}.$$

Again, when  $b = 1$ , this is equivalent to  $p > (5^{1/2} - 1)/2 = 0.618$  (the golden mean). Thus, when minimizing the risk of extinction, more than one reserve is preferred when the probability of persistence is sufficiently high if all the available habitat were placed in a single reserve (fig. 2).

A useful approximation in determining the optimal number of reserves can be obtained by treating  $n$  in equation (6) as a continuous variable. Thus, if we differentiate

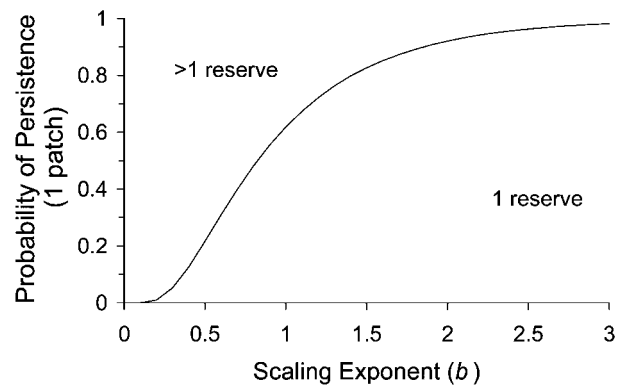


Figure 2: The optimal reserve configuration for different parameter combinations of the scaling exponent ( $b$ ) and probability of persistence when all habitat is in one reserve ( $p$ ). One reserve is optimal for minimizing the risk of extinction, in the absence of dispersal, for parameter combinations below the line.

$f(n)$  with respect to  $n$  and set the resulting expression equal to 0, we obtain

$$by^* \ln y^* = (1 - y^*) \ln(1 - y^*), \text{ or}$$

$$b = \frac{E^* \ln E^*}{(1 - E^*) \ln(1 - E^*)} \quad (7)$$

(see appendix), where  $E^* = 1 - y^*$  is the optimal risk of local extinction. Equation (7) means that for a given value of  $b$  (the parameter describing the rate at which the mean time to extinction increases with patch area), there is an optimal risk of local extinction (see fig. A1 in the online edition of the *American Naturalist*). Equation (7) may be solved for  $E^*$  numerically or approximated by expressing  $\ln E^*$  as a linear function of  $b$  (see the appendix).

Once the optimal risk of local extinction is determined for a given value of  $b$ , and assuming a given total reserve area (and therefore a given  $p$ ), there is an optimal number of patches,

$$n^* = \left[ \frac{\ln(1 - E^*)}{\ln p} \right]^{1/b} \quad (8)$$

(appendix; fig. 1).

An approximation for equation (8) is

$$n^* \approx \left[ -\frac{1}{b \ln p} \right]^{1/b} \quad (9)$$

(appendix), which is valid when  $p^{(n^*)}$  is small.

Given that there is an optimal risk of local extinction, this optimal risk corresponds to a particular size for each reserve, which we refer to as the optimal reserve size. This optimal reserve size will be overestimated if catastrophic extinctions occur that are independent of the size of the reserve. Such catastrophes can be included in the above model by assuming that they occur independently among local reserves. If the local reserves face the same risk of catastrophe, then let  $s$  be the probability of avoiding a catastrophic extinction at each reserve within the time frame of the analysis ( $1 - s$  is the probability of a catastrophic extinction occurring). Therefore, the chance of a species remaining in each reserve is equal to  $sy$ , and the probability of extinction in all reserves is given by  $f(n) = (1 - sy)^n$ . The optimal reserve size decreases as  $s$  varies from 1 to 0, but the influence of  $s$  is relatively weak. If the same approximation as in equation (9) is used,  $s$  has no influence on the optimal reserve design. In fact, equation (9) is the limiting solution as  $s$  approaches 0 for the equation  $f(n) = (1 - sy)^n$  (i.e., as persistence becomes dominated by catastrophes rather than reserve area).

Therefore, in the presence of catastrophes, the optimal number of reserves will lie between the solutions provided by equation (8), assuming  $s = 1$ , and equation (9), assuming  $s = 0$ .

### Mean Time to Extinction

The mean time to extinction of  $n$  patches ( $M_n$ ) can be obtained by integrating  $1 - f(n)$  over the time horizon variable  $T$  (eqq. [3] and [4]). This results in the expression

$$M_n = aH^b n^{-b} \left( 1 + \frac{1}{2} + \frac{1}{3} + \dots + \frac{1}{n} \right) \quad (10)$$

(see also Quinn and Hastings 1987).

Again, for given  $b$ , it is not difficult to determine the integer  $n$  that maximizes  $M_n$ . For example, when  $b = 1$ , it is more or less obvious that the optimal  $n$  is unity. A simple calculation comparing  $M_1$  and  $M_2$  also shows that more than one reserve is optimal when  $b < \ln 3 / \ln 2 - 1 \approx 0.585$  (fig. 3).

For small values of  $b$ , the optimal  $n$  will be large, in which case one can use the asymptotic form  $(1 + 1/2 + 1/3 + \dots + 1/n) = \ln n$  (see also Quinn and Hastings 1987) and treat  $n$  in equation (10) as a continuous variable. Differentiating the (asymptotic) expression for  $M_n$  with respect to  $n$  then shows that the optimal  $n$  (for small  $b$ ) is  $n^* = e^{1/b}$  (eq. [2]), which was obtained previously by McCarthy (1995; see also McCarthy and Lindenmayer 1999). More than one reserve is optimal when the value of  $b$  is small, and the optimal number of reserves increases as  $b$  decreases (fig. 3). The optimal number of reserves depends only on  $b$  when maximizing the mean time to extinction, not the total area being reserved.

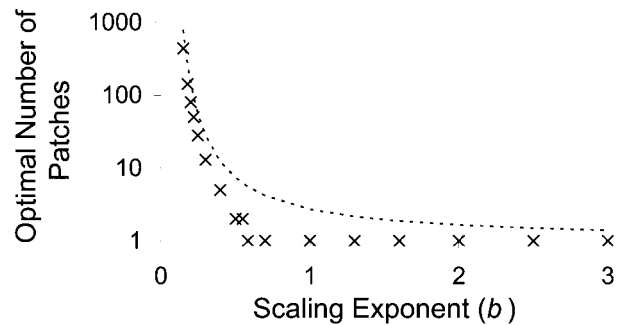


Figure 3: The optimal number of reserves for maximizing the mean time to extinction, assuming no dispersal. The crosses are exact solutions, treating  $n$  as a discrete variable (eq. [10]). The dotted line is the approximation based on  $(1 + 1/2 + 1/3 + \dots + 1/n) \approx \ln n$  and treating  $n$  as a continuous variable (eq. [2]).

*Colonization and Correlation*

In the above analyses it was assumed that extinctions occurred independently among reserves and that empty reserves were not recolonized, both of which are unlikely to be true if reserves are close together. In this section we develop a model to consider whether it is better to have one or two reserves when colonization and correlation are both present.

A two-reserve system can be in one of three possible states: 0, 1, or 2 reserves occupied. Transition probabilities among these states (0, 1, and 2) from one year to the next can be described by a  $3 \times 3$  matrix ( $\mathbf{M}_{ij}$ ). The transition probabilities from state 0 are straightforward to calculate, being 0 for transitions to nonzero states and 1 for remaining in state 0.

The transition from state 1 to state 0 requires that the species goes extinct in the occupied reserve and does not recolonize the empty reserve. This occurs with probability  $e(1 - c)$ , where  $e$  is the per-reserve annual extinction rate and  $c$  is the probability of colonization of the empty reserve from the occupied reserve. The transition probability from state 1 to 2 is equal to the probability of the species not going extinct in the occupied reserve multiplied by the probability that the empty reserve is colonized  $[(1 - e)c]$ . State 1 can be retained either by the occupied reserve remaining extant and the empty reserve remaining empty  $[(1 - e)(1 - c)]$  or by both reserves changing occupancy ( $ec$ ).

The transition from state 2 to state 0 requires that both reserves go extinct. The probability of this transition would equal  $e^2$  if extinctions were independent. However, if the correlation in the incidence of extinction equals  $\delta$ , then the probability is equal to  $e[e + (1 - e)\delta]$  (McCarthy and Lindenmayer 1998). This expression can be derived from the definition of the Pearson product moment correlation coefficient and conditional probability (McCarthy and Lindenmayer 1998). Similarly, the probability of both reserves remaining occupied is equal to  $(1 - e)[1 - e(1 - \delta)]$ , and the probability of one reserve remaining occupied while the species goes extinct in the other is equal to  $2e(1 - e)(1 - \delta)$ .

Thus, the transition matrix is given by

$$\mathbf{M} = \begin{bmatrix} 1 & e(1 - c) & e[e + (1 - e)\delta] \\ 0 & (1 - e)(1 - c) + ec & 2e(1 - e)(1 - \delta) \\ 0 & c(1 - e) & (1 - e)[1 - e(1 - \delta)] \end{bmatrix}.$$

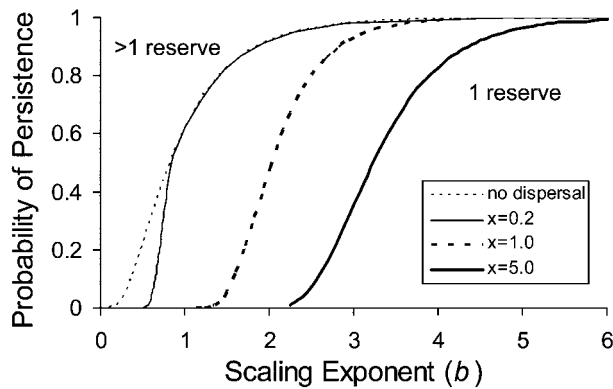
If it is assumed that the correlation in the incidence of extinction ( $\delta$ ) and the colonization rate ( $c$ ) both decline with distance between the two reserves ( $d$ ) according to an exponential function (Akçakaya and Atwood 1997,  $\delta = \exp[-\alpha d]$  and  $c = \exp[-\beta d]$ ), then  $\delta$  can be ex-

pressed as a function of  $c(\delta = c^{\alpha/\beta} = c^x)$ , where  $x$  describes how quickly the correlation declines with distance relative to the colonization rate. When  $x$  is large, the correlation in the incidence of extinction is weak. The correlation declines faster than the colonization rate when  $x > 1$ . A more complex function could be chosen (e.g.,  $\delta = \exp[-\alpha d^x]$ ), but we have selected a basic exponential function for the sake of simplicity.

Matrices of this form ( $\mathbf{M}$ , with an absorbing state, which is extinction in this case) can be analyzed by deleting the first row and column of the matrix (the row and column associated with the absorbing state) to produce matrix  $\mathbf{R}$  (Day and Possingham 1995). The maximal eigenvalue of  $\mathbf{R}$  is proportional to the probability of annual persistence, so extinction risk of the metapopulation is maximized when the eigenvalue is maximized (Day and Possingham 1995). Thus, for a two-patch system, it is possible to determine the optimal value of  $c$ , which corresponds to an optimal distance between patches (see appendix).

For the two-patch scenario, the matrix  $\mathbf{M}$  can be raised to the power of  $T$  to determine the probability of extinction, which is the transition probability from state 2 to state 0 for the matrix  $\mathbf{M}^T$ , given that both patches are initially occupied and are an optimal distance apart. The risk of extinction under the optimal two-reserve configuration can be compared to the risk of extinction if the area to be reserved were restricted to a single patch to determine which is better. This latter value equals  $1 - [(1 - e)^{2-b}]^T$  (appendix). When correlation in the incidence of extinction declines slowly with distance relative to the dispersal rate ( $x = 0.2$ ), the threshold value for the scaling parameter at which more than one reserve is optimal is similar to the case without dispersal and without correlation (fig. 4). However, when the correlation declines more quickly with distance, there is a greater range of situations in which more than one reserve is optimal (fig. 4). Nevertheless, the general pattern holds, with one reserve being optimal when the probability of persistence is low and when risks decline rapidly with increases in habitat area ( $b$  is large).

The similarity between the case  $x = 0.2$  and the model that ignores correlation and dispersal (fig. 4) occurs because when the correlation declines more slowly than the dispersal rates, the optimal configuration is to have individual reserves considerable distances apart. In this case, both dispersal rates and correlation are low, making the model without dispersal and correlation a reasonable approximation. Simulations of larger numbers of reserves (M. McCarthy, unpublished data) appear to confirm that this approximation holds for all optimal reserve configurations when  $x$  is small.



**Figure 4:** The optimal reserve configuration for different parameter combinations of the scaling exponent ( $b$ ) and probability of persistence over 200 years when all the habitat ( $H$ ) is in one reserve ( $p$ ). One reserve is optimal for minimizing the risk of extinction for parameter combinations below the line. The different lines represent the relative rate at which the correlation in the incidence of extinction and the dispersal rate decline with distance ( $x$ ). These results are compared to the situation where there is no dispersal and no correlation (from fig. 2).

### Examples

We will illustrate the implementation of these models with two examples. The first is the greater glider (*Petauroides volans*), an arboreal marsupial of eastern Australia (McKay 1995). McCarthy and Lindenmayer (1999) used a stochastic population model to predict that the mean time to extinction increased with patch size according to the equation

$$M = 8.40A^{0.87},$$

where  $A$  is the size of the patch (ha). Given that the exponent ( $b = 0.87$ ) is  $>0.585$ , a single patch will maximize the mean time to extinction. When evaluated in terms of minimizing the extinction risk of isolated patches, the optimal local extinction risk ( $E^*$ ) is equal to 0.578 (eq. [7]). Assuming that extinction risk is equal to  $1 - \exp(-T/M)$ , where  $T$  is the time frame of the analysis, it is possible to plot the optimal reserve size ( $A^*$ ) as a function of  $T$  (see fig. A2 in the online edition of the *American Naturalist*), demonstrating that larger patches are favored as the time frame of the analysis increases. With a time frame of 200 years, the optimal patch size is approximately 45 ha. This can be compared to the optimal reserve size of approximately 33 ha, which was obtained using the approximation given by equation (9).

For the greater glider model (McCarthy and Lindenmayer 1999), correlation in the incidence of fires, which are assumed to kill greater gliders, declines with distance  $d$  approximately as  $\exp(-0.5*d)$ , while colonization prob-

abilities declines approximately as  $\exp(-2.5*d)$ . Assuming that fires are the only source of local extinction, correlation in the incidence of extinction declines slowly with distance relative to colonization probabilities, with  $x = 0.2$ . For  $x = 0.2$  and  $b = 0.87$ , the probability of persistence over 200 years if all the habitat were in one patch would have to be  $>0.533$  (equivalent to  $\sim 65$  ha) for more than one patch to be optimal. This is the same threshold as that obtained when assuming patches are independent and there is no dispersal (fig. 4).

The second example is for mountain sheep in the United States. Data on the persistence of sheep populations over a 40-year period (Wehausen 1999) were used to derive a regression relationship between the mean time to extinction and population size

$$M = 26.6K^{0.556},$$

where  $K$  is used to measure the number of individuals in the population instead of habitat area.

Given that the exponent ( $b$ ) is  $<0.585$ , more than one patch will maximize the mean time to extinction, with the optimal number of patches (obtained numerically) equal to 2 (cf. 6 from the approximation eq. [2]). The difference between the approximation and the optimal value occurs because the approximation is only accurate when the optimal number of reserves is large. When evaluated in terms of minimizing the extinction risk of isolated patches, the optimal local extinction risk ( $E^*$ ) is equal to 0.799 (eq. [7]). The relationship between the optimal reserve size ( $K^*$ ) and the time frame of the analysis (see fig. A3 in the online edition of the *American Naturalist*) has a similar form to that for greater gliders. With a time frame of 200 years, the optimal local population size is  $\sim 16$  individuals to minimize the risk of extinction. This can be compared to the optimal population size of  $\sim 13$  individuals, which is obtained using the approximation given by equation (9).

### Discussion

When evaluated in terms of the risk of extinction and the reserves are independent, multiple reserves are only favored for those species that are relatively secure. For example, if  $b = 1$ , more than one reserve minimizes the risk of extinction only when the probability of persistence in a single reserve is  $>0.62$ . The general result from these analyses is that the probability of persistence of the most threatened species is maximized with a relatively small number of reserves. A second consequence of the dependence on the risk faced by the species is that the optimal number of patches will decrease as the time frame of the

analysis increases (figs. A2, A3). This occurs because risks increase as we forecast over longer intervals.

The optimal configuration of a reserve system depends on the formulation of the management objective. When maximizing the mean time to extinction, the optimal number of reserves is largely independent of the amount of available habitat for the reserve system, with  $n^* \approx e^{1/b}$ . In contrast, the risk of extinction is minimized when individual reserves are equal to an optimal patch size, which is represented in equation (7) by the optimal risk of local extinction. Therefore, the optimal number of reserves is linearly proportional to the amount of available habitat (appendix). The difference occurs because the shape of the distribution of times to extinction, not just its mean, changes with the number of reserves. Therefore, the risk of extinction (the area under the tail of the distribution) is not necessarily closely related to the mean. Which of these two management objectives (or an alternative) is most suitable may depend on the particular management scenario.

Perhaps the most important point is that the optimal design can change qualitatively depending on this choice of objective, a result that is not particularly intuitive. Further, the solution does not necessarily converge as the time frame becomes arbitrarily long. Minimizing the risk of extinction is attractive because minimizing the sum of these values over all species of concern will maximize the number that are conserved. However, this does require specifying the time frame of management concern. In short, the best choice of management objective is not clear, but the optimal management strategy depends profoundly on this choice. In such circumstances, perhaps a better management objective is to obtain a reserve configuration that is most robust to uncertainty in the model and its parameters. This is an area of current research.

In many cases, a reserve system will already be present, and the question is how best to add reserved areas. If the aim is to minimize the risk of extinction, and current reserves are already larger than the optimal size, the optimal solution is to create new reserves of the optimal size. However, if some of the existing reserves are smaller than the optimal size, it may be possible to expand the current reserve. Provided the total area of new habitat is sufficient to bring all the current reserves to the optimal size, the optimal solution is to do just this. However, when there is not sufficient habitat to achieve this, the problem becomes one of constrained optimization, and a numerical solution appears to be required.

The result that area should be added to reserves such that they are of the optimal size also has application to habitat restoration. For species with a high risk of extinction, the optimal number of reserves is small, so habitat restoration should tend to occur at the site of current

populations rather than at a different site (all else being equal). Similarly, if the aim is to maximize the mean time to extinction, the advantage of adding to current reserves can be compared to establishing new reserves.

Analysis of the model that included correlation and dispersal was limited to considering whether one patch was optimal, not the optimal number of patches. This latter problem is relatively difficult to solve because it is necessary to define how correlation in the incidence of extinction changes not just with distance but also patch size. This is important because correlation in the incidence of extinction among small patches might be lower because demographic stochasticity will have a greater effect on extinction than in larger patches. At the same time, larger patches may be buffered somewhat by catastrophic events because they will be less likely to affect the entire patch. This might reduce the correlation in extinction among large patches. The consequence of these two counteracting factors is unclear. Our results demonstrate the importance of considering the relative rate at which dispersal and correlation in extinction change with distance (fig. 4). It is likely that changes in correlation with patch size will also have an important influence on the optimal reserve configuration.

When the aim is to minimize the risk of extinction, the optimal solution depends on determining the local extinction risk. It is difficult to obtain precise estimates of this for most species, although it may be possible to obtain unbiased predictions across a range of species (Brook et al. 2002; Ellner et al. 2002). Reserves are usually established to conserve multiple species, so obtaining unbiased predictions may be more important than obtaining precise predictions for each species. Extending these results to apply to conservation of multiple species is an area of further study.

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## Appendix from M. A. McCarthy et al., “Theory for Designing Nature Reserves for Single Species”

(Am. Nat., vol. 165, no. 2, p. 250)

### Details of Mathematical Solutions for the Optimal Number of Reserves

#### *Extinction Risk of Independent Reserves*

Assume that the amount of habitat in each local reserve is  $A_i$ . If there are  $n$  reserves, then the total area of habitat is  $H = \Sigma A_i$ . Assume that the local extinction risk of each reserve  $h(A_i)$  is a function of habitat area. Then the overall risk of extinction of reserves that are independent is the product of all the local extinction risks:

$$L = \Pi h(A_i).$$

This can be minimized with Lagrange minimization, subject to the constraint  $H = \Sigma A_i$ . Thus,

$$\mathcal{L} = \Pi h(A_i) - \lambda \Sigma A_i,$$

where  $\lambda$  is the Lagrange multiplier, and the derivative of the Lagrangian ( $\mathcal{L}$ ) with respect to the size of any reserve  $k$  is

$$\frac{d\mathcal{L}}{dA_k} = \frac{h'(A_k)\Pi h(A_i)}{h(A_k)} - \lambda.$$

Setting this expression to 0 leads to

$$\frac{h'(A_k)}{h(A_k)} = \frac{\lambda}{\Pi h(A_i)}.$$

Thus, the term  $h'(A_k)/h(A_k)$  is the same for all reserves when the risk of extinction  $L$  is minimized. The expression  $h'(A_k)/h(A_k)$  is the proportional change in the extinction risk for small changes in reserve area. If the function  $h(A_i)$  is the same for all reserves and  $n$  is unrestricted, there are at most two solutions for  $A_i$  (using our functional form for  $h[A_i]$ ) that satisfy the constraint that  $h'(A_k)/h(A_k)$  is a constant for all reserves. However, it is possible to show that only one of these will minimize  $L$ . It follows that  $L$  is minimized when  $A_i = H/n$ , so

$$L = \Pi h\left(\frac{H}{n}\right) = \left[h\left(\frac{H}{n}\right)\right]^n.$$

In cases where habitat quality differs among reserves, the function  $h(A_i)$  will also differ. In such circumstances, these results are still useful because they demonstrate that the optimal configuration is such that the proportional change in local extinction risk with a small increase of reserve size is the same for all reserves.

The value of  $n$  that minimizes the function  $L = (1 - y)^n = \{1 - \exp[-T/a(H/n)^b]\}^n$  can be obtained by taking the derivative of  $L$  and setting the resulting expression equal to 0. In general, when  $f(n) = [g(n)]^n$ ,

$$f'(n) = ng'(n)[g(n)]^{n-1} + \ln[g(n)][g(n)]^n.$$

So, given that  $g(n) = 1 - \exp[-T/a(H/n)^b] = 1 - p^{n^b}$  in this case,

$$g'(n) = -p^{n^b}bn^{b-1}\ln p,$$

and

$$\begin{aligned}
 f'(n) &= -np^{nb}bn^{b-1}\ln p[1-p^{nb}]^{n-1} + \ln[1-p^{nb}][1-p^{nb}]^n \\
 &= -p^{nb}bn^b\ln p[1-p^{nb}]^{n-1} + \ln[1-p^{nb}][1-p^{nb}]^n \\
 &= -p^{nb}b\ln p^{nb}[1-p^{nb}]^{n-1} + \ln[1-p^{nb}][1-p^{nb}]^n \\
 &= -yb\ln y[1-y]^{n-1} + \ln[1-y][1-y]^n,
 \end{aligned}$$

where  $y = p^{nb}$ , which is the probability of local persistence. Setting  $f'(n) = 0$  to obtain the optimal number of reserves ( $n^*$ ) leads to

$$b = \frac{\ln[1-y^*][1-y^*]}{y^*\ln y^*} = \frac{E^*\ln E^*}{(1-E^*)\ln(1-E^*)},$$

where  $E^*$  is the optimal risk of local extinction ( $E^* = 1 - y^*$ ).

The equation  $b = E^*\ln E^*/(1-E^*)\ln(1-E^*)$  may be approximated by a linear function to obtain an expression for  $E^*$ . Taking the first term of a Taylor series expansion around the point ( $E^* = 0.1, b = 2.428$ ) leads to

$$\ln E^* \approx 0.345 - 1.09b,$$

which is a close approximation for equation (7), especially for  $b < 4$  if  $E^*$  is truncated to be  $< 1.0$  (fig. A1). For  $b > 4$ , a close approximation is  $\ln E^* \approx -b$  (using the approximations  $\ln(1-E^*) \approx -E^*$  and  $1-E^* \approx 1$  for small values of  $E^*$ ). Once  $E^*$  is obtained, it is straightforward to obtain  $n^*$ , the optimal number of patches from the equation  $1 - E = p^{nb}$ .

It is relatively straightforward to show that  $n$  is linearly related to  $H$ , the total area to be reserved. Rearranging  $y^* = p^{nb}$  leads to

$$n^* = \left[ \frac{\ln(y^*)}{\ln(p)} \right]^{1/b}.$$

Since  $p = \exp(-T/aH^b)$  (the probability of persistence if all available habitat is placed in a single reserve),  $\ln(p) = -T/aH^b$ , which, when substituted into the above expression, leads to

$$n^* = H \left[ -\frac{a \ln(y^*)}{T} \right]^{1/b},$$

demonstrating that the optimal number of reserves is proportional to the total area being reserved ( $H$ ).

A second solution for  $n^*$  can also be obtained by approximating equation (6) by

$$f(n) = (1-y)^n \approx 1 - yn = 1 - p^{(nb)}n,$$

which is valid when  $p^{(nb)}$  is small. Taking the first derivative of this equation and setting the resulting expression equal to 0 to obtain the minimum leads to

$$n^* \approx \left[ -\frac{1}{b \ln p} \right]^{1/b}.$$

This approximation has an advantage over the linear approximations for  $b$  and  $E^*$  because the optimal number of reserves can be obtained directly from the values for  $b$  and  $p$  (rather than first requiring  $E^*$ ), although the optimum  $n$  is overestimated (fig. 1).

*Colonization and Correlation*

Persistence of the two-patch metapopulation is maximized when the following eigenvalue of the reduced matrix  $\mathbf{R}$  is maximized:

$$q = \frac{c(2e-1) - (e-1)[2 + (c^x-1)e] + \sqrt{4(e-1)[(c+e-1)(e-1) - c^x e(e-c-1)] + [2-3e-c^x e(e-1) + e^2 + c(2e-1)]^2}}{2}.$$

The value of  $c$  that maximizes  $q$  can be obtained by differentiating  $q$  with respect to  $c$ , and setting the resulting expression to 0:

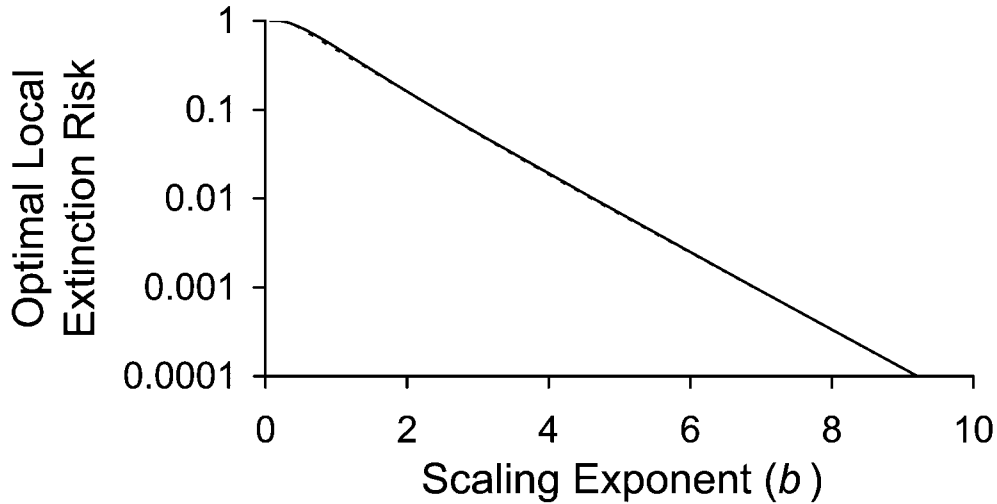
$$\begin{aligned} \frac{dq}{dc} = & \left\{ 2e - 1 + c^{x-1}ex - c^{x-1}e^2x + \{c[c(1-2e)^2 + (e-1)e(2e-3)] \right. \\ & \left. + c^{2x}(1-e)^2e^2x - c^x(e-1)e[(e-1)ex + c(2e-3)(x+1)] \right\} \\ & / c \sqrt{4(e-1)[-c^x e(e-c-1) + (e-1)(e+c-1)] + [2-3e-c^x(e-1)e + e^2 + c(2e-1)]^2} / 2. \end{aligned}$$

For the case  $x = 1$ , the optimal colonization rate is

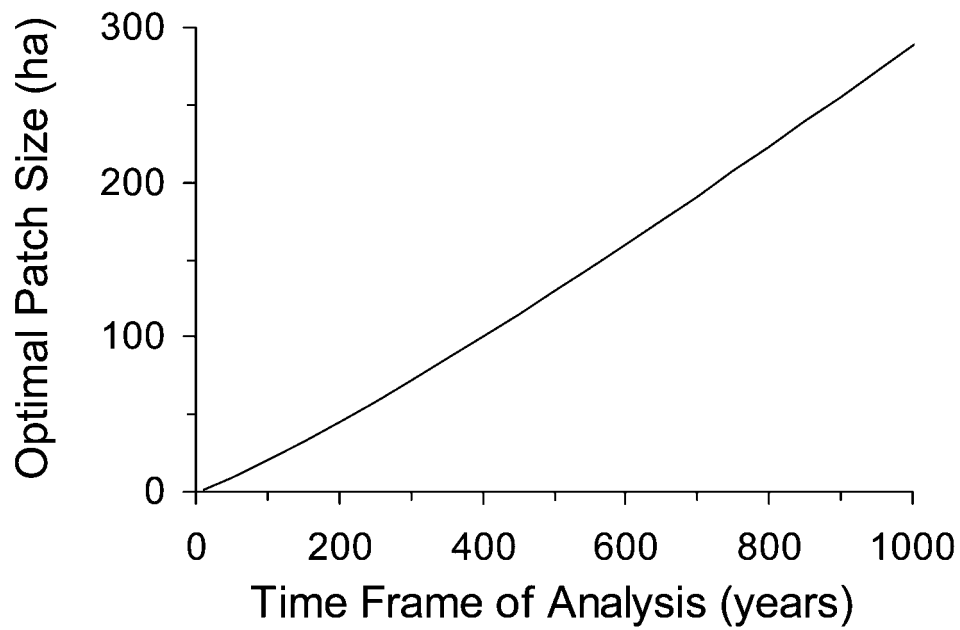
$$c^* = \frac{\sqrt{(2e)(1-e)[1-e(3-e)] + (e-1)e[3+(e-3)e]}}{1 + (e-1)e[10 + e(e-5)]}.$$

For other values of  $x$ , the solution of  $dq/dc = 0$  can be found numerically. The extinction risk for this solution can also be compared to the case when  $c = 0$  (in which the two patches are entirely isolated and independent) to determine the two-patch system that has the greatest persistence.

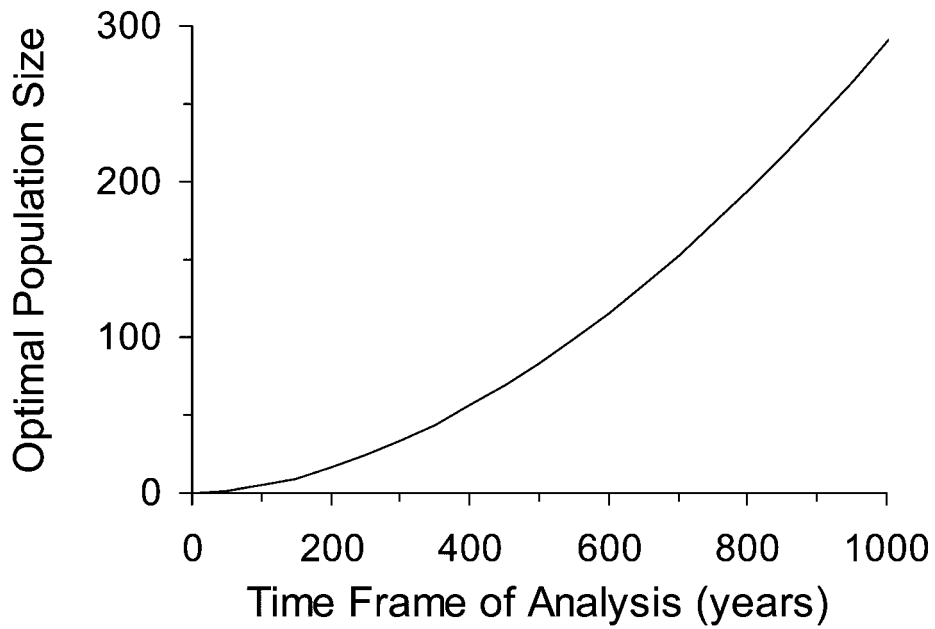
Assuming that the mean time to extinction is a power function of habitat area (eq. 4), the annual probability of persistence of each reserve  $(1 - e)$  would equal  $P^{2^b}$ , where  $P$  is the annual probability of persistence if the habitat were in a single reserve (4). Thus,  $1 - e = P^{2^b}$ , leading to  $P = (1 - e)^{2^{-b}}$ , and the probability of the species persisting for  $T$  years is  $[(1 - e)^{2^{-b}}]^T$  if placed in a single reserve. This single-patch case can be compared to the two-patch case to determine which has the lowest risk of extinction.



**Figure A1:** The optimal risk of local extinction versus the scaling exponent ( $b$ ), assuming no dispersal between reserves. The solid line is the exact solution (eq. [7]), while the dashed lines (largely obscured by the solid line) are the approximations  $\ln E = 0.345 - 1.09b$ , for  $b < 4$ , and  $\ln E = -b$  for  $b > 4$ .



**Figure A2:** The optimal size of individual reserves ( $A$ ) versus the time frame of the analysis when minimizing the risk of extinction of the greater glider, obtained by solving equation (7) and assuming that the mean time to extinction is given by  $M = 8.4A^{0.87}$ .



**Figure A3:** The optimal size of individual populations ( $K$ ) versus the time frame of the analysis when minimizing the risk of extinction of mountain sheep, obtained by solving equation (7) and assuming that the mean time to extinction is given by  $26.6K^{0.556}$ .