

Cost-efficient fenced reserves for conservation: single large or two small?

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Abstract. Fences that exclude alien invasive species are used to reduce predation pressure on reintroduced threatened wildlife. Planning these continuously managed systems of reserves raises an important extension of the Single Large or Several Small (SLOSS) reserve planning framework: the added complexity of ongoing management. We investigate the long-term cost-efficiency of a single large or two small predator exclusion fences in the arid Australian context of reintroducing bilbies *Macrotis lagotis*, and we highlight the broader significance of our results with sensitivity analysis. A single fence more frequently results in a much larger net cost than two smaller fences. We find that the cost-efficiency of two fences is robust to strong demographic and environmental uncertainty, which can help managers to mitigate the risk of incurring high costs over the entire life of the project.

Key words: conservation fencing; cost-effectiveness; exclusion fences; feral cat, *Felis catus*; greater bilby, *Macrotis lagotis*; invasive alien species; Lorna Glen, Western Australia; reintroduction; reserve size vs. number; return on investment; SLOSS.

INTRODUCTION

The optimal reserve design to maximize conservation outcomes for metapopulations is frequently debated (Quinn and Hastings 1987, McCarthy et al. 2005, Blowes and Connolly 2012). The decision to create either a single large or several small (SLOSS) reserves in a fragmented landscape is based on the tension between two factors: the effects of spatially correlated environmental catastrophes (providing risk-mitigation benefits to numerous small reserves); and the lower local extinction risk offered by large reserves (giving viability benefits to fewer, larger reserves). The optimal number and spacing of reserves is therefore specific to the landscape, species, and objectives of the conservation scenario (Etienne and Heesterbeek 2000, Ovaskainen 2002, McCarthy et al. 2005).

Since the SLOSS question was first posed (Diamond 1975), the debate has focused on systems of unmanaged reserves. It is assumed that no ongoing management costs are incurred after the initial outlay to purchase the land. In a continuously managed system, however, these

ongoing costs (which can be both deterministic and stochastic) can outweigh the initial acquisition costs (Armsworth et al. 2011), and add further complexity to the optimal reserve design. Ongoing costs will not necessarily be equal for a single large or several small managed reserves; larger areas benefit from economies of scale with respect to management (Balmford et al. 2003); separated reserves have a higher edge to area ratio, which increases perimeter monitoring costs (Dickman 2012).

Differing ongoing costs alter the well-studied SLOSS calculus. The management objectives must shift from being performance-based (such as absolute probability of persistence or population size) to considering the cost-efficiency of the different decisions over time. When choosing between conservation projects with differing costs, the decision that maximizes the ecological benefit gained per dollar invested represents the best use of limited conservation resources (Naidoo et al. 2006).

Reserves surrounded by predator exclusion fences are a classic example of a continuously managed system (Short and Turner 2000, Clapperton and Day 2001, Long and Robley 2004, Moseby and Read 2006, Hayward and Kerley 2009, Scoffield et al. 2011, Somers and Hayward 2011, Burns et al. 2012, Dickman 2012).

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Constructing a predator exclusion fence around an area within a reserve, and eradicating invasive predators from within, can mitigate high predation pressure on a population of threatened species. Threatened Australian marsupials that are susceptible to predation are regularly reintroduced successfully into well-managed fenced enclosures (e.g., Winnard and Coulson 2008, Moseby et al. 2009, Miller et al. 2010), although these are limited mainly to those with frequent monitoring and high-quality fences (Short 2009).

The day-to-day reality of management planning is complex, and short funding cycles from uncertain sources mean that building a single large fence is not always feasible. Additional funding following the demonstrated success of an enclosure can be used to leverage further investment to extend the original fence or to establish a new, smaller enclosure some distance away. There are examples of both approaches in Australia (for example, Arid Recovery in South Australia has been extended four times). The SLOSS question naturally arises here, both at the outset of a new project and with increased funding after a successful fencing program: is it more efficient to spend limited conservation resources by constructing a single large fence, or should managers instead construct multiple spatially separated fences?

Formulating a plan for fenced enclosures entails trade-offs between cost, fragmentation, and mitigating the risk of catastrophe. Incursion by predators is an ever-present threat, and these events can cause massive mortality of threatened species (Winnard and Coulson 2008, Moseby et al. 2009, Short 2009, Bode and Wintle 2010). Creating two fenced populations creates a higher fence to area ratio, increasing incursion risk per unit area. However a two-fence system also ensures that the entire population is never threatened by a single incursion. Likewise, numerous reserves separated by larger distances are less likely to be threatened by the same catastrophe (e.g., a fire, flood, or the outbreak of disease) than a single fence. The continuous management of fenced reserves also allows for recolonization attempts in the event of local extinction in a two-fence system. The use of the second reserve as an insurance population means that a threatened species will only be lost if a catastrophe affects both populations at the same time. However, separating reserves increases management costs and fragments the population into units that house smaller populations, which are more susceptible to demographic stochasticity (Lande 1993). Given that both a single large fence and several small fences for conservation have both benefits and costs, under what situations is each the optimal choice?

We employ a decision theoretic framework to choose between a single large and two small fences. We show that in some cases it is optimal to build multiple fences by considering different budgetary constraints, catastrophe frequencies, and demographic parameters. We will also show that doing so significantly reduces the risk

of unexpectedly high costs, especially in the presence of parametric uncertainty. Decision theory allows us to construct a framework to quantitatively consider this question. It allows decision-makers to consider the cumulative effects of these benefits and costs on a common management goal: to maximize the conservation benefit for a threatened species gained per dollar invested.

METHODS

We use simulation-based population viability analyses to assess the performance of two fencing strategies: a single large or two smaller fenced reserves. We track both the population sizes and the cumulative expenditure for both strategies, applying our methods to a case study of the greater bilby *Macrotis lagotis* in the arid zone of Australia. These results will be used to compare which strategy provides the most cost-efficient conservation benefits under varied objectives.

Objectives

We consider a manager who plans to use fences (see Plate 1) to exclude introduced predators to increase the viability of a newly released population of a threatened species. The decision between constructing a single large fence or two smaller fences must be made, and if a two-fence system is chosen, the optimal distance between the two fences must also be determined. We assume that the manager will have access to the same initial budget for either fencing strategy, and that the aim is to maximize cost-efficiency over the lifetime of the fenced system. We consider two distinct measures of success to quantify conservation benefit: the average abundance of the threatened species, and its probability of persistence over a fixed time horizon.

To assess these objectives, we model a population in a single-fence system and also populations in a two-fence system with a range of distances between the fences. We consider a fencing project with a fixed budget B for the initial construction phase of the enclosures. We run the model for 50 years, or until the populations are extinct, and compare the outcomes to determine whether a single large or two small fences provide the most cost-efficient benefits. We assume that the introduced predators are distributed evenly throughout the landscape, and will invade the enclosure opportunistically. We define C^L as the lifetime cost of the large fence, N_t^L as the number of females at time t in the large fence. We track only the females in the population, and assume that males are saturating. Likewise, we define for $i = \{1, 2\}$, $C^i(d)$ as the lifetime cost and $N_t^i(d)$ as the population at time t of each small fence i . Both of these quantities are functions of the distance d between the fences.

We first consider a manager who aims to maximize the population size per unit dollar. This manager will choose to build a two-fence system if the average cost (net present value) per female individual per year is smaller than it would be for a single large fence:

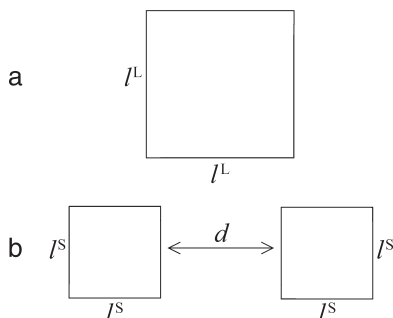


FIG. 1. Schematic diagram of the two reserve designs: (a) a single large enclosure (superscript L) or (b) two small fenced enclosures (superscript S) separated by the distance d , where l is the length of one side of the fence.

$$\frac{C^1(d)}{\sum_{t=1}^T N_t^1(d)} + \frac{C^2(d)}{\sum_{t=1}^T N_t^2(d)} < \frac{C^L}{\sum_{t=1}^T N_t^L} \tag{1}$$

On the other hand, some managers may aim to maintain the existence of the population for as long as possible, with less of an emphasis on the average size of the population. In this case, the manager would choose two fences if the probability of persistence at time T per dollar invested in a two-fence system was larger than that of a single fence:

$$\frac{\Pr(N_T^1(d) + N_T^2(d) > 0)}{C^1(d) + C^2(d)} > \frac{\Pr(N_T^L > 0)}{C^L} \tag{2}$$

This objective explicitly favors long-persisting populations; however, the population size is an implicit factor because smaller populations are more prone to stochastic extinction events (Lande 1993).

The manager’s goal should determine which of the two objective equations (Eqs. 1 or 2) she will use to optimize the fenced reserve design. Two fences should be constructed if the chosen inequality holds true; otherwise, it is more cost-efficient to construct a single fenced reserve. We compare the outcomes of the two fencing strategies based on their lifetime costs. It is reasonable to assume that the money being spent on monitoring the fences in a decade has been in the bank in a trust accumulating interest in the meantime. To capture this possibility, we discount future spending by some rate, r , per annum.

Construction of the fences

It is reasonable to assume that fencing projects receive a large amount of funding at the outset of the program while ongoing costs are funded from a yearly budget cycle. For example, a fenced enclosure might be constructed as a conservation offset funded by a mining company or land developer with a lump-sum payment, and the yearly running of the reserves might fall to a government department. The construction cost of the fences is determined by an initial available budget B ,

such that $B = c_0^L = c_0^S$. This initial budget will determine the relative sizes of the fences for each potential strategy.

The initial construction phase of a fenced enclosure has two stages: the construction of the fence itself, followed by the eradication of the introduced predator species. We consider square fences with side length l^L for the single large fence, and l^S for each of the smaller fences in a two-fence system (where l^L and l^S are defined by the budget; see Fig. 1). We assume a building cost per kilometer of the fence (c_F , including materials and labor; see Table 1); an initial eradication cost (c_{E0}), which increases linearly with area; and travel cost between the two fences for transport of personnel in the construction phase (c_T per km, where the two fences are separated by d km). The total initial cost of building one and two fenced enclosures, respectively, is the sum of the building, eradication, and travel costs:

$$\begin{aligned} c_0^L(l^L) &= 4c_F l^L + c_{E0}(l^L)^2, \text{ and} \\ c_0^S(l^S) &= 8c_F l^S + 2c_{E0}(l^S)^2 + c_T d. \end{aligned} \tag{3}$$

We set $c_0^L = c_0^S$ to determine the relative sizes of one or two fences for given cost parameters and initial budget. Solving these simultaneous equations for l^L and l^S , we obtain a nonlinear relationship between the size of the single fence and the total size of the two-fence system, $l^S = (2c_{E0})^{-1}[-4c_F + \sqrt{c_{E0}^2(l^L)^2 + 4c_{E0}c_F l^L + 16c_F^2 - dc_T c_E}]$. This relationship always results in a larger total area in the single-fence system. Although this relationship is dependent on the distance between the two fences, the travel cost (in 2012 Australian dollars) is negligible compared to the total budget that we consider in this case study ($c_0^S(l^S) = \text{AU}\$500,000$), so there is no change in the relative sizes of the fences when separated by different distances.

We also consider scenarios in which the two fences are not of equal size. Eq. 3 is altered to reflect the disparate allocation of the initial construction budget according to different ratios ($\alpha \in [0,1]$).

$$\begin{aligned} c_0^S(l^{S1}, l^{S2}) &= 4c_F(\alpha l^{S1} + (1 - \alpha)l^{S2}) \\ &+ c_{E0}(\alpha(l^{S1})^2 + (1 - \alpha)(l^{S2})^2) + c_T d. \end{aligned} \tag{4}$$

General model

For a single large fenced reserve, the population size in year t is N_t^L . This population changes each year according to the current population size and a vector of n stochastic demographic parameters, \mathbf{x}_t , each drawn from known probability distributions. Each year, catastrophic environmental events and predator incursions occur according to Bernoulli probability distributions. The probability of environmental catastrophe, q_t , depends on the area of the fenced reserve; a larger area has more opportunity for fire or flood (see Appendix). The probability of a predator incursion, I_t , increases with the length of the perimeter. The mortalities when these events occur are also stochastic variables μ_q and μ_I , indicating the proportion of the population killed. These

TABLE 1. Model parameters, including best estimates (costs are in 2012 Australian dollars AUS).

Term	Description	Value	Dependent factor
B	Initial budget	AUS500 000	fixed
c_0^i	Construction cost of fence i	AUS500 000	B
c_F	Reserve fence construction cost	AUS24 000/km†	perimeter
c_{E_0}	Initial eradication cost	AUS1394/km ²	area
c_M	Monitoring cost	AUS6.09/km per visit†	perimeter
c_N	Maintenance cost	2.5% of initial construction cost per year (Clapperton and Day 2000)	perimeter
c_T	Travel cost between two fences	AUS2.03/km†	separation distance and frequency of monitoring
c_R	Cost of restocking after local extinction	AUS2000/breeding pair	population relocated
c_I	Cost of eradicating incursion	AUS1091/km ² †	area
N_0	Initial population released	30	
K	Carrying capacity (breeding females)	98 (single fence), 26 (each of two equal fences)	area
l^S	Length of one side of each fence in two-fence system	2.49 km (superscript S denotes small reserve)	B
l^L	Length of one side of single fence	4.86 km (superscript L denotes large reserve)	B
ϕ	Frequency of monitoring	three times per week (Long and Robley 2004)	
p_b	Annual binomial probability of breach	0.0109/km (Bode and Wintle 2010)	perimeter
μ_I	Incursion mortality	16 individuals (8 females)	based on probability of incursion
r	Discount rate	0.05	
q_t	Binomial probability of environmental catastrophe	0.0452 (single fence), 0.0362 (two equal fences)	area

† Personal communications, Western Australian Department of Parks and Wildlife (2013).

factors all interact according to a function of population dynamics, f , resulting in the population size in the single large fence (with area a^L and perimeter $4l^L$) at time $t + 1$ being

$$N_{t+1}^L = f(N_t^L, \mathbf{x}_t, q_t(a^L), \mu_q, I_t(l^L), \mu_I). \quad (5)$$

In a two-fence system, the total population is $N_{t+1}^S = N_{t+1}^1 + N_{t+1}^2$. The separate populations N_t^1 and N_t^2 change in a fashion similar to that of the single-fence system. In this model we allow each fence to be used as an insurance population in the event of a local extinction in the other fence. The probabilities of environmental catastrophes are correlated in space, so the probabilities of catastrophe in each fence (q_t^1 and q_t^2) are correlated according to the distance between the two fences, d . The other parameters are drawn from the same probability distributions as the single-fence system. Thus we define the population growth in each of the fences ($i, j \in \{1, 2\}$) by

$$N_{t+1}^i = f(N_t^i, N_t^j, \mathbf{x}_t, q_t^i(a^i, d, q_t^j), \mu_q, I_t(l^i), \mu_I). \quad (6)$$

Both fencing systems incur deterministic costs each year. Monitoring and maintenance must be carried out with a weekly frequency of ϕ , each time incurring a cost of c_M , which scales linearly with the size of the fenced area (Bode et al. 2012). Additionally, every time the two-fence system is monitored, the distance between the two fences must be traveled, incurring a travel cost c_T that depends on the distance d between the two fences.

When environmental catastrophes and incursions occur, the stochastic costs c_q (rebuilding after fence

destruction) and c_I (eradicating an incursion) must be paid. For a single fence, these ongoing costs add to the initial construction cost c_0^L to give

$$C^L = c_0^L + \phi c_M + \sum_{t=1}^T \frac{1}{(1+r)^{T-t}} [q_t(a^L)c_q + I_t(a^L)c_I]. \quad (7)$$

In the event of a local extirpation and repopulation from the second fence, a translocation cost per animal moved c_R is required. The number of animals moved depends on the size of the population at the remaining fence. Assuming that one team manages all fences within the same fencing project, there is also a travel cost between the fences in a two fence system. This cost, ϕc_T (d), depends both on the distance between the fences, d (to be traveled twice, once in each direction), and ϕ . Therefore the total cost for one of the fences is

$$C^1 = c_0^S + \phi(c_M + c_T(d)) \sum_{t=1}^T \frac{1}{(1+r)^{T-t}} \times [q_t(a^1)c_q + I_t(a^1)c_I + c_R^1(N_t^1, N_t^2)]. \quad (8)$$

The total cost for the second fence is calculated in the same manner.

The functions and probability distributions of the random variables are all general here. The forms of these are determined by the threatened species being released into the fences, the invasive species to be eradicated, the location of the fences, and the current labor and material costs. We parameterize the system using bilbies

TABLE 2. Greater bilby population parameters (Southgate and Possingham 1995).

Term	Description	Value
N_t	Population size (females only)	varies with time (t)
Y_t	Number of female offspring born	varies with t
A_t	Surviving female adults	varies with t
μ_a	Adult mortality rate	0.09
S_t	Female settlers	varies with t
R_t	Female recruits	varies with t
μ_j	Juvenile mortality rate	0.79
b_t	Birth rate of female offspring	stochastic, $\sim N(2.8, 0.9)$
K	Female carrying capacity (ceiling)	fenced area/female home range

(*Macrotis lagotis*) and the predator exclusion fence in Lorna Glen, Western Australia, as a case study.

Parameterization of the model

To parameterize the model, we used financial data from the 1080-ha predator-exclusion fenced enclosure at Lorna Glen in the arid zone of central Western Australia (see Table 1). Cost estimates for construction, the initial eradication of predators, and monitoring were used in this model (Bode et al. 2012).

Population model.—We illustrate the application of our methods by considering the management of the greater bilby (*Macrotis lagotis*), a nocturnal burrowing bandicoot native to arid Australia (Moseby and O'Donnell 2003). The bilby exemplifies the important role that fenced enclosures can play in threatened species conservation; the species is managed in five fencing projects across Australia. Predation by cats and foxes, habitat degradation by rabbits and farming, in addition to altered fire regimes, have driven the lesser bilby *Macrotis leucura* to extinction, and have reduced the greater bilby's range by 80%. Successful reintroduction of bilbies to previous habitat has been shown to depend heavily on the continued absence of ongoing predation pressure (Moseby et al. 2011). Consequently, nearly all successes have been behind well-managed fences.

Bilbies were reintroduced to the proposed Lorna Glen Conservation Park (128 captive-bred individuals) between 2007 and 2010 (Pertuisel 2010). Animals were "hard released" (without the aid of a predator exclusion fence) following the control of feral cats using poison baits. Preliminary modeling suggests that the population may be on a slow decline to local extinction (Pertuisel 2010). However, the levels of mortality included in the model may be elevated owing to the method of release, and new recruits born on site may experience lower mortality rates. Determining the current population size, therefore, is an area of active research (e.g., Burrows et al. 2012). Subsequent reintroductions of other threatened species of mammals at Lorna Glen have used a "soft release" via a predator exclusion fence. The fenced enclosure has an area of 1080 ha, stands 1.8 m in height, and has three electrified wires (see Bode et al. 2012). For this paper, therefore, we consider the scenario of bilbies being reintroduced to Lorna Glen inside the predator exclusion fence. This is a realistic scenario, because

bilbies are regularly reintroduced behind similar predator exclusion fences across Australia's semiarid/arid zone. The fence does not allow dispersal of the native species from inside the enclosure, so we assume that the population of bilbies is closed.

We use demographic parameters (see Table 2) taken from a population viability analysis in the Watarrka National Park in the Northern Territory (Southgate and Possingham 1995). Each fenced enclosure is populated with N_0 breeding pairs at the outset of the project (divided evenly in the two-reserve system). We model the population dynamics in each fencing system in discrete time (with yearly time steps).

We model a density-dependent metapopulation in discrete time. Only the females are tracked in the model, under the assumption that mating is polygynous and males are saturating. The maximum density of the population is defined as the total area divided by the home ranges of females, which are assumed to be nonoverlapping (Southgate and Possingham 1995).

In this population model, reproduction occurs first, with the number of young (Y_t) born in year t being proportional to the population size N_t and the annual birth rate b_t . Adults (A_t) then die according to a binomial probability with a mean mortality rate of μ_a . The juveniles in excess of the carrying capacity K die (creating a population ceiling); otherwise, these individuals (S_t) recruit to the adult population with a binomial probability ($1 - \mu_j$), to give the number of new recruits, Q_t , for the breeding season. The population in the subsequent year is thus composed of the surviving adults and new recruits (where $B(n, p)$ denotes a variable drawn from a binomial distribution with n trials and p probability of success of each trial):

$$Y_t = b_t N_t$$

$$A_t = N_t - B(N_t, \mu_a)$$

$$S_t = \min(Y_t, K - A_t)$$

$$Q_t = S_t - B(S_t, \mu_j)$$

$$N_{t+1} = A_t + Q_t. \quad (9)$$

We assume a landscape of viable habitat, which has uniform quality; this allows the two fences to be separated by any distance.

Environmental catastrophes.—Although our general framework (Eqs. 1 and 2) allows for consideration of any spatially correlated catastrophes (for example, droughts or cyclones), here we consider only fires and floods. These large-scale environmental catastrophes pose a constant threat in the arid zone of Australia (Southgate and Possingham 1995); the threats are compounded for enclosed populations, where fences create barriers to escape (Hayward and Kerley 2009). In these catastrophic events, in addition to the demographic costs, the fence itself can be severely damaged (Long and Robley 2004). Although fire prevention techniques can be employed to minimize the risk of fire (e.g., vegetation control and back burning), the risk of fire and flood must still be considered in the model. Historical data from the 244 000-ha wildlife reserve at Lorna Glen in Western Australia’s arid zone was used to model fire frequency, beta-distributed intensity, and spatial correlation (see Appendix).

Incursions by predators.—Fences are not impregnable barriers, and we must therefore consider the realistic probability that fences fail and incursions by predators occur (Long and Robley 2004, Bode and Wintle 2010). With a given probability of breach rate per kilometer of a fence, p_b , the probability of failure (incursion), I , at any point along the perimeter of a fenced enclosure scales nonlinearly with the length L of the perimeter according to Bode and Wintle (2010):

$$I(L) = 1 - (1 - p_b)^L. \tag{10}$$

Frequent monitoring of the perimeter ϕ times per week at a cost of c_M Australian dollars per kilometer is required for prompt detection of any breaches; the cost of eradication in the event of a breach is c_I (Table 1). We consider a fixed cost for successful eradication, however stochastic success dependent on effort could also be considered. We assume that each incursion event results in a fixed amount of bilby mortality, μ_I .

Local extirpation.—Local extirpation is possible through catastrophic mortality (environmental or by incursion), or through demographic mortality. If extirpation occurs in a single-fence system, we assume that the fencing program terminates. In the event of a local extirpation event in a two-fence system, however, the reserve will be repopulated with individuals from the other fence. The number of individuals moved from fence 2 (with current population N_2) to fence 1 is $\min\{N_2/2, N_0\}$ where N_0 is the size of the population initially released into each fence (determined by the manager). This relocation incurs cost c_R per individual translocated.

Solution method

We simulate the population in each of the fence designs (a single fence and two fences with different size

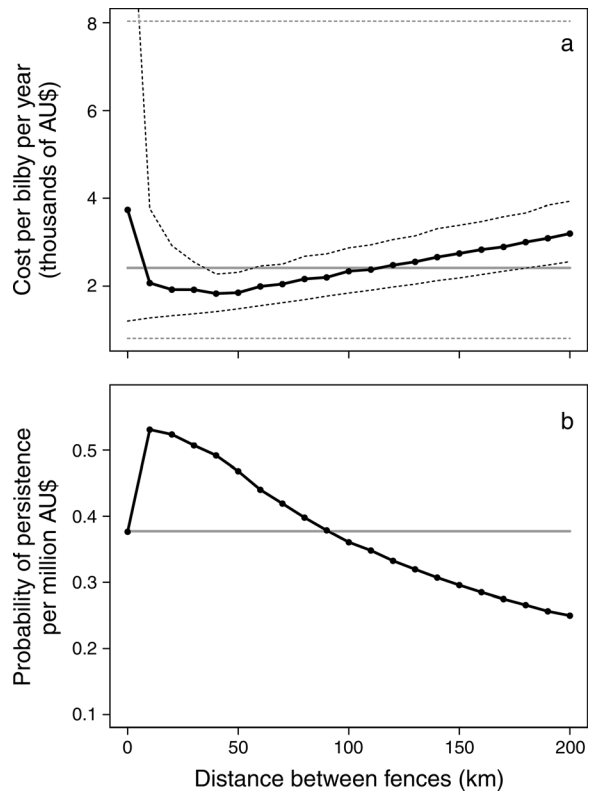


FIG. 2. The performance of each fencing strategy as simulated for bilbies (*Macrotis lagotis*) in Lorna Glen, Western Australia. Cost-efficiency under both objectives, (a) minimizing the cost per bilby per year, and (b) maximizing the probability of persistence per million dollars invested, depends on the separation between the two fences. Cost is given in Australian dollars (AU\$). The mean performance of a single fence, which does not have any distance dependency, is given by the solid light gray line; the mean performance of a two-fence system is given by the black line. Panel (a) includes the respective 5th and 95th percentiles as light gray and black dashed lines.

ratios) with 5000 repetitions each in R version 2.12.1 (R Development Core Team 2010). With each repetition we track the female population size, environmental catastrophes, incursion events, and both the deterministic and stochastic costs incurred. At the termination of each simulation (either at the defined time horizon or when the population is extinct), we calculate the cost-efficiency measured by the two different objective functions, using the yearly population size (Eq. 1) and the persistence at the time horizon (Eq. 2). Then we take the mean performance of the 5000 repetitions. We present the results for both objectives, and make recommendations to the manager accordingly (aiming to maximize objective one and minimize objective two).

RESULTS

Case study: bilbies in the arid zone

Our simulations show that the optimal fencing strategy depends on the distance between the two fences

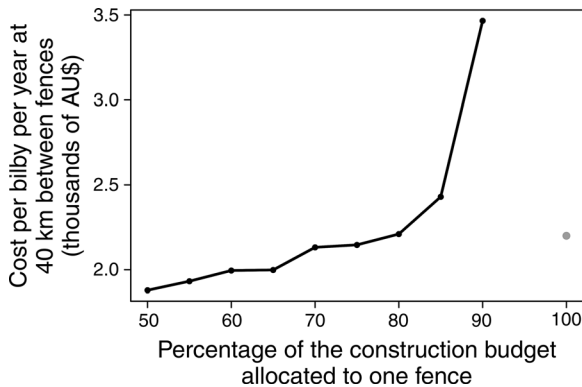


FIG. 3. The performance of a single fence (light gray circle) vs. a two-fence system (black) with an unequal allocation of the initial construction budget. Because we consider a maximum of two fences, the second associated fence is constructed with the remaining percentage of the budget.

as well as the manager's objective for the case study of bilbies in the arid zone of Australia (Fig. 2a, b). If land is available separated by a distance between 10 km and 100 km, constructing two fenced reserves is more cost-efficient when considering cost per bilby per year. The optimal separation is 40 km, resulting in a cost per bilby per year of AU\$1830 and a 0.53 probability of persistence per million Australian dollars. If land is not available at this distance, it becomes more expensive to manage the two-fence system; according to this objective, the better choice is to construct a single fence. However, a manager whose objective is to maximize the probability of persistence per million dollars has a clearer optimal solution: a single fence is only the best choice if the two fences would be more than 90 km apart. Under this objective, two fences separated by 10 km achieve 140% of the benefit per dollar invested in a single fence.

Mitigating the risk of overspending

The cost-efficiency of any fenced population is highly stochastic. Population dynamics, a stochastic environment, and probabilistic extinction events combine to create a highly unpredictable situation. A risk-averse manager may aim to reduce the chance that these random factors cause unexpectedly high costs, thereby threatening the entire program for a reason other than extinction.

A single fence is at a much greater risk of incurring very high costs than a two-fence system (Fig. 2a). A two-fence system (when separated by a distance of 40 km) costs less than AU\$3000 per bilby per year in 95% of our simulations. The risk of a very high cost in the single-fence system proved to be much higher, with 5% of simulations costing over AU\$8000 per bilby per year. Two fences separated by any distance is a more risk-averse choice than a single fence.

Unequal split of construction budget

The most cost-efficient way to split the construction budget in a two-fence system is exactly in half (Fig. 3). However, two fences split unevenly up to a size ratio of 1:3 (a 75% split) separated by 40 km are more cost-efficient than a single fence in the Lorna Glen case study. This indicates that there is some benefit to having even a small secondary population to act as an insurance population (a 75% split gives a carrying capacity of 14 breeding females in the smaller fence).

A ratio of greater than 1:3 between the sizes of the two fences approximates a single large fence with a few spatially separated breeding pairs. However, a system of two fences with this split has a smaller total area than a single fence because a greater perimeter needed to be constructed initially, and it has higher ongoing costs due to constant travel between the locations. The benefits of such a small insurance population are outweighed by these increased costs and a single fence is more cost-efficient.

Most parameter combinations that we investigate preserve the dominance of the equally split two-fence system over any unequal split, so these results have been omitted for clarity. Where these results are omitted, a manager should aim for two fences of equal size where recommended, or revert to a single fence wherever it proves to be more cost-efficient.

Probability of environmental catastrophe

Two fences help to mitigate the risk of extinction when the probability of environmental catastrophe is uncertain. This annual probability only weakly affects the cost-efficiency of two equally sized fences (Fig. 4a, b). The second fence provides an insurance population in the event of catastrophe; spatial separation drastically decreases the chance of the entire population being threatened by a single event, and provides a source of individuals for repopulation if a local extinction occurs in one of the fences. Comparatively, the relationship is strong in the single fence: with higher probability of catastrophe, the cost per bilby per year increases quickly (Fig. 4a) and the probability of persistence per million dollars decreases dramatically (Fig. 4b).

An unevenly split two-fence system also shows a high sensitivity to the frequency of catastrophe, being dominated by two evenly split fences when fires are as frequent or more frequent than those seen at Lorna Glen. The proportion of the population killed in an environmental catastrophe is beta-distributed, with smaller areas skewed more to the right (because smaller fences are more likely to burn completely). This means that the population in the smaller fence in an unevenly split two-fence system is more likely to be extirpated completely as the frequency of environmental catastrophe increases.

Two fences with an uneven split cost less per bilby per year with low probabilities of environmental catastrophe

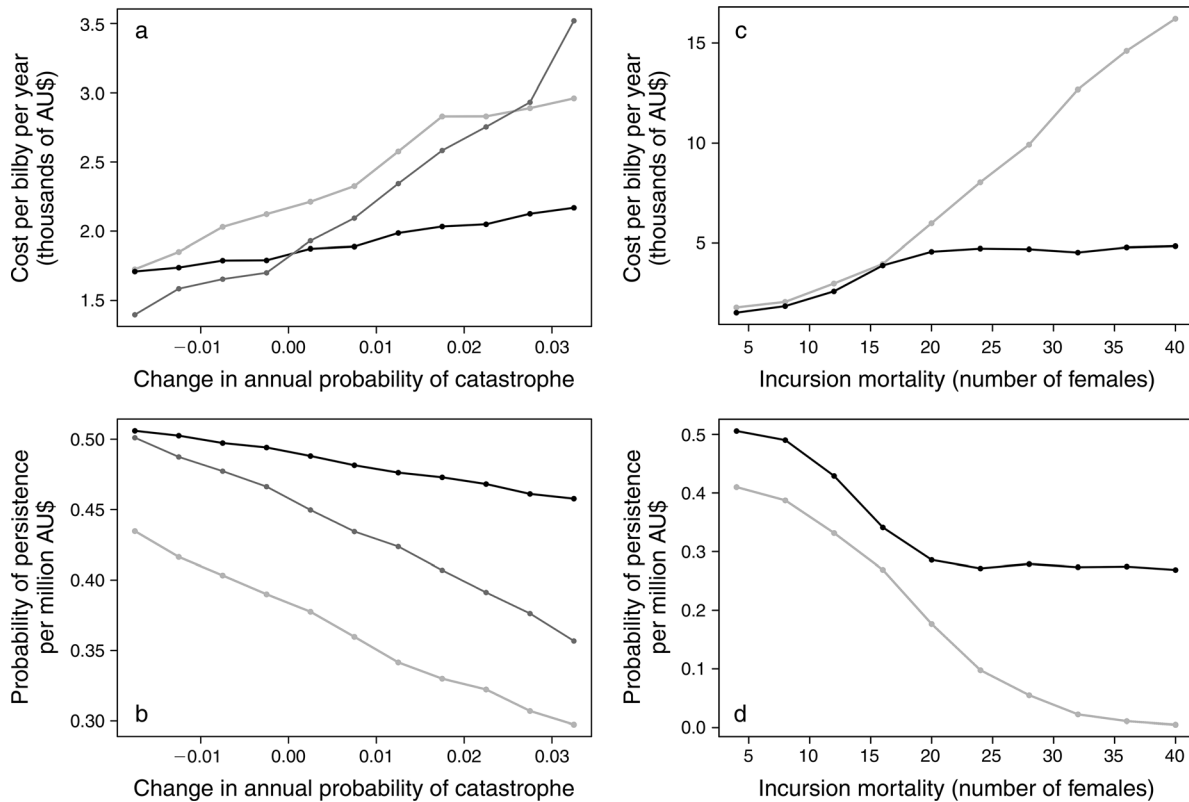


FIG. 4. Sensitivity analysis on the performance of each fencing strategy. The single large fence is shown in light gray; the system of two small, evenly sized fences (separated by 40 km) is in black; the system of two small, unevenly sized fences is in dark gray. Under both objectives, the two-fence system is more robust to increases in probability of environmental catastrophe (a, b) and incursion mortality (c, d). The dark gray line for two unevenly sized small fences has been omitted for clarity in (c, d) because the performance of this system falls between the evenly sized and single large fences here and is never optimal.

than do evenly split fences (Fig. 4a). In the absence of frequent environmental catastrophes, the main drivers for extinction are demographic stochasticity and mortality from incursion. When the fences are unevenly split, one of the two fences houses a larger population, which is less influenced by demographic stochasticity (Lande 1993). Additionally, the smaller insurance population will experience fewer incursions because their probability depends only on perimeter length.

Incursion mortality

The cost per bilby per year of the single-fencing system increases sharply with the number of females that are killed in a single incursion by a predator (Fig. 4c). The probability of persistence of the population in a single fence per million dollars invested declines steadily (Fig. 4d). The performance of a two-fence system is much more robust to increases in incursion mortality. Incursions threaten at most one of the two populations; this means that if a predator enters one fence and eliminates the population, then the other fence is a source of individuals for repopulation. We see that the cost-efficiency of the two-fence system is robust with respect to the number of females that are killed during

each incursion. The mortality of an incursion is unpredictable: it is a result of many interacting factors including the number of predators involved, their attack rate, their ability to evade capture once detected, and the manager’s detection abilities. Where this parameter might be underestimated, the robustness of the two-fence system would minimize the unpredicted negative effects of high incursion mortality.

Under the Lorna Glen parameterization, the carrying capacity in each small fence is 26 females vs. 98 in the single fence (Table 1). With an incursion mortality of 26 or more females, two fences are more cost-efficient under both objectives than is the single fence. This demonstrates that two fences are more cost-efficient even if one population is extirpated with each incursion event than if the single-fenced population declines by approximately 25%. This flexibility is due to the repopulation of the empty fence from the remaining population, requiring both populations to go extinct at the same time for a global extinction to occur.

Threatened species demographics

Analysis of the results’ sensitivity to birth rate shows that the two-fence system dominates at low birth rates,

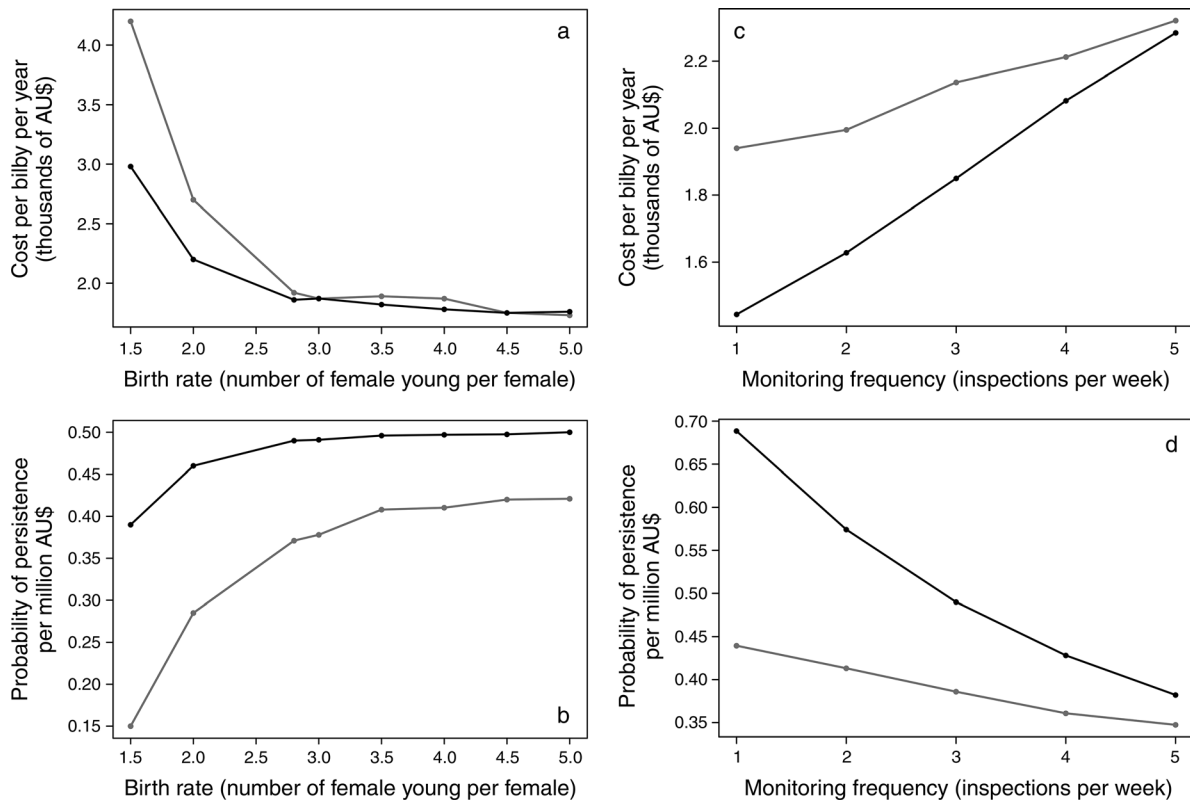


FIG. 5. The effect of the birth rate (number of female young per year per female bilby) and monitoring frequency (the number of times each fence is visited by a manager for any routine monitoring and maintenance) on the performance of each fencing strategy. The single fence is shown in light gray, the evenly split two-fence system (separated by 40 km) in black.

and the two strategies are comparably cost-efficient at birth rates higher than 3. At very high birth rates ($b \geq 5$, almost double that of bilbies in the arid zone), the cost per bilby per year of both fencing strategies almost converge to the same value (AU\$1700). At these high birth rates, the populations will reach carrying capacity for much of their lifetime, which results in many more individuals to share the costs in a single-fence system. Driving this objective is demographic stochasticity, which has a lesser effect on larger populations (Lande 1993). In contrast, aiming to maximize the probability of persistence per million dollars gives results that are more robust to demographic changes; two fences have a consistent advantage over a single fence under this objective even at very high birth rates. This result is driven by environmental stochasticity, which affects the two-fence system less due to the spatial correlation of environmental catastrophes declining with distance, and the potential for repopulation.

Costs and monitoring

The optimal strategy is robust to variations in costs: both initial (construction, eradication) and ongoing (maintenance, travel, eradication, repopulation). However, the results are sensitive to the frequency of monitoring. Because travel between the two fences is

required with each monitoring event, the two-fence system is disadvantaged by frequent monitoring (Fig. 5c, d). If the system is monitored five times per week or more, it is optimal under both objectives to construct a single fence.

Decreasing the discount rate from 5% quantitatively alters the recommendations of our model (see Fig. 6a, b for the optimal solution to the case study with a discount rate of 2%). The qualitative recommendation is somewhat robust, however: at an optimal distance, two fences are at least as cost-efficient per bilby per year as a single fence with discount rates as low as 2% per annum. The flexibility in the distance between the two fences is restricted under both objectives (Fig. 6a, b), but the flexibility in size ratio up to 1:3 is preserved. Also preserved is the mitigation of potential cost blowout. Even at low discount rates, the upper bound of the single-fence system was up to 220% more expensive than the two-fence system in our simulations (comparing the 95th quantiles of the cost per bilby per year; Fig. 6a).

DISCUSSION

We used a return on investment approach to choose between constructing a single large or two small fences for conserving a species threatened by an introduced predator. The primary benefit of a single large fence is

that it is cheaper on a per-unit-area basis: a larger fence can be constructed with the same initial budget; it therefore has a higher total carrying capacity than a two-fence system. On the other hand, two smaller fences can mitigate risks of both catastrophic damages and system-wide extinction. These risk mitigation benefits are heightened because managers can redistribute the effects of environmental stochasticity by translocating individuals between the two fenced exclosures.

In this study we considered two management objectives. A manager planning a fencing program for a threatened species with multiple existing fenced populations (such as bilbies in Australia) may place a higher importance on maintaining a larger population in a new fence, even if the trade-off is a lower probability of persistence at 50 years. In that management scenario, the objective is to minimize the cost per bilby per year, because this metric will be minimized when there are more individuals to share in the construction and operating costs. This is likely to be the objective when a manager wants to use the population as a source for new introductions and she is concerned about inbreeding depression and loss of genetic variability. However, if the persistence of the new fenced population is extremely important (for example if it will be one of the only secure populations of the threatened species), the manager should aim to maximize the probability of persistence per million dollars invested. Under this objective, more secure populations have a high benefit even if they are small. This second objective promotes the construction of two small fences under a much wider range of parameters than the first, highlighting the trade-offs between decreased total size of the fenced area, recolonization potential, and risk of extinction. The two objectives give opposing recommendations in scenarios with some parameter combinations; this emphasizes the need for a clear management objective in the planning stages of any fencing project.

Where a manager's objective is not captured by either of the two objectives we considered, we can place constraints on the acceptable solutions and then choose the most cost-efficient of those. For example, by considering cost-efficiency, we did not consider the absolute probability of persistence. Plans to recover a threatened species sometimes aim for a particular probability of persistence; this can be a requirement for down-listing a species. A minimum probability threshold will drive the decision in some cases, because a single fenced population has a lower probability of persistence. Adding this constraint may alter the optimal recommendation to a less cost-efficient solution. For example, two fences may be required to meet the persistence threshold, but if the only available land parcels were separated by large distances, this would not be cost-effective.

Two-fenced reserves are a stereotypical example of risk mitigation. Not only is the project much less likely to experience severe cost blowouts (with projected

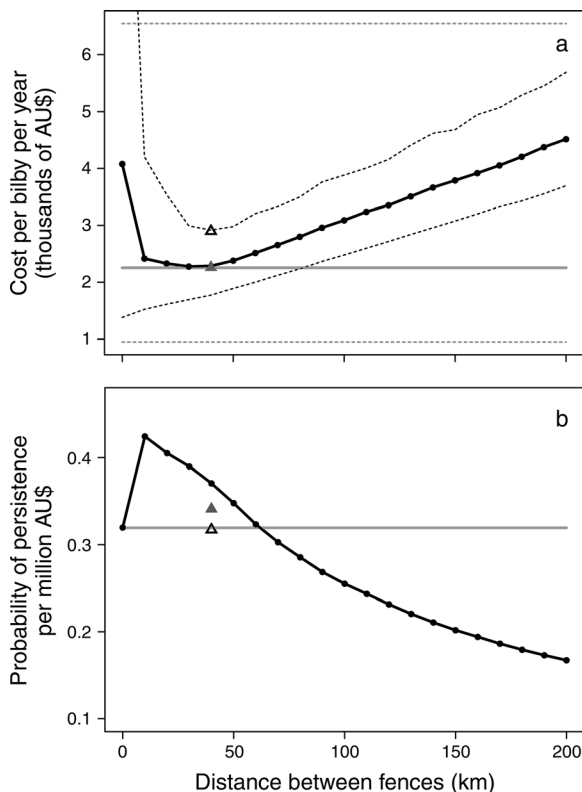


FIG. 6. The performance of each fencing strategy with a discount rate $r = 0.02$ at different distances. The mean performance of a single fence, which does not have any distance dependency, is given by a solid light gray line and the mean performance of a two-fence system by a black line. The gray triangle is the performance of a two-fence system with a 1:3 ratio in size; the open triangle is a two-fence system with a 1:9 split. Panel (a) includes the respective 5th and 95th quantiles as dashed gray and black lines.

savings of hundreds of dollars per bilby per year), but the two-fence system is also more robust to inaccurate estimations of the frequency and intensity of catastrophic events. This would be extremely useful, because most conservation management scenarios have unpredictable catastrophes and poor information (Halpern et al. 2006). In particular, the absence of historical flood data for the Lorna Glen region introduces environmental uncertainty to this model. Severe drought is a danger throughout Australia; in this paper we have assumed that the effects would be so widespread as to affect all exclosures equally and that supplemental feeding would be implemented to prevent loss of life. We recognize, however, that some parts of the landscape may function better as drought refugia (Stafford Smith and Morton 1990).

The optimal strategy depends heavily on the distance between the available reserve sites for two reasons: first, environmental catastrophes are spatially correlated; second, ongoing management costs (particularly monitoring) scale with the distance between fences. Our model suggests that there is a specific distance (40 km for



PLATE 1. The predator exclusion fence at Lorna Glen in Western Australia used as a case study in this paper (for a description of the fence see Bode et al. [2012]). Photo credit: Keith Skelley, Western Australian Department of Parks and Wildlife.

the Lorna Glen case study) below which it is optimal, under both objectives, to construct two fences. At larger distances, the expected cost-efficiency of a single fence is better than that of two fences, because the greater distance does not reduce the probability of simultaneous catastrophes, but continues to increase ongoing management costs. At sufficiently short distances, two fences do not mitigate environmental risks because catastrophes are likely to impact both fences simultaneously.

In almost all situations where a two-fence system is recommended, the optimal size ratio of the two fences is 1:1. If land is not available to adhere strictly to this ratio, however, there is substantial leeway to split the areas unevenly. For the Lorna Glen case study, disparate splits of up to 1:3 (if separated by 40 km) are still more cost-efficient than a single-fence system. This means that our recommendations are much more flexible and feasible for real-world management scenarios.

Comparisons of Australian marsupial populations have revealed that fenced populations have lower genetic diversity than unfenced populations (de Tores and Marlow 2011), and smaller fences would be expected to have correspondingly lower diversity. The different genetic diversity of one- or many-fence solutions would therefore operate to improve the relative performance of a single-fence decision (either by incurring lower genetic management costs, or by experiencing higher fitness through less inbreeding). However, it is unlikely that these differences would be of

sufficient magnitude to affect our conclusions, and therefore we did not include them. Although the alternative fences would support markedly different populations, the rate of loss of genetic diversity would be quite similar because both are still relatively small (Miller et al. 2009). The management of genetic diversity under each of the alternatives would attract a similar total cost, and therefore would not impact the relative priority of the different options. Over the lifetime of the fence, the expected loss of genetic diversity would also be low (<8%) under either action (Miller et al. 2009). Evidence indicates that such a change would be unlikely to dramatically impact fitness (Chapman et al. 2009), and, through it, the population dynamics.

The findings that under many scenarios two fences are better than one can help to directly inform management decisions about how many fences to construct and at what distance they should be placed for the conservation of the greater bilby in the arid zone of Australia. Through our sensitivity analyses, we found that as the expected mortality from environmental catastrophe and incursion increases, two-fence systems outperform single-fence systems by an increasing amount. These results are also extremely robust to cost estimates. These sensitivity analyses broaden the applicability of our results to the conservation of greater bilbies in any landscape. Additionally, our investigation of the effect of differences in demographic parameters means that these results can also help to guide conservation fencing

decisions for different threatened species, in entirely different countries and contexts.

Fences are long-term investments, and over time it is possible that our parameterizations will have reduced accuracy. However, robustness to changes in ongoing costs indicates an enduring aspect of this study over time. With reduced costs due to technological advances and improved techniques, the quantitative results presented here will still hold. This robustness also ensures the applicability of the results to different landscapes, remoteness, and excluded invasive species, all of which can dramatically affect the project costs (Long and Robley 2004). If fencing materials and technology are improved in the future, the reliability of a new fence might be increased and the frequency of monitoring required could be decreased, resulting in higher cost-efficiency for the two fences. On the other hand, for risk-averse managers who might monitor the system daily, a single fence would be a better choice.

We have considered only the conservation of a single-species metapopulation here. This also captures fencing projects that will house multiple species, but where the project is designed to maximally benefit one particular threatened species. In reality, fences are likely to house a number of species, and the interactions between these may affect the optimal fencing strategy. Some threatened species may also provide critical services that benefit the entire ecosystem (Lawton 1994, James and Eldridge 2007), which we have not considered here. Species interactions and ecosystem services could be incorporated into this framework through the demographic model and the calculation of the conservation benefit.

On a practical level, this research extends the Single Large or Several Small (SLOSS) debate by including fenced enclosures; by allowing the consideration of ongoing monitoring, management, and translocation costs as well as initial expenditure; and by including spatially correlated environmental stochasticity, as well as demographic variation. As with models of SLOSS in reserves, our results show that the optimal management decision—whether to construct a single large fence or two smaller fences—is complex and contextual (McCarthy et al. 2005). At a broader level, our results provide novel emphasis to the two contrasting factors that drive the SLOSS question: the risk-spreading benefits of multiple independent projects, and the various benefits (ecological and economic) of acting at a large-scale. Fenced enclosures highlight very common issues that nevertheless receive relatively little attention in the SLOSS debate—ongoing costs and active management—because the debate around the utility of fences as a management strategy focuses closely on their ongoing expenses. These factors can drive managers in opposing directions: ongoing costs emphasize the economies of scale offered by single reserves, whereas active interventions allow managers greater scope for managing risks. Interestingly, the cumulative result of

these novel factors does not simplify the SLOSS problem. Instead, they will exacerbate the consequences of mistakes. They therefore make a clear understanding of the nuances of specific projects even more important.

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SUPPLEMENTAL MATERIAL

Appendix

Parameterizing the model of environmental catastrophe (*Ecological Archives* A024-205-A1).