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Title: Costs are key when reintroducing threatened species to multiple release sites

Running head: Costs are key when reintroducing species

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Abstract

Threatened species with reduced and fragmented habitats can be reintroduced into their historical ranges to establish new populations. Multiple sites might be options for reintroductions; therefore, managers must determine when to open sites (e.g., establish infrastructure and improve conditions), release individuals into those sites, and eventually cease releases. Careful planning of this schedule, incorporating the cost of actions, is imperative at the outset of a program. To address this challenge, we consider a reintroduction plan under different cost scenarios for three potential reintroduction sites. In particular, we investigate the implications of having no ongoing site-management cost, a financial ongoing site-management cost, and a demographic cost of continuous releases. We couple population and management models to find a schedule that maximizes total abundance over time of bridled nailtail wallaby *Onychogalea fraenata* (released in fixed numbers each breeding season from a stable source population) using stochastic dynamic programming. We find that the type of ongoing cost influences the structure of the optimal schedule. If active release sites cost nothing to maintain, there is no incentive to cease releases. In that case, the optimal schedule is to open sites sequentially, then release individuals to the smallest active population for the entire length of the program. A financial cost for managing active sites alters this result; once all sites are open and have populations of a critical threshold size, sites should be closed sequentially. A higher mortality rate (demographic costs) at active compared to inactive sites completely changes the structure of the optimal strategy. Instead of opening all sites in the first few management stages, only one site should be active any time to reduce the demographic impact of releases. Our general results provide a guide for planning future reintroduction

programs and illustrate the importance of categorizing and understanding ongoing costs for reintroduction planning.

1 Introduction

Establishing new threatened species populations is a promising but expensive conservation strategy. For species with highly restricted and fragmented ranges, the only opportunity for recolonization into secure habitat is through assisted introduction or reintroduction (Griffith et al. 1989, Sarrazin and Barbault 1996, Hoegh-Guldberg et al. 2008). Given the huge conservation opportunities available through establishing new populations, useful management rules have been established for captive-to-wild reintroductions in the absence of ongoing financial costs (Fischer and Lindenmayer 2000, Tenhumberg et al. 2004, Hardman and Moro 2006, Rout et al. 2009, Converse et al. 2013a, Runge 2013). However, despite wide recognition that considering costs when making conservation decisions with a limited budget increases management efficiency and impact, reintroduction-planning science has largely omitted ongoing financial costs (Naidoo et al. 2006, Bottrill et al. 2008, Evans et al. 2015, McDonald et al. 2015). Reintroductions can be expensive, so ongoing costs may have a substantial impact on the cost-efficiency of these programs (Morris et al. 2015). Where an ongoing stream of individuals are available for release each year (e.g. Mawson 2004), repeated decisions must be made to distribute the releases between new populations to improve the overall outcome for the species while considering these financial costs.

Threatened species reintroduction program costs fall broadly within three categories: cost of providing individuals for release (either breeding and rearing costs, or surveying wild source populations); site preparation costs; and the ongoing monitoring and maintenance costs at active release sites. Site preparation costs go beyond just land acquisition. Even if the management organization already owns the release site, the main local extinction driver must be addressed before any releases can begin (Kleiman et al. 1994). Harmful invasive species must either be locally eradicated (Bode et al. 2013, Helmstedt et al. 2016) or continuously managed (Helmstedt et al. 2014); habitat restoration might be required (Miller and Hobbs 2007); and management infrastructure must be constructed. Detailed baseline ecological data about the release site is needed (IUCN 2013), and population modeling and assessment should be undertaken prior to starting releases especially where the reintroduction schedule depends on the site carrying capacity (Seddon et al. 2007). Careful planning of each reintroduction is key to success of the newly established population (Chauvenet et al. 2013). Post-release monitoring is effective not only to increase success of the new populations, but also to inform future translocation programs of the same species (Armstrong and Seddon 2008). Additionally, there are costs to ceasing active releases to a site; detailed ecological assessments and reporting procedures may be required. While these initial costs are high there is no reason to assume they eclipse ongoing management costs (Kleiman et al. 1991). Management costs often exceed startup costs over the lifetime of a program even with discounting and must be considered in any planning effort (Armsworth et al. 2011).

Creating additional wild populations is expensive but imperative for the bridled nailtail wallaby *Onychogalea fraenata* persistence (McKnight 2008). These endangered

Australian marsupials were thought to be extinct until a population was discovered in 1973 in Dingo, Queensland (Gordon and Lawrie 1980). New populations have since been reintroduced at two additional sites, each isolated within a matrix of unsuitable habitat and introduced predators. A reintroduced population at Avocet National Park was established through 14 releases (averaging 4.85 females per release) from 2001-2005. The wallabies breed up to three times per year, ensuring a frequent stream of individuals for release from captive breeding facilities and established sites (Kingsley et al. 2012). Identifying new potential translocation sites is a primary goal set out by the WWF action plan for Bridled nailtail wallabies (Roache 2011). We investigate the next stage in the recovery process: when multiple sites have been identified, how should the releases proceed?

When faced with multiple potential reintroduction sites, a manager must determine when to prepare a new release site, and where to allocate bridled nailtail wallabies. Should they release to each site until it is very close to carrying capacity before moving on to the next? Or should they invest in preparing each release site at the outset and then alternate between releasing to each site year to year? We will use structured decision making to show that the optimal schedule is between these two extremes – focusing on a single site vs spreading resources equally. We aim to optimize a single-species release program by considering the process of opening potential reintroduction sites, releasing individuals and ceasing releases. We will consider three different cost structures for continuing active releases at a site. First, we ignore any ongoing costs, assuming that there are only three financial requirements: initially establishing the release site, producing individuals for release, and finishing active releases. We retain and add to these costs for the next two scenarios. Second, we consider a scenario where the financial cost of maintaining an active release site could alternatively be spent conserving bridled nailtail wallabies through a separate conservation program, therefore decreasing the net benefit to the species of running the release program. Third, we assume that there is a demographic cost to a population at any site that is receiving active releases (e.g. through higher mortality in released individuals, see Pople et al. 2001, Seddon et al. 2007, Shier and Swaisgood 2012, or inability to find a mate Servanty et al. 2014) or is being intensively monitored. Runge (2013) incorporated similar demographic costs to design an age-structured release strategy to a single griffon vulture (*Gyps fulvus*) population. Previous studies have investigated how to use limited funds when releasing individuals to establish a single reintroduced population (Haight et al. 2000, Canessa et al. 2014), and how to allocate individuals between multiple release sites without cost considerations or the potential to stop releases (Collazo et al. 2013). However, this is the first study that explores ongoing cost and the subsequent trade-off between number of populations and the number of individuals released.

By investigating the way different cost structures affect the optimal management strategy for bridled nailtail wallabies, we will highlight the need to thoroughly consider the costs incurred in specific reintroduction scenarios. We will develop specific guidelines for bridled nailtail wallaby reintroductions, but also infer general rules that are applicable to many reintroduction programs. These guidelines can act as a decision support tool for the cost-efficient management of reintroductions to improve the outcomes for threatened species conservation for the limited funds available.

2 Materials and Methods

We consider the management of a reintroduction program that has three potential but unprepared release sites of equal quality for bridled nailtail wallabies. We assume a reliable source of adults for release (such as the successful captive breeding population established at Gregory mine site in Queensland or the original population at Taunton National Park, Kingsley et al. 2012), but we do not explicitly model the source population. We construct a population transition model that accounts for demographic stochasticity for each newly established wild population (see Supporting Information, Caswell 2001, Tenhumberg et al. 2004, Rout et al. 2009). Assuming females drive population dynamics and that an equal number of males are released, we will consider only females in our model. We couple the population model with an explicit management model: in each breeding season, a manager is required to choose one of a finite set of actions. We optimize the schedule of these actions through time, depending on the populations at the release sites.

2.1 Management objective

The ultimate goal of this program is to establish multiple reintroduced wild populations, and the manager's direct objective is to maximize the current and future abundance of the threatened species across the new populations. The state of the system is the population size at each of N reintroduction sites, $s = \{n_1, n_2, \ldots, n_N\}$. At each time-step in our planning horizon, the immediate reward gained by the manager is the total reintroduced population size, given by

$$R(s,a) = \sum_{1}^{N} n_i(t) + m_{s,a}$$

Equation 1

where $n_i(t)$ is the population of the threatened species at site i at time t, and $m_{s,a}$ is the number of individuals released, defined by the action a and the state s.

The overall objective is to maximize the abundance summed over the lifetime of the project (from $t = 0$ to $t = T$ breeding seasons), defined by Bellman's equation (Bellman 1954)

$$V(s,t) = \max_{a} \left[R(s,a) + \sum_{s'} T_a(s,s') V(s', t+1) \right].$$

Equation 2

$T_a(s,s')$ is the probability of the populations at each site transitioning from state s to state s' after action a is taken (see Population Dynamics section).

2.2 Population Dynamics

We construct a Markovian population model with a truncated carrying capacity for each released population. In this model, reproduction occurs followed by demographic mortality in each breeding season. For full details of the population model, see the Supplementary Materials. For a description of the population parameters, see Table 2.

2.3 Management model

After each breeding season, the manager must take an action (summarized in Table 1). Opening a site requires preparing the site for a newly released population, with potential activities ranging from constructing infrastructure to habitat modification or invasive species removal. In this model, we assume that each site being considered requires the same preparation. Every site begins in an unprepared state with no individuals, which we define as U. If the site i is opened (the action o_i), the site is empty (state $n_i = 0$) but is active and prepared to received releases in the following time-step. When a site is active, infrastructure and monitoring is maintained at the site, and individuals can be released to that site (action r_i). We assume that these adult individuals are integrated into the breeding population immediately (although we relax this assumption when considering the demographic cost of management). Alternatively, an active site can cease future releases (action c_i) moving the site to a finished state (f). At this stage, intensive monitoring for the translocation program stops (although might continue if managers have other goals outside the scope of this project), infrastructure is no longer necessarily maintained, and if a physical manager presence was needed this ceases. We assume that once a site is finished, it can not be reopened; however a site can be in the active state but not receiving releases in any given year.

[Table 1 about here]

2.4 Management costs

We consider three classes of management cost: releasing individuals (including breeding and capturing them), costs of site actions (preparing a release site and ceasing releases at one), and costs of maintaining an active release site. The implicit tradeoff between cost and abundance is reflected in the reward function. We make the assumption that releases, opening a site, and ceasing future releases have the same financial and temporal cost. Therefore we restrict the manager to only one action (open, release, or cease) at each time-step, forcing a trade-off to be made: opening a new reintroduction site to allow a new population in the future, or ceasing future releases to save ongoing maintenance costs incurs an immediate cost to the wild population numbers.

Maintaining an active site for potential future releases also incurs a cost. We explicitly model three classifications of ongoing site maintenance costs. First, in our base case, we present the optimal release schedule without any ongoing management cost. Second, we include a financial cost for each active site. We assume that the money spent maintaining a site open for releases, including the cost of intensive monitoring (Kleiman et al. 1991), could have otherwise been spent conserving individuals of this species in another project external to the reintroduction program. We incorporate this into the model by reducing the immediate reward gained (Equation 1) by the number of active sites A:

$$R(A, a) = \sum_{1}^{N} n_i(t) + m_{s,a} - A.$$

Third, we consider the possibility that active sites incur a demographic cost. Although there has been no evidence of a mortality impact of monitoring activities at the Bridled nailtail wallaby release site at Avocet, monitoring has been short and infrequent, and resulted in population estimates with large confidence intervals (Kingsley et al. 2012). Implementing a population-based action plan requires frequent and precise population estimates, which increases the required monitoring frequency and intensity. Even a small error in population estimates can result in large strategy changes, and the need for population estimates in every time-step amplifies any small effects. Therefore ongoing, intensive monitoring is needed, which has the potential to disrupt the population and cause increased mortality. Although this demographic impact is likely to be minimal, fewer females breed at capacity at Avocet National Park than at their native sites, indicating potential population pressure in released populations (Kingsley et al. 2012). We investigate how increases in mortality of up to 30% (increasing the adult mortality from 0.4 to 0.52) in active sites would affect the optimal release schedule.

Post-release effects have been reported in reintroduced populations, and are likely to be widespread but perhaps under-detected (Panfylova et al. 2016). It is possible that only the newly released individuals experience an increased mortality rate, not the entire population. We do not model this scenario here because it reduces to a variation of the no cost scenario with a smaller number of individuals successfully released. Therefore, we only investigate a scenario where maintaining an active site affects the demographics of the entire population. We assume this effect occurs every year, because the elements of an active site (i.e., maintaining intensive monitoring, infrastructure, and personnel activity) are not specific to release times.

2.5 Optimization method

Bridled nailtail wallabies breed three times a year – this means that every four months managers are required to make a decision about if and where to release individuals from captivity, so we have a time-step length of four months. We consider a program length of 40 breeding seasons (equating to 13.3 years, acting three times a year), roughly the time required to establish three populations comparable in size to that at Avocet National Park. We consider a captive breeding program that consistently produces four females per breeding cycle.

[table 2 about here]

Using Stochastic Dynamic Programming (Bellman 1957, Mangel and Clark 1988), we find the optimal schedule for opening three potential reintroduction sites and releasing Bridled nailtail wallabies under each of our three cost structures.

3 Results

3.1 Bridled nailtail case study

[Fig. 1 about here]

With no cost for keeping sites open for release, and with $K = 50$, the optimal schedule that the manager should follow depends both on the number of active sites (sites that have been opened) and the population within those sites (Fig. 1a, 2a). With no cost for keeping sites open for releases, sites should be opened one by one as the active sites reach critical population sizes. For the bridled nailtail wallaby case study, the second site should be opened as soon as the first site reaches a population of $n^* \geq 12$ individuals. The third site should be opened as soon as both of the first two sites reach $n^{**} \geq 18$. At all other time-steps, the available individuals should be released to the active site with the smallest population. In sites with larger carrying capacities, the critical populations increase in proportion with the carrying capacity (Fig. 3a,c, red lines). Each site should be filled to around 40% of the maximum population before the next is opened.

[Fig. 2 about here]

Approximately equal populations should be maintained at each active site. All sites should eventually be open at the same time. Since this initial scenario does not include a cost to maintaining active release sites, there is no incentive to cease reintroductions to sites. The releases continue to the smallest population for the duration of the program.

3.2 Financial cost

We first expand the management model to consider a case where the funds required to maintain an open release site could be invested in conserving one breeding pair of the same species elsewhere (Fig. 1b, 2b). Sites should be opened according to the same schedule as the previous scenario (in the absence of ongoing costs). With a carrying capacity of $K = 50$, once all sites are open and have reached a threshold population of

$n_f = 22$, active releases should cease to the largest population. At this point, the probability of falling to an irrecoverable level is low and financial resources are more productively spent on other conservation efforts. Releases are ceased at one site at a time, and if any of the active populations drop below n_f, supplemental releases should be made until all are back at that critical population. The critical population n_f increases in proportion to the carrying capacity (Fig. 3a,) with sites being closed when they are about 80% full. The required population is very close to carrying capacity (Fig. 3c). In sites with carrying capacities of fewer than 20 individuals it is never optimal to finish a site, it should always be kept open for potential future releases.

3.3 Demographic cost

If a population at an active site experiences mortality rates within 30% of inactive sites, the optimal release schedule is unchanged and adheres to the no cost scenario (Fig. 1a). However, when active sites experience a mortality rate more than 30% higher than finished sites it is optimal to only have one site active at any time (Fig. 1c, 2c). A site is opened, released to, and then finished before another site is opened. Sites are never active but not receiving releases, because this results in wasted individuals. The required population at each site before ceasing releases increases with the number of already established populations. A population of $n_f = 12$ is required before ceasing releases to the first site and moving on to the second regardless of the carrying capacity of each site (Fig. 3b). The critical population for the second site is slightly higher (around $n_{ff} = 14$ to 18 individuals, increasing with carrying capacity), and the third is higher again ($n_{fff} =$ 18 to 24 individuals, increasing with carrying capacity). These populations are much lower at all carrying capacities than when a direct penalty is incurred (55% vs. 90% if $K = 50$, Fig. 3c). Again, there is a special case when the carrying capacity is 10 or smaller, indicating a minimum viable population size. It is never optimal to finish a population in such a small site, and the optimal schedule is identical to the first management case with no ongoing costs.

3.4 Optimal schedule through time

As the fixed end of the program approaches and there are fewer time-steps remaining for rewards to accrue, Bellman's equation (Equation 2) places more emphasis on immediate than future rewards. Therefore, as time progresses the optimal action tends toward ceasing releases at smaller populations to prevent immediate penalties. However, for bridled nailtail wallabies all changes in actions tend to be completed within the first 20 timesteps (Fig 2). The optimal schedule that we have reported here holds for the first 35 (of 40 total) timesteps; this is likely to cover the entire active decision-making portion of the translocation program.

4 Discussion

We used stochastic dynamic programming to find the optimal schedule for reintroductions to multiple release sites that incur an initial establishment cost and ongoing management costs. This approach allowed us to find decisions that are optimal in the long-term over the entire lifetime of the project rather than myopic decisions that increase only immediate rewards. We found that the structure of ongoing management costs drives the qualitative patterns of how we make tradeoffs between: opening new release sites, releasing individuals and ceasing releases within cost restrained scenarios.

With very low ongoing management costs, our results showed that a bridled nailtail wallaby reintroduction manager should open sites and reintroduce small populations one by one, until all sites are simultaneously open. The population sizes at open sites dictates which one the manager should release to: always the smallest, with the aim of keeping all populations equal. Keeping the sites open with intensive monitoring and the possibility of further releases maximizes the managers' flexibility; if a population starts to dip, managers can respond quickly and alter their strategy. If this flexibility is comes at no additional cost, it will always be the best management situation. The critical population sizes required before opening the next site increase concavely with carrying capacity. At relatively large populations (up to 50 individuals considered here), the populations need to reach less than 50% of the carrying capacity before a manager can be reasonably confident in that population and should spread their efforts to open a new reintroduction site.

Without considering ongoing management costs, we showed that there is little incentive to stop actively releasing to a population. This is untrue where a financial cost is incurred by active sites. If the money being spent maintaining each open release site could have been invested elsewhere on conservation for the same (or an equally valued) species, the optimal schedule for opening the reintroduction sites and establishing small populations is unaffected. However, once all the sites are open and have all reached a critical population size, translocations should cease at each site one by one. This critical population size is consistently large: around 90% of the total carrying capacity. This result indicates that the financial burden is not severe enough to justify ceasing releases to sites because of cost. Since stochastic dynamic programming looks into the future rather than optimizing myopically, adding individuals to a site now will provide future benefits even if the same number of individuals is subtracted from the immediate reward. It is better to achieve a healthy and self-sustaining population at each site before spending time and money closing down a reintroduction program to one site. Ceasing releases to a site is a risky decision; the infrastructure is no longer available to supplement a declining population with extra individuals at a finished release site (and in fact since intensive monitoring of the state has ceased, this decline may go undetected). Reestablishing releases to avoid failure at sites that have been prematurely closed would be expensive financially, require time to change the policy and set up the required physical infrastructure, and allow additional population decline due to delayed detection and action.

We treated all financial costs as a trade-off between actions rather than including explicit costs, by assuming that the cost of keeping a site open for releases for one year could otherwise be spent on a conservation project external to this reintroduction program. This assumption exposes a fundamental question in conservation decision theory: if money is saved on one project, where should it next be spent? A substantial literature exists for prioritizing how funds should be spent between multiple different projects (Joseph et al. 2009, Bennett et al. 2014, Helmstedt et al. 2016), and we do not undertake this process here. The value of this tradeoff is case-specific; it depends on the species, the alternate project, and the relative weight the manager places on each identified objective (Converse et al. 2013b). While these trade-offs are simplistic and do not capture every element of real-world funding, they allow us to incorporate costs into the stochastic dynamic programming structure. Failing to consider costs in conservation problems can lead to extreme differences in actions and outcomes (Baxter et al. 2006, Naidoo et al. 2006), and we have made a valuable step away from that issue for reintroduction programs here.

Captive-bred individuals can suffer from higher mortality rates than wild-born individuals (Beck et al. 1994, Haque and Smith 1996, Stoinski et al. 2003, Whiteside et al. 2015) due to decreased fitness and lack of predator awareness in captivity (Snyder et al. 1996). Although this increased mortality is contested, our results suggest that managers should invest in knowing it. We identified a tipping point for bridled nailtail wallabies (an increase of 30% mortality at active release sites). Below this tipping point, the optimal policy is identical to the no-cost scenario and releases should not be ceased. Above this tipping point, we see a change in the qualitative result: a manager should never have more than one bridled nailtail wallaby release site open at a time. Sites should be opened, filled to a critical population level (a small fraction of the carrying capacity) and then we move to releases at another site. This change in release strategy is because keeping a site open and continually monitored for active releases increases the mortality in this scenario, outweighing the lower likelihood of long-term survival of a smaller reintroduced population. As the number of established populations increases, the total number of individuals released to the next new sites also increases. This captures the benefit of free individuals created in established populations; in the time required to release a population at a new site, the other established populations are growing at no additional cost.

Future applications of this method to specific case studies might broaden knowledge of the costs or benefits for any specific conservation problem. In reintroduction programs that are particularly concerned with genetic variation (especially where there are few existing populations), augmenting populations after ceasing translocations may be beneficial to slow the decline of genetic diversity (Ottewell et al. 2014). Intensive modeling and management programs can increase the long-term viability of reintroduced populations by increasing their genetic viability (Bach et al. 2010). In this case study we assume that genetic exchanges are equally necessary regardless of the initial schedule used to establish the release populations, resulting in equal cost requirements for each strategy we consider. Therefore, we have omitted this ongoing cost from the scope of this study. Translocations can provide broad benefits to entire ecosystems, such as that resulting from wolf reintroduction in Yellowstone National Park (Fortin et al. 2005, Ripple and Beschta 2012, Ewen et al. 2014). If this is a primary goal of translocation programs, the reward function in Bellman's equation should be altered to reflect ecosystem changes. Our study is restricted only to projects with a sustainable stream of individuals to be released either from a captive breeding program or a large, stable wild population; scenarios where the release of individuals reduces the viability of the source population (such as bearded vultures *Gypaetus barbatus*) are excluded (Bustamante 1996).

Our findings show that there are vast differences in the recommended structure of a reintroduction program when ongoing financial costs and demographic costs to maintaining active release sites are considered. We found general rules to inform future translocation or captive breeding release programs. By incorporating initial setup, release and management costs we increase the realism of our reintroduction model, and our results can be used by managers and decision makers as a decision support tool.

Reintroductions, translocations and increasingly assisted colonizations are frequently used to mitigate human impacts on threatened species, and increase their chance at persistence. Where species' ranges have contracted beyond the potential for natural recolononization such as is the case for bridled nailtail wallabies, managed reintroductions represent the only opportunity for new populations to be created. These findings will help to ensure that these efforts and funds are leveraged for the highest possible impact on bridled nailtail wallabies, and threatened species in general.

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Tables

Table 1 The actions possible when a site is in a particular state, and the resulting population growth.

State	New state if no action is taken	Available action	New state after action
U	Remains unprepared	Open site	0
n	$n' = f(n)$	Release m individuals Cease translocations	$n' = f(n+m)$ C, with pop $f(n)$
C	C with pop $f(n)$	No actions available	No actions available

Table 2 Demographic parameters for bridled nailtail wallabies (Rout et al. 2009) and management parameters

Parameter	Definition	Value
β	birth rate (number of offspring per female per 4 months)	0.9
f	probability offspring are female	0.5
μ	adult mortality rate	0.4
$1-\lambda$	juvenile mortality	0.1
m	number of females released each time-step	4
N	number of sites	3
K	carrying capacity	25 females

Figures

Fig. 1

Optimal actions for each site identified by solving the stochastic dynamic programming problem. Grey indicates no action at that site, green open site, yellow close site, and blue release. Where multiple sites are eligible for the "release" action, the manager should release to the site with the smallest population.

Fig. 2

Population growth at three single-replicate simulations of optimally managed release sites. Each main plot shows the abundance at the three sites over time, while the lines below the axis indicate which sites are active (have been opened and not yet ceased receiving releases). Three different ongoing cost structures are considered: (a) no ongoing costs; (b) the financial cost of maintaining an active site could be spent conserving one breeding pair of the species elsewhere; (c) open sites experience increased mortality.

Fig. 3

The critical population to change the management action for different carrying capacities. (a) Red line shows opening schedule for the scenarios with no ongoing site management costs and with financial cost, which are identical. The second population should be opened when the first reaches the solid red line, and the third when the first two reach the dashed red line. With no management costs, translocations never cease. With ongoing financial costs, the sites should cease translocations one at a time when all populations reach the green line. (b) Adult mortality is doubled at open sites. Only one site should be open at any time: the first should cease translocations at the solid blue line (always n = 12), then the second should be opened until it reaches the dashed blue line, and then the third until it reaches the dotted blue line. (c) All critical populations in panels (a) and (b) as proportions of carrying capacity.

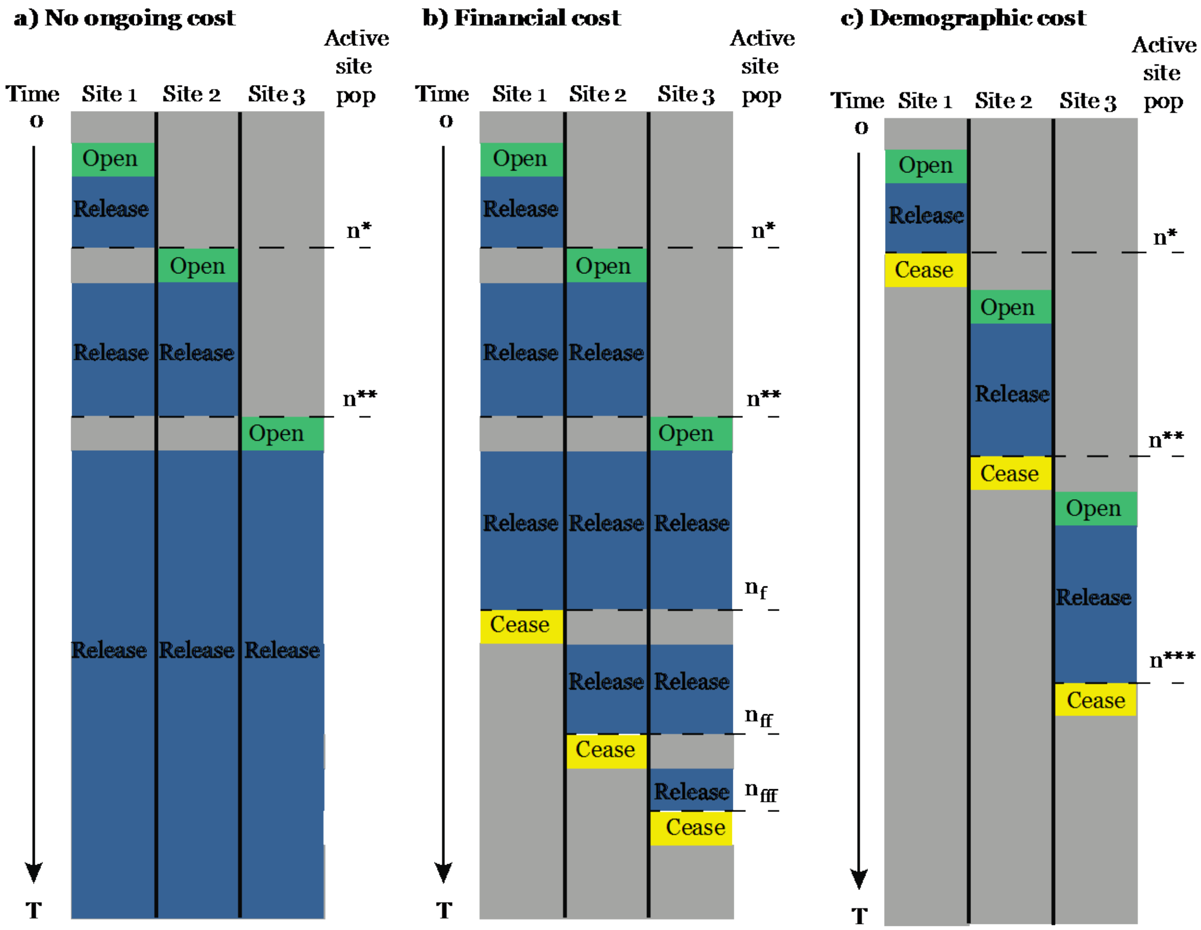
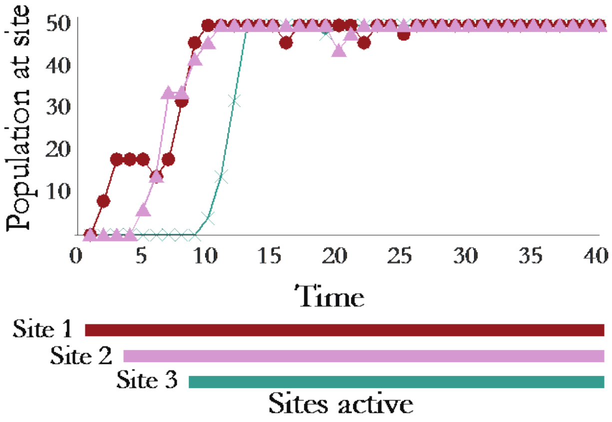
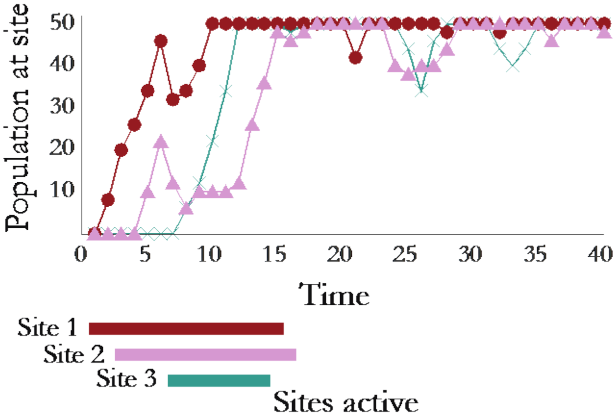

a) No ongoing cost
Time
Site 1
Site 2
Site 3
Active site pop
0
Open
Release
n*
Open
Release
Release
n**
Open
Release
Release
Release
T
b) Financial cost
Time
Site 1
Site 2
Site 3
Active site pop
0
Open
Release
n*
Open
Release
Release
n**
Open
Release
Release
Release
n_f
Cease
Release
Release
n_{ff}
Cease
Release
n_{fff}
Cease
T
c) Demographic cost
Time
Site 1
Site 2
Site 3
Active site pop
0
Open
Release
n*
Cease
Open
Release
n**
Cease
Open
Release
n***
Cease
T

Fig 1.

(a) No ongoing costs



(b) Financial cost



(c) Demographic cost

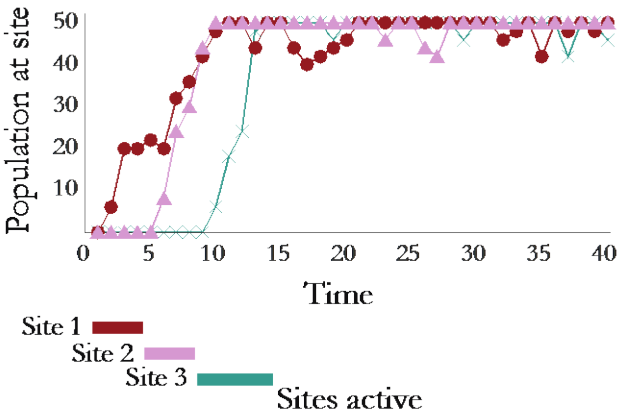


Fig. 2

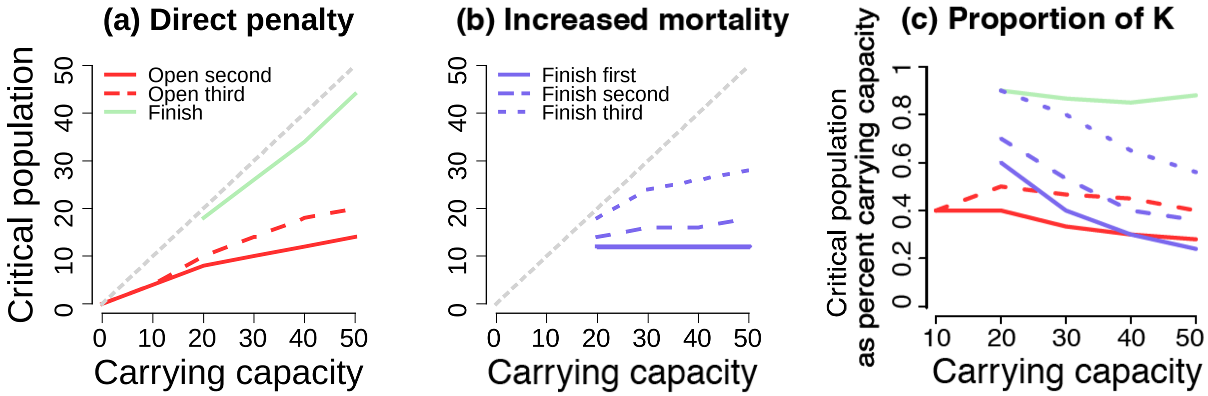

(a) Direct penalty
Critical population
Carrying capacity
Open second
Open third
Finish
0
10
20
30
40
50
(b) Increased mortality
Finish first
Finish second
Finish third
(c) Proportion of K
Critical population as percent carrying capacity
0.2
0.4
0.6
0.8
1

Fig. 3