

Optimal adaptive management for the translocation of a threatened species

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Abstract. Active adaptive management (AAM) is an approach to wildlife management that acknowledges our imperfect understanding of natural systems and allows for some resolution of our uncertainty. Such learning may be characterized by risky strategies in the short term. Experimentation is only considered acceptable if it is expected to be repaid by increased returns in the long term, generated by an improved understanding of the system. By setting AAM problems within a decision theory framework, we can find this optimal balance between achieving our objectives in the short term and learning for the long term. We apply this approach to managing the translocation of the bridled nailtail wallaby (*Onychogalea fraenata*), an endangered species from Queensland, Australia. Our task is to allocate captive-bred animals, between two sites or populations to maximize abundance at the end of the translocation project. One population, at the original site of occupancy, has a known growth rate. A population potentially could be established at a second site of suitable habitat, but we can only learn the growth rate of this new population by monitoring translocated animals. We use a mathematical programming technique called stochastic dynamic programming, which determines optimal management decisions for every possible management trajectory. We find optimal strategies under active and passive adaptive management, which enables us to examine the balance between learning and managing directly. Learning is more often optimal when we have less prior information about the uncertain population growth rate at the new site, when the growth rate at the original site is low, and when there is substantial time remaining in the translocation project. Few studies outside the area of optimal harvesting have framed AAM within a decision theory context. This is the first application to threatened species translocation.

Key words: active adaptive management; Bayesian statistics; bridled nailtail wallaby; decision theory; *Onychogalea fraenata*; optimization; Queensland, Australia; reintroduction; stochastic dynamic programming; translocation; wildlife management.

INTRODUCTION

Managers of natural systems must make difficult decisions in the face of considerable uncertainty. This uncertainty presents itself in three ways (Parma and NCEAS Working Group on Population Management 1998). First, process uncertainty comes from variability and unpredictability in natural processes that are beyond the manager's control. For example, a wildlife manager cannot predict a population growth rate that is highly weather dependent. Second, model uncertainty arises from an inability to understand exactly how a system works, for example, knowing how a species will respond to changes in habitat availability. Finally, observational uncertainty comes from our inability to directly and precisely measure the state of a system, such

as the number of individuals of a particular species in a predefined area.

One way to deal with uncertainty when managing is to take an adaptive management approach. Adaptive management recognizes uncertainty and can reduce model uncertainty if that reduction can improve future performance (Walters 1986). It involves specifying a number of candidate hypotheses or models of how the system is functioning, and updating the level of belief in each model as the results of management are observed. There are two forms of adaptive management: passive and active. The difference between the two lies in whether the learning potential of management actions is considered when making decisions. In passive adaptive management, learning is valued, but is not part of the management plan. In active adaptive management (AAM), the ability to learn influences management decisions: there is a balance between achieving the objective in the present and learning for improved management in the future.

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Although AAM has been widely advocated for wildlife management (Parma and NCEAS Working Group on Population Management 1998, Shea et al. 2002, Aldridge et al. 2004, Folke et al. 2004, Grafton and Kompas 2005, Takagawa et al. 2005, Morita et al. 2006, Schmiegelow et al. 2006), its application has been limited (Lee 1999, Allan and Curtis 2005); exceptions include Sainsbury (1991) and Walters et al. (1993). Existing management cultures may not encourage the acknowledgment of uncertainties (MacDonald and Rice 2004, Allan and Curtis 2005). Experimental actions can be perceived as failures or bad management when there are short-term losses, even if this outcome reduces model uncertainty (Lee 1999). The cost of forgoing returns during short-term experimentation may be too great, particularly when the ecological "short-term" translates to years or even decades (Walters et al. 1993). In cases where there is a clearly defined objective, decision theory offers a rational and transparent framework for AAM. We can determine the precise amount of learning that will be repaid by improved future management, maximizing expected returns over the entire time frame in question. A careful choice of time horizon and discount factor indicates the level of tolerance for short-term losses (Walters and Green 1997).

Decision theory is a formal approach to decision making that involves clearly specifying objectives and acknowledging uncertainty (Clemen 1996, Shea and NCEAS Working Group on Population Management 1998). It can be implemented with qualitative methods or complex mathematical tools (Shea and NCEAS Working Group on Population Management 1998, Possingham et al. 2001). A decision-theoretic approach requires a clear statement of management objectives, a list of management options, identification of the important variables to monitor, and at least one plausible description of the dynamics of the system (Shea and NCEAS Working Group on Population Management 1998). A quantitative decision-theoretic approach to adaptive management has been applied extensively to problems of optimal harvest, particularly of fish (Walters and Hilborn 1976, Smith and Walters 1981, Walters 1981, Walters et al. 1993) and waterfowl (Nichols et al. 1995, Williams and Johnson 1995, Johnson and Case 2000). However, only recently has it been applied to other areas of wildlife management, such as designing marine reserves (Gerber et al. 2005), managing forests to maintain old-growth habitat (Moore and Conroy 2006), and planning revegetation (McCarthy and Possingham 2007).

In this paper we optimize the AAM of bridled naitail wallaby (*Onychogalea fraenata*) translocation, as an extension of the translocation problem described in Rout et al. (2007). AAM has been advocated repeatedly for species translocations (Sarrazin and Barbault 1996, Brook et al. 2002, Stockwell and Leberg 2002, Hirzel et al. 2004, Seddon et al. 2007), although it is seldom applied (Blumstein 2007). A recent exception is Arm-

strong et al. (2007), who applied an AAM approach to the reintroduction of the New Zealand Hihi to Mokoia Island. Although the reintroduction itself failed, the use of an AAM approach allowed them to gain useful information from the process, which they then utilized in reintroductions of the species to other islands. However, their adaptive management manipulations were based on more traditional experimental design, rather than a decision-theoretic approach.

We examine the AAM of the translocation of bridled naitail wallabies, an endangered species found in central Queensland, Australia. Once believed to be extinct, bridled naitail wallabies were rediscovered at a single location in what is now Taunton National Park. They have since been successfully translocated to Idalia National Park and Avocet Nature Refuge, and a substantial captive population has been established (Johnson 2003, Lundie-Jenkins and Lowry 2005). To satisfy the conditions of recovery, as specified in its 2005–2009 Recovery Plan, the species needs to be reestablished at two more sites (Lundie-Jenkins and Lowry 2005).

METHODS

We construct an AAM plan for a manager who must choose where to translocate wallabies over time, with a choice of two possible sites. We assume that the manager has good knowledge of population growth at the first site. A second new site is available for translocations, but there is limited information on its suitability as habitat for this species. The only way to learn about its suitability is to translocate there and monitor the outcome. The choice of whether to invest translocated animals in the original site or the new site depends heavily on what the population growth rates are at the two sites (Rout et al. 2007). How much effort should be put into learning about the new site, as opposed to just managing with the information already available? This scenario allows us to look directly at learning and managing in an AAM context.

Formulating the problem

Assume that wallabies from a captive source population can be translocated to two different sites. The captive population produces two "excess" individuals available for translocation in each time step. The growth rate of our population at the "original" translocation site is known, whereas the growth rate is uncertain at the other "new" site, and we will have opportunities to learn its value by translocating animals to that site and following their fate. Management must decide where to translocate available captive animals, and we represent this decision with variable d (the number of individuals translocated to the new site). Both animals can be translocated to the original site ($d = 0$), both can be translocated to the new site ($d = 2$), or one animal can be translocated to each site ($d = 1$).

TABLE 1. Reasonable ranges for demographic parameters of bridled naitail wallabies

Parameter	Definition	Established range	Source
λ	birth rate (probability of a female giving birth to one offspring in a 4-month period)	0.89–1.00	Johnson (1997), Fisher et al. (2000)
f	ratio of female to male newborns	0.5	McCallum et al. (1995)
μ_B	mortality rate (probability of an individual dying in a 4-month period)	0.01–0.46	Fisher (1998), Fisher et al. (2000), Pople et al. (2001)

Population dynamics

We use a first-order Markov chain stochastic population model to describe the dynamics of each population. We label the new and original populations A and B , respectively, and limit them to maximum sizes of K_A and K_B . This population size limit can be interpreted as the carrying capacity of each population site. We only track female wallabies: there are n_t^A females in population A at time t , and n_t^B females in population B at time t . Each time step in the SDP is equal to four months. In each time step, animals are translocated, then the entire population is subject to natural mortality, and then there is reproduction. Translocated animals experience the same mortality rate as the rest of the population; we assume that there is no additional mortality associated with translocation. The translocation project runs for four years, or 12 time steps ($T = 12$).

Stochastic births and deaths in the populations are represented using matrices, with elements that give the probability of shifting from one population size to another within a time step. Both populations A and B have the same recruitment matrix \mathbf{L} . (It is simple to construct different recruitment matrices for each site if it is relevant to the translocated species.) A female can give birth to a maximum of one newborn in a time step. This occurs with a probability λ , and there is a probability f that the newborn will be female. Because we assume a female cannot have more than one newborn in a time step, the probability that a single female has i female newborns in a time step is

$$b_{i,1} = \begin{cases} (1 - \lambda) + \lambda(1 - f) & \text{if } i = 0 \\ \lambda f & \text{if } i = 1 \\ 0 & \text{otherwise.} \end{cases}$$

Following from this, the probability that j females have i female newborns is

$$b_{i,j} = \begin{cases} ib_{1,1} + (j - i)b_{0,1} & \text{if } i \leq j \\ 0 & \text{otherwise.} \end{cases}$$

At population densities close to the carrying capacity K , reproduction is truncated to ensure that the population does not exceed its carrying capacity. Each element $l_{m,n}$ of the recruitment matrix \mathbf{L} is the probability that the population changes from n to m individuals due to reproduction:

$$l_{m,n} = \begin{cases} b_{m-n,n} & \text{if } n \leq m < K \\ 1 - \sum_{i=n}^{K-1} b_{i-n,n} & \text{if } m = K \\ 0 & \text{if } m < n \text{ or } m > K. \end{cases}$$

Population B has a known mortality rate μ_B . Each element $s_{i,j}^B$ of the survival matrix \mathbf{S}_B is the probability of j individuals surviving to become i individuals in the next time step, where i and j are both $\leq K_B$. This is given by the binomial probability

$$s_{i,j}^B = \begin{cases} \binom{j}{i} \mu_B^{j-i} (1 - \mu_B)^i & \text{if } 0 \leq i \leq j \\ 0 & \text{otherwise.} \end{cases}$$

The Markov chain transition matrix for this population from time step (t) to time step ($t + 1$) is $\mathbf{M}_B = \mathbf{L}\mathbf{S}_B$, the matrix product of the recruitment matrix \mathbf{L} and the survival matrix \mathbf{S}_B . We do not consider processes of immigration and emigration, because, in cases of threatened species with isolated translocation sites and low population densities, dispersing animals are unlikely to survive and reproduce.

We chose demographic parameters within reasonable ranges for bridled naitail wallabies, as outlined in Table 1. The birth probability for both populations (λ) is kept constant at 0.9, and we examine three possible mortality rates for population B (μ_B): 0.4, 0.3, and 0.2. The per capita growth rate r of population B can be approximated as the expected number of female offspring resulting from one female (Tenhumberg et al. 2004):

$$r = \sum_{i=1}^{K_B} im_{i,1}^B$$

where $m_{i,1}^B$ is an element of the transition matrix \mathbf{M}_B . We thus examine situations in which population B is known to be decreasing ($\mu_B = 0.4, r = 0.87$), roughly stable ($\mu_B = 0.3, r = 1.015$), or increasing ($\mu_B = 0.2, r = 1.15$).

The carrying capacities of the populations, K_A and K_B , are both set at 30 individuals. These were not chosen as realistic population limits for bridled naitail wallabies, but are rather an upper limit on what we can reasonably compute with the program. To ensure that this does not bias our conclusions, we analyze results for when the original population is both far from and close to its carrying capacity, to examine its effect on the optimal strategies.

To describe our limited knowledge of the mortality rate in population A (μ_A), we use a beta probability distribution. It has the following density function (with shape parameters α and β):

$$f(\mu_A) = \frac{\mu_A^{\alpha-1}(1-\mu_A)^{\beta-1}}{B(\alpha, \beta)}$$

where $B(\alpha, \beta)$ is a beta function that acts as a normalizing constant. Constructing the survival matrix for population A is more complicated than for population B due to the uncertain mortality rate μ_A . Because we do not know the mortality rate exactly, we cannot construct the survival matrix S_A exactly. Instead we must integrate over all possible values for μ_A , weighting by the probability that each is the true mortality rate (using the beta distribution). After some algebraic manipulation (see Appendix A), the expected survival matrix for population A can be shown to be

$$E_{\mu_A}(s_{h,n_t^A+d}^A | \alpha, \beta) = \begin{cases} \frac{\binom{n_t^A + d - h + \alpha - 1}{n_t^A + d - h} \binom{h + \beta - 1}{h}}{\binom{n_t^A + d + \alpha + \beta - 1}{n_t^A + d}} & h \leq n_t^A + d \\ 0 & h > n_t^A + d \end{cases}$$

(when we assume that α and β are positive integers), where $s_{h,n_t^A+d}^A$ is the probability that $n_t^A + d$ wallabies at time t become h wallabies at time $t + 1$ due to mortality ($h \leq n_t^A + d$). $E_{\mu_A}(\cdot)$ is the expected value taken over all possible values of mortality rate μ_A . We only consider cases where the beta parameters α and β are positive integers. In Appendix A, we give an alternative formulation for any positive real α and β .

We assume that animals translocated to the new site are monitored for the time step of their translocation, and we receive data on whether they survive that time step. These translocated individuals have the same mortality rate as the rest of population A , and can thus be viewed as a sample of the larger population. (If translocation increases mortality, the mortality rate of translocated animals is then a conservative estimate of the mortality of the larger population.) Data on the death and survival of translocated animals give us further information about the mortality rate μ_A , which can be combined with the present understanding of the mortality rate (a beta distribution) using Bayes' theorem. The monitoring of death and survival is a type of binomial sampling, which is known to be a conjugate for a beta prior distribution (Casella and Berger 1990). This means that the posterior combination of new data and a beta prior is also a beta distribution with different parameters. We can therefore update our knowledge of the mortality rate quite easily: for binomial sampling with g deaths and $d - g$ survivors from n translocations, the beta distribution can be updated as $(\alpha + g, \beta + d - g)$

(McCarthy 2007). That is, to update the mortality rate, we add the number of animals that die to α , and add the number of animals that survive to β .

Parameters α and β can take any positive value, yet it is necessary to choose a finite set of values at which to calculate the optimal management strategy. Throughout the four-year translocation project there is a maximum of 22 opportunities to learn about the new site (translocation occurs in time steps 1 to 11; in each, two animals at most can be translocated to the new site). If we were to begin the translocation project with a uniform beta distribution ($\alpha = 1, \beta = 1$), and we have at most 22 learning opportunities, we could arrive at any combination of $\alpha = 1, 2, \dots$ and $\beta = 1, 2, \dots$ such that $\alpha + \beta \leq 24$. To allow for other more informative prior distributions, we imposed a much higher ceiling of 52 on $\alpha + \beta$. Any additional data obtained that would cause the parameters to violate this condition are ignored. We analyze results only up to $\alpha + \beta \leq 24$ to ensure that this upper bound on learning does not interfere with the strategies observed.

Finding the optimal management strategy

To determine the optimal management decisions, we use a mathematical method known as stochastic dynamic programming, or SDP. SDP determines the exact optimal decision for each possible management state, which in this case is defined by the number of animals at each site. It can be applied to any stochastic system with a finite number of states, and where sequential decisions are made (Bellman 1957, Mangel and Clark 1988, Lubow 1996). SDP has been applied to ecological management problems such as harvesting a wild population (Walters 1981, Johnson et al. 1997), biocontrol (Shea and Possingham 2000), fire management (McCarthy et al. 2001), allocation of conservation effort (Yokomizo et al. 2003, Wilson et al. 2006), and landscape reconstruction (Westphal et al. 2003), as well as translocation (Lubow 1996, Tenhumberg et al. 2004, Rout et al. 2007).

The first step of any optimization is to define the objective. We aim to maximize the total number of animals in both populations at the end of the translocation period. That is,

$$V(T, \alpha, \beta, n_T^A, n_T^B) = n_T^A + n_T^B \tag{1}$$

where V is the value of the strategy. We subsequently calculate the value of the optimal strategy at earlier time steps in the translocation project (assuming that all subsequent decisions are optimal) as the expected total population size at terminal time T . Stochastic dynamic programming produces state-dependent optimal decisions, which in this case means that an optimal decision is found for each population state, i.e., for every possible number of animals in each population (n_T^A, n_T^B), and a range of states of belief regarding the uncertain mortality rate (positive integer values of α and β such that $\alpha + \beta \leq 52$). At the terminal time T , the final reward

is calculated for each population state based on the objective function. The SDP then steps backward, to evaluate each possible decision for each possible state in the previous time step, using transition probabilities given by the population models. Of all the possible decisions to be made, the one that yields the highest expected returns is selected as the optimal decision for that system state at that time step.

Passive adaptive management

Although we are principally concerned with optimizing active adaptive management, we first calculate the equivalent optimal passive adaptive strategies. These are essential for identifying situations in which it is optimal to learn under AAM. By comparing optimal strategies, we can find situations where it is optimal to add to the new population under active adaptive management, but not under passive adaptive management; these are decisions driven by the need to learn.

The dynamic programming equation for passive adaptive management is

$$\begin{aligned}
 &V(t, \alpha, \beta, n_t^A, n_t^B) \\
 &= \max_{d=\{0,1,2\}} \sum_{i=0}^{K_A} \sum_{j=0}^{K_B} \sum_{h=0}^{n_t^A} \sum_{g=0}^d V(t+1, \alpha, \beta, i, j) \\
 &\quad \times E_{\mu}(s_{h,n_t^A}^A | \alpha, \beta) E_{\mu}(s_{d-g,d}^A | \alpha, \beta) l_{i,h+d-g}^A m_{j,n_t^B+2-d}^B
 \end{aligned}$$

where V is the expected final population size (across both sites) under optimal passive adaptive management, and it depends on the current time step in the translocation project (t), current knowledge about the mortality rate in population A (a beta distribution with parameters α and β), and the current size of each population (n_t^A and n_t^B). It is found by determining the expected final population sizes under each possible translocation choice d and choosing the maximum. These expected values are calculated by weighting all of the possible outcomes over the next time step by their probability of occurrence and summing the results. The SDP is calculated backward, so it begins by calculating the expected value V in the final time step T of the translocation project (Eq. 1). It then steps back to the previous time step $T - 1$, to calculate the expected final population sizes under each possible translocation choice, and finds the translocation for each state that will give the highest expected final population size. It continues to step backward, repeating this process and finding the optimal translocation d for each state in each time step.

We assume we observe that g of the d animals translocated to population A die within the time step. Population A has size i in year $t + 1$, while population B has size j . The probability of population B having size j is the probability of $n_t^B + 2 - d$ animals after translocation becoming j animals through births and deaths, and this can be read from the matrix \mathbf{M}_B . To

investigate the size of population A at time $t + 1$, we use the expected survival matrix to determine the probability that h of the initial n_t^A animals survive, and the probability that $d - g$ of the d translocated animals survive. Examining these probabilities separately is not necessary under passive adaptive management, but allows the beta distribution to be updated under active adaptive management, as we will describe. The surviving $h + d - g$ individuals reproduce to become i animals, and the probability of this occurring is read from the recruitment matrix \mathbf{L} .

Our observation that g of the d animals translocated to population A die within the time step gives us new information about the mortality rate of population A . However, as previously mentioned, the learning potential of actions is not considered when determining the value of a management decision under passive adaptive management. Hence, α and β are not updated with this new information when finding the optimal decision. When putting these optimal decisions into practice, new information about the mortality rate would not be ignored. In each time step, we would implement the optimal decision for the current state, which includes the current estimate of the new population mortality rate (described by α and β). If we were to learn new information about this mortality rate, in the next time step we would implement the optimal decision for the new estimate of the mortality rate. Thus learning may still occur, but under passive adaptive management the optimal decisions do not take into account the value of learning.

Active adaptive management

The dynamic programming equation for active adaptive management is

$$\begin{aligned}
 &V(t, \alpha, \beta, n_t^A, n_t^B) \\
 &= \max_{d=\{0,1,2\}} \sum_{i=0}^{K_A} \sum_{j=0}^{K_B} \sum_{h=0}^{n_t^A} \sum_{g=0}^d V(t+1, \alpha + g, \beta + d - g, i, j) \\
 &\quad \times E_{\mu}(s_{h,n_t^A}^A | \alpha, \beta) E_{\mu}(s_{d-g,d}^A | \alpha, \beta) l_{i,h+d-g}^A m_{j,n_t^B+2-d}^B.
 \end{aligned}$$

This is the same as for passive adaptive management, except that α and β are updated with new information that we receive from translocating to population A . Consequently, our updated understanding of the mortality rate in population A is a beta distribution with parameters $\alpha + g$ and $\beta + d - g$.

RESULTS

We present optimal translocation strategies as a function of the expected mortality rate $E(\mu_A) = \alpha/(\alpha + \beta)$ and $(\alpha - 1) + (\beta - 1)$, rather than considering α and β directly. The expected mortality rate is our best point estimate of the true underlying mortality rate at any time, whereas $(\alpha - 1) + (\beta - 1)$ gives the number of observations made if we begin with a uniform ($\alpha = \beta = 1$)

prior distribution for the mortality rate. Thus, it is a measure of the confidence we have in our estimated mortality rate. Furthermore, we focus our discussion of results on the optimal balance between learning and managing for a translocation project. We aim to answer this question: When should we learn to improve future management and when should we just manage as best we can with the information we have? Due to the complexity of the SDP and the volume of results generated, it is impossible to display the optimal management strategies in their entirety. Instead we focus on overall patterns in the results and illustrate our discussion with relevant examples.

Passive adaptive management

The optimal translocation to population A under passive adaptive management depends only on the expected mortality rate, and not on the uncertainty around that mortality rate ($[\alpha - 1] + [\beta - 1]$); see Figs. 1 and 2. If both sites are empty at the start of the translocation project ($t = 1$), optimal passive adaptive decisions are not affected by the carrying capacity of the original site (Fig. 1a, c, e). In this case, the expected mortality rate informs translocation decisions in the same way that the known mortality rate did previously (Rout et al. 2007). Generally, the optimal passive adaptive strategy is to translocate both wallabies to the site with the lowest (expected) mortality rate (Fig. 1a, c, e). If the original population is stable or increasing, optimal passive adaptive decisions are slightly affected by the carrying capacity of the new site (Fig. 1c, e). If the new site has a very low estimated death rate, instead of translocating both animals to the new population it is best to translocate one animal into each population. This is because the new site is expected to grow at such a rate that it will reach its carrying capacity within the translocation period, so the benefit of adding extra animals is diminished.

If the original population has a high mortality rate of 0.4, the passive adaptive decisions are not affected by the number of wallabies in that population (compare Fig. 1a and b). However, if the original population has a lower mortality rate, optimal passive adaptive decisions when it is close to carrying capacity are significantly different than those when it is empty. If the original population is stable ($\mu_B = 0.3$), it is optimal to translocate to the new site if it is expected to have a mortality rate of 0.37 or less, 0.07 higher than when the original site is empty (compare Fig. 1c and d). If the original population is increasing ($\mu_B = 0.2$), it is optimal to translocate to the new site if it is expected to have a mortality rate of 0.65 or less, 0.45 higher than when the original site is empty (compare Fig. 1e and f). In both these cases, the original population is likely to increase to carrying capacity within the time horizon without the aid of translocation. Any animals added to this population when it is at carrying capacity have a mortality rate of 1. In general, it is optimal to add to the population with the lowest

mortality rate. Thus, as the original population approaches carrying capacity it becomes optimal to translocate individuals to the new site over a broader range of (expected) mortality rates. The optimal passive adaptive strategy is thus driven only by the expected growth rates of the two sites in relation to their carrying capacities, not by the uncertainty in the unknown mortality rate at the new site.

Learning for active adaptive management

By comparing the passive and active adaptive strategies, we can determine the importance of learning about the mortality at the new site. The passive and active adaptive strategies show a marked difference in the early stages of the translocation project. For example, consider that both sites are empty, and the original population has a high mortality rate of 0.4 (Fig. 1a). There are many instances in which it is optimal to translocate to the new site under the active adaptive strategy, but not under the passive adaptive strategy. This is because the passive adaptive strategy is to translocate to the site with the lowest (expected) mortality rate and maximize expected population growth over the translocation project. However, under the active adaptive strategy it is sometimes optimal to translocate to the new site even when we suspect it has the lower population growth rate, so that we can learn more about the mortality rate there. Any losses incurred by translocating to a site with a higher mortality rate are outweighed by the benefit to future management of reducing uncertainty about the true mortality rate at the new site. Put more simply, the optimal decisions in these instances are driven by a need to learn.

Effect of prior knowledge on learning

As we would expect, it is more beneficial to learn when the estimated mortality rate at the new site is highly uncertain. For example, consider again that both sites are empty at the start of the translocation project, and the original population has a high mortality rate of 0.4 (Fig. 1a). When we have a low amount of prior information from which to estimate the new site mortality rate ($[\alpha - 1] + [\beta - 1] = 1$), we translocate to the new site up to an expected mortality rate of 0.67. Thus, if we are very uncertain, it is best to learn about the new site if we think it may have a mortality rate up to 0.27 higher than the mortality rate of the original population. When we have a large amount of prior information ($[\alpha - 1] + [\beta - 1] = 22$, for example) and thus have more confidence in our estimate of the mortality rate, it is best to learn about the new site up to an estimated mortality rate of 0.46, only 0.06 higher than the mortality rate of the original population.

Effect of mortality rate at the original site on learning

The importance of learning is also affected by the mortality rate of the original population. In Fig. 1 we compare strategies across different mortality rates for

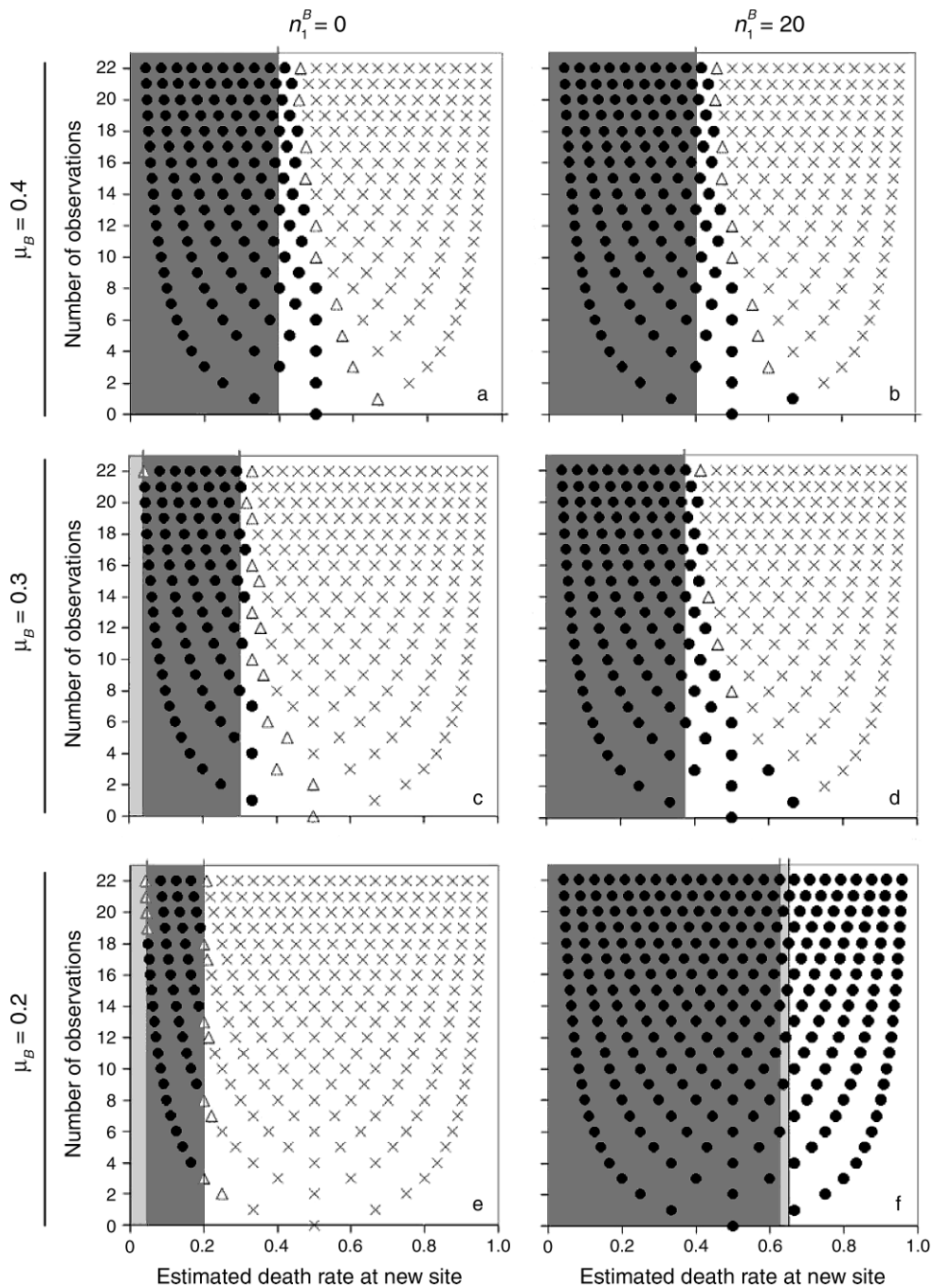


FIG. 1. Adaptive translocation strategies at the beginning of the project ($t = 1$) when the new site is empty ($n_1^A = 0$), where n_1^A is the number of females in population A at time t . The original site (n_1^B) is either empty (a, c, e) or consists of 20 wallabies (b, d, f). Shading indicates the optimal passive adaptive strategy: translocate both wallabies to the new site ($d = 2$, dark shading), one wallaby to each site ($d = 1$, light shading), or both wallabies to the original site ($d = 0$, no shading), where d is the number of individuals translocated to the new site. Symbols indicate the optimal active adaptive strategy: translocate both wallabies to the new site ($d = 2$, solid circles), one wallaby to each site ($d = 1$, triangles), or both wallabies to the original site ($d = 0$, crosses). Three different mortality rates for the original population (μ_B) are shown: 0.4 in the top row, 0.3 in the middle row, and 0.2 in the bottom row.

the original population, at the start of the translocation project. If the original population is empty and has a mortality rate of 0.4 (Fig. 1a), we learn about the new site if it has an estimated mortality rate up to 0.27 higher

than the original population. If the original population is empty and has a mortality rate of 0.3 (Fig. 1c), we learn about the new site if it has an estimated mortality rate up to 0.2 higher. If the original population is empty

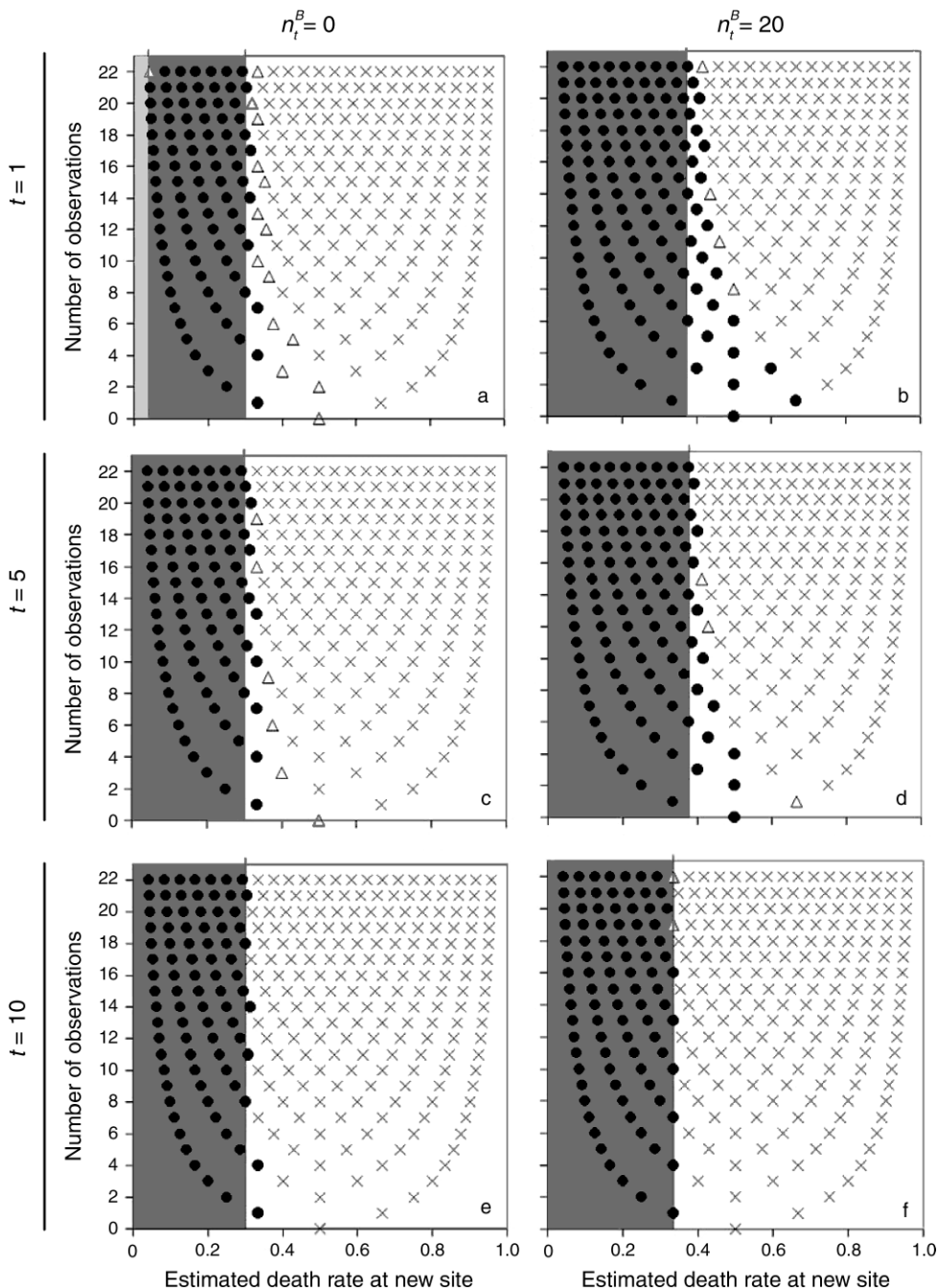


FIG. 2. Adaptive translocation strategies when the original population has a mortality rate of 0.3 ($\mu_B = 0.3$) and the new site is empty ($n_t^A = 0$). Strategies are shown across time: at the start of the translocation project 3 years 8 months remaining, $t = 1$), in the middle (2 years remaining, $t = 5$), and close to the end (8 months remaining, $t = 10$). The original site (n_t^B) is either empty (a, c, e) or consists of 20 wallabies (b, d, f). Shading indicates the optimal passive adaptive strategy: translocate both wallabies to the new site ($d = 2$, dark shading), one wallaby to each site ($d = 1$, light shading), or both wallabies to the original site ($d = 0$, no shading). Symbols indicate the optimal active adaptive strategy: translocate both wallabies to the new site ($d = 2$, solid circles), one wallaby to each site ($d = 1$, triangles), or both wallabies to the original site ($d = 0$, crosses).

and has a mortality rate of 0.2 (Fig. 1e), we learn about the new site if it has an estimated mortality rate up to 0.05 higher. Thus, the extent of learning decreases as the mortality rate of the original population decreases. If the original population has a low mortality rate,

there is less pressure to explore the alternative. However, if the original population has a higher mortality rate, it becomes important to determine whether a population established at the new site will fare any better. It is also less risky to translocate to the

new site if the benefit of translocating to the original population is small.

This observation does not hold when learning is influenced by the carrying capacity. Instances of learning can increase as the mortality rate of the original population decreases, if the original population is close to its carrying capacity or likely to reach its carrying capacity during the translocation period (Fig. 1b, d, f). For example, consider that the original population has a mortality rate of 0.2 at the start of the translocation project. If it is empty, it is optimal to learn about the new site if it has an estimated mortality rate of up to 0.25, which is 0.05 higher than under the passive adaptive results (Fig. 1e). However, if the original population is close to its carrying capacity, it is optimal to translocate to the new site for the entire range of estimated mortality rates, which is up to 0.35 higher than under the passive adaptive results (Fig. 1f). As previously noted, any animals added to a population at carrying capacity die immediately and are effectively “wasted.” Translocating to the new site (and learning the population mortality rate there) is therefore encouraged when the original population is likely to achieve the carrying capacity without translocation: the risk of failing when learning is outweighed by the risk of translocating to a full population. Translocation to the new site also has the added benefit of improving future management.

Effect of time remaining on learning

Instances of learning decrease as the translocation project progresses through time. For example, consider that the mortality rate of the original population is 0.3 and the new site is empty. If the original site is also empty at the start of the translocation project, learning is an important driver of optimal decisions up to an expected new site mortality rate of 0.5 (Fig. 2a). By the middle of the project, the extent of this learning decreases (Fig. 2c), and close to the end of the project (the second-to-last time step), learning only occurs up to an expected new site mortality rate of 0.33 (Fig. 2e). In the final time step of the project, no learning occurs at all. Again, we can see that when the original population is close to its carrying capacity, the range of expected mortality rates over which it is optimal to translocate to the new site is increased, and the range over which it is optimal to learn is increased (Fig. 2b, d, f). However, we still observe the same pattern of decreased instances of learning over time. The importance of learning decreases over time because its potential benefit to future management decreases. In the final time step there is no prospect of future management, so there is no benefit to learning.

Simulating active adaptive translocation

An example of the active adaptive management of a translocation project is shown in Fig. 3. Initially, the original and new sites hold 15 and 0 wallabies,

respectively. The mortality rate at the original population is known to be 0.3; the mortality rate at the new site is uncertain and a beta(3, 7) prior distribution is set for it. This is a somewhat vague distribution with a mean of 0.3, attaching roughly equal weight to the possibilities of an increasing or a declining population at the new site. In the first three time steps, all captive wallabies are translocated to the new site with the purpose of learning the mortality rate at this site. All six translocated wallabies survive their first time step in this new environment, and the manager’s perception of the mortality rate decreases. Furthermore, wallabies begin reproducing at the new site. The manager is now sufficiently confident that the new site is superior to the original site and all wallabies are translocated to the original population over the next three time steps. However, by chance the new population actually declines slightly, so the manager supplements the new population. The new population thrives over the second half of the project, and the estimated mortality rate for the new population is refined to a value near 0.2 as the translocation successes and failures are observed. The original population has 20 wallabies at the end of the project and the final population size at the new site is 27 wallabies, consisting of surviving translocated wallabies and their offspring.

We generated multiple simulations of translocation management over a range of parameter values (Appendix B). Active adaptive management produced mean final population sizes that were consistently greater than or roughly equal to those from passive adaptive management. The improvement of active over passive adaptive management is generally only 1–3% but can be as great as 20%. This occurs when the new site has an underlying mortality rate of $\mu_A = 0.2$ while the original population is known to be steady with $\mu_B = 0.3$. When both sites are empty, an active adaptive manager will translocate to the new site and quickly learn that a population can grow rapidly there. By contrast, a passive adaptive manager will spend much of the project establishing a steady population at the original site before translocating wallabies to the new site of unknown quality.

DISCUSSION

We have constructed a translocation strategy that incorporates uncertainty in the mortality rate of translocated animals at a site. Under passive adaptive management, the expected mortality rate at the new site is treated as the true value when making decisions. Under active adaptive management, there is opportunity to learn the true mortality rate and improve future management as a result. Learning is most beneficial to management: (1) when the original population has a high mortality rate; (2) when the original population is likely to reach carrying capacity; (3) when the mortality rate of the new site is highly uncertain; and (4) when more time remains for the benefits of learning to be

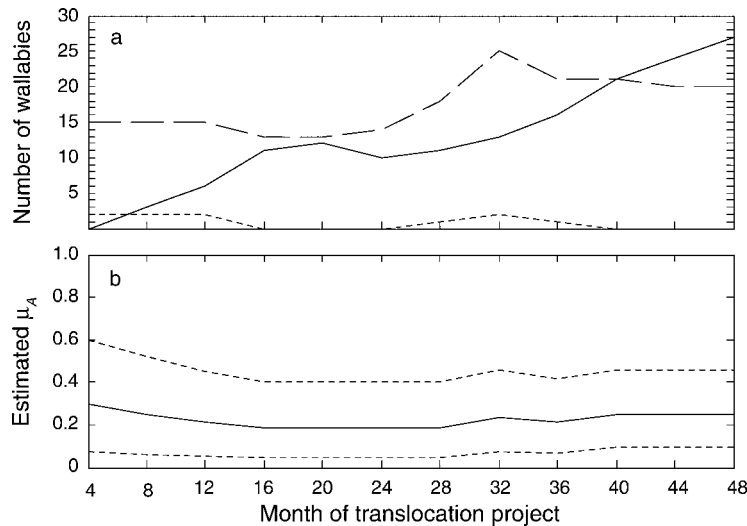


FIG. 3. An example simulation of active adaptive management of a four-year translocation project. (a) Number of wallabies at the new site, n_t^A (solid line), number of wallabies at the original site n_t^B (long-dashed line), and d , the number of wallabies translocated to the new site (short-dashed line). (b) Estimated mortality rate μ_A at the new site, denoted by the mean (solid line), with 2.5th and 97.5th percentiles on the beta distribution (short-dashed lines). The true mortality rates of the populations at the original and new sites are $\mu_B = 0.3$ and $\mu_A = 0.2$, respectively. Initially the original population consists of 15 wallabies, the new site is empty, and the prior distribution for the uncertain mortality rate at the new site is Beta(3, 7).

realized. The benefits to management can be significant: our simulations show that learning can increase the final number of animals by as much as 20%.

We have shown that the optimal strategies are influenced by the imposed carrying capacity. The specific carrying capacities imposed here are a necessity of the computational method, and may not reflect the biological reality for our case study of bridled nailtail wallabies. By analyzing results for when the original population is both far from and close to its carrying capacity, we have been able to examine the effect of this carrying capacity on the optimal strategies as well as the extent of learning. We have focused mainly on the carrying capacity of the original population, because we expect that a population translocated entirely to a new site is unlikely to approach such a limit over the course of the project.

We used a beta distribution to represent our knowledge of the uncertain parameter. In combination with the binomial observation process, this allows us to model belief of all values on the interval $[0, 1]$ using only two state variables, α and β , and to update model belief simply. The approach reduces computational requirements substantially and has potential application in a range of ecological management scenarios, such as measuring revegetation success (McCarthy and Possingham 2007) and modeling transitions in population size (Hauser and Possingham 2008).

There are several ways in which this framework could be made more realistic. By assuming that translocated animals have the same mortality rate as the larger population, we do not account for any increase in mortality caused by the translocation itself. We could

instead assume that there is some functional relationship between the mortality rate of translocated animals and that of the larger population. This would add complexity to the model, and the method of updating the expected mortality rate. We could also expand the framework to account for uncertainty in more than one model parameter. Incorporating uncertainty for more parameters would entail adding at least two more states to the SDP for each uncertain parameter, with each addition creating a geometric increase in computational requirements. Also, the results from such a program would be extremely difficult to interpret, especially when determining which factors drive optimal decisions. This model also ignores the effect of environmental stochasticity, such as the impact of weather on mortality. Incorporating this would involve tracking a variable mortality rate over time, which would also involve a significant increase in computational requirements as well as complexity of results. As with any model, there is a trade-off between realism and simplicity. As the first application of a Bayesian SDP to translocation, our model is a simpler one that can be built upon. If the complexity of this model were to be increased, it might be more appropriate to use a different decision analysis method to find an approximate rather than optimal solution.

Our simulations required specifying a prior probability for the mortality rate of the new site that could be updated when learning. We tried to select a vague prior: setting the mean of our prior to be 0.3 gives even weights to the possibilities of a declining population and a growing population. We could instead use a uniform distribution, which gives an initial mean mortality rate

of 0.5. However, as the mortality rate values for the original population range between 0.2 and 0.4, this means that the new site initially would be considered less suitable than the original site. Under passive adaptive management (where the expected mortality rate is treated as the true rate), the new site would never be utilized. Under active adaptive management, there is still an incentive to learn about the new site despite the prior belief of a high mortality rate. In this case, active adaptive management greatly outperforms passive adaptive management because, through learning, the new site can be discovered to be better than initially thought. In general, it is intuitive that the experimental approach of the active adaptive manager will perform well if the new site is highly suitable and will cause mortality when the site is unsuitable. This structured decision theoretic approach indicates when a manager should withdraw from an unsuitable site and utilize a new suitable location for species translocation. When applying these strategies in practice, ideally there might be information about the species and habitat quality that would allow the manager to construct a prior appropriate to the specific situation.

The translocation of threatened species could be an appropriate venue for the application of active adaptive management. Because of its threatened status, it may not be possible to delay the translocation of a species to learn about the suitability of candidate translocation sites. When managing in an actively adaptive way, this learning is incorporated into the management process, which can then begin without delay. By using decision theory to find the best management strategies, experimentation can be undertaken only when the benefits to future management are greater than the risk of losing animals.

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APPENDIX A

Derivation of the expected mortality rate of population A (*Ecological Archives* A019-022-A1).

APPENDIX B

Summary statistics of translocation project simulations (*Ecological Archives* A019-022-A2).