

Active adaptive conservation of threatened species in the face of uncertainty

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Abstract. Adaptive management has a long history in the natural resource management literature, but despite this, few practitioners have developed adaptive strategies to conserve threatened species. Active adaptive management provides a framework for valuing learning by measuring the degree to which it improves long-run management outcomes. The challenge of an active adaptive approach is to find the correct balance between gaining knowledge to improve management in the future and achieving the best short-term outcome based on current knowledge. We develop and analyze a framework for active adaptive management of a threatened species. Our case study concerns a novel facial tumor disease affecting the Australian threatened species *Sarcophilus harrisii*: the Tasmanian devil. We use stochastic dynamic programming with Bayesian updating to identify the management strategy that maximizes the Tasmanian devil population growth rate, taking into account improvements to management through learning to better understand disease latency and the relative effectiveness of three competing management options. Exactly which management action we choose each year is driven by the credibility of competing hypotheses about disease latency and by the population growth rate predicted by each hypothesis under the competing management actions. We discover that the optimal combination of management actions depends on the number of sites available and the time remaining to implement management. Our approach to active adaptive management provides a framework to identify the optimal amount of effort to invest in learning to achieve long-run conservation objectives.

Key words: active adaptive management; Bayesian updating; decision theory; learning; Markov decision process; *Sarcophilus harrisii*; stochastic dynamic programming; Tasmania, Australia; Tasmanian devil facial tumor disease.

INTRODUCTION

Conservation management faces the challenge of making good decisions despite uncertainty about both the ecology of the system to be managed and impact of the management options on that system (Burgman et al. 2005). Uncertainty can manifest itself in a number of aspects of knowledge (Regan et al. 2002). There may be uncertainty around parameter estimates which lead us to question the output of models (Caswell 2001). Managers may also be uncertain about the model they have chosen

to represent the system (Chatfield 1995, Regan et al. 2002). Because models provide valuable tools with which to investigate the response of systems to different management scenarios and are commonly used to make conservation decisions (e.g., Possingham et al. 1993, Punt and Smith 1999), a number of techniques have been proposed that quantify model uncertainty (Burnham and Anderson 2002, Wintle et al. 2003) and facilitate decisions that are coherent in the face of model uncertainty (Burgman et al. 1993, Drechsler et al. 1998, Shea and Possingham 2000, Yokomizo et al. 2003, Regan et al. 2005, 2006).

Some uncertainty is effectively irreducible (e.g., natural variation/stochasticity), while other forms of uncertainty may be reduced through learning. What is not captured within most uncertainty analyses is our ability to learn about a system while we are managing

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that system. Adaptive management, a systematic process for improving management through learning, has long been advocated as a suitable approach for “learning while doing” (Holling 1978, Walters and Hilborn 1978, Walters 1986). The conservation literature contains numerous examples of adaptive approaches being proposed as a way to improve knowledge, management actions, and thus our ability to achieve our objectives, without delaying implementation (Parma and NCEAS Working Group on Population Management 1998, Shea and Possingham 2000, Shea et al. 2002, Varley and Boyce 2006, Rout et al. 2009). Until recently, however, almost all illustrations have used a “passive” approach to this adaptive process. In passive adaptive management, the consequences of management are repeatedly evaluated but, as the name suggests, no attempt is made to impose a management action specifically with the intention of learning and improving management (cf. Walters 1986, McCarthy and Possingham 2007).

Conservation managers are often faced with multiple competing hypotheses about the functioning of the systems they manage (e.g., Johnson et al. 1997). Ambiguity about the true nature of the system may be driven by competing beliefs of experts and perpetuated through inconclusive observations of the system via monitoring. When faced with a range of competing management options, some of those options may better enable managers to reduce uncertainty about the way the system functions and thus better achieve their management objective. However, in many instances, the action that most accelerates learning may not be the action that initially appears most likely to achieve the best outcomes. Hence, there is invariably a tension between implementing the best action given current knowledge and implementing actions that will allow rapid learning about system function and improve future decision making. An emerging discipline in conservation biology is “active” adaptive management, which seeks to balance both short-term management objectives and a desire to learn so as to achieve optimal long-term management outcomes. In this way, active adaptive management is a form of management that places an explicit value on learning that could improve future management (Holling 1978, Walters and Hilborn 1978, Walters 1986, McCarthy and Possingham 2007).

Active adaptive management is a logical and compelling approach to conservation management. However, although discussed widely, it has until recently evaded practical application within decision-making frameworks (see McCarthy and Possingham 2007, Rout et al. 2009). One reason for this is that computational limitations have made it challenging to find optimal solutions to the trade-off between gaining knowledge and implementing management in complex ecological systems. Application of active adaptive management has generally focused on uncertainty in a single parameter within a model of system functionality (Walters et al. 1992, Gerber et al. 2005, McCarthy and Possingham

2007, Hauser and Possingham 2008, Rout et al. 2009). In addition, it may be politically or socially unpalatable to implement an apparently suboptimal (in the short term) management option to gain knowledge and make better future decisions. In this way, the concept of active adaptive management can appear to be at odds with a narrow view of “best practice.”

In this paper, we advance our understanding of how to manage ecological systems through active adaptive management. We focus on investigating how management should proceed when there is uncertainty about how a system functions and there are multiple possible models of functionality. Should managers invest in learning early in the management timeframe by implementing several different management actions and thus hone their understanding of system functions? Should they instead learn nothing actively, implement one management action and thus take a chance on their belief and improve management via passive knowledge gain?

Decision theory is the mathematical theory about rational decision making. It involves systematic consideration of the goals of the decision maker, the choices available, the possible outcomes and the probability of their occurrence (Maguire 1986, Possingham et al. 2001). Decisions can then be made based on their likelihood of meeting the stated goals. We establish our active adaptive management problem within such a framework, enabling optimal decisions to be made about which management action to implement when there is a need to protect a population of a threatened species and learn about a component of how the system functions to improve management.

We illustrate an active adaptive management approach by investigating the management of a disease affecting populations of the Tasmanian devil, *Sarcophilus harrisii*, in Australia. This once common species has suffered a rapid decline in the last decade due to the impact of a fatal facial tumor disease (Jones et al. 2007, McCallum et al. 2007, McCallum 2008) (see Plate 1). The situation has demanded an urgent response by managers in view of the dramatic impact, the novel status of this disease, and the cultural value of this species. The novelty of the disease has led to multiple hypotheses regarding disease dynamics, including uncertainty about the rate of transmission of the disease and the length of the period between infection and appearance of disease symptoms, known as latency. Thus, while the long-term fundamental objective is to maintain devil populations, there is also a short-term-means objective to understand which of these hypotheses is correct so that an appropriate course of management can be implemented. More generally, this work provides a protocol for examining the relationship between learning and management when there are multiple hypotheses of how a system functions, a feature that is present in most, if not all, conservation settings.

METHODS

We outline the elements of an adaptive management framework for a conservation problem where there are multiple hypotheses about system function. We define the potential actions, the alternative population models, the monitoring design, and the management objectives. We also describe the analytical methods used to find the optimal solutions for the case study of the Tasmanian devil, *Sarcophilus harrisii*.

Case study

Tasmanian devil facial tumor disease is a recent conservation threat that has significantly increased the probability of extinction of the Tasmanian devil in the wild (Jones et al. 2007, McCallum et al. 2007, McCallum 2008). The disease is an infectious cancer that is transmitted individual to individual through open wounds, almost exclusively between adults (McCallum 2008). In situ conservation actions are currently limited to the removal of infected individuals from a population. Removal of diseased individuals is expected to break transmission by reducing the basic reproductive rate of the disease in the population. By suppressing disease prevalence, management aims to give the devil population a better chance at recovery, that is, to increase the expected population growth rate to >1 . Thus, we can view the overall aim of management as maximizing the growth rate of the population over the management horizon.

Due to the large spatial extent of devil home ranges, it is only feasible to implement disease suppression in isolated or semi-isolated subpopulations of the species. As such, implementation of management actions is restricted to two areas of mainland Tasmania ($n = 2$). We explore the role of adaptive management where only one site is available for implementation and then extend it to consider a scenario where management is undertaken at two sites.

Actions

There are a number of possible management actions that involve the removal of different classes of individuals from an infected devil subpopulation. These actions have been proposed by different experts that include researchers, managers, and experts on wildlife disease and the Tasmanian devil, and reflect different underlying hypotheses regarding disease latency. We consider three possible actions: (1) remove no individuals (do nothing), (2) remove all visibly diseased adults, and (3) remove all adults from the subpopulation.

Each action can affect the long-term fate of a subpopulation by changing the size, age, and sex structure of the population (and thus the reproductive potential). This in turn influences the prevalence, spread and persistence of the disease. The effect of each action on the recovery of a subpopulation is determined by the subpopulation growth rate. There is uncertainty about

how the subpopulation will respond to these actions and we express this through three alternative models.

Models

Advocates for different management actions disagree, in part, because they have different beliefs about how the system functions. For example, if disease transmission rates are low and the subpopulation is small, removal of any animals would be detrimental to the short-term persistence of the subpopulation, thus favoring the removal of no animals (action 1). Those who argue for removing all diseased adults (technically, those showing signs of disease, action 2), implicitly believe that transmission rates are high but the latency period of the disease is short and that few individuals not showing symptoms of the disease will be infected by the disease. Thus, removal of animals showing signs of disease is all that is required to effectively remove the disease. A long latency period, coupled with high disease transmission rates by adults, would favor removal of all adults from the subpopulation (action 3) in an effort to make sure that no asymptomatic but diseased animals were left in the subpopulation to continue to transmit the disease.

The response of the system is measured through the annual growth rate of the devil subpopulations as a function of an action a_j [for the number of potential actions J] under each of the alternative models, i [with mean predicted growth rate $f_i(a_j)$]. We consider m models of how the system functions such that the subpopulation response (growth rate) following action a_j at time t given model i is defined as

$$\lambda_{\text{site},t}(a_j, \text{model } i) = f_i(a_j) + \varepsilon_{\text{site},t}$$

where $j = 1, \dots, J$; site = 1, \dots , S ; $t = 1, \dots, T$; $i = 1, \dots, m$, and $\varepsilon_{\text{site},t} \sim \mathcal{N}(0, \sigma_{ij}^2)$.

We assume the process error, $\varepsilon_{\text{site},t}$, is normally distributed with mean 0 and action- and model-specific variance, σ_{ij}^2 , and further, that the sites are independent. Thus, σ_{ij} is the standard deviation associated with how subpopulation growth responds to management action j given model i is true. Note that the λ values are the actual growth rates of the subpopulations, and thus σ^2 is strictly process variance and in this case does not include observation error.

Having defined a set of models and the expected subpopulation responses given a particular action and model, we now set up a process where our belief in each model can change given the subpopulation response when an action is implemented.

Monitoring

Let w_{it} be the belief in a model relative to other considered models such that

$$\sum_{i=1}^m w_{it} = 1$$

and

$$w_{it} \geq 0 \quad \text{for all } i, t.$$

Thus w_{it} is the probability at time t that model i best represents the system ($w_{it} = \Pr(\text{model } i)$ given the data to date). As actions are taken and the outcomes of these actions are observed through monitoring, the plausibility of each model is reassessed by updating the weights w_{it} . Here full confidence in a model is indicated when $w_{it} = 1$, and no confidence when $w_{it} = 0$.

In each year, monitoring is implemented and an estimate of the growth rate of each subpopulation, $\hat{\lambda}_{\text{site},t}$, is obtained. This information is used to update our beliefs in each of the alternative models, using Bayes' theorem:

$$\begin{aligned} w_{i,t+1}(\hat{\lambda}_{1,t}, \hat{\lambda}_{2,t}, a_{1,j}, a_{2,k}) \\ &= \Pr(\text{model } i \mid \hat{\lambda}_{1,t}, \hat{\lambda}_{2,t}, a_{1,j}, a_{2,k}) \\ &= \frac{\Pr(\hat{\lambda}_{1,t}, \hat{\lambda}_{2,t} \mid \text{model } i, a_{1,j}, a_{2,k}) \Pr(\text{model } i)}{\sum_{l=1}^m \Pr(\hat{\lambda}_{1,t}, \hat{\lambda}_{2,t} \mid \text{model } l, a_{1,j}, a_{2,k}) \Pr(\text{model } l)} \\ &= \frac{\varphi\left(\frac{\hat{\lambda}_{1,t} - f_i(a_{1,j})}{\sigma_{ij}}\right) \varphi\left(\frac{\hat{\lambda}_{2,t} - f_i(a_{2,k})}{\sigma_{ik}}\right) w_{i,t}}{\sum_{l=1}^m \varphi\left(\frac{\hat{\lambda}_{1,t} - f_l(a_{1,j})}{\sigma_{lj}}\right) \varphi\left(\frac{\hat{\lambda}_{2,t} - f_l(a_{2,k})}{\sigma_{lk}}\right) w_{l,t}}. \end{aligned} \quad (1)$$

where k represents the action for site 2 and j for site 1. The model weights at time $t + 1$ depend on the actions applied to each site and the observed subpopulation growth rates at time t in each site. To the extent that the observed growth rate, $\hat{\lambda}_{\text{site},t}$, is an estimate of the realized growth rate, $\lambda_{\text{site},t}$, the variance terms in Eq. 1 should include both the process variance and the observation variance. We assumed that observation error is negligible, so the variance term includes only the process variance. We comment on this assumption in the *Discussion*.

Objective

We considered an objective that focuses on management performance by seeking the greatest long-term growth of the subpopulation(s). That is, we seek to maximize the geometric mean annual growth rate at each site over the time horizon, T . We can convert this from a product to a sum by taking the logarithm. This is equivalent to maximizing

$$\sum_{\text{site}=1}^2 \sum_{t=0}^{T-1} \ln \lambda_{\text{site},t}. \quad (2)$$

Specifically, for the Tasmanian devil case study our objective is to maximize the net expected growth in the subpopulation/s over the next 20 years ($T = 20$).

We use stochastic dynamic programming (SDP) to determine the optimal strategies for managing Tasmanian devil facial tumor disease to maximize expected population growth across sites, taking into account the process and value of learning about disease dynamics. This method is applicable to management scenarios where a set of sequential decisions must be made and the underlying system dynamics are Markovian (Bellman 1957, Mangel and Clark 1988, Lubow 1996, McCarthy et al. 2001). Stochastic dynamic programming determines the management action to apply to each site, depending on the objective, time, and the current state of the system. In our problem, the state variable is an information state or belief in each model, $w_{i,t}$ (see Williams 1996). A set of recursive equations are set up to calculate the expected value of the objective function from one time step to the next, stepping backward from the final outcome at the terminal time T . For each time step, all possible decisions are evaluated for every possible combination of a discretized set of model weights, $\mathbf{w}_t = \{w_{1,t}, w_{2,t}, \dots, w_{m,t}\}$. Thus, the SDP depends on defining probabilities of transition from one information state to another and the value of being in that state. These transition probabilities are calculated based on information obtained at each time step using Bayes' theorem (see Eq. 1).

We use $V^*(\mathbf{w}_t, t)$ to denote the expected value of applying the optimal management strategy from time t to the terminal time T . The value function $V^*(\mathbf{w}_t, t)$ is a cumulative sum of the log of the expected annual subpopulation growth rate at each site (see Eq. 2), and there is no reward received at the terminal time T , so

$$V^*(\mathbf{w}_T, T) = 0 \quad \text{for all } \mathbf{w}_T.$$

Over other time steps $t = 0, 1, 2, \dots, T - 1$ the optimal actions $a_{1,j}, a_{2,k}$ to apply at each site satisfy

$$\begin{aligned} V^*(\mathbf{w}_t, t) = \max_{j,k=1,\dots,J} \sum_{i=1}^m w_{i,t} \int \int_{\hat{\lambda}_{1,t} \hat{\lambda}_{2,t}} & \left[\ln \hat{\lambda}_{1,t} + \ln \hat{\lambda}_{2,t} \right. \\ & + V^*(\mathbf{w}_{t+1}(\hat{\lambda}_{1,t}, \hat{\lambda}_{2,t}, a_{1,j}, a_{2,k}), t + 1) \Big] \\ & \times \varphi\left(\frac{\hat{\lambda}_{1,t} - f_i(a_{\text{site},j})}{\sigma_{ij}}\right) \\ & \times \varphi\left(\frac{\hat{\lambda}_{2,t} - f_i(a_{\text{site},k})}{\sigma_{ik}}\right) d\hat{\lambda}_{1,t} d\hat{\lambda}_{2,t}. \end{aligned}$$

We use a weighted sum of future returns over the plausible models of disease dynamics ($i = 1, 2, \dots, m$), and over a discretized set of plausible subpopulation growth rates, $\hat{\lambda}_{1,t}$ and $\hat{\lambda}_{2,t}$, that we could observe at the two sites in the next time step after taking our action. The updated model weighting \mathbf{w}_{t+1} comes from Eq. 1,

TABLE 1. Expected population growth rate, $f_i(a_j)$, of Tasmanian devil, *Sarcophilus harrisii*, populations based on expert opinion, under three different models of facial tumor disease dynamics, for each of three control actions (do nothing, remove diseased individuals, and remove all adults).

Variable	Expected population growth rate, $f_i(a_j)$			
	Disease dynamic			Model mean
	Model $i = 1$, disease will not progress	Model $i = 2$, short latency	Model $i = 3$, long latency	
Control action				
Action $j = 1$, remove no individuals	1.20	0.90	0.90	0.903
Action $j = 2$, cull all diseased	1.15	1.05	0.95	1.012
Action $j = 3$, cull all adults	1.01	1.01	1.01	1.010
Model weights (current/initial)	0.01	0.39	0.60	na
Best action (growth rate)	1.20	1.05	1.01	1.036

Notes: Each model favors one potential action (favored value in boldface). Also shown are the current model weights for the three models and the expected growth rate in the face of model uncertainty for each action. The growth rate under the “best action” is achieved by knowing the model before taking action. The expected value of perfect information is the difference between the expected growth rate under certainty (1.036) and the highest expected growth rate in the face of uncertainty (1.012). All means are weighted geometric means.

and it is this updating process that ensures our management is adaptive in nature.

As an approximation to the dynamic problem, and to help us better understand the dynamic solutions, we also performed a traditional one-time-step decision analysis, which does not provide learning benefits. That is, we calculated the expected value in the face of uncertainty by finding

$$\exp\left\{\max_a E_i[\ln f_i(a)]\right\}$$

where the expectation is taken over the models, using the initial model weights \mathbf{w}_0 . We also calculated the amount by which the expected growth rate could be increased by resolving model uncertainty before taking action, known as the expected value of perfect information:

$$\exp\left\{E_i[\max_a \ln f_i(a)]\right\} - \exp\left\{\max_a E_i[\ln f_i(a)]\right\}.$$

Parameters: Tasmanian devil case study

Information on annual population growth rates for Tasmanian devils was elicited from a small group of experts (S. Lachish, H. McCallum, M. Jones, and N. Beeton, *personal communication*) to parameterize the three candidate models. The group was given the set of action/model combinations as in Table 1 and asked, as a group, to assign an annual subpopulation growth rate to each combination of three possible management actions, varying in severity in their direct impact on the subpopulation through removal of individuals, and three alternative models of how experts believe the disease may behave within the subpopulations (see Table 1). The severity of the action in terms of its direct impact on subpopulation growth was therefore assessed based on the component of individuals removed from the subpopulation under this action. The values assigned to each action/model combination were bounded by current estimates of subpopulation growth rates in both

a healthy population ($\lambda \approx 1.2$; Lachish et al. [2007]) and a diseased population that is left unmanaged ($\lambda \approx 0.9$; Lachish et al. [2007]). The standard deviation associated with each model was estimated as 0.1 (H. McCallum, *personal communication*). We examined the impact of the magnitude of the variability in parameter estimates assumed for our models by also looking at the optimal decisions under a standard deviation of 0.5.

The SDP was run over a 20-year time horizon ($T = 20$) with both one and two sites in which management could be implemented. The possible values for observed subpopulation growth rate were set between $\hat{\lambda} = 0$ and $\hat{\lambda} = 2$ and discretized into increments of 0.05. Model weights were discretized into increments of 0.01.

Simulations of change in belief and subpopulation size

To assess the change in belief in each model and the potential trajectory of the subpopulations over the management horizon, we simulated the implementation of the optimal strategy from the SDP. Simulations were run from realistic starting states for the Tasmanian devil case study for both initial subpopulation size ($N_0 = 70$ individuals; Lachish et al. [2007]) and for the current belief in the three candidate models ($w_1 = 0.01$, $w_2 = 0.6$, and $w_3 = 0.39$). Simulations were run for a single subpopulation system and a two subpopulation system, and for each of these subpopulation scenarios simulations were repeated for each model being set as the true model of how the system functioned.

At each time step, the optimal action from the SDP was implemented in the subpopulation(s), given the current model weights (w_1 , w_2 , w_3). Realized growth rates ($\hat{\lambda}_{1,t}$ and $\hat{\lambda}_{2,t}$) were drawn from the normal distribution with the mean given by the underlying true model and last action taken, and a standard deviation of 0.1. Based on these observed growth rates, the belief in each model was updated using Eq. 1, and the sizes of the subpopulations were projected using a simple growth model, where

$$N_{t+1} = \sum_{\text{site}=1}^S \lambda_{\text{site},t} N_{\text{site},t}.$$

The process of implementing actions from the SDP, obtaining observations of subpopulation growth rates and updating our belief in each model and the overall population size across sites continued for the full 20-year time horizon and iterated 10 000 times. The mean belief in each model, the mean population size across sites, and the proportion of actions implemented in each year were recorded.

RESULTS

The optimal strategies are presented as ternary plots, with the optimal action as the response, and the axes our belief in each of the three alternative models (belief in model 1, w_1 ; belief in model 2, w_2 ; and belief in model 3, w_3) (Hill and Lewicki 2005). Fig. 1a illustrates how such plots are interpreted. The corners of the plot represent the regions in which managers have high belief in one model and low belief in both other models (e.g., at the top of the triangle, belief in model 3, w_3 , is high, and beliefs in model 1, w_1 , and 2, w_2 , are low), while the center of the plot represents an equal belief in all three models ($w_1 = w_2 = w_3$). The horizontal reference lines (gray lines) represent the degree of belief in model 3, while the reference lines parallel to the other sides of the triangle represent the degree of belief in models 1 (red lines) and 2 (black lines).

The static one-step solution to this problem represents the recommended action in the face of uncertainty and is a function of the initial model weights (Fig. 1b). The solution is equivalent to a classical decision analysis that presents the action with the highest expected growth rate across all models (see Table 1). The current initial model weights ($w_1 = 0.01$, $w_2 = 0.60$, and $w_3 = 0.39$) for the Tasmanian devil case study favor action 2 (shown with the blue circle in Fig. 1b; see Table 1), an action also favored over a large range of model weights. If the initial belief in model 3 was increased (w_3 increased), action 3 would be favored. Action 1 (do nothing) is favored only when there is a high degree of belief in model 1, and a low belief in model 2. Such a classical decision analysis does not allow for the opportunity to learn through time; however, we can calculate the expected value of information: the amount by which the expected growth rate could be increased by resolving model uncertainty before taking action. The expected value of information is 0.024, that is, the expected growth rate could increase from 1.012 to 1.036 if perfect information could be acquired (see Table 1). As with most problems, not all the potential actions are equally informative. Here if action 1 (no treatment) were taken and there was no process or observation error, model 1 could be quickly distinguished from models 2 and 3, but models 2 and 3 could not be distinguished, as they predict the same growth rate under action 1. Action 2 (cull all diseased animals) is the most informative, as all three models

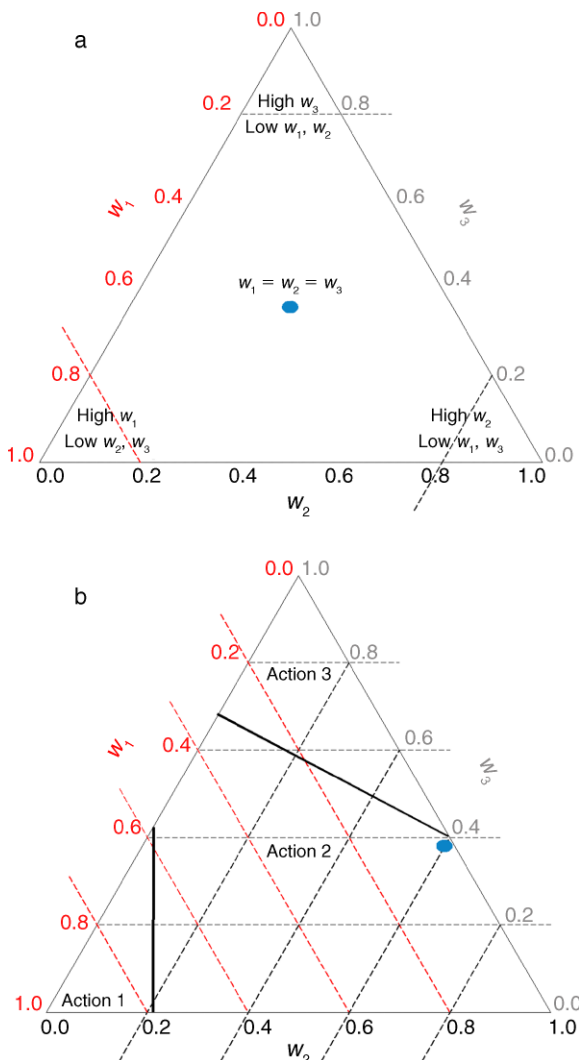


FIG. 1. (a) Diagram of a ternary plot showing how the three coordinates are interpreted in the case of facial tumor disease in the Tasmanian devil, *Sarcophilus harrisii*. Here the axes are the beliefs in each of the three models: model 1, w_1 , that the disease will not progress; model 2, w_2 , that the disease has a short latency period; and model 3, w_3 , that the disease has a long latency period. The solid blue circle represents the point at which our belief in each model is equal ($w_1 = w_2 = w_3$). (b) Optimal strategy for one time step in the face of uncertainty. The belief plot is divided into three regions, each of which corresponds to an optimal action: (1) remove no individuals (do nothing), (2) remove all visibly diseased adults, and (3) remove all adults from the subpopulation. The initial belief state is shown with a solid blue circle; the optimal strategy is action 2 (cull all diseased individuals).

predict a different response while action 3 (cull all adults) is not informative at all, as all three models predict the same response.

The optimal active adaptive management strategy is driven by the degree of belief in each model being the true model of our system, the benefit arising from each action under each model, and the number of sites available to implement an active adaptive strategy (Figs.

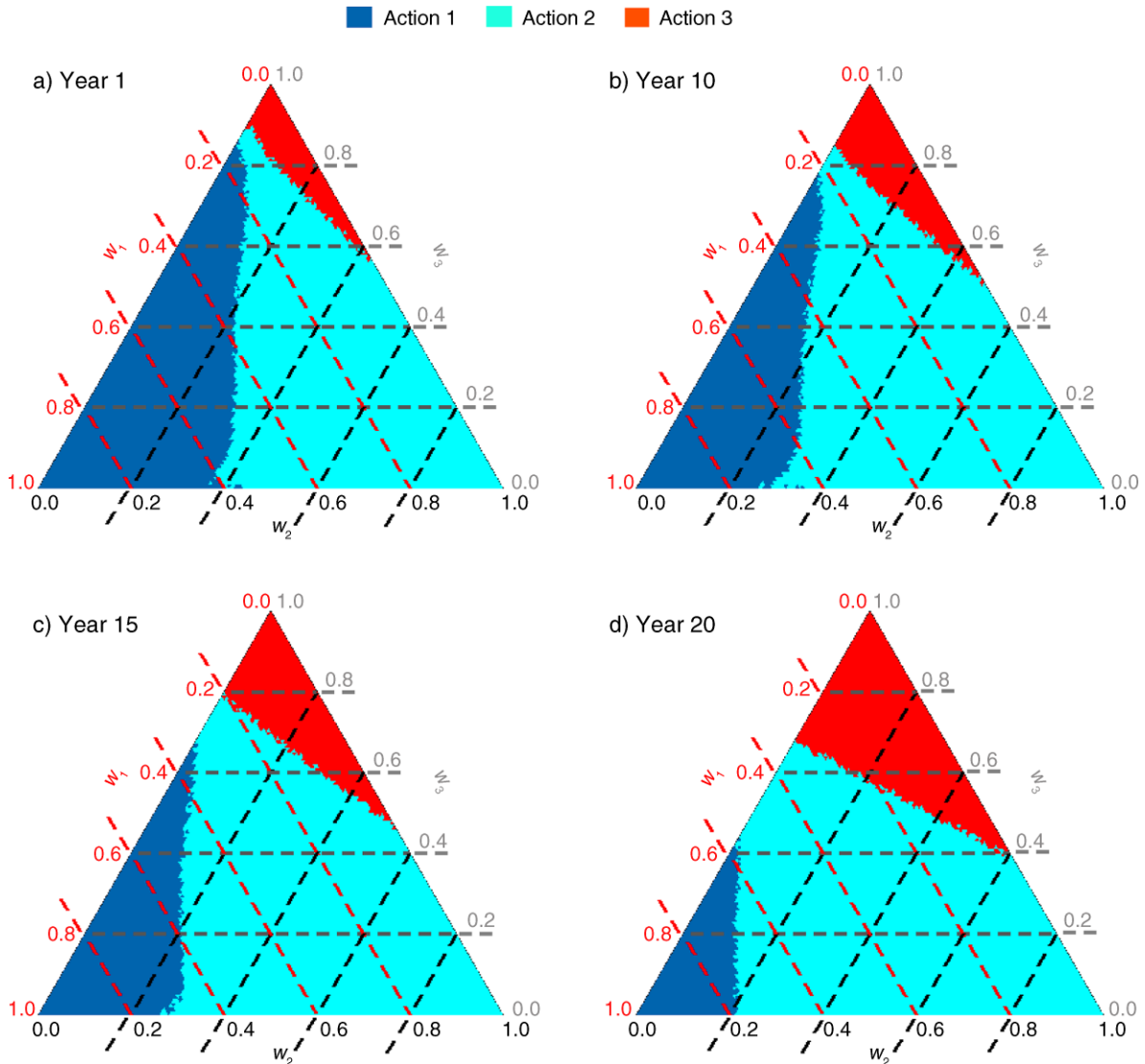


FIG. 2. Optimal active adaptive strategy in one site, given beliefs in each of three models (see Fig. 1) at (a) year 1, (b) year 10, (c) year 15, and (d) year 20 of a 20-year time horizon. Results in this plot are based on elicited judgments about mean population growth rate for Tasmanian devils (see Table 1) and a standard deviation of 0.1.

2–6). When management can only be implemented in one area, the optimal strategy is a function of the model weights and the time remaining to manage (Fig. 2). At $t = 20$, when no additional time remains to manage the population, the optimal strategy (Fig. 2d) is identical to the one derived from a static analysis (Fig. 1b). Here learning holds no benefit and the best actions are determined by the *expected* growth rate in the face of uncertainty, which is a function of our belief in each model. As the time remaining to manage increases, so too does the time available to accrue the benefits of knowledge gain and the value of learning. Even with just a few years remaining to learn ($t = 15$), the model weights over which action 3 is optimal decreases (recall that action 3 produces no learning), and the model

weights over which actions 1 and 2 are optimal increase (Fig. 2c). This pattern becomes more pronounced as the time to manage increases (Fig. 2a, b). At $t = 1$, action 2 (the most informative action) is chosen over much of the belief space, action 3 is chosen only when there is a very high initial belief in model 3, but action 1 shows a significant probing region, especially when model 1 is likely but model 2 is not (Fig. 2a). For the initial model beliefs identified for the Tasmanian devil case study, the optimal action at $t = 1$ is action 2.

Given a low starting belief in model 1 ($w_1 = 0.01$) and a slightly higher belief in model 2 ($w_2 = 0.6$) than model 3 ($w_3 = 0.39$), learning rate depended on which model of the system was reality and how informative the action associated with that model was (Fig. 3), as well as the

magnitude of the observation error (results not shown). If the disease had no impact (model 1 true) then it took ~13 years to learn with 70% certainty ($w_1 = 0.7$; Fig. 3a). Initially, diseased individuals were removed from the population with a steady increase in the frequency with which doing nothing (action 1) was implemented. In this circumstance, model 3 was eliminated from consideration as a plausible model relatively quickly, but it took much longer to distinguish model 1 from model 2; in the interim, action 2, the more informative action, was favored. If in reality the disease had a short period of latency (model 2), then attaining a belief of 70% in this model took 3 years (Fig. 3b), with action 2 being implemented in three quarters of the iterations and action 3 being optimal in all others. In those iterations in which action 3 was favored, no further learning occurred; as a result, the mean model weight stabilized at almost 80% ($w_2 = 0.79$). A similar rate of learning occurred if the disease had a long latency (model 3), with action 2 being implemented initially but then the action to remove all adults (action 3) being optimal after about six years of management (Fig. 3c). Once it was clear that action 3 was favored, no further learning occurred and the model weights stabilized. Population size increased dramatically when the disease was not impacting the population (Fig. 3a). If the disease had a short latency and mainly diseased individuals were being removed, then the population size steadily increased (Fig. 3b). On the other hand if the disease had a long latency and all adults were being removed the population remained relatively stable at the initial population size (Fig. 3c).

Many threatened species persist in a small number of subpopulations (Harrison and Bruna 1999), and thus adaptive management can feasibly be implemented in more than one site. For Tasmanian devil recovery, adaptive management can be implemented in two subpopulations. In the first few years, when there is the potential for learning, we see a similar result to that of the one-population problem where it is optimal to do nothing in both sites, over a wide range of beliefs that the disease will not progress (model 1; Fig. 4a). Likewise, if managers have strong belief in short latency (model 2) or long latency (model 3) being the best representation of the system, they should implement the action that gives the largest growth rate for that model (action 2 or 3, respectively). However, having two sites in which to implement management alters how one should act under the specific circumstances in which, previously, one would choose to switch from one action to another when only one site was available for management (see Fig. 2). When this is the case under the two population problem, managers should implement a mixed strategy that is a combination of the bordering action in either site. When there is no time remaining to implement management, and thus no future benefit from learning, our results mirror that for single-site management (Figs. 1b and 2d) and managers should implement the same action across both areas (Fig. 4d). The benefits of implementing a

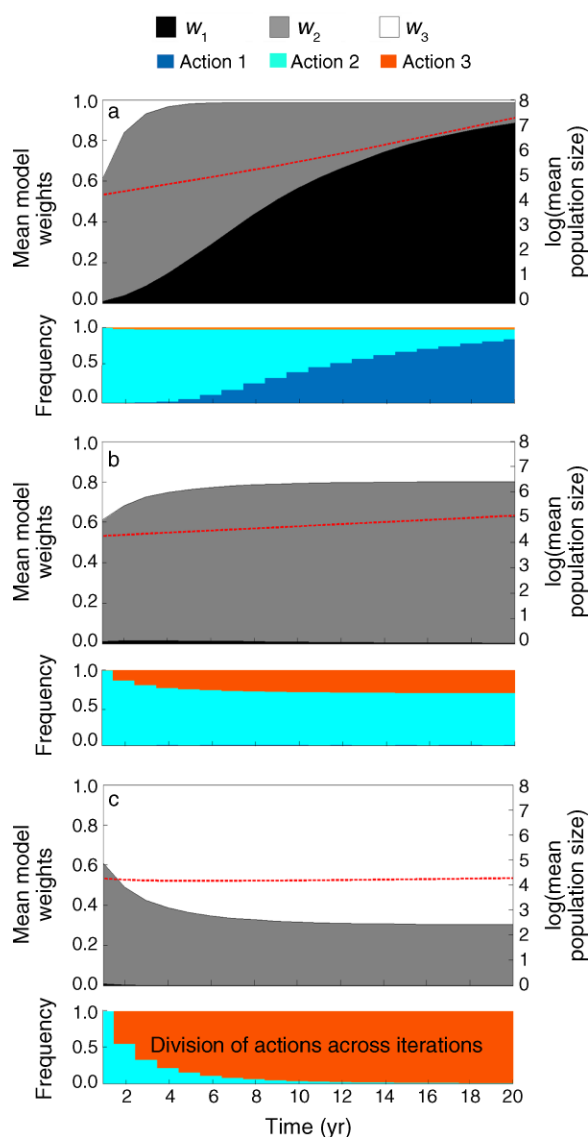


FIG. 3. Mean belief in each model (white, gray, and black shaded areas) and mean population size (dashed lines) plotted against time, as the optimal strategy for one population is implemented and observations are attained, given that (a) model 1 (w_1), (b) model 2 (w_2), or (c) model 3 (w_3) is the true model of the system. The initial population size is set to 70 individuals. The mean growth rate is taken from Table 1, and the standard deviation is set to 0.1. The colored bars beneath the black and white graph show the frequency with which each action is implemented through time.

mixed strategy decrease not only with the time remaining to implement management (Figs. 2 and 4) but also with an increase in the process variance (from 0.1 to 0.5) under each model/action combination (Fig. 5).

Having two subpopulations to manage enables managers to learn more rapidly than with one site (Fig. 6). To be 70% sure that there is no impact of the disease (model 1) took only about seven years of

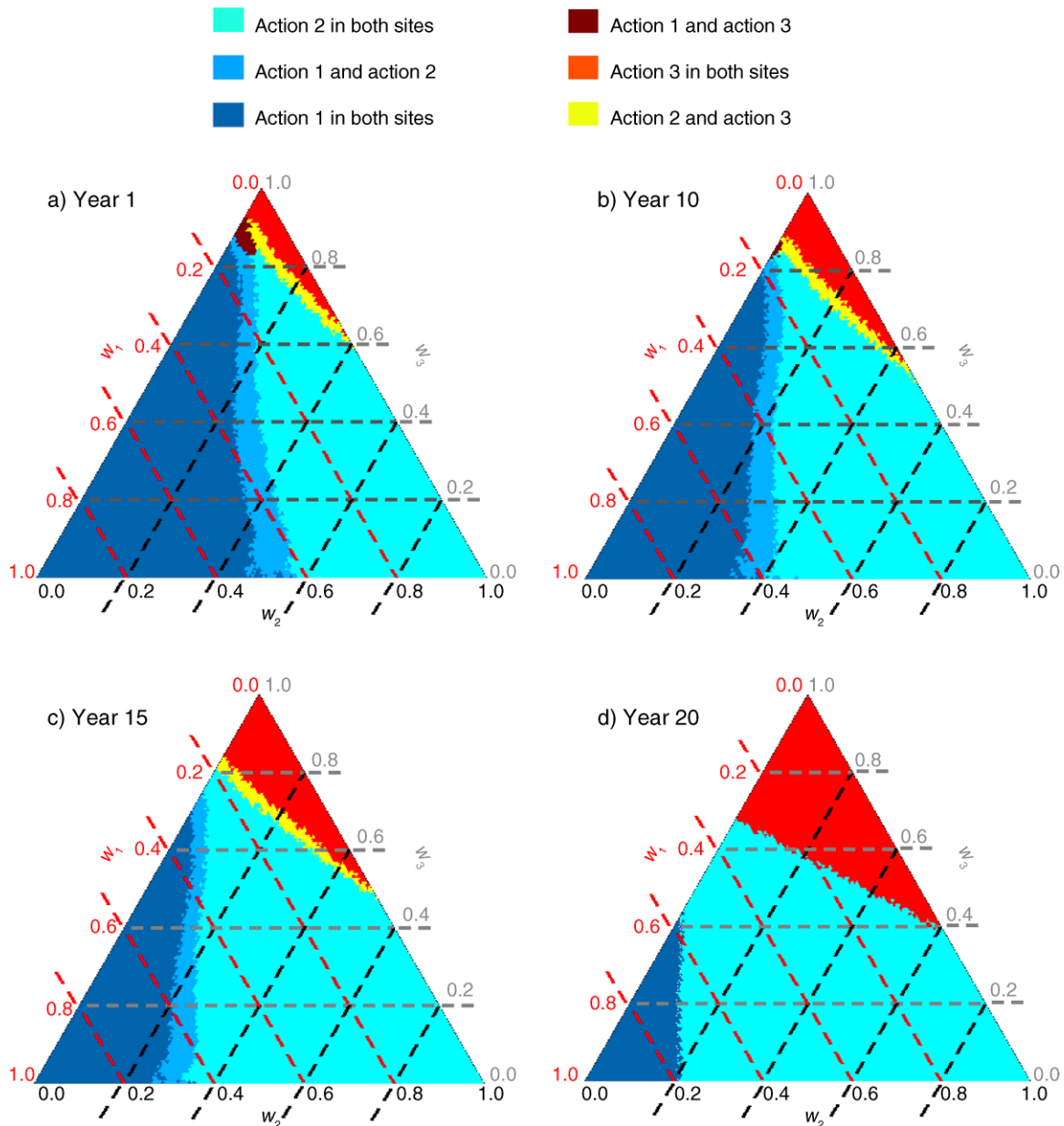


FIG. 4. Optimal active adaptive strategy in each of two populations, given belief in each of three models (see Fig. 1) at (a) year 1, (b) year 10, (c) year 15, and (d) year 20 of a 20-year time horizon. Results in this plot are based on elicited judgments about mean population growth rate for Tasmanian devils (see Table 1) and a standard deviation of 0.1.

management (Fig. 6a) with the optimal action shifting rapidly from removing diseased individual from both sites (action 2) to doing nothing in either (action 1). If in reality the disease had a short period of latency (model 2), then learning occurred rapidly with 70% certainty occurring in two years but reaching a maximum belief in this model of 88% within 11 years of management (Fig. 6b). A similar rate of learning occurred if the disease had a long latency (model 3) reaching 70% belief in model 3 in three years. Action 2 was optimal in both sites initially but then the action to remove all adults (action 3)

quickly became the best strategy (Fig. 6c). A similar pattern in the change in overall population size was observed for two subpopulations as for one subpopulation managed in isolation (see Figs. 3 and 6). The overall population size was higher on average when model 1 was the true model of the system and no individuals were removed (Fig. 6a) and were significantly lower if all adults were being removed as the disease had a long latency (Fig. 6c). The mean overall subpopulation size was always double that for when one subpopulation was being considered.

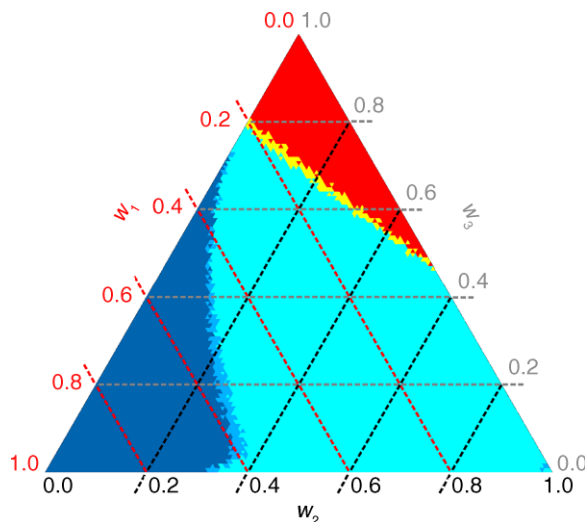


FIG. 5. Optimal active adaptive strategy in each of two populations, given belief in each of three models in the first year of management, when the standard deviation of the observed growth rates is high ($\sigma_{ij} = 0.5$). Compare to Fig. 4a; the same color key as for Fig. 4 applies here.

DISCUSSION

Uncertainty about how ecological systems function makes management decisions difficult (Peterson et al. 1997, Drechsler et al. 1998, Shea and Possingham 2000, Regan et al. 2003). Managers must often address multiple competing hypotheses about how the system they are trying to manage actually functions. If there exists substantial uncertainty about the veracity of competing hypotheses and, therefore, the best course of action, it is useful to see whether learning can help to achieve overall conservation objectives. This may lead managers to consider actions that are nominally suboptimal based on the model with the highest initial credibility. In the absence of “certainty,” learning strategies can be incorporated explicitly within the decision-making process. This active adaptive management approach seeks to balance both our short-term management objectives and our desire to learn to achieve optimal long-term management outcomes. While some highly credible adaptive management programs have shown how to reduce model uncertainty and improve management outcomes (Johnson et al. 1997, Nichols and Williams 2006), we provide the first example of using *active* adaptive management to reduce model uncertainty for threatened species management, and one of very few conservation applications (see Rout et al. 2009).

In conservation management problems, feasible actions often have differing benefits to the threatened population and offer different potential in terms of learning. In our case study, benefits to the Tasmanian devil population are measured in terms of the geometric mean growth rate and different abilities to inform future management from actions based on removing individ-

uals from the populations. Culling diseased animals (action 2) is both the best action to take in the face of uncertainty, and the most informative action; it is thus no surprise that this is the best action to implement over a large range of beliefs in the three models of disease behavior. Indeed, as the time remaining to manage increases, we are even more likely to implement this action as the short-term benefits of removing all adults

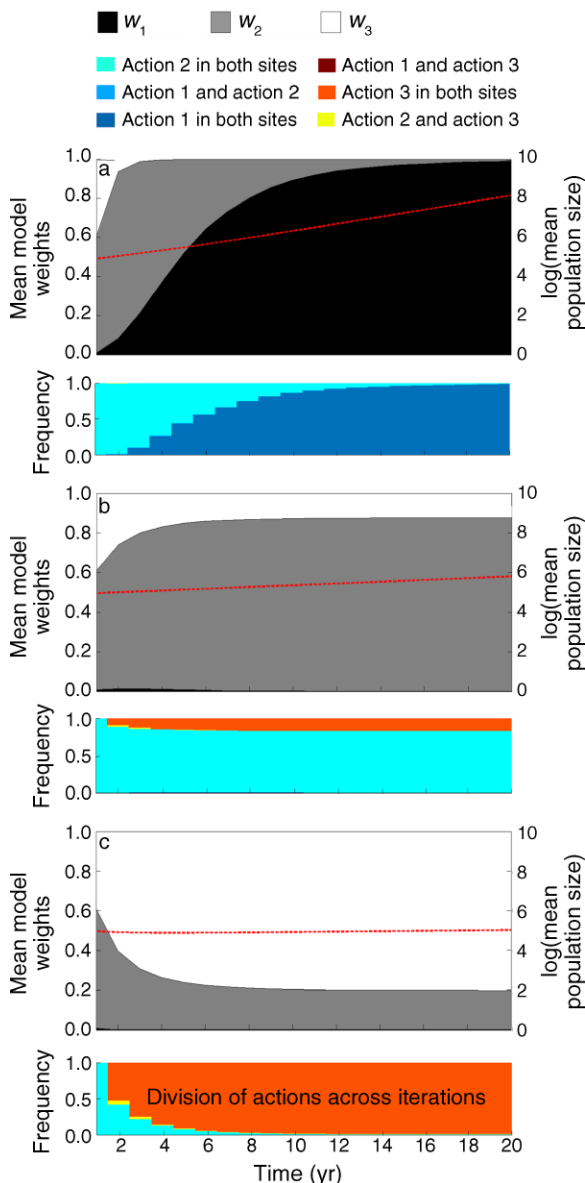


FIG. 6. Mean belief in each model (white, gray, and black shaded areas) and mean total population size (both subpopulations, shown by the dashed line) plotted against time, as the optimal strategy for two populations is implemented and observations are attained, given that (a) model 1, (b) model 2, or (c) model 3 is the true model of the system. The initial population size in each subpopulation is set to 70 individuals (total initial population size 140). The color bar shows the frequency with which each action is implemented through time.

(action 3) from the population is offset with the long-term value of learning the underlying model to improve future management. This action is even optimal when there is high confidence that the disease will not progress, because only the diseased individuals in the subpopulation would be removed and a growth rate close to that of a healthy subpopulation would be maintained ($f_1(2) = 1.15$).

An important question to address is this: why would we ever implement no management when we are concerned about a threatened species? Doing nothing to directly manage a threatened species (action 1 in our case study) can seem counterintuitive for a conservation management program. The answer rests with the ability of this action to enable us to improve future management by helping us choose between competing models. In the case of the Tasmanian devil, this was important because of the wide difference in population growth rates predicted under the different hypotheses (model 1, $f_1(1) = 1.20$ vs. models 2 and 3, $f_2(1) = f_3(1) = 0.90$). Thus, if there is a reasonable belief that the disease will not progress (say, $w_1 > 0.2$), and particularly if there is low belief that the disease has a short latency (model 2) then it is worth doing nothing to quickly determine whether model 1 is the best description of the system. It is worth noting that the value of doing nothing as a learning strategy decreases as the process variance of the model increases (e.g., Fig. 5). With high process variance, model 1 cannot be quickly discriminated from the other two models, and thus it is better to implement the action that will give not only the biggest benefit in the face of uncertainty (action 2) but also be the most informative for distinguishing between models.

Many threatened species now only persist in a small number of relatively isolated subpopulations (Harrison and Bruna 1999) and numerous management programs worldwide distribute resources between subpopulations in an attempt to ensure the persistence of threatened species (e.g., Sumatran tiger, *Panthera tigris sumatrae* [Linkie et al. 2006]; Gunnison's Sage Grouse, *Centrocercus minimus* [Oyler-McCance et al. 2001]; the golden lion tamarin, *Leontopithecus rosalia* [Pinto and Rylands 1997]; Caribbean staghorn coral, *Acropora cervicornis* [Vollmer and Palumbi 2007]; and Japanese woodland primula, *Primula sieboldii* [Washitani et al. 2005]). Predictably, the number of subpopulations or areas available to implement management actions affects how learning can take place. If there are multiple subpopulations to manage and managers are unsure which hypothesis (or system model) best fits reality, then they can implement different strategies in different areas. The benefit from implementing a mixed strategy could be twofold. In the Tasmanian devil case study, by implementing the two actions that maximize subpopulation growth under two of the competing models, managers can guard against the potential loss from acting solely on the "wrong" model. This could be considered the conservation equivalent of hedging one's

bets, in that potentially large losses are buffered at the cost of moderately reducing the maximum overall population growth (for both subpopulations). However, there can be more to a mixed strategy than hedging our management investments; indeed, implementing two different actions can also accelerate learning, by simultaneously testing two hypotheses.

In deriving this example of active adaptive management, we have made a number of simplifying assumptions that allowed us to focus on the central dynamics of the problem. The question is this: are these assumptions undermining the inference from the case study? First, as an objective, we used the geometric mean growth rate over time as a proxy for the likelihood of persistence. Such a substitution is common to threatened species management (Caswell 2001, Baxter et al. 2008). In contrast to other objectives, such as maximizing persistence, maximizing growth by incorporating learning may not guarantee the persistence of the species in the system. Further, using growth as a proxy for persistence or extinction may encourage actions and population responses that are risky or socially unacceptable in the system we are trying to manage (e.g., a string of low growth rates, leading to a very small population before a sequence of high growth rates leading to recovery). Using extinction risk or population size as an objective, instead of growth rate, might lead to strategies that avoid actions that risk low growth rates (like action 1). In doing so these alternative objectives may value learning differently, possibly avoiding the most informative actions and slowing the rate of learning. A key consideration is how quickly learning is expected to occur. If learning is expected to occur quickly, before extinction risk accumulates, then the objective focusing on growth rate will be a good proxy for extinction risk. If, on the other hand, learning is expected to accrue slowly relative to the risk of extinction, then we may inadvertently allow extirpation of the species in the process of learning about the problem.

We assumed that the process error on the realized growth rates was normally distributed; however, there are alternative distributions that could be considered. Perhaps the best alternate candidate is the log-normal distribution that would confine the growth rates to positive values and increase the likelihood of low realized growth rates (right-skewed distribution). This difference, however, is not likely to have a major effect on the optimal strategies as the magnitudes of the realized growth rates are due to process variance, which is not under the control of the managers. A more important consequence of the distribution of the realized growth rates concerns the risk of significant decline. The right skew of a log-normal distribution will produce a small left tail, meaning a lower risk of population decline than for a normal distribution; in such a case, the use of growth rate as a proxy objective for extinction risk might be even more safely assumed.



PLATE 1. (Left) Tasmanian devil *Sarcophilus harrisii* without Tasmanian devil facial tumor disease and (right) one with the disease. Photo credits: right, M. E. Jones; left, Rodrigo Hamede.

In assessing how active adaptive management might apply in more than one area, we have assumed that the two subpopulations being managed have identical dynamics; hence the best model of the system is valid in both areas. If the subpopulations did not have the same dynamics, then information gained via management in these areas could be contradictory and our ability to understand the overall system, improve management, and thus better achieve our conservation objectives, would be diminished. If there is a preconceived notion that subpopulations in different areas may have different dynamics, for example one subpopulation of the Tasmanian devil has short disease latency while the other long, then a more sophisticated model of learning would be required. Here the optimal strategy for adapting management could be based on implementation of a one-subpopulation strategy independently in each area to enable improved management in each subpopulation.

The Tasmanian devil is a highly valued and iconic species in Australia. There has been a significant amount of funding allocated to saving the species from extinction (Government of Tasmania 2006, Commonwealth of Australia 2008). In this paper, we have assumed not only that there is enough funding to implement the actions proposed, but that the monetary cost of implementing all these management actions is equal. In reality this is not the case for most threatened species management programs; some actions will cost more than others. For the Tasmanian devil, doing nothing in an area, in terms of monetary investment, costs us nothing beyond the monitoring effort, while removing diseased individuals or all adults from a subpopulation will require significant and varied investment in staff time and training, equipment, and potentially a public relations campaign to deal with the public response to euthanizing a native animal, especially if that animal has no visible symptoms (action 3). The difference in these costs will determine how much of a given action can be implemented within a fixed budget. This may, in turn, influence the choice of

management strategy (Chadès et al. 2008). For simplicity, we assume that the cost of monitoring is negligible (or equal across management options), a fact that may be true in some conservation scenarios (e.g., assessing revegetation density; McCarthy and Possingham 2007), but is often far from reality (Field et al. 2004, Hauser et al. 2006). Indeed assessing subpopulation growth rates can require a long-term, intensive, and costly monitoring program.

We also assumed that our monitoring could tell us current subpopulation growth exactly. In reality, detecting population change of even a common species is difficult and the precision of the estimates obtained varies with the amount of resources invested. For the Tasmanian devil, significant resources are invested in monitoring, particularly the two subpopulations in question, so the observation error is likely to be dominated by the process error. The more general application does require consideration of how process and observation error both play a role in determining the optimal strategy. The model described in this paper could be extended to incorporate partial observability of the system and even to identify the optimal investment in monitoring (Chadès et al. 2008), but such an extension is beyond the scope of the current work. Incorporating imperfect observation of the system and the cost of implementing monitoring could significantly alter the benefits of learning and thus an active adaptive management strategy.

Most management programs do not explicitly record and incorporate failures or observations that disagree with a preconceived notion of system function (see Armstrong et al. 2007). In the framework we provide, our certainty in each model of system function is explicitly incorporated, such that all potential models of system function are evaluated in deciding how best to manage. Without such a framework, would we ever consider the notion that doing nothing to manage a threatened species could actually provide the best future outcome? The reality is that rarely would this strategy be considered due to the perception that doing nothing

means failing to act. However, our work shows that despite the risk from leaving our system unmanaged, doing nothing can be the best action if it provides both significant learning potential (our current belief is uncertain) and/or a strong benefit (belief in model 1 is warranted: e.g., the facial tumor disease will not progress; see Fig. 2c and Table 1). This work provides a case study of how active adaptive management can be utilized to make difficult decisions in a transparent and justifiable manner. Further it reinforces the role of active adaptive management in distinguishing among competing ideas about how an ecological system functions and how best to manage it. Active adaptive management has been hailed as the way forward for effective conservation management, and indeed for managing our environment in a changing world (Peterson et al. 1997). We hope this work will contribute to wider adoption of the useful but difficult concept of active adaptive management.

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LITERATURE CITED

- Armstrong, D. P., I. Castro, and R. Griffiths. 2007. Using adaptive management to determine requirements of reintroduced populations: the case of the New Zealand hihi. *Journal of Applied Ecology* 44:953–962.
- Baxter, P. W. J., J. L. Sabo, C. Wilcox, M. A. McCarthy, and H. P. Possingham. 2008. Cost-effective suppression and eradication of invasive predators. *Conservation Biology* 22: 89–98.
- Bellman, R. E. 1957. *Dynamic programming*. Princeton University Press, Princeton, New Jersey, USA.
- Burgman, M. A., S. Ferson, and H. R. Akçakaya. 1993. *Risk assessment in conservation biology*. Chapman and Hall, London, UK.
- Burgman, M. A., D. B. Lindenmayer, and J. Elith. 2005. Managing landscapes for conservation under uncertainty. *Ecology* 86:2007–2017.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference*. Second edition. Springer, New York, New York, USA.
- Caswell, H. 2001. *Matrix population models*. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.
- Chadès, I., E. McDonald-Madden, M. A. McCarthy, B. A. Wintle, M. Linkie, and H. P. Possingham. 2008. When to stop managing or surveying cryptic threatened species: an optimal decision theoretic approach. *Proceedings of the National Academy of Sciences (USA)* 105:13936–13940.
- Chatfield, C. 1995. Model uncertainty, data mining and statistical inference. *Journal of the Royal Statistical Society, Series A (Statistics in Society)* 158:419–466.
- Commonwealth of Australia. 2008. Budget paper no. 2 2008/09. Commonwealth of Australia, Canberra, Australia.
- Drechsler, M., M. A. Burgman, and P. W. Menkhurst. 1998. Uncertainty in population dynamics and its consequences for the management of the Orange-bellied Parrot *Neophema chrysogaster*. *Biological Conservation* 84:269–281.
- Field, S. A., A. J. Tyre, N. Jonzen, J. R. Rhodes, and H. P. Possingham. 2004. Minimizing the cost of environmental management decisions by optimizing statistical thresholds. *Ecology Letters* 7:669–675.
- Gerber, L. R., M. Beger, M. A. McCarthy, and H. P. Possingham. 2005. A theory for optimal monitoring of marine reserves. *Ecology Letters* 8:829–837.
- Government of Tasmania. 2006. *Tasmanian budget 2006–2007—at a glance*. Government of Tasmania, Hobart, Tasmania, Australia.
- Harrison, S., and E. Bruna. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? *Ecography* 22:225–232.
- Hauser, C. E., A. R. Pople, and H. P. Possingham. 2006. Should managed populations be monitored every year? *Ecological Applications* 16:807–819.
- Hauser, C. E., and H. P. Possingham. 2008. Experimental or precautionary? Adaptive management over a range of time horizons. *Journal of Applied Ecology* 45:72–81.
- Hill, T., and P. Lewicki. 2005. *Statistics: methods and application, a comprehensive reference for science, industry and data mining*. StatSoft, Tulsa, Oklahoma, USA.
- Holling, C. S. 1978. *Adaptive environmental assessment and management*. Blackburn Press, Caldwell, New Jersey, USA.
- Johnson, F. A., C. T. Moore, W. T. Kendall, J. A. Dubovsky, D. F. Caithamer, J. R. Kelley, and B. K. Williams. 1997. Uncertainty and the management of mallard harvests. *Journal of Wildlife Management* 61:202–216.
- Jones, M. E., P. J. Jarman, C. M. Lees, H. Hesterman, R. K. Hamede, N. J. Mooney, D. Mann, C. E. Pukk, J. Bergfeld, and H. McCallum. 2007. Conservation management of Tasmanian devils in the context of an emerging, extinction-threatening disease: devil facial tumor disease. *Ecohealth* 4: 326–337.
- Lachish, S., M. Jones, and H. McCallum. 2007. The impact of disease on the survival and population growth rate of the Tasmanian devil. *Journal of Animal Ecology* 76:926–936.
- Linkie, M., G. Chapron, D. J. Martyr, J. Holden, and N. Leader-Williams. 2006. Assessing the viability of tiger subpopulations in a fragmented landscape. *Journal of Applied Ecology* 43:576–586.
- Lubow, B. C. 1996. Optimal translocation strategies for enhancing stochastic metapopulation viability. *Ecological Applications* 6:1268–1280.
- Maguire, L. A. 1986. Using decision analysis to manage endangered species populations. *Journal of Environmental Management* 22:345–360.
- Mangel, M., and C. W. Clark. 1988. *Dynamic modeling in behavioral ecology*. Princeton University Press, Princeton, New Jersey, USA.
- McCallum, H. 2008. Tasmanian devil facial tumour disease: lessons for conservation biology. *Trends in Ecology and Evolution* 23:631–637.
- McCallum, H., D. M. Tompkins, M. Jones, S. Lachish, S. Marvanek, B. Lazenby, G. Hocking, J. Wiersma, and C. E. Hawkins. 2007. Distribution and impacts of Tasmanian devil facial tumor disease. *Ecohealth* 4:318–325.
- McCarthy, M. A., and H. P. Possingham. 2007. Active adaptive management for conservation. *Conservation Biology* 21:956–963.
- McCarthy, M. A., H. P. Possingham, and A. M. Gill. 2001. Using stochastic dynamic programming to determine optimal fire management for *Banksia ornata*. *Journal of Applied Ecology* 38:585–592.
- Nichols, J. D., and B. K. Williams. 2006. Monitoring for conservation. *Trends in Ecology and Evolution* 21:668–673.
- Oyler-McCance, S. J., K. P. Burnham, and C. E. Braun. 2001. Influence of changes in sagebrush on Gunnison sage grouse

- in southwestern Colorado. *Southwestern Naturalist* 46:323–331.
- Parma, A. M., and NCEAS Working Group on Population Management. 1998. What can adaptive management do for our fish, forests, food and biodiversity? *Integrative Biology: Issues, News and Reviews* 1:16–26.
- Peterson, G., G. A. De Leo, J. J. Hellmann, M. A. Janssen, A. Kinzig, J. R. Malcolm, K. L. O'Brien, S. E. Pope, D. E. Rothman, E. Shevliakova, and R. R. T. Tinch. 1997. Uncertainty, climate change, and adaptive management. *Ecology and Society* 1:1–7.
- Pinto, L. P. D., and A. B. Rylands. 1997. Geographic distribution of the golden-headed lion tamarin, *Leontopithecus chrysomelas*: implications for its management and conservation. *Folia Primatologica* 68:161–180.
- Possingham, H. P., S. J. Andelman, B. R. Noon, S. Trombulak, and H. R. Pulliam. 2001. Making smart conservation decisions. Pages 225–244 in M. E. Soule and G. H. Orians, editors. *Conservation biology: research priorities for the next decade*. Island Press, Washington, D.C., USA.
- Possingham, H. P., D. B. Lindenmayer, and T. W. Norton. 1993. A framework for the improved management of threatened species based on Population Viability Analysis (PVA). *Pacific Conservation Biology* 1:39–45.
- Punt, A. E., and A. D. M. Smith. 1999. Management of longlived marine resources: a comparison of feedback-control management procedures. Pages 243–265 in J. A. Musick, editor. *Life in the slow lane: ecology and conservation of long-lived marine animals*. American Fisheries Society Symposium 23. American Fisheries Society, Bethesda, Maryland, USA.
- Regan, H. M., H. R. Akçakaya, S. Ferson, K. V. Root, S. Carroll, and L. R. Ginzburg. 2003. Treatments of uncertainty and variability in ecological risk assessment of single-species populations. *Human and Ecological Risk Assessment* 9:889–906.
- Regan, H. M., Y. Ben-Haim, B. Langford, W. G. Wilson, P. Lundberg, S. J. Andelman, and M. A. Burgman. 2005. Robust decision making under severe uncertainty for conservation management. *Ecological Applications* 15:1471–1477.
- Regan, H. M., M. Colyvan, and M. A. Burgman. 2002. A taxonomy and treatment of uncertainty for ecology and conservation biology. *Ecological Applications* 12:618–628.
- Regan, T. J., M. A. McCarthy, P. W. J. Baxter, F. D. Panetta, and H. P. Possingham. 2006. Optimal eradication: when to stop looking for an invasive plant. *Ecology Letters* 9:759–766.
- Rout, T. M., C. E. Hauser, and H. P. Possingham. 2009. Optimal adaptive management for the translocation of a threatened species. *Ecological Applications* 19:515–526.
- Shea, K., and H. P. Possingham. 2000. Optimal release strategies for biological control agents: an application of stochastic dynamic programming to population management. *Journal of Applied Ecology* 37:77–86.
- Shea, K., H. P. Possingham, W. W. Murdoch, and R. Roush. 2002. Active adaptive management in insect pest and weed control: intervention with a plan for learning. *Ecological Applications* 12:927–936.
- Varley, N., and M. S. Boyce. 2006. Adaptive management for reintroductions: updating a wolf recovery model for Yellowstone National Park. *Ecological Modelling* 193:315–339.
- Vollmer, S. V., and S. R. Palumbi. 2007. Restricted gene flow in the Caribbean staghorn coral *Acropora cervicornis*: implications for the recovery of endangered reefs. *Journal of Heredity* 98:40–50.
- Walters, C., L. Gunderson, and C. S. Holling. 1992. Experimental policies for water management in the Everglades. *Ecological Applications* 2:189–202.
- Walters, C. J. 1986. *Adaptive management of renewable resources*. Blackburn Press, Caldwell, New Jersey, USA.
- Walters, C. J., and R. Hilborn. 1978. Ecological optimization and adaptive management. *Annual Review of Ecology and Systematics* 9:157–188.
- Washitani, I., F. Ishihama, C. Matsumura, M. Nagai, J. Nishihiro, and M. A. Nishihiro. 2005. Conservation ecology of *Primula sieboldii*: synthesis of information toward the prediction of the genetic/demographic fate of a population. *Plant Species Biology* 20:3–15.
- Williams, B. K. 1996. Adaptive optimization and the harvest of biological systems. *Mathematical Biosciences* 136:1–20.
- Wintle, B. A., M. A. McCarthy, C. T. Volinsky, and R. P. Kavanagh. 2003. The use of Bayesian model averaging to better represent uncertainty in ecological models. *Conservation Biology* 17:1579–1590.
- Yokomizo, H., P. Haccou, and Y. Iwasa. 2003. Conservation effort and assessment of population size in fluctuating environments. *Journal of Theoretical Biology* 224:167–182.