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Allocating conservation resources between areas where persistence of a species is uncertain

EVE MCDONALD-MADDEN,[1,2,8] IADINE CHADÈS,[1,2,3,4] MICHAEL A. MCCARTHY,[5] MATTHEW LINKIE,[6] AND HUGH P. POSSINGHAM[1,7]

[1]*Applied Environmental Decision Analysis Centre, School of Biological Sciences, University of Queensland, St Lucia, Queensland 4072 Australia*
[2]*CSIRO Sustainable Ecosystems and Climate Adaptation Flagship, St Lucia, Queensland 4072 Australia*
[3]*Australian Centre of Excellence for Risk Analysis, School of Botany, University of Melbourne, Parkville, Victoria 3010 Australia*
[4]*ARC Centre of Excellence for Mathematics and Statistics of Complex Systems, Discipline of Mathematics, University of Queensland, Queensland 4072 Australia*
[5]*Applied Environmental Decision Analysis Centre, School of Botany, University of Melbourne, Parkville, Victoria 3010 Australia*
[6]*Durrell Institute of Conservation and Ecology, University of Kent, Canterbury, Kent CT27NR United Kingdom*
[7]*Department of Mathematics, University of Queensland, St Lucia, Queensland 4072 Australia*

Abstract. Research on the allocation of resources to manage threatened species typically assumes that the state of the system is completely observable; for example whether a species is present or not. The majority of this research has converged on modeling problems as Markov decision processes (MDP), which give an optimal strategy driven by the current state of the system being managed. However, the presence of threatened species in an area can be uncertain. Typically, resource allocation among multiple conservation areas has been based on the biggest expected benefit (return on investment) but fails to incorporate the risk of imperfect detection. We provide the first decision-making framework for confronting the trade-off between information and return on investment, and we illustrate the approach for populations of the Sumatran tiger (*Panthera tigris sumatrae*) in Kerinci Seblat National Park. The problem is posed as a partially observable Markov decision process (POMDP), which extends MDP to incorporate incomplete detection and allows decisions based on our confidence in particular states. POMDP has previously been used for making optimal management decisions for a single population of a threatened species. We extend this work by investigating two populations, enabling us to explore the importance of variation in expected return on investment between populations on how we should act. We compare the performance of optimal strategies derived assuming complete (MDP) and incomplete (POMDP) observability. We find that uncertainty about the presence of a species affects how we should act. Further, we show that assuming full knowledge of a species presence will deliver poorer strategic outcomes than if uncertainty about a species status is explicitly considered. MDP solutions perform up to 90% worse than the POMDP for highly cryptic species, and they only converge in performance when we are certain of observing the species during management: an unlikely scenario for many threatened species. This study illustrates an approach to allocating limited resources to threatened species where the conservation status of the species in different areas is uncertain. The results highlight the importance of including partial observability in future models of optimal species management when the species of concern is cryptic in nature.

Key words: decision theory; detectability; partially observable Markov decision process; poaching; return on investment; Sumatran tiger; surveying; threatened species management.

INTRODUCTION

The enormity of environmental issues worldwide means that monetary investment in conservation management is distributed sparsely. Resources allocated to individual regions or conservation programs are limited (James et al. 1999). Often managers are making decisions about which areas to manage with limited funding. With such finite resources and an urgency to implement conservation strategies, managers need quantitative frameworks to aid decision making. These frameworks must explicitly incorporate trade-offs between the costs and benefits of management options allowing resources to be allocated to achieve conservation objectives efficiently and transparently (Possingham et al. 2001, Murdoch et al. 2007). In the world of finance such allocations are achieved using a measure of enterprise known as "return on investment" (Bodie et al. 2004). In conservation, the concept of return on investment has become a focus of theoretical conserva-

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[8] E-mail: eve.mcdonald-madden@csiro.au

tion research (O'Connor et al. 2003, Wilson et al. 2006, Murdoch et al. 2007, Wilson et al. 2007) and is becoming a useful tool for allocating funds between actions or areas to get the best return from our conservation dollar (e.g., New Zealand Department of Conservation [Joseph et al. 2009], The Nature Conservancy [E. Game. *personal communication*]). Such approaches, however, are myopic and the dynamic nature of conservation problems has led to a flurry of research on how to temporally allocate resources between actions and areas (e.g., Johnson et al. 1997, Milner-Gulland 1997, McCarthy et al. 2001, Westphal et al. 2003, Tenhumberg et al. 2004, Bode and Possingham 2005, Wilson et al. 2006, Drechsler and Watzold 2007, McDonald-Madden et al. 2008). The majority of this research has converged on modeling problems as Markov decision processes (MDP). Indeed, the use of MDP in the conservation literature increased considerably in the last decade and is becoming an essential tool in the theoretical conservationists' toolkit.

Markov decision processes, most often solved using stochastic dynamic programming (SDP), give an optimal strategy driven by the current state of the system being managed, for example; the number of extant populations of a threatened species (McDonald-Madden et al. 2008), the level of establishment of a biological control (Shea and Possingham 2000), the number of individuals in a population of concern (McCarthy et al. 2001), or even the number of parcels reserved in an area (Wilson et al. 2006). Most, if not all, threatened species are cryptic and thus difficult to observe. The difficulty in observing threatened species means the states of the populations we are managing are typically uncertain, a fact that could seriously impair our conservation decisions. For example, if deciding between management of multiple areas depends on whether a threatened species is extant in an area or not, using an allocation strategy that assumes the presence of the threatened species is completely observable (e.g., MDP), could potentially waste resources by allocating funds to areas where the threatened species has already disappeared. The penalty for this error might be reduced funding to those areas that are important for the species persistence. Alternatively, resources may not be allocated to areas where the species remains extant but unobserved, a result that could be devastating for the persistence of the species.

Monitoring can enable managers to gain the information needed to make state-dependent management decisions (Nichols and Williams 2006, Chadès et al. 2008). Yet monitoring, as with management, costs money, and affects the funds available for other conservation activities, such as further management. Where funds are limited, the cost of monitoring can mean a trade-off exists between taking a management action known to reduce the risk of extinction, versus gaining information that will hopefully make our management more efficient, and our threatened species even more secure. To make this tradeoff between information gain and direct management when allocating resources our allocation approach must incorporate the value of information in making these decisions (see Howard 1966, Polasky and Solow 2001, Chadès et al. 2008). Allocation approaches that assume we have perfect information on the state of the system (e.g., MDP), do not explicitly value further information gained through monitoring, and therefore cannot be used to evaluate tradeoffs between information gain and immediate management action. The trade-off between information gain and direct management is mathematically and computationally difficult to evaluate and to date only relatively simple problems have been explored (Johnson et al. 1997, Gerber et al. 2005, Regan et al. 2006, McCarthy and Possingham 2007, Chadès et al. 2008, Rout et al. 2009). Importantly, incorporating this trade-off into resource allocation requires that we undertake an adaptive approach to decision making in light of our uncertainties about the state of the system being managed (see Nichols and Williams 2006).

In this paper, we provide the first adaptive framework for dynamically allocating resources to either management or monitoring across more than one area important to the persistence of a threatened species. To do this we use a relatively new approach to conservation science, a partially observable Markov decision process (POMDP). POMDP allows us to determine the best action to implement (monitoring or management), based on uncertain information about the presence of the species in different areas. Chadès et al. (2008) describe the use of POMDP in making optimal management decisions for a single population of a threatened species. Here we extend that work to a more realistic scenario, the management of two populations of the Sumatran tiger (*Panthera tigris sumatrae*) in Kerinci Seblat National Park, Indonesia. Demonstrating the use of POMDP in two populations allows us to compare the outcomes from this adaptive framework (POMDP), to decisions that rely on complete knowledge of the state of each population (MDP). We explore how assumptions about uncertainty in our knowledge of the system state, affects whether we survey, manage, or do nothing in these areas, and how differences in the level of uncertainty drive the selection of different strategies. We conduct the first comparison of POMDP resource allocation behavior between systems where the expected return on investment from management is either the same for all populations or variable across populations.

Methods

Problem definition

We consider a cryptic threatened species that exists in two populations in remnant habitat patches, referred to as population A and population B. The populations are isolated from each other, so there is no chance of recolonization once a population becomes locally extinct. A program with a fixed budget is in place to

TABLE 1. Definition of parameters and values of parameters used for the Sumatran tiger case study (Linkie et al. 2006; M. Linkie, *unpublished data*).

Parameter	Definition	Values
T	management time horizon	20 years
C	budget available to conservation program	current, \$47 723; reduced, \$31 815
C_s	cost of surveying one population	\$10 235
d_s	detection probability of species when surveying	current, 0.780; reduced, 0.260
d_m	detection probability of species when managing	current, 0.010; increased, 0.210
p_0	annual probability of extinction in a population when **not** managing	high extinction risk, 0.0880; low extinction risk, 0.0102
p_m	annual probability of extinction in a population when managing *both*	current C, 0.00330, 0.00130; reduced C, 0.0277, 0.00640†
p_m	annual probability of extinction in a population when managing *one*	current C, 0.0000285, 0.0000115; reduced C, 0.000340, 0.000137†

Note: Here high extinction risk is equivalent to high return on investment while low extinction risk is equivalent to a lower return on investment.

† For both current and reduced C, the first value is for high extinction risk, and the second value is for low extinction risk.

manage this species. We examine the difference in management strategies when we model our problem as an MDP, were it is assumed we know the state of the system, and when we model our problem as a POMDP, where the state of the system is uncertain.

Objective

The first step in formulating the conservation resource allocation problem is to define a quantifiable objective. Our aim is to find the optimal allocation of resources given a fixed budget, C, that gives the greatest long term benefits for the conservation of a cryptic threatened species. Specifically our objective in both cases is to maximize the expected number of populations of a threatened species that remain extant over a 20-year management horizon (time $T = 20$).

Actions

In the fully observable MDP one of two actions can be implemented in each population (1) to manage and (2) to do nothing. The budget is fixed and is traded off between both populations thus we explored four possible overall conservation actions, a, using MDP:

1) manage both population A and population B (MM);
2) manage population A and do nothing in population B (MN);
3) do nothing in population A and manage population B (NM); and
4) do nothing in both populations (NN).

System states

The state of the system is based on whether populations are extant or extinct. Given this, the system can be characterized by one of four possible states (1) both populations extant, (2) both populations extinct, (3) population A extant and population B extinct, and (4) population A extinct and population B extant. These states are known as the set of "real" states of the system, S.

Transition probabilities

The probability of extinction when we manage a population depends on the action taken in the other population. That is, if we manage population A and B then the budget must be split and thus the probability of extinction in each population will be greater than for a population that receives all available resources for management. However, if we were to manage one population then this would have a lower probability of extinction while the second population would not be managed and have a higher risk of extinction. Thus, there is a clear trade-off between the probability of extinction of an individual population and our ability to save both populations given a fixed budget, C.

The stochastic consequences of a reserve-manager's actions on the population are represented by transition probabilities. The transition probabilities represent the probability distribution of moving from any real state s in S at time t, to any real state s' in S at time $t+1$, given an action a is implemented at time t ($P(s' \mid s, a)$). The probability of extinction of a managed population, p_m, is less than the probability of extinction when a population is not managed, p_0 ($p_m < p_0$; see Table 1 for summary of parameters). We assume that recolonization is not possible and thus extinct populations remain extinct.

Reward function

A reward function is specified based on the real state of our system at each time step ($R(s)$). Here we use a reward function that gives a score of one point for each population that is not extinct each time step. This exactly reflects the objective function, which aims to maximize the expected value of the reward function over the entire management time horizon.

TABLE 2. Relationship between observations and real states using a partially observable Markov decision process (POMDP) framework in terms of the probability of an observation, z, given the real state, s, based on detectability, d.

	Observations, z			
Real states, s	aa	ap	pa	pp
EE	1	0	0	0
EE_x	$1-d$	d	0	0
E_xE	$1-d$	0	d	0
E_xE_x	$(1-d)^2$	$(1-d)d$	$d(1-d)$	d^2

Notes: The value of d varies depending on the action performed. Within a completely observable Markov decision process (MDP) framework the relationship assumed 100% detection: that is, if nothing is observed in both populations than the real state is assumed to be extinct in both areas. Real states: EE is extinct in both, EE_x is extinct in population A and extant in B, E_xE is extant in population A and extinct in B, and E_xE_x is extant in both. Observations: aa is not observed in both, ap is not observed in population A and observed in B, pa is observed in population A and not observed in B, and pp is observed in both.

Completely observable Markov decision process

We solve the MDP using a mathematical optimization method known as stochastic dynamic programming (Bellman 1957, Mangel and Clark 1988, Lubow 1996, McCarthy et al. 2001). Stochastic dynamic programming determines the exact optimal strategy depending on the management objective, time, and the current state of the system. Stochastic dynamic programming works by stepping backwards from the terminal time T. For each time step all possible decisions are evaluated over all four possible real states. Thus, the optimal strategy through time maps real states to actions (π: States$_t \rightarrow$ Action$_t$) and is determined by the dynamic programming equations:

$$V_T^*(s) = R(s),$$

and

$$V_t^*(s) = R(s) + \max_{a \in A} \gamma \sum_{s' \in S} V_{t+1}(s') \Pr(s' \mid s, a)$$

where $t = 1, 2, \ldots, T-1$ represents the management years, V is the maximum value of the function, $R(s)$ is the reward function and $P(s' \mid s, a)$ is the probability of transition from real state s to s' given action a is implemented in s (Mangel and Clark 1988, Williams 2009). A discounting factor, γ, is used during the value iteration to facilitate reaching a finite sum (the algorithm converges). The value of γ also dictates the relative value placed on future rewards compared to immediate rewards, where a discount factor close to one values the future more than a factor close to zero. We use a discount rate of 4% ($\gamma = 0.96$) to ensure convergence of the MDP to an exact solution over the 20 year time horizon. Over this time horizon such a small discount rate will not affect the optimal strategy derived only the time taken to compute the strategy.

Deriving an optimal management strategy incorporating species' detectability

To derive an optimal strategy given uncertainty in the real state of the system, S, we need to incorporate imperfect detection of the species. We achieve this by posing the problem as a partially observable Markov decision process (POMDP) and solving a multi-time-step scenario using the incremental pruning algorithm (Cassandra et al. 1997). Our POMDP adds three elements to the regular MDP: the action to survey; a set of observations, z (detection or non-detection of the species in each population, termed presence or absence); and the probabilities of these observations. Thus the suite of potential actions is extended to include the following:

5) survey population A and manage population B (SM);
6) manage population A and survey population B (MS); and
7) survey both populations (SS).

The probability of observing the species in a population given it is present depends on the resources allocated to that action. This detection probability equals d_s when surveying or d_m when managing (where $1 \geq d_s \geq d_m \geq 0$; see Table 1 for summary of parameters). These probabilities represent the likelihood of an observation, z, at time $t+1$, given the real state of the system, s', at time $t+1$, and the action taken, a, at time t [$\Pr(z \mid a, s')$] (see Table 2 for description of the relationship between observations and real states).

The optimal action derived using the POMDP algorithm depends on the history of previous observations, z, and actions, a, rather than the real state, which is unobserved. Keeping track of the complete observation–action history is computationally infeasible; instead POMDP synthesizes this information into one variable known as a "belief state." A belief state, b, is a probability distribution over all real states capturing the relative likelihood of being in each of our four real system states (see Table 3 for example of belief state in each of four real states given three hypothetical observation/action histories). The POMDP algorithm finds an optimal action each year given the current belief about the real state of the species (extant or extinct) in each population (see Williams 2009 for further details on

TABLE 3. Belief state for the real state of the system, s, given three hypothetical scenarios of detection history in each population and management being implemented in both populations.

	Scenario		
Real states, s	1	2	3
EE	0.01	0.02	0.07
EE_x	0.05	0.04	0.2
E_xE	0.05	0.25	0.2
E_xE_x	0.89	0.69	0.53

Notes: Scenario 1, species detected in both populations two years ago; scenario 2, species detected in population A two years ago but not in population B (detected 10 years ago); scenario 3, species not detected in either population recently (detected 10 years ago). Real states: EE is extinct in both, EE_x is extinct in population A and extant in B, E_xE is extant in population A and extinct in B, and E_xE_x is extant in both.

POMDP). Thus, the optimal strategy through time maps belief states to actions (π: Belief$_t \rightarrow$ Action$_t$).

In order to apply the optimal solution, decision-makers first need to determine the probability that the species is extant in each population. This can be done by answering two simple questions: when is the last time we saw the species in each population and how have we acted in each area since seeing the species? These answers will provide enough information to compute the current belief state. For example if it has been a long time since we have observed the species in an area and we have implemented a lot of monitoring in that area than we will have low belief that the species remains extant in that area. From a starting belief state, b, an action, a, is selected, leading to an observation z. Using this information, the previous belief, b, is updated to give the current belief state [$b_z^a(s')\ \forall s'$] (see Fig. 1 for a diagram of this process). Bayes' theorem enables us to update the belief state throughout our management time horizon for all possible combinations of actions that could be implemented and the observed states:

$$b_z^a(s') = \frac{P(z \mid a, s') \times \sum_{s \in S} P(s' \mid s, a) \times b(s)}{P(z \mid b, a)}.$$

The POMDP algorithm iterates through our decision-making horizon calculating at each time step, t, the action, a, that gives the maximum value, $V_t^*(b)$, based on the reward function, $R(s)$, the current belief of being in state s, $b(s)$, the real state transitions, $P(s' \mid a, s)$, the observation probabilities, $P(z \mid a, s')$, and the expected cumulated rewards in the future time step, $V_{t+1}^*(b_z^a)$:

$$V_T^*(b) = \sum_{s \in S} b(s)R(s) \quad \forall b$$

$$V_t^*(b) = \sum_{s \in S} b(s)R(s) + \max_{a \in A} \gamma \sum_{s \in S} \sum_{s' \in S} \sum_{z \in Z} b(s)P(s' \mid a, s) \times P(z \mid a, s')V_{t+1}^*(b_z^a) \quad \forall b.$$

As with the MDP to facilitate convergence of the POMDP algorithm we use a discount rate of 4% ($\gamma = 0.96$). The action with the maximum value at each time step is the optimal management strategy, π, for a specific ecological scenario.

Case study: Sumatran tiger

The Sumatran tiger is critically endangered due to poaching and reduced abundance of prey and habitat (Kenny et al. 1995, Wikramanayake et al. 1998, Linkie et al. 2006, Dinerstein et al. 2007). The 36 400-km^2 Kerinci Seblat region of west-central Sumatra is designated as part of a level 1 "tiger conservation landscape" (Dinerstein et al. 2007) and significant resources are spent annually to conserve this population. Linkie et al. (2006) investigated the effect of resources invested in anti-poaching protection on the probability of losing the different tiger populations within this landscape. Two important management strategies for this species are reducing the level of tiger and prey poaching by patrolling the population, and assessing its status through surveying. Currently, about \$47 800 is spent annually on these two actions with approximately one-fifth of this budget spent on surveying (C_s = \$10 235) and the remainder on protection measures (C_m; M.

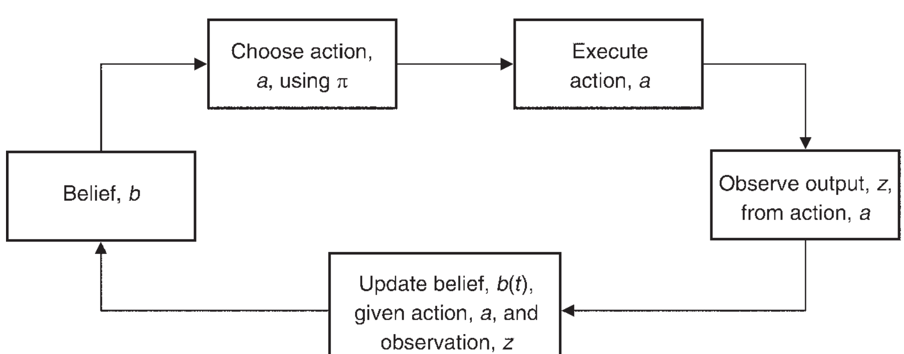

FIG. 1. Procedure for iteratively applying the optimal strategy and updating the belief that the population is persisting as implemented in the partially observable Markov decision process.

Linkie, *unpublished data*). The budget set here is based on the cost of implementing patrols in the periphery of two populations and does not include the ongoing costs of overheads for this long-term program.

The probabilities of transition between states of the tiger population were calculated from the probabilities of extinction (and its complement, the probability of survival) of each tiger population depending on the action implemented. In each year the total budget of C is expended; thus, if we manage one population then this population has a probability of extinction given an investment of C, whilst the other has a probability of extinction given no investment (doing nothing). If we manage both populations, each population has a probability of extinction assuming half the budget is invested in management at each population. When surveying a population, a cost C_s is incurred, thus there are $C - C_s$ resources available to manage the second population. We derived a local extinction probability for a population given the resources spent on poaching patrols based on a population viability analysis of this Sumatran tiger population relating probability of population extinction over 50 years to the number of tigers poached from a population annually (Linkie et al. 2006). This model indicates a relatively high probability of extinction of a population in a 50-year time frame when no management occurs ($p_0 = 0.99$). To reduce tiger poaching by 50% requires an investment of \$18 744 (M. Linkie, *unpublished data*), and this value was used to fit a logistic function to relate probability of extinction in a 50-year time horizon to dollars invested in management, $P(C_m)$, where (see Fig. 2a):

$$P(C_m) = p_0\left[1 - \frac{1}{(18\,744/C_m)^{\theta} + 1}\right].$$

Here θ was derived by fitting this logistic curve to data from the population viability analysis from Linkie et al. (2006) to maintain a similar change in probability of extinction given increasing investment as from a reduction in tigers poached ($\theta = 7$). We used the same logistic curve with a reduced probability of extinction over a 50-year period without management ($p_0 = 0.4$) to construct a curve relating probability of extinction to dollars invested in management for a low return on investment population (see Fig. 2a). From these curves we interpolate the probability of extinction over 50 years given a particular action was implemented (e.g., manage both populations; see Fig. 2a) and derived annual transition probabilities of a population of Sumatran tigers, p_m, where $p_m = 1 - [1 - P(C_m)]^{1/50}$.

Observation transitions are calculated based on the probability of detecting a tiger given they persist in a population (d) and the complementary probability of non-detection given persistence ($1 - d$). The transitions are constructed given the real state of the system, the observed state of the system and the action implemented. Thus, if both populations persist and we survey in population A and manage in population B then our probability of observing a tiger in population A and B will be the product of the probability of detecting a tiger given they persist in a population if we survey (d_s) and if we manage (d_m; see Table 2). Linkie et al. (2006) estimated that there is a 50% chance of detecting a tiger at a survey point, given that it is in the vicinity. Based on this figure we derived the binomial probability that at least one tiger would be detected during surveys of 10% of survey points (where the total number of survey point is 500) and approximately 30 female tigers remain extant ($d_s = 0.78$; see Fig. 2b). We explore the impact of survey efficiency, and variation in crypticness of the species being managed, by assuming a reduction in the chance of detecting a tiger at a survey point to 10% ($d_s = 0.26$; see Fig. 2b). We assume that there is almost no chance of detecting a tiger when anti-poaching patrols are implemented as we are not actively searching for tigers in the area ($d_m = 0.01$); thus, there is little opportunity to reduce our uncertainty about the state of a population unless we survey. By increasing this value we assess how the optimal management strategy would change if the species is more likely to be detected during management ($d_m = 0.21$), for example if surveying could be implemented simultaneously with management actions for no extra cost or animals are less cryptic.

A summary of all parameter values for the Sumatran tiger example is given in Table 1.

Simulations: why incorporate partial observability?

We assess the performance of the optimal strategy determined by the POMDP and that from the MDP over a 20-year time horizon using forward simulation. Performance is based on the percentage of the total possible reward achieved in that period averaged across all iterations. We investigate how performance changes as the detectability of the species during management or level of cryptsis, d_m, increases from 0.01 (low detectability during management, equivalent to Sumatran tiger) to 1 (completely observable during management). We investigate this pattern for both the current budget and the reduced budget, and also when the risk of extinction in both populations is equal and when they differ. Simulations were run over 1000 iterations.

Results

The MDP gives an optimal strategy based on the real states of each population, whether they are extant or extinct. The optimal strategy from the MDP for whether to actively manage or simply do nothing in a population is influenced by the budget available for management and the differences between populations in terms of extinction risk and thus return on investment from management. With the current budget available to manage the Sumatran tiger the optimal strategy is to manage the populations that are extant. A reduction in funding means there is not enough money to effectively manage both populations and affects only our optimal

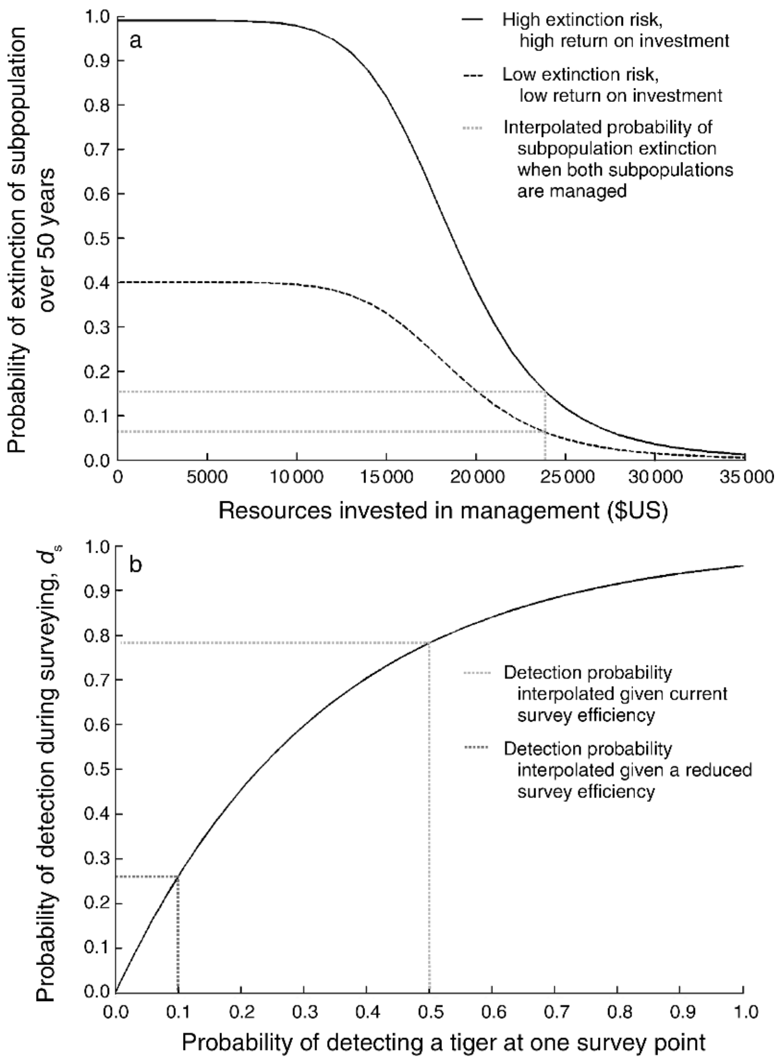

FIG. 2. (a) Assumed relationship between probability of extinction in 50 years of a population and the money invested in managing a population. Each curve represents an extinction risk/return on investment measure, high or low. The black curve is derived from probability of extinction data from Linkie et al. (2006) and cost data for the Sumatran tiger (M. Linkie, *unpublished data*). The gray dashed lines show the probability of extinction interpolated from these relationships given two populations are managed. (b) Assumed relationship between detection probability from surveying and the probability of detecting a tiger at one sample point. This curve is based on the probability that a population of tigers would be detected during surveys when $10 235 is invested in surveying (M. Linkie, *unpublished data*) and approximately 30 female tigers remain extant. The gray dashed lines show the detection probability, d_s, given there is a 50% chance of detecting a Sumatran tiger at a survey point (Linkie et al. 2006) and a 10% chance of detecting a Sumatran tiger at a survey point. This reduction represents the impact on detection if a less efficient survey technique was used or a more cryptic species was being managed.

action in the state where both populations are extant. The optimal strategy in this case is to manage the population that gives the biggest return on investment.

Using a partially observable approach our decision is now based on our understanding of the state of each population and thus the axes represent a manager's belief in the persistence of the Sumatran tiger in each population (Figs. 3–6). When the belief in both populations approaches one (equivalent to both populations being extant) or belief in one population approaches one whilst the other approaches zero (equivalent to one population being extant and the other extinct) then the optimal decision from the POMDP is the same as that derived from the MDP. The optimal strategy from the POMDP for whether to actively manage, survey, or simply do nothing in a population is influenced not only by the budget available for management and the differences between populations in terms of return on investment but also interestingly, by how sure we are that the species persists in each area and the disparity in these beliefs. The decisions to survey in both populations or to do nothing in both populations are never optimal for any combination of extinction risk or funding explored. In short,

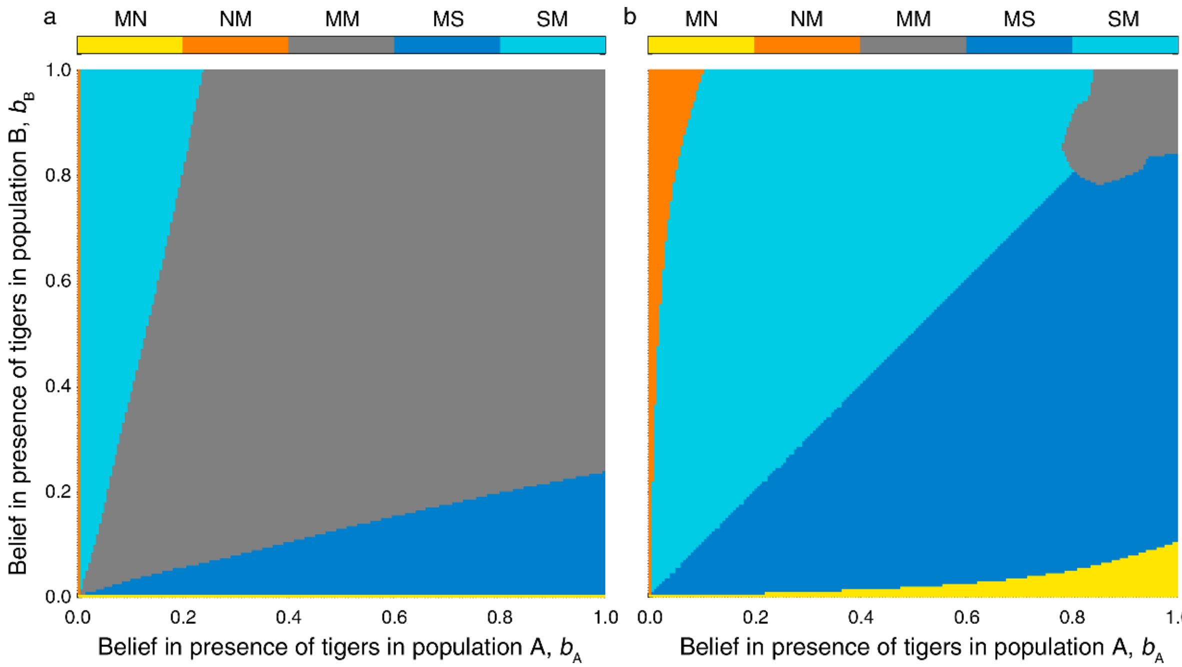

FIG. 3. The optimal decision for Sumatran tigers in the first year of action (20 years remaining to manage) dependent on our belief in the presence of tigers in population A, b_A, and our belief in the presence of tigers in population B, b_B, when (a) both populations have high probability of extinction (inhabit low quality habitat) and (b) both populations have a high probability of extinction and budget is reduced by one-third. Detectability, $d_s = 0.78$. Key to abbreviations: MN, manage population A and do nothing in population B; NM, do nothing in population A and manage population B; MM, manage both populations; MS, manage population A and survey in population B; and SM, survey in population A and manage population B.

neither of these strategies is efficient as some form of management can always improve the final outcome.

The current budget available to manage two populations of the Sumatran tiger enables active management in both populations to be optimal over a wide range of certainty in the presence of tigers (Fig. 3a). If, however, there is a large disparity in our belief about the presence of tigers in both areas, it is no longer optimal to manage the population in which our belief in the presence of tigers is low. Under these circumstances we should invest in gaining information on the presence or absence of tigers in this population by surveying and updating our belief in their presence. When our belief in the presence of tigers in a population is less than 0.5%, it is no longer worth monitoring in this population. Abandoning a population at this belief state is optimal regardless of changes in budget or the potential return on investment (extinction risk). If the funding available to manage the Sumatran tiger were cut by a third, the option to manage both populations, irrespective of our certainty in the presence of tigers, would reduce the effectiveness of anti-poaching patrols in each population (Fig. 3b). Indeed, under a reduced budget both populations should only be managed if we have seen tigers in both areas in the last 7 years ($b_A \geq 80\%$ and $b_B \geq 80\%$; Fig. 3b). The most efficient strategy under a reduced budget is to manage the population in which we are more certain tigers are present, whilst surveying and gaining information in the other population. If funding is reduced then we should cease management in one population when the chance it is extant is less than 10% ($b_A \leq 0.1$ or $b_B \leq 0.1$).

Changes in the detection probability when we monitor, for example, the use of a less effective survey method or the study of a more cryptic species, affect the optimal strategy (Fig. 4a). If the probability of detection during surveying is decreased then the benefits of surveying are also lower, and the area of the strategy for which it is optimal to survey in one population is reduced (Fig. 4a, see Fig. 3b for comparison with high, d_s). Indeed, if the budget is low we would both increase the optimality of managing both populations and increase the optimality of doing nothing instead of surveying (Fig. 4a). When the budget is higher than only the area over which we manage both populations increases. There is also a possibility of detecting tigers while managing, d_m, which may increase if surveillance can be integrated into patrolling or if we are managing a less cryptic species. When we increase this value, we see a similar result from the increase in d_s, with the belief space over which it is optimal to survey decreasing and the belief space over which management of both population is optimal increasing (Fig. 4b, see Fig. 3b for comparison with low d_m). There is no change in the optimality of actions that incorporate doing nothing

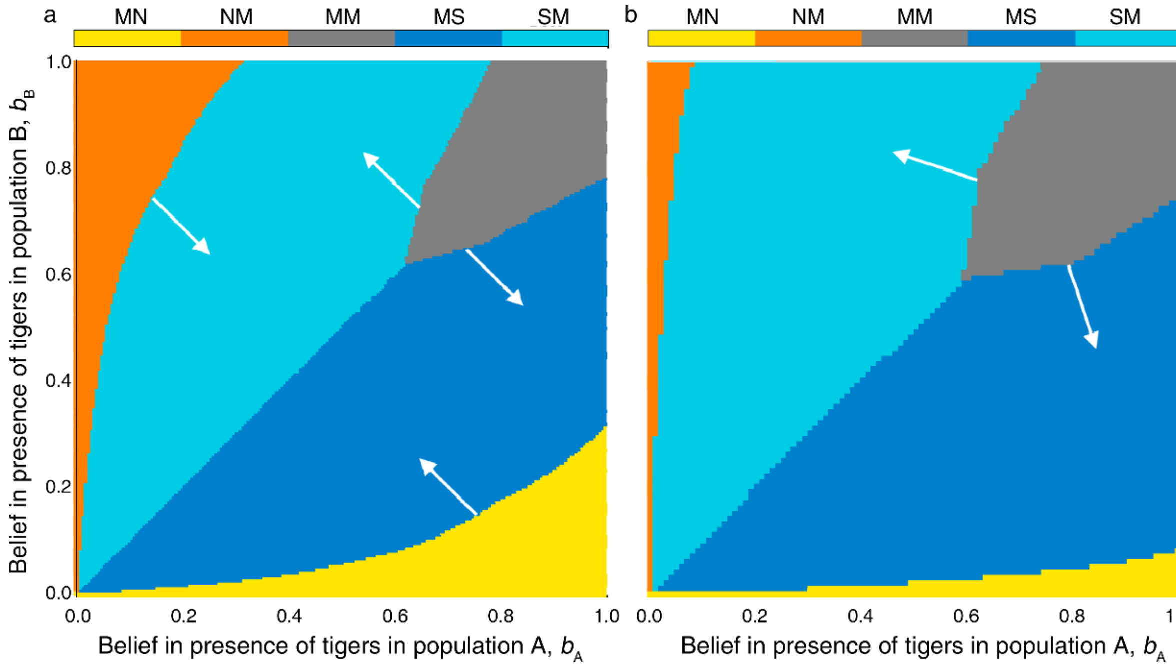

FIG. 4. The optimal decision for Sumatran tigers in the first year of action (20 years remaining to manage) dependent on our belief in the presence of tigers in population A, b_A, and our belief in the presence of tigers in population B, b_B, (a) when the probability of detection from surveying is reduced, $d_s = 0.26$, and (b) when the probability of detection when managing in increased, $d_m = 0.21$. Here both populations have high probability of extinction (high return on investment), and the budget is reduced by one-third. The arrows show how the optimality of surveying (MS and SM) has reduced given these changes in detection (see Fig. 3b for comparison). Key to abbreviations: MN, manage population A and do nothing in population B; NM, do nothing in population A and manage population B; MM, manage both populations; MS, manage population A and survey in population B; and SM, survey in population A and manage population B.

(MN and NM) when the probability of detecting tigers while managing, d_m, is increased.

Return on investment (extinction risk) in a population can differ for a number of reasons, for example, the habitat in each population could differ in quality or populations could have different levels of human encroachment. A difference in the potential return on investment in the populations, affects how we should allocate resources between our tiger populations (Fig. 5). In the population with low extinction risk (return on investment) the optimal action is to survey when our belief in the presence of tigers in that population is below that of the second population which has high risk of extinction (return on investment) (Fig. 5a; see Table 1 for extinction risk values). Otherwise, when our belief is higher in the low risk population, we manage this population as well. We only cease managing the population at high risk (high return on investment), and concentrate management in the low risk area, when our belief in the presence of tigers in the high risk area is low. With less funding we cannot effectively manage both populations when we consider the distinction in extinction risk (Fig. 5b). The optimal decision is to manage the population in the high risk area if our certainty in the presence of tigers there is above approximately 40% and implement no action in the population at lower risk (with low return on investment). Even if our initial certainty in the presence of tigers in this population is less than 40% we still manage this population, however, we now survey the other population. Only when our initial belief in the presence of tigers in the population at low risk of extinction is markedly higher than that of the high risk area do we implement management in this low risk population. We do not, however, stop acting in the high risk population we merely shift focus from management to surveillance.

The optimal decision is not only influenced by our belief in the presence of tigers in each population but also by the time horizon of management and whether or not a tiger is observed in either population during our previous actions (Fig. 6). As we progress towards the final year of management, the benefits of surveying diminish. Indeed surveying will never be optimal in our final year irrespective of our belief in the presence of tigers in either population as information gained cannot influence management decisions. Not only do the optimal decisions change each year, but the optimal action in each population will change depending on our previous action, and any observations, which influence the current belief about the presence of tigers. If both populations are the same and we start with equal certainty that tigers are present in both areas and we do

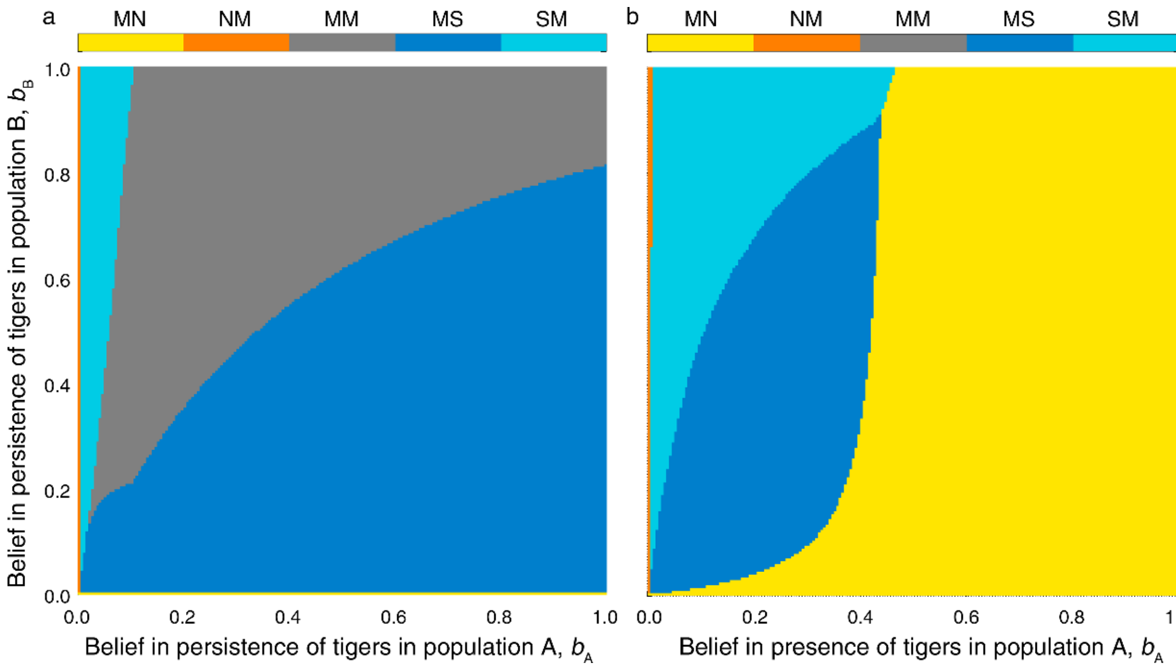

FIG. 5. The optimal decision for Sumatran tigers in the first year of action (20 years remaining to manage) dependent on our belief in the presence of tigers in population A, b_A, and our belief in the presence of tigers in population B, b_B, when (a) population A has a high probability of extinction (high return on investment) and population B has a low probability of extinction (low return on investment) and (b) population A has a high probability of extinction (high return on investment) and population B has a low probability of extinction (low return on investment) and the budget is reduced by one-third. Detectability, $d_s = 0.78$. Key to abbreviations: MN, manage population A and do nothing in population B; NM, do nothing in population A and manage population B; MM, manage both populations; MS, manage population A and survey in population B; and SM, survey in population A and manage population B.

not observe tigers in either population for five years, a likely scenario for many cryptic threatened species, then our belief in the presence of tigers in both areas declines evenly and we implement the same actions in both (Fig. 6). If the history of sightings of tigers in both areas is different, for example we might be 60% sure tigers are in population B but only 40% sure they are present in population A, the optimal actions and the changes in our certainty of the presence of tigers would differ (Fig. 6). In implementing this optimal strategy we affect our belief in the presence of tigers in each population in the next management period differently, and as we obtain no positive observations of tiger presence our beliefs decline. Thus, in population B where we implement management our belief in the presence of tigers only declines marginally while in population A, in which we survey and see nothing, our certainty in the presence of tigers declines markedly. In the next year, our actions will be driven by our new and now different beliefs in the presence of tigers in each population and as our belief in the presence of tigers at population B is markedly higher we will manage only this population.

In general ignoring the cryptic nature of the species and managing assuming the problem can be repeated as an MDP can significantly diminish our conservation outcomes. The performance of management based on the optimal solutions from the POMDP depends much more on the budget available to manage the Sumatran tiger but very little of the population detectability (Fig. 7a, b). When the budget is low the POMDP reaches an average performance level of 75–80% of the maximum possible reward over 20 years (Fig. 7a), but reaches almost 100% performance when the budget is increased (Fig. 7b). Here 100% performance means that both populations remain extant over the 20 year management horizon. The optimal decision from the MDP is to manage all extant population/s irrespective of return on investment or the budgets we explored, that is if no tigers are observed in a year than the optimal action is not to manage in both areas. As the detectability of the species during management increases so too does the performance of management based on the optimal solution from the MDP (Fig. 7a, b). However, this increase in performance is marginal until detectability is high. Indeed, the MDP solution performs up to 90% worse than the POMDP for highly cryptic species (low detectability during management; Fig. 7b) and even when the observability reaches 90%, the performance of the MDP solution is at least 40% lower than the performance of the POMDP solution (Fig. 7a). Only when there is a 100% chance of observing the species when we manage the population does the performance of the MDP and the POMDP converge. The results for the performance of the POMDP compared to the MDP do not differ if the populations have an equal risk of extinction (return on investment) or their extinction risk differs.

Discussion

Threatened species managers need to decide how to allocate their limited funds within conservation programs not only between management actions but often between areas to be managed. In recognition of the cost and objectives of conservation programs a number of decision-making frameworks have been explored to show how to achieve the best return on investment (e.g., McCarthy et al. 2008). These frameworks have provided significant insight into the best way to achieve objectives for threatened species management. Implementation of the best action from these frameworks almost always requires knowledge of the state of the system: management actions are state-dependent (e.g., Shea and Possingham 2000, McCarthy et al. 2001). The cryptic nature of most threatened species means that in reality conservation managers may not know with certainty the state of the species they are trying to protect (Chadès et al. 2008, MacKenzie 2009). Managers confronting such issues need more comprehensive allocation frameworks that incorporate not only the objectives of their management plan but an understanding of their budget, the benefit and costs of different actions, and their uncertainty in population or system states that drive management. Our work on the Sumatran tiger in two populations shows for the first time that ignoring uncertainty about the presence of the species leads to significantly suboptimal decision-making.

A key limiting factor in almost all threatened species management programs is money. Indeed, the amount of funding available can have a significant impact on the best management strategy to implement (e.g., McCarthy et al. 2008). Interestingly, spending more money in one area does not necessarily imply a consistent incremental increase in return from that investment: there are likely to be diminishing returns. This means that if our budget is large enough we can get better returns by investing in a second population as well. However, if funding is small and the risk of extinction of the species in both areas high, we get a better return by concentrating our management in one population, in effect invoking the concept of a triage (Bottrill et al. 2008, McDonald-Madden et al. 2008). Deciding when to change from managing both areas to implementing management in one population depends heavily on the framework used to optimally allocate resources. A strategy based around the real state of the system (MDP) provides hard boundaries for when to make a decision to cease management in an area. Such an approach could have two outcomes: managers might make this decision too early and risk extinction of a population, or they might continue investment in a population that is beyond recovery and thus waste resources that could be reallocated where management can still benefit the species.

Treating surveys as a possible action is a key difference between a completely observable and a partially observable approach to resource allocation between populations of a threatened species. Surveying with the aim of detecting a species can significantly alter our understanding of the real state of the populations, and thus guide better management. Monitoring is important in areas in which our belief in the presence of a threatened species is low. In many ways, this form of monitoring enables managers to make informed decisions to either reinstate or cease management in an area when funding is insufficient to secure both populations. This provides an informed and justifiable decision to triage the management of a threatened species in some areas. Of course, the benefits of gaining information on the presence of a species in a populations is strongly influenced by how much time we have left to learn, a factor that may be beyond the control of most managers. However, if surveying can be improved by increasing the detection capability of surveys, without increasing cost, then the benefits of monitoring will increase and thus our effectiveness in learning the state of the system we are managing may improve. In contrast, if our survey technique is less efficient or the threatened species we are managing is more cryptic than the Sumatran tiger the benefits of surveying will decrease and we should either do nothing or implement management depending on our belief in the presence of our species in that area (see Fig. 4a). Information gain can also occur during management actions, for example we may observe a tiger when we are implementing anti-poaching patrols. For the Sumatran tiger we have assumed that detection during management is rare. Detection during management may increase if, for example, we are managing a less cryptic species or we can implement surveys during management for no extra investment. If detection of the species during management is increased, then management also provides the benefits of gaining information on the status of the population and thus, as one might expect, monitoring alone is rarely optimal (Fig. 4b). The impact of detection from both surveillance and management highlights the importance of incorporating information gain into the decision-making framework.

The importance of considering the uncertainty in the system state is further highlighted by the considerable difference in performance of the MDP and POMDP in reaching our conservation objective. Including the possibility that the species can be detected (or not) while managing and explicitly integrating the value of information significantly improves the performance of management. Interestingly, an increase in funding available to implement our management strategy will increase the performance of POMDP but does not affect that from the MDP strategy. In fact no matter how much we increase the budget available to management,

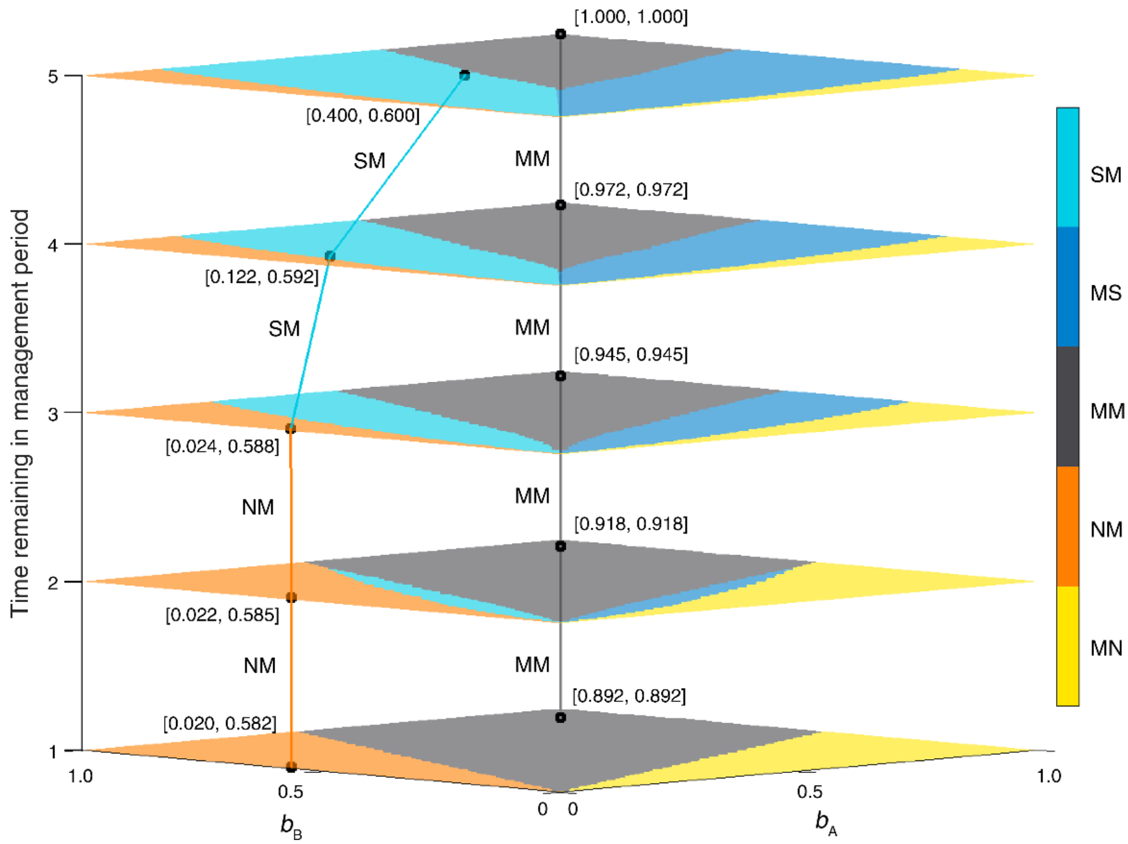

FIG. 6. The optimal decision for Sumatran tigers over the last five years of management dependent on our belief in the presence of tigers in population A, b_A, and our belief in the presence of tigers in population B, b_B, when both population have high probability of extinction (high return on investment) and the budget is reduced by one-third. The lines show how our beliefs in the persistence of tigers in each population change through time given that no tigers are detected (numbers in square brackets are x- and y-coordinates of points at each time step). The two line sequences show two different initial belief states: (1) where we have full belief in the persistence of tigers in each population ($b_A = 1$ and $b_B = 1$) and (2) when we have differing beliefs in each population ($b_A = 0.4$ and $b_B = 0.6$). The color of the line represents the action that should be taken from the optimal strategy in the preceding year (actions are also labeled). Detectability, $d_s = 0.78$. Key to abbreviations: MN, manage population A and do nothing in population B; NM, do nothing in population A and manage population B; MM, manage both populations; MS, manage population A and survey in population B; and SM, survey in population A and manage population B.

even enough to always manage two populations effectively, the MDP strategy is still state dependent and driven by what we detect in the population during management. Hence, if we do not see the species in both populations (observation absent/absent) we will assume that the species is not present in each area and thus not manage in either area as given by the optimal MDP strategy for that population state. In essence we could be not managing when the species still persists, an error that in reality could lead to increased extinction risk for the species. Comparable performance between the two approaches is only achieved when the detectability of the species through passive observation during management is close to 100%. Here the benefits of monitoring are essentially removed and the system state can be effectively observed during management. In reality, this case is uncommon as threatened species are invariably rare and often cryptic. In many cases, the observability of the species during management will be less than 100% and thus following a strategy derived assuming perfect detectability of the system could lead to very suboptimal results. Of course there are some cases where species must be detected during management for management to be implemented successfully, for example vaccination or weed fumigation. The requirement for detection to occur for the benefits from these management actions to be obtained essential puts a caveat on the implementation of these actions; it does not however mean that detection of the species during such management actions is certain (100%). The direct link between management actions and detection required here can be incorporated into the POMDP framework but cannot be explored within a framework that assumes that the system is completely observable (i.e., MDP).

Despite the significant improvement in performance of a strategy that incorporates uncertainty and our ability to learn about the state of the system, there are some important drawbacks to POMDP we need to

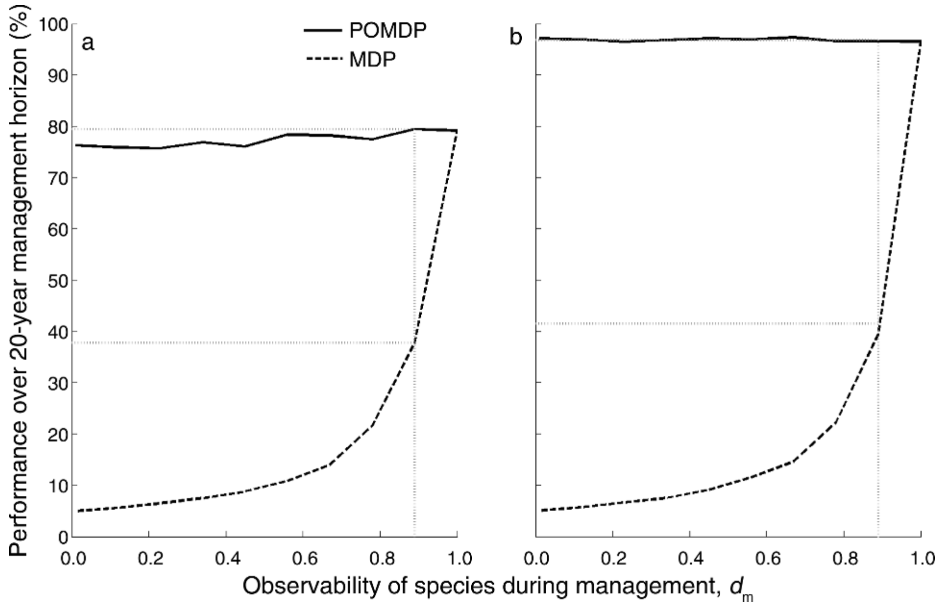

FIG. 7. The performance over a 20-year management horizon of a partially observable Markov decision process (POMDP) and fully observable (MDP) optimization of threatened species management with increasing observability of that species during management, d_m. The figure shows results based on (a) low budget and (b) high budget. Here 100% performance means that both populations remain extant over the 20-year management horizon. Dashed gray lines represent the performance of both strategies assuming observability of 90% ($d_m = 0.9$). The effectiveness of surveying does not affect the comparison of these two techniques.

highlight. Using POMDP we assumed that we know the probability of detection of a species when we survey an area. Such information is often difficult to estimate but can be approximated for cryptic species by repeated sampling methods (MacKenzie 2006). We also assume that we know the relationship between extinction risk and investment in management. In other words, we know the effectiveness of our direct management actions. Such functions are essential for deriving the transition probabilities necessary to utilize both the MDP and POMDP methods. Structural uncertainty in these functions can be considered by incorporating into the decision-making framework multiple functions of how management benefit might change and our ability to learn which is the true function of management benefit based on the actions implemented (Nichols and Williams 2006, MacKenzie 2009, Williams 2009, McDonald-Madden et al. 2010). In essence incorporating such uncertainty would lead to an adaptive framework that enabled decision-makers to deal with not only uncertainty in the state of the system being managed and but also the structural uncertainty within the parameterization of the problem. Answering this fully adaptive management problem with both forms of uncertainty would require solving a multi-dimensional POMDP. Further, the complexity of problems that can be explored using POMDP is limited. Deriving an exact optimal strategy using POMDP is expensive in terms of computational time and memory. This means that we are also haunted by the curse of dimensionality (Bellman 1957) and thus the state space over which we can optimize is limited. Here we explore the optimal allocation of resources between two populations of a threatened species but if we extend the reality of the problem to more populations we cannot derive an exact optimal strategy using POMDP. However approximation methods can be explored to derive an allocation strategy given our uncertainty in the state of the system with more realism—essentially enabling us to escape this curse of dimensionality (Ross et al. 2008). In addition to the state space limitation, the complexity of solving a POMDP increases exponentially with the time horizon. Here we have provided an exact solution to the POMDP for a finite time horizon of 20 years, allowing us to show how the optimal strategy will change as the time remaining in a management program declines. While some management programs are limited to a finite management period, for example they have a defined investment timeframe from a funding body; other threatened species programs with the aim of conservation will not have a finite management horizon and may instead plan to manage the species in perpetuity. In this case, what is needed is an optimal strategy that managers can implement for as long as the program continues, deemed in the artificial intelligence literature as an infinite time horizon solution (Puterman 1994). In our case, deriving an infinite horizon solution is not computationally feasible; however, this solution may be approximated by the first time step (in this case year 20). New approximation methods do not allow us to completely escape the problem of a more complex state space (i.e., moving from a simple extant/extinct state space to a individual based state space) using POMDP. The solutions from complex POMDP are difficult to interpret and represent in a way that can facilitate conservation management. To improve our ability to manage rare species we need to find new ways to incorporate partial observability that allow for increased system complexity and utility of the optimal strategies. The essential next step must happen with the collaboration of Artificial Intelligence researchers and ecologists.

Uncertainty is inherent in conservation problems and a handful of studies have explored optimization of management decisions in light of such uncertainties (see McCarthy and Possingham 2007, Rout et al. 2009). Studies thus far have focused on uncertainty in particular parameters of the system and optimized over one starting belief state related to the estimate of this parameter. Our knowledge of the state of the systems that we manage is never complete. It is therefore remarkable that this study is one of the first utilizing an optimization procedure that deals directly with this type of incomplete knowledge (POMDP). Using POMDP has allowed us to confront the rarely-framed question of whether uncertainty surrounding our belief in the state of threatened species populations should change our actions. Our answer is simple: in the current climate of limited conservation funding this uncertainty does indeed impact how we should manage a threatened species. If we are to make the best decisions for threatened species management we must allocate funding based not only on the bang we get for our buck but on our "certainty" in achieving those results.

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