Optimal allocation of conservation effort among subpopulations of a threatened species: How important is patch quality?

Aliénor L. M. Chauvenet,[1] Peter W. J. Baxter,[1,2,3] Eve McDonald-Madden,[1] and Hugh P. Possingham[1]

[1]*University of Queensland, The Ecology Centre and Applied Environmental Decision Analysis Centre,
School of Biological Sciences, St. Lucia, Queensland 4072 Australia*
[2]*Australian Centre of Excellence for Risk Analysis, School of Botany, University of Melbourne, Parkville, Victoria 3010 Australia*

Abstract. Money is often a limiting factor in conservation, and attempting to conserve endangered species can be costly. Consequently, a framework for optimizing fiscally constrained conservation decisions for a single species is needed. In this paper we find the optimal budget allocation among isolated subpopulations of a threatened species to minimize local extinction probability. We solve the problem using stochastic dynamic programming, derive a useful and simple alternative guideline for allocating funds, and test its performance using forward simulation. The model considers subpopulations that persist in habitat patches of differing quality, which in our model is reflected in different relationships between money invested and extinction risk. We discover that, in most cases, subpopulations that are less efficient to manage should receive more money than those that are more efficient to manage, due to higher investment needed to reduce extinction risk. Our simple investment guideline performs almost as well as the exact optimal strategy. We illustrate our approach with a case study of the management of the Sumatran tiger, *Panthera tigris sumatrae*, in Kerinci Seblat National Park (KSNP), Indonesia. We find that different budgets should be allocated to the separate tiger subpopulations in KSNP. The subpopulation that is not at risk of extinction does not require any management investment. Based on the combination of risks of extinction and habitat quality, the optimal allocation for these particular tiger subpopulations is an unusual case: subpopulations that occur in higher-quality habitat (more efficient to manage) should receive more funds than the remaining subpopulation that is in lower-quality habitat. Because the yearly budget allocated to the KSNP for tiger conservation is small, to guarantee the persistence of all the subpopulations that are currently under threat we need to prioritize those that are easier to save. When allocating resources among subpopulations of a threatened species, the combined effects of differences in habitat quality, cost of action, and current subpopulation probability of extinction need to be integrated. We provide a useful guideline for allocating resources among isolated subpopulations of any threatened species.

Key words: decision theory; endangered species conservation; habitat fragmentation; Kerinci Seblat National Park (KSNP), Indonesia; management efficiency; optimization; Panthera tigris sumatrae; *rule of thumb; stochastic dynamic programming (SDP); Sumatran tiger.*

Introduction

Habitat destruction due to human activity (e.g., building of roads, housing expansion, and fire) or natural events (e.g., disease, flood, storm, and fire) is considered one of the most significant threats to species worldwide (Baguette and Schtickzelle 2003, Keller et al. 2005, Wiegand et al. 2005, Johst et al. 2006). This destruction can fragment the population of a species into several smaller subpopulations. In such fragmented landscapes the metapopulation paradigm implies that movement among subpopulations enables recolonization and thus persistence of a metapopulation if connectivity is maintained (Hanski and Gilpin 1997,

Baguette and Schtickzelle 2003). Unfortunately, habitat fragmentation often results in complete separation of subpopulations, and therefore many threatened species exist as suites of isolated subpopulations. As a consequence of this isolation, each subpopulation may be vulnerable to local extinction through demographic, stochastic, or genetic effects (Keller et al. 2005), with no possibility of natural recolonization upon local extirpation (Harrison and Bruna 1999). In order to persist, these species require adequate management that ultimately requires smart conservation decision making (Possingham et al. 2001).

A key limiting factor in the conservation of threatened species is the funding available to implement management (Guikema and Milke 1999). As a result of this limitation, managers are often faced with the difficult decision of how to allocate their money between subpopulations of a species in order to get the best results. Furthermore, it has been shown that ignoring

[3] Corresponding author. E-mail: p.baxter@uq.edu.au

the cost of conservation when deciding how to manage species can lead to misdirected effort and ultimately wastes management resources (Baxter et al. 2006, Wilson et al. 2006). Consequently, there is a need for a decision-making approach that enables managers to make practical management decisions that use resources efficiently (Possingham et al. 2001).

Despite the recognition of the importance of careful allocation of scarce resources and widespread acknowledgment of the threats posed by habitat fragmentation (Keller et al. 2005, Wiegand et al. 2005), there has been little research combining these aspects into a coherent decision-making framework for among-subpopulation resource allocation. McDonald-Madden et al. (2008a) were the first to use a decision-theoretic approach to investigate how best to allocate resources among isolated subpopulations of a threatened species. With the constraint of a fixed budget, they consider the problem of managing several isolated subpopulations with the objective of maximizing the expected number of extant subpopulations and derive an expression for the optimal number of subpopulations to manage given the costs associated with management. One of the major assumptions of this work is that all subpopulations are identical. Although such an assumption simplifies the problem, in many real situations there will be significant differences in quality between the patches in which the subpopulations persist, such as the habitat area and location, the number of predators, the cost of doing conservation management, the levels of disturbance and threat, and food availability.

We aim to provide managers with a framework for optimally allocating a fixed budget between isolated subpopulations distributed in patches of different quality. In doing so we address key questions such as: should we manage all subpopulations, allocating resources evenly, risking the loss of all subpopulations due to inadequate investment? Should we use a triage approach (Walker 1991), increasing the individual chance of persistence for some, but possibly sacrificing others? And if we distribute money or effort nonuniformly, what characteristics of a patch will determine where most money is allocated: the highest quality patch, the patch where actions are cheapest?

We solve the problem of optimal budget allocation with a mathematical optimization approach, which is underpinned by relationships between the probability of extinction of a subpopulation and the money invested in its conservation. We assume that subpopulations are distributed in isolated patches of dissimilar quality such that each has a different set of parameters. The habitat quality influences two variables: each subpopulation's current probability of extinction and the effectiveness of management efforts to decrease this extinction risk. The model also depends on fixed costs: the total budget available for the project, the indirect cost of management of a species, and the cost of specific management items (also see McDonald-Madden et al. 2008a). Here

our overall management objective is to minimize the chance of losing one or more subpopulations (Nicholson and Possingham 2006). We solve the budget allocation problem through time using stochastic dynamic programming (SDP), an optimization technique. Stochastic dynamic programming compares different management options for each possible state of the system of interest as the system changes through time; for example, in our case, identification of which subpopulations are extant at the current time could serve as a system state variable that induces selection of a specific management action. It has been used to solve problems in several conservation studies, e.g., fire management (Richards et al. 1999, McCarthy et al. 2001), translocation (Lubow 1996, Tenhumberg et al. 2004, Rout et al. 2005), and population management (Shea and Possingham 2000).

To assess the performance of the state-dependent optimal solution and other simple heuristic management options, we compare them using simulations and demonstrate the approach using the Sumatran tiger, *Panthera tigris sumatrae*, as a case study. The Sumatran tiger is exposed to numerous threats which, combined with its low population numbers, has resulted in its classification as critically endangered on the IUCN red list (Cat Specialist Group 1996). The major threats to its survival are habitat destruction, excessive poaching for illegal trade (Nowell and Jackson 1996, Morell 2007), prey depletion, and persecution by humans because of the threat to livestock (Linkie et al. 2003, 2006, Nyhus and Tilson 2004). Linkie et al. (2006) studied the occurrence and population viability of the tigers in the Kerinci Seblat National Park, Sumatra. Following repeat surveys of the region, they identified four core subpopulations living in suitable habitats and the level of anti-poaching measures (and thus cost) necessary to maintain those subpopulations. We can therefore answer the question: How should we split the management budget between these subpopulations in order to minimize the chance of losing one or more subpopulations?

METHODS

Consider a species divided into several isolated and independent subpopulations. We model the probability of extinction of one subpopulation given an investment of amount b as

$$P(\text{extinction}|\$b) = \frac{P_0}{\phi\left(\dfrac{b - c_{\mathrm{f}}}{c_{\mathrm{m}}}\right) + 1} \tag{1}$$

following McDonald-Madden et al. (2008a); the effect of alternative model forms is discussed in McDonald-Madden et al. (2008b). Each subpopulation has a probability of extinction if no action is taken, P_0, which decreases as money is invested into that subpopulation's management (Fig. 1). The exact effect of a given monetary investment on the probability of extinction depends on the ease of management of the subpopula-

tion, ϕ (shape parameter of the curve, reflecting response to effort). The smaller ϕ is, the more difficult it is to reduce the probability of extinction, $P(\text{extinction} | \$b)$. The fixed cost of management of each subpopulation (indirect costs that indirectly influence the subpopulations' probabilities of extinction, such as the costs of travel, hiring field staff, and getting permits) is represented by c_f. The cost per unit effort of a management action (e.g., meter of fencing, poison bait, anti-poaching patrol) is symbolized by c_m. The probability of extinction of a subpopulation can therefore be reduced by the product of the management efficiency (ϕ, effort^{-1} units, e.g., per-patrol efficiency) and the number of management items that can be afforded with the annual fixed budget b once the cost of managing the subpopulation c_f has been subtracted (McDonald-Madden et al. 2008a).

In this paper we consider cases in which each subpopulation i can have a different unmanaged extinction probability P_{0i} and management efficiency parameter ϕ_i. Therefore, a subpopulation i will be allocated a percentage α_i of the total budget:

$$P_i(\text{extinction} | \$\alpha_i b) = \frac{P_{0i}}{\phi_i \left(\dfrac{\alpha_i b - c_f}{c_m} \right) + 1}. \qquad (2)$$

We also consider subpopulations that are isolated from one another and thus assume that any factor affecting one subpopulation will not affect the others. In other words, we assume that the probability of extinction of one subpopulation is not related to the probability of extinction of the others for any other reason than the allocation of resources between subpopulations. Hence the probability of losing one or more subpopulations, the value we are trying to minimize, is one minus the probability we lose no subpopulations or one minus the product of all the probabilities that each subpopulation is extant.

State-dependent optimization

We find the state-dependent optimal solution using stochastic dynamic programming (SDP). This method lets us take the current state of the system into account at each time step and therefore allows the management action to respond to the state of the system as it changes. Stochastic dynamic programming can be used on any system that can be represented by a fixed number of states, with transitions between states driven by a first-order Markov chain (Intriligator 1971, Mangel and Clark 1988). It works by backwards iteration (based on the condition that the optimal path is followed at all subsequent time steps) comparing different management options for the system. To formulate the optimization problem we take the following steps:

1) State an objective and time horizon (number of time steps in the management plan). In this case the objective is to have all the subpopulations extant at the final time step of the management plan. We chose a
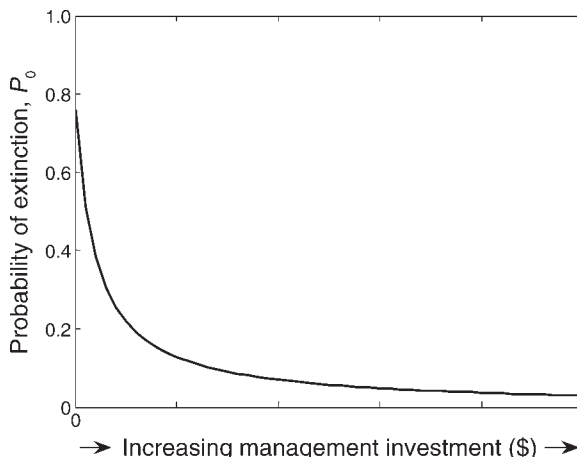

FIG. 1. Hypothetical relationship between the probability of extinction of a subpopulation and the budget invested into its conservation.

management time frame of 50 years. This is the expected time frame within which the KSNP Sumatran tigers will go extinct without adequate protection (Linkie et al. 2006).

2) Define all possible states of the system. Here, the states are defined by which subpopulations are extant and which ones are not, giving 2^n possible states for a system of n subpopulations (Day and Possingham 1995).

3) Assign a reward at the final time step to each state based on the objective. This is the value to management for having arrived at a particular system state by the end of the time frame. To reflect the management objective stated above, we assigned a reward of one to the state where all subpopulations are extant and a reward of zero to all other states.

4) Define the management options that we want to consider for the system. Because we look at splitting an annual budget b between several subpopulations, each management option corresponds to a different combination of allocation proportions $\alpha_i \in \{0, 0.01, 0.02, \ldots, 1\}$ with the sum of the α_i being equal to 1.

5) Calculate the transition probabilities from one state to another, given each management strategy. In our case we can find the transition probabilities using Eq. 2 and a given set of allocations α_i. The transition probabilities are calculated as follows. Consider the subpopulations i, which each have a probability of going extinct $P(\text{extinction} | \$\alpha_i b)$, as in Eq. 2. If a state contains N subpopulations extant at time t then the probability of subpopulations $i = 1, 2, \ldots, X$ going extinct (and subpopulations $i = X + 1, \ldots, N$ remaining extant) within one time step is

$$\prod_1^X P_i(\text{extinction} | \$\alpha_i b) \times \prod_{X+1}^N [1 - P_i(\text{extinction} | \$\alpha_i b)].$$

$$(3)$$

ALIÉNOR L. M. CHAUVENET ET AL.

TABLE 1. Case study parameters for three core subpopulations (CS1, CS3, and CS4).

Parameter	Term	Value
Unmanaged probability of extinction	P_0	
CS1		0.205
CS3		0.088
CS4		0.088
Management efficiency	ϕ	
CS1		0.060
CS3		0.016
CS4		0.046
Total budget (US$)	b	52 704
Fixed cost of managing each subpopulation (US$)	c_f	1728
Cost of a management action (US$)	c_m	220

This formulation can be applied to any combination of any number of subpopulations N.

One-step optimization

We derive a one-step optimization for a system of two subpopulations, A and B. The overall budget b is to be split between those subpopulations. Each subpopulation i receives a proportion α_i of the budget, with

$$\alpha_A + \alpha_B = 1.$$

Then,

$$P(\text{extinction}|\$b)$$

$$= \frac{P_{0A}}{\left[\phi_A\left(\dfrac{\alpha_A b - c_f}{c_m}\right) + 1\right]} + \frac{P_{0B}}{\left[\phi_B\left(\dfrac{\alpha_B b - c_f}{c_m}\right) + 1\right]}$$

$$- \frac{P_{0A}}{\left[\phi_A\left(\dfrac{\alpha_A b - c_f}{c_m}\right) + 1\right]} \times \frac{P_{0B}}{\left[\phi_B\left(\dfrac{\alpha_B b - c_f}{c_m}\right) + 1\right]}. \tag{4}$$

By minimizing Eq. 4 with respect to α_A and α_B, we find a one-step optimization that can serve as a rule of thumb in the case of a two-subpopulation system.

Simulation

We use forward simulation to compare the optimal solution from the state-dependent optimization (the SDP) to the following simple heuristic management options:

1) Split the budget equally among all extant subpopulations.

2) Split the budget among subpopulations in proportion to their probabilities of extinction (P_{0i}).

3) Give all the money to subpopulation A.

4) Give all the money to subpopulation B.

5) Give all the money to subpopulation C (in the three-subpopulation case only).

6) Split the money equally between the two most threatened subpopulations (higher P_{0i}; three-subpopulation case only).

7) Split the money equally between the two least threatened subpopulations (lower P_{0i}; three-subpopulation case only).

8) Split the money equally between the two subpopulations that are easier to manage (larger management efficiency, ϕ_i; three-subpopulation case only).

For each subpopulation i managed with each option, the simulation compares the probability of its extinction given the money spent on its conservation, $P_i(\text{extinction}|\$\alpha_i b)$, with a uniform random number sampled from [0, 1]. At each time step, the subpopulation survives if $P_i(\text{extinction}|\$\alpha_i b)$ is smaller than the random number. The process is repeated for 50 years over 5000 iterations. The mean time to extinction of at least one subpopulation is used to compare the performance of management options.

We investigate a number of scenarios. For two and three subpopulations we examine factorial combinations of ease of management vs. threat status, and seven different budget levels (US$10 000, $30 000, $60 000, $100 000, $300 000 and $500 000). For example, for a three-subpopulation system ($P_{0A} > P_{0B} > P_{0C}$ always), we looked at the mean time to extinction of at least one subpopulation under each management strategy when $\phi_A > \phi_B > \phi_C$ for every budget size.

Sensitivity to change in parameters

For the two-subpopulation system and the three budget sizes (small, medium, and large), we assess the state-dependent optimization performance for its sensitivity to P_{0A}, P_{0B}, ϕ_A, and ϕ_B (10% change). This allows us to determine the sensitivity to changes in probabilities of extinction and management efficiencies of our conclusions.

Case study: Sumatran tigers

From Fig. 4 of Linkie et al. (2006) we are able to determine the relationship between resource investment and the probability of extinction of the subpopulations. We then used Fig. 1 of Linkie et al. (2006) to determine the probability of extinction of each subpopulation i if no action is taken, P_{0i}, and used Eq. 1 (after McDonald-Madden et al. 2008a) to fit overlaying curves and establish the subpopulations' management efficiencies ϕ_i. Core subpopulation 2 is not in immediate danger of extinction and therefore we assume it does not require any action to stay extant. We focus therefore on the remaining three subpopulations: core subpopulations 1, 3, and 4 (Linkie et al. 2006). We also estimate the costs of implementing management in a subpopulation c_f, the cost of a management action (anti-poaching patrols) c_m, and the total yearly budget available for this management option, b (M. Linkie, *unpublished data*). Table 1 shows the values of each parameter for the case study.

In order to find the best management option to minimize the extinction probability, we look at the budget allocations recommended by the exact optimization (SDP) and the other heuristics. We then assess

FIG. 2. Percentage of the budget allocated to each subpopulation over a 50-year period for budgets ranging from US$10 000 to US$500 000. Subpopulation A is the most endangered and most efficient to manage, while subpopulation C is the least endangered and least efficient to manage (scenario 1).
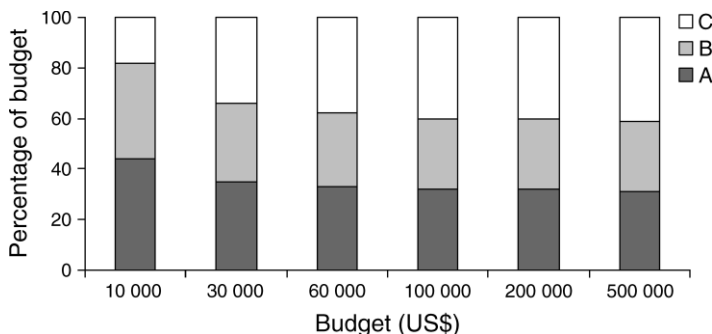
their relative performances by repeating the simulation procedure above with the tiger parameters (Table 1).

RESULTS

State-dependent optimization

The state-dependent optimization tells us how to allocate the budget over time in order to minimize the chance of losing at least one subpopulation (i.e., losing one or more subpopulations). However, for our model, the optimal budget allocation is the same regardless of the time left until the end of the management. The subpopulations receive the same amount of money when 50 years are left as when one year is left. This is due to the persistent nature of threats, such as poaching, which require the same preventive action every year in order to meet our objective of keeping all the subpopulations extant.

We describe the state-dependent optimization results, focusing on the state of most interest, i.e., when all subpopulations are still extant. We look at two scenarios for each system: when the most endangered subpopulations are more efficient (scenario 1, $\phi_A > \phi_B > \phi_C$) and less efficient (scenario 2, $\phi_C > \phi_B > \phi_A$) to manage.

Two subpopulations

When the more threatened subpopulation is the more efficient to manage, the subpopulation less efficient to manage receives the bigger percentage of the budget for almost all budget sizes. If the budget is very small (e.g., US$10 000), however, the subpopulation that is more efficient to manage gets more money. For scenario 2, regardless of the budget size, the subpopulation that is the less efficient to manage (but more endangered) receives the greater percentage of the budget.

When the less efficient subpopulation to manage is the more endangered, the difference between proportions received by the two subpopulations is greater than when it is the less endangered.

Three subpopulations

For scenario 1, if the budget is very small, the subpopulation that is most efficient to manage (and most threatened) receives the most money followed by the second-most efficient to manage (Fig. 2). As the

budget increases a little, the subpopulations receive an almost equal amount of money. Finally, for a medium-to-large size budget, the subpopulation that is the least efficient to manage (and least endangered) receives the biggest percentage, followed by the subpopulation that is the most efficient to manage (and most endangered). The remaining subpopulation, with intermediate levels of threat and ease of management, receives the lowest amount of money.

For scenario 2 (Fig. 3), regardless of the budget size, the subpopulation that is the least efficient to manage (and most endangered) receives the most money followed by the subpopulation that is the second-least efficient to manage. The subpopulation that is the most efficient to manage, and least threatened, receives the least money.

One-step optimization

As indicated by the state-dependent optimization, the optimal solution is not dependent upon the length of the management time frame. Hence we can find the exact optimization with a one-step optimization. For a two-subpopulation system, the proportions that minimize the chance of losing at least one subpopulation in one time step are

$$\alpha_A^* = \big\{\Phi[c_f(x + y) - bx + c_m(-P_{0A} - P_{0B} + \beta)]$$

$$+ \sqrt{\beta\Phi(\chi + c_m x)(\chi + c_m y)}\big\}/[\Phi(x - y)b] \quad (5)$$

$$\alpha_B^* = 1 - \alpha_A^*$$

with $\Phi = \phi_A\phi_B$, $\beta = P_{0A}P_{0B}$, $x = P_{0A}\phi_B$, $y = P_{0B}\phi_A$, and $\chi = \Phi(2c_f - b) - c_m(\phi_A + \phi_B)$.

Simulation

In this section we present the results of the simulation of 50 years of management of two- and three-subpopulation systems with three different annual budgets: small (US$30 000), medium (US$100 000), and large (US$300 000). Without loss of generality, we assume that $P_{0A} > P_{0B} (> P_{0C})$ in all cases. We assess the performances of the management options using the mean time to extinction of at least one subpopulation.
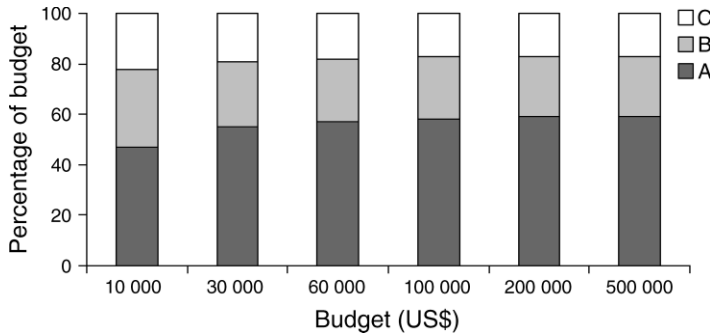
Fig. 3. Percentage of budget allocated to each subpopulation over a 50-year period. Subpopulation A is the most endangered and least efficient to manage, and subpopulation C is the least endangered but most efficient to manage (scenario 2).

The strategy that always gives the longest mean time to extinction of at least one subpopulation is that of the dynamic optimization. In Table 2 we present the options that are second-best for both scenarios 1 and 2 and further possible combinations of rankings of threat and efficiency not investigated with the exact optimization. For a two-subpopulation system, there are only two scenarios possible; when the more threatened subpopulation is more efficient to manage (scenario 1), the option of splitting the money equally between the two subpopulations performs second only to the optimal solution. When the most threatened subpopulation is less efficient to manage (scenario 2), the second-ranked guideline is to split the money in proportion to the unmanaged probabilities of extinction of each subpopulation (hereafter, "proportionally"). For a three-subpopulation system, there are six possible combinations of management efficiencies. We can group them into two categories: the first is when the least threatened subpopulation (C) is more efficient to manage than the subpopulation that is neither the most nor the least threatened (B). In these cases, regardless of the management efficiency of A (the most threatened subpopulation), the strategy that comes second to the optimal solution is to split the money proportionally between the subpopulations. The second is when B is more efficient to manage than C, regardless of the position of A. For those combinations, the second-best

strategy is to split the money equally between the subpopulations. For every scenario (combinations of management efficiencies), the ranking of the management options is independent of the budget size. In any case, the worst management option would be to assign the entire budget to a single subpopulation, yielding mean time to extinctions up to 40 times worse than the optimal solution.

Sensitivity to changes in parameters

For a two-subpopulation system, the optimization consistently yields the best mean time to extinction. In every case, the worst option is to give all the money to one subpopulation. If $\phi_A > \phi_B$, the second-best option is always to split the money equally between all the subpopulations, and if $\phi_B > \phi_A$, the second-best option is always to split the budget proportionally to the subpopulations' unmanaged probabilities of extinction (see Table 3).

Case study: Sumatran tigers

We find the optimal budget allocations for Sumatran tiger management in order to minimize the probability of losing one or more of the endangered subpopulations (present in core areas 1, 3, and 4; Linkie et al. 2006). Core subpopulation 1 (CS1) has the highest unmanaged probability of extinction, whereas CS3 and CS4 have smaller, equal probabilities of extinction. Core subpop-

TABLE 2. Second-best management options, depending on the budget size (the best option is always the optimization).

Management efficiency	Two subpopulations (A and B), any size budget	Three subpopulations (A, B, and C), any size budget
$\phi_A > \phi_B > \phi_C$ (scenario 1)	equally	equally
$\phi_C > \phi_B > \phi_A$ (scenario 2)	proportionally	proportionally
$\phi_B > \phi_A > \phi_C$		equally
$\phi_B > \phi_C > \phi_A$		equally
$\phi_A > \phi_C > \phi_B$		proportionally
$\phi_C > \phi_A > \phi_B$		proportionally

Notes: The measure of performance is the mean time to extinction of at least one subpopulation. The management options are: "equally," equal allocation; "proportionally," allocation proportional to the unmanaged probability of extinction of each subpopulation (P_0). The budget sizes are small (US$30 000), medium (US$100 000), and large (US$300 000). For all case scenarios $P_{0A} > P_{0B} > P_{0C}$.

TABLE 3. Sensitivity analysis of a 10% change in the parameters P_{0A}, P_{0B}, ϕ_A, and ϕ_B for a two-subpopulation (A and B) system.

Budget size	Small	Medium	Large
Case scenario $\phi_A > \phi_B$			
Minimum and maximum difference between the optimization and the second-best option ("equally")	2.3 to 5.5	1.7 to 3.2	1.2 to 1.7
Minimum and maximum difference between the optimization and the worst option (all money to one subpopulation)	41.3 to 57.8	40.4 to 60.5	38.7 to 54.9
Case scenario $\phi_B > \phi_A$			
Minimum and maximum difference between the optimization and the second-best option ("proportionally")	2.6 to 6.6	1.8 to 4.2	1.2 to 1.9
Minimum and maximum difference between the optimization and the worst option (all money to one subpopulation)	39.2 to 58	42 to 58.8	39.4 to 60.8

Notes: The sensitivity was tested for three budget sizes: small (US$30 000), medium (US$100 000), and large (US$300 000). The table shows the relative performance (measured by mean time to extinction) of the optimization compared to the second-best option and the worst option. For example, with a small budget and for the first case scenario, the optimization yields a mean time to extinction that is between 2.3 and 5.5 times better than the second-best option. See Table 1 for an explanation of variable abbreviations.

ulation 1 is the easiest to manage, followed by CS4, then CS3. That is $P_{0,CS1} > P_{0,CS4} \approx P_{0,CS3}$ and $\phi_{CS1} > \phi_{CS4} > \phi_{CS3}$. The total yearly budget for tiger management is just over $50 000 (Table 1).

There is only one optimal solution for the resource allocation as the subpopulations receive the same amount of money regardless of the management time frame. Core subpopulation 1, which is the most endangered subpopulation but also the most efficient to manage, should receive the biggest proportion of the budget (40%), followed by CS3 (33%; the second most efficient to manage), and CS4 should receive 27%.

We next examine the mean times to extinction of at least one subpopulation. As expected, the optimization gives the best result with a mean time to (at least one) local extinction of 10.2 years. The second-best strategy is to split the overall budget equally between all three subpopulations, achieving a mean time to extinction of 9.3 years. The worst strategy would be to invest all the money into managing one subpopulation, regardless of the subpopulation. It yields a mean time to extinction as low as 2.4 years.

We tested the sensitivity of these results to ±10% changes in parameter values and found that the optimization always performs at least two times and up to eight times better than the worst option. We also found that the optimization can achieve a mean time to extinction from 1.04 times to 1.5 times better than the second-best option (split the money equally between all subpopulations).

DISCUSSION

The aim of this study is to produce management guidelines for species existing as suites of isolated subpopulations. We focus on finding the optimal way to allocate a fixed budget between isolated subpopulations of a threatened species when they occur in patches of dissimilar quality. The optimal solution accounts for the fact that different patches have different qualities

and costs of management. Here quality is represented by the risk of extinction of each subpopulation and how that risk declines with investment (Fig. 1).

The stated objective is to minimize the probability of losing at least one subpopulation, which aims to secure the survival of all of them. We find that, by using this objective, what would normally be a time-dependent optimization problem becomes essentially a time-independent optimization problem, and we must therefore apply the same management option every year. This can be explained by the persistent nature of threats to the subpopulations (e.g., poaching), which are managed on a year-to-year basis. As soon as one population goes extinct, we have irreversibly failed to meet our management objective and hence it is best, at every time step, to minimize this possibility. In other circumstances, for example if we could permanently improve habitat quality by expanding a reserve, the optimal strategy may change between years.

Under a limited budget, a triage approach would be to favor one subpopulation over another, sacrificing the one(s) whose management would be too costly or too difficult. The results of our optimization, driven by our objective to save all subpopulations, do not allow this scenario. Our optimization gives money to all subpopulations considered at all times of management. Moreover, instead of investing in the subpopulations that are more efficient to manage and thus less costly to save, in most cases it gives the biggest percentage of the budget to the subpopulations that are less efficient to manage. This result is due to the objective of keeping all subpopulations extant. The optimization recommendations compensate for the lack of management efficiency and the high probability of extinction by giving more money to those subpopulations that have a lower chance overall of persistence. The only exception is for an extremely small budget when a subpopulation that is both more endangered and more efficient to manage receives the biggest percentage of money. In that case the budget is not big enough to meet the objective (the

mean time to extinction of all subpopulations with the optimization is only approximately two years) and giving more money to the least efficient keeps all subpopulations extant for a shorter time than giving to the most efficient to manage.

In the case of a two-subpopulation system, the exact allocation solution given by the one-step optimization is a usable equation that is less time-consuming than, but equivalent to, the full optimization. Nonetheless it is not very straightforward and therefore we tried to find simpler allocation options. When compared with the optimization, the heuristics performed almost as well (Table 2), depending on the case scenario. Two heuristics, split the money equally and split the money proportionally between the subpopulations, consistently yield the second-best mean time to extinction after the optimal solution. By using those heuristics, we stay true to the solution suggested by the state-dependent optimization, which is to prioritize the subpopulations less efficient to manage; e.g., for the three-subpopulation system, the best heuristic is to split the money proportionally, hence giving more money to A and B, when those two are the less efficient to manage.

To protect the Sumatran tigers of the Kerinci Seblat region there is a need for anti-poaching patrols (Linkie et al. 2006), an action that is costly given the limited funding available. Finding a solution that gives optimal and efficient ways to allocate resources between these subpopulations is thus important. The state-dependent optimization, which is the best management option, recommends that we give more money to CS1, which is the most endangered and most efficient to manage, followed by CS3, which is the least efficient to manage, and CS4. Because CS3 is the least efficient to manage and one of the two most endangered we would have expected it to receive the biggest amount of money. The reason for this optimal allocation is that the available budget ($\sim$US\$50 000) is too small to meet the objective of keeping all tiger subpopulations extant. We tested tiger management strategies for bigger budgets (results not presented), and the results indeed reflect case scenario 1: for a medium-size budget, all subpopulations receive almost equal amounts ($\alpha_{CS1} \approx \alpha_{CS3} \approx \alpha_{CS4}$), and for a large budget $\alpha_{CS1} > \alpha_{CS4} > \alpha_{CS3}$, which is what we would expect as $\phi_{CS1} > \phi_{CS4} > \phi_{CS3}$. In order for all the subpopulations to remain extant at the end of the 50-year management period, they would require an annual investment of \$10 000 000. Thus under the current state of funding it is not efficient to manage all subpopulations; indeed, a significant amount of money would be needed to save all three subpopulations.

For the case study, we assume that CS2 does not require any financial investment to stay extant because it is not currently endangered (Linkie et al. 2006). More realistically, as money is invested into the other three subpopulations and anti-poaching patrols are implemented, it would deter the poachers from CS1, CS3, and

CS4 (Caro et al. 1998) and thus possibly increase poaching activity in the remaining, currently secure, subpopulation (CS2). In addition, after a few years of management one or more of the other subpopulations' abundance might increase enough so they are no longer at risk. As we assume that the subpopulations are independent, the model does not take into account these possible changes in threat level, and thus a reassessment of the subpopulations' states after a number of years of management may be needed in order to refocus or confirm the optimal budget allocation (see Chadès et al. 2008, McDonald-Madden et al. 2008*a*). The optimization approach we present can readily accommodate such factors, for example by making P_{0i} dynamically change with the status of other subpopulations $j \neq i$.

Two of the main assumptions of this study are that the management costs c_f and c_m are the same for every subpopulation and that the subpopulations are isolated from one another (the probability of extinction of one does not affect the other and there is no significant dispersal between them). Because c_m is the cost of a management item, it is likely to be the same for all subpopulations if they all require the same management such as anti-poaching patrols. As a result the assumption that all subpopulations have the same c_m is reasonable for this case study. On the other hand, c_f is the cost of implementing management for the subpopulations, and it is partly influenced by the cost of travel to and between the subpopulations, which may differ greatly depending on the spatial arrangement of the subpopulations. We assumed that the subpopulations are isolated from one another, which happens in the wild (Harrison and Bruna 1999), and it is a reasonable assumption that dispersal is limited by habitat fragmentation and loss. Nonetheless, for species for which dispersal significantly modifies the composition of the subpopulations, this model might not be best suited and further studies may need to be undertaken in order to investigate the manner in which dispersal rates change the probability of extinction of each subpopulation and thus shift the optimal management effort.

In conclusion, this model aims at producing a guideline for managers when it comes to allocating a fixed budget between isolated subpopulations and making the most of the resources available. It is limited by the fact that the input parameters do not change as the management deadline approaches. That is, as money is invested into the subpopulations, some initial parameters may be affected and change. Another consequence is that it cannot be used for species for which there is significant dispersal between the subpopulations as it may change the management efficiency of the subpopulations or their unmanaged probability of extinction. To counterbalance this limitation, we recommend monitoring the states of the subpopulations after a few years of management to reassess the budget allocation.

Literature Cited

Baguette, M., and N. Schtickzelle. 2003. Local population dynamics are important to the conservation of metapopulations in highly fragmented landscape. Journal of Applied Ecology 40:404–412.

Baxter, P. W. J., M. A. McCarthy, H. P. Possingham, P. W. Menkhorst, and N. McLean. 2006. Accounting for management costs in sensitivity analyses for matrix population models. Conservation Biology 20:893–905.

Caro, T. M., N. Pelkey, M. Borner, K. L. Campbell, B. L. Woodworth, B. P. Farm, J. Ole Kuwai, S. A. Huish, and E. L. M. Severre. 1998. Consequences of different forms of conservation for large mammals in Tanzania: preliminary analyses. African Journal of Ecology 36:303–320.

Cat Specialist Group. 1996. *Panthera tigris* ssp. *sumatrae. In* 2007 IUCN Red List of Threatened Species. ⟨www.iucnredlist.org⟩

Chadès, I., E. McDonald-Madden, M. A. McCarthy, B. Wintle, M. Linkie, and H. P. Possingham. 2008. When to stop managing or surveying cryptic threatened species. Proceedings of the National Academy of Sciences (USA) 105:13936–13940.

Day, J. R., and H. P. Possingham. 1995. A stochastic metapopulation model with variability in patch size and position. Theoretical Population Biology 48:333–360.

Guikema, S., and M. Milke. 1999. Quantitative decision tools for conservation programme planning: practice, theory and potential. Environmental Conservation 26:179–189.

Hanski, K., and M. E. Gilpin. 1997. Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego, California, USA.

Harrison, S., and E. Bruna. 1999. Habitat fragmentation and large-scale conservation: What do we know for sure? Ecography 22:225–232.

Intriligator, M. D. 1971. Mathematical optimization and economic theory. Prentice-Hall, Eaglewood Cliffs, New Jersey, USA.

Johst, K., M. Drechsler, J. Thomas, and J. Settele. 2006. Influence of mowing on the persistence of two endangered large blue butterfly species. Journal of Applied Ecology 43:333–342.

Keller, I., L. Excoffier, and C. R. Largiadèr. 2005. Evaluation of effective population size and detection of a recent population decline coinciding with habitat fragmentation in a ground beetle. Journal of Evolutionary Biology 18:90–100.

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.

Linkie, M., D. J. Martyr, J. Holden, A. Yanuar, A. T. Hartana, J. Sugardjito, and N. Leader-Williams. 2003. Habitat destruction and poaching threaten the Sumatran tiger in the Kerinci Seblat National Park, Sumatra. Oryx 37:41–48.

Lubow, B. C. 1996. Optimal translocation strategies for enhancing stochastic metapopulation viability. Ecological Applications 6:1268–1280.

Mangel, M., and C. W. Clark. 1988. Dynamic modeling in behavioral ecology. Princeton University Press, Princeton, New Jersey, USA.

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.

McDonald-Madden, E., P. W. J. Baxter, and H. P. Possingham. 2008a. Subpopulation triage: how to allocate conservation effort among populations. Conservation Biology 22:656–665.

McDonald-Madden, E., P. W. J. Baxter, and H. P. Possingham. 2008b. Making robust decisions for conservation with restricted money and knowledge. Journal of Applied Ecology 45:1630–1638.

Morell, V. 2007. Can the wild tiger survive? Science 317:1313–1314.

Nicholson, E., and H. P. Possingham. 2006. Objectives for multiple-species conservation planning. Conservation Biology 20:871–881.

Nowell, K., and P. Jackson. 1996. Wild cats: status survey and conservation action plan. International Union for the Conservation of Nature and Natural Resources (IUCN), Gland, Switzerland.

Nyhus, P. J., and R. Tilson. 2004. Characterizing human–tiger conflict in Sumatra, Indonesia: implications for conservation. Oryx 38:68–74.

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. Soulé and G. H. Orians, editors. Conservation biology: research priorities for the next decade. Island Press, Washington, D.C., USA.

Richards, S. A., H. P. Possingham, and J. Tizard. 1999. Optimal fire management for maintaining community diversity. Ecological Applications 9:880–892.

Rout, T. M., C. E. Hauser, and H. P. Possingham. 2005. Minimise long-term loss or maximise short-term gain? Optimal translocation strategies for threatened species. Ecological Modelling 201:67–74.

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.

Tenhumberg, B., A. J. Tyre, K. Shea, and H. P. Possingham. 2004. Linking wild and captive populations to maximize species persistence: optimal translocation strategies. Conservation Biology 18:1–11.

Walker, B. H. 1991. Biodiversity and ecological redundancy. Conservation Biology 6:18–23.

Wiegand, T., E. Revilla, and K. A. Moloney. 2005. Effects of habitat loss and fragmentation on population dynamics. Conservation Biology 19:108–121.

Wilson, K. A., M. F. McBride, M. Bode, and H. P. Possingham. 2006. Prioritizing global conservation efforts. Nature 440:337–340.