LETTER

Resource allocation for efficient environmental management

Abstract

Michael A. McCarthy,¹* Colin J. Thompson,² Cindy Hauser,¹ Mark A. Burgman,¹ Hugh P. Possingham,³ Melinda L. Moir,¹ Thanawat Tiensin^{4,5} and Marius Gilbert^{6,7} Environmental managers must decide how to invest available resources. Researchers have previously determined how to allocate conservation resources among regions, design nature reserves, allocate funding to species conservation programs, design biodiversity surveys and monitoring programs, manage species and invest in greenhouse gas mitigation schemes. However, these issues have not been addressed with a unified theory. Furthermore, uncertainty is prevalent in environmental management, and needs to be considered to manage risks. We present a theory for optimal environmental management, synthesizing previous approaches to the topic and incorporating uncertainty. We show that the theory solves a diverse range of important problems of resource allocation, including distributing conservation resources among the world's biodiversity hotspots; surveillance to detect the highly pathogenic avian influenza H5N1 virus in Thailand; and choosing survey methods for the insect order Hemiptera. Environmental management decisions are similar to decisions about financial investments, with trade-offs between risk and reward.

Keywords

Avian influenza, biodiversity hotspots, biodiversity loss, infectious diseases, insect surveys.

Ecology Letters (2010) 13: 1280-1289

INTRODUCTION

Global environmental problems include loss of biodiversity, emerging infectious diseases and climate change. There are insufficient resources to eliminate completely this broad range of environmental problems, and hence it is necessary to prioritize (Possingham *et al.* 2001; Brooks *et al.* 2006). Recent developments have moved from ground-breaking work that ranks threats (Mace & Lande 1991; Myers *et al.* 2000) to determining efficient strategies for reducing threats. Decision theory provides the tools to identify these efficient strategies. Fundamental aspects of decision theory include an objective function that defines the goal of management, and a method to determine the combination of management strategies that optimizes the objective function (Possingham *et al.* 2001).

doi: 10.1111/i.1461-0248.2010.01522.x

Examples of decision theory in conservation include allocating conservation resources among regions (McCarthy *et al.* 2006; Wilson *et al.* 2006; Murdoch *et al.* 2007; Bode *et al.* 2008), designing nature reserves (Possingham *et al.* 2000; Moore *et al.* 2004; McCarthy *et al.* 2005), allocating funding to species conservation programs (McCarthy *et al.* 2008; Joseph *et al.* 2009), designing biodiversity surveys and monitoring programs (Bar-Shalom & Cohen 1976; Moir *et al.* 2005;

¹ School of Botany. The University of Melbourne. Parkville	⁵ Department of Livestock Development, Phyathai Road
Vic. 3010, Australia	Bangkok 10400, Thailand
² Department of Mathematics and Statistics, The University of	⁶ Université Libre de Bruxelles, Av FD Roosevelt 50,
Melbourne, Parkville, Vic. 3010, Australia	B-1050 Brussels, Belgium
³ The Ecology Centre, Schools of Integrative Biology and	⁷ Fonds National de la Recherche Scientifique, rue d'Egmont 5,
Physical Sciences, The University of Queensland, Brisbane,	B-1000 Brussels, Belgium
Qld 4072, Australia	*Correspondence: E-mail: mamcca@unimelb.edu.au
⁴ Faculty of Veterinary Medicine, Utrecht University, Yalelaan 7,	
3584 CL Utrecht, The Netherlands	

Hauser & McCarthy 2009), managing threatened, migratory or invasive species (Baxter *et al.* 2006; Martin *et al.* 2007) and investing in greenhouse gas mitigation schemes (Springer 2003). These problems have a common structure that seeks to optimize an outcome subject to constraints. Furthermore, uncertainty is prevalent in environmental management, and needs to be considered to manage risks (e.g., Polasky *et al.* 2000; Burgman 2005; Drechsler 2005; Halpern *et al.* 2006). Ignoring uncertainty is risky, can lead to over-confidence in the chosen management strategy, and exposes managers to unexpected failure (Burgman 2005).

This article has two major aims: to show (1) how a simplified version of conservation problems can be usefully applied to a broad range of examples, and (2) that the particular structure of this simplification allows these approaches to incorporate uncertainty about the state of the world and the response to management. We illustrate the breadth of the approach using three very different case studies: (1) allocation of resources among biodiversity hotspots, (2) surveillance of avian influenza in Thailand and (3) choice of methods for surveying insect biodiversity. This provides a theory to help guide environmental management in the face of uncertainty.

METHODS

Models

Environmental management can be characterized by considering a manager who must decide how to allocate finite resources among a set of options to best achieve an objective. For example, a manager of an endangered species might need to decide how to allocate effort among options such as habitat protection, habitat restoration, captive breeding and control of predators and disease. Mathematically, this can be expressed as a manager seeking to optimize the function $L = f(x_1, x_2, ..., x_n)$ by choosing the values of x_i , the amount invested in each of the *n* options, subject to a budget constraint $(\sum_{i=1}^{n} x_i = B)$. The function f() defines how the expenditures on the options (the x_i s) combine to influence the management outcome L. For example, in reserve design, a manager might wish to maximize the amount of biodiversity protected by allocating a finite budget to reservation of land, subject to the costs of management and other constraints (Possingham et al. 2000).

A range of nonlinear optimization methods are available to solve problems of this form (e.g., Nocedal & Wright 1999; Boyd & Vandenberghe 2004). However, we propose that this general form for L can be approximated usefully by the simplified function

$$L = \sum_{i=1}^{n} p_i(x_i) \tag{1}$$

in which returns on investment in each of the *n* management options are assumed to be additive. The outcome of option *i* $(p_i(x_i))$ is the reward function when aiming for large values of *L*. Naming $p_i(x_i)$ the penalty function might be more apt when seeking small values of *L*, but we use the term reward function in all cases for simplicity. As examples, the reward functions might be the probability of species persistence (*L* is the expected number of species persisting; McCarthy *et al.* 2008) or the probability of sites containing an undetected invasive species (*L* is the expected number of such sites; Hauser & McCarthy 2009). Here, we show that the approximation (eqn 1) helps to highlight a common structure of environmental management problems, and provides a natural mechanism for incorporating uncertainty into decision-making.

The management outcome L (eqn 1) can be optimized subject to the budget constraint $\sum_{i=1}^{n} x_i = B$ using Lagrange optimization (Sundaram 1996; see Supporting Information). Regardless of the form of the reward functions, the optimal solution is to invest in the options for which the marginal benefits are large, and invest to a level in each such that the marginal benefits are equal. For example, the simplest function for $p_i(x_i)$ has linear changes in the outcome for each management option $p_i(x_i) =$ $p_i + b_i x_i$. This might be suitable when changes in management outcomes are sufficiently small that diminishing management returns do not occur. In this case, the strategy to optimize the expected outcome is to invest in the single option where the marginal benefit is greatest (Cannon 2009). If the amount of resources that can be invested in each option is limited $(x_i^* \leq x_i^{\max})$, then it is equivalent to the Project Prioritization Protocol of Joseph et al. (2009).

Hauser & McCarthy (2009) provide analytical solutions for the optimal investment in each option when the reward functions are exponential $p_i(x_i) = p_i e^{-b_i x_i}$ (see also the Supporting Information). Another alternative is to assume a hyperbolic function $p_i(x_i) = p_i(1 + \varphi_i x_i)^{-\theta_i}$, which has proportionally smaller improvements in $p_i(x_i)$ as more money is invested compared with the exponential form. Being a power function, the hyperbolic model also applies to cases where benefits of conservation reserves accrue according to a species-area relationship (e.g., as used by Murdoch *et al.* 2007). When the different options have a common value for $\theta_i = \theta$, the expected outcome is optimized when the level of investment in option *i* is:

$$x_i^* = (B/n + 1/b_{\varphi})v_i/\overline{v} - 1/\varphi_i, \text{ provided } x_i^* > 0,$$

and $x_i^* = 0$ otherwise, (2)

where $v_i = (\varphi_i p_i)^{1/(\theta+1)} / \beta_i$, \overline{v} is the arithmetic mean of v_i , and h_{φ} is the harmonic mean of φ_i . Results must be obtained numerically when θ_i are not equal.

Incorporating uncertainty

In the above formulation of the problem, we optimized $L = \sum_{i=1}^{n} P_i(x_i)$. This ignores uncertainty in the possible outcomes that may arise, for example, due to uncertainty in the parameter values that define the functions $p_i(x_i)$. Financial investments have recognized the importance of uncertainty for several decades (Markowitz 1952, 1991), and there are parallels with investment in environmental strategies (Springer 2003; Edwards *et al.* 2004). Optimizing the expected return without regard to uncertainty in the reward functions $p_i(x_i)$ is a risky strategy in environmental management, just as it is in finance (Markowitz 1952, 1991). Instead, we might wish to maximize the probability that L achieves a minimally acceptable outcome T (satisficing; Simon 1982) or use some other method for dealing with uncertainty such as worst-case analysis or minimizing regrets (French 1986).

Uncertainty in the outcome of each management option can be considered by treating each $p_i(x_i)$ as a random variable. The overall management outcome L is then simply the sum of *n* random variables, the mean and variance of which is well known (Ross 2009; see Supporting Information). The probability distribution for L will depend on the probability distribution of $p_i(x_i)$. As the number of options n increases, the distribution of Lwill approach a Gaussian (normal) due to the central limit theorem, which simplifies how to determine the strategy that maximizes the probability of achieving a minimally acceptable outcome T. When the number of strategies is not sufficiently large to justify a normal assumption, the distribution of L can be calculated explicitly (i.e., by the convolution of multiple random variates) or by using some other assumption (e.g., that the sum of lognormal distributions is approximately lognormal; Fenton 1960). Once the probability distribution of L is determined, one can optimize the probability that L achieves at least the minimally acceptable outcome T.

There is a simple solution when outcomes among all management options are linear and uncorrelated, and a normal distribution for L for can be assumed (see Supporting Information) as in the hotspots example below. In this case, the probability of exceeding a minimally acceptable outcome T is maximized by allocating to option iin proportion to $y_i^* = (\mu_i - T/B)/\sigma_i^2$, (provided $y_i^* > 0$) where *B* is the available budget, μ_i is the expected value of b_i (the efficiency of investment in option *i*), and $\sigma_i = \sqrt{V(b_i)}$, the standard deviation of b_i . Thus, we should invest in all options for which the expected efficiency is at least minimally acceptable ($\mu_i > T/B$). In this case, options receive more funding as the expected outcome μ_i increases, and as the outcome becomes more certain (σ_i decreases). In the linear case, greater uncertainty relative to the expected benefits of an option leads to greater spreading of resources

among the other options. Correlations between management options modify this optimal allocation (see Supporting Information).

CASE STUDIES

We applied our theory to three case studies that can be characterized by the three different reward functions. These case studies required allocation of: (1) conservation resources among the world's biodiversity hotspots (linear model), (2) surveillance effort to detect a strain of the highly pathogenic avian influenza (HPAI) H5N1 virus in Thailand (exponential model) and (3) effort among methods in a biodiversity survey (hyperbolic model).

Biodiversity hotspots

Biodiversity hotspots support many endemic species but face high levels of threat (Myers et al. 2000). We examined how best to allocate an annual budget of US\$310 million over 20 years to conserve endemic plant species in 34 of the world's hotspots. Allocating finite conservation resources among biodiversity hotspots can minimize the expected number of endemic plant species becoming extinct (Bode et al. 2008). We replicate the study of Bode et al. (2008) and then extend it to account for uncertainty. In addition to threat (a function of the level of protection and the rate of vegetation clearance) and endemism, the cost of acquiring land is a key variable driving the optimal allocation of resources among areas (Ando et al. 1998; Wilson et al. 2006; Bode et al. 2008). The model accounts for the number of endemic species S_i in region *i*, which accumulates with area A_i according to $S_i = k_i A_i^{z}$, with z = 0.18 (Bode *et al.* 2008). It also accounts for the area of land a_i that is already reserved in region *i*, the area of unreserved land u_i , the per-unit-area cost of land c_i , the expenditure x_i in each region, and the proportion δ_i of the unreserved land that is cleared each year. In this case, the predicted number of species saved from extinction by land acquisition is approximately $x_i \chi \kappa_i \delta_i (a_i + u_i(1 - \delta_i))^{\chi - 1} / c_i$ (see Supporting Information). This becomes a simple optimization when the objective is to minimize the loss of species because the number of species in a region saved from extinction is approximately linear with respect to expenditure (x_i) in that region. To minimize the expected loss of species, land is bought in the region with the greatest value of $\chi \kappa_i \delta_i (a_i + u_i (1 - \delta_i))^{\chi - 1} / c_i$ subject to the annual budget constraint and the amount of uncleared land that is available.

The above optimization requires parameter values for z_i , c_i , a_i , u_i , δ_i and κ_i . Estimates for z_i , c_i , a_i , u_i and δ_i , which are the species-area exponent, land costs, and information on land clearing and reservation are likely to be reliable, and

were obtained from Bode et al. (2008). However, the number of species that are likely to be saved for a particular area of reserved land is uncertain for several reasons. For many taxonomic groups, such as invertebrates, the relative number of endemic species in a region (κ_i) will be poorly estimated. For many species, their distribution within areas bought for conservation reserves will be unknown. Additionally, the long term persistence of species (i.e., the effectiveness of the reserve system) is also uncertain. These sources of uncertainty can be modelled by treating the term κ_i as a random variable with mean λ_i so the number of species saved per unit of expenditure has mean $E(b_i) = \lambda_i \chi \delta_i (a_i + u_i (1 - \delta_i))^{\chi - 1} / c_i$. We assumed that the coefficient of variation in the term κ_i is the same in all regions $(V(b_i) = k(\lambda_i \chi \delta_i (a_i + u_i(1 - \delta_i))^{\chi - 1}/c_i)^2$; i.e., the uncertainty is proportionally equal, given by k), that κ_i is normally distributed, and that the estimated number of species in a reserve is an unbiased estimate of the number that will persist. We then determined the strategy that will save at least T endemic plant species per year from extinction.

In the case study, we determined the optimal allocation of the annual US\$310 million budget in each of 20 years (from Bode *et al.* 2008), with the amount of reserved land (a_i) increasing annually with previous investment, and the amount of available land (u_i) decreasing annually as unreserved land is cleared or purchased. Results were expressed in terms of the total investment in each hotspot over the 20 years.

The expected number of endemic plant species saved from extinction is maximized by spending money in only 8 of the 34 hotspots because investments in other regions are expected to be less efficient (Fig. 1). These results are equivalent to those obtained in the original study (Bode *et al.* 2008), with resources allocated to single regions for several years until the available land is bought. For example, the Tropical Andes receives the entire annual budget for 10 consecutive years.

The results are very different from the original study (Bode *et al.* 2008) when uncertainty is considered. Rather than investing the annual budget until all suitable land in a hotspot is bought, a more uniform distribution of resources among regions occurs when the aim is to maximize the probability of saving at least T plant species per year (for $T \leq 3$, Fig. 1). Some regions that did not receive any funding when minimizing the expected number of extinctions received funds under this risk-averse strategy. With a very modest goal of at least some positive outcome, it is optimal to invest in more hotspots, with 13 receiving >1% each of the total funds. This bet hedging helps buffer the investment against an unexpectedly poor outcome in one hotspot by a greater chance of an unexpectedly good outcome in another.



Figure 1 The optimal allocation of resources over a 20-year period to the world's biodiversity hotspots when minimizing the expected number of extinct endemic plants species [Min E(L)], or when maximizing the probability of saving at least T endemic plant species per year. Results are only shown for hotspots receiving > 1% of the total funding. The Coastal Forests of East Africa receive 0.6–0.7% of funds in all cases. Maputaland-Pondoland-Albany, Philippines and Tumbes-Chocó-Magdalena should receive some funding (< 1%) when saving at least one endemic plant species per year (T = 1).

H5N1 surveillance

A strain of HPAI H5N1 virus emerged in Asia in the mid 1990s. Thailand and other countries in southeast Asia experienced numerous epidemic waves of HPAI H5N1 in 2004, 2005 and 2006, causing high social and economic impact. Although relatively rare compared with the epidemic in poultry, human infections by HPAI H5N1 have frequently been fatal. A great concern is that a mutation of this virus to permit efficient human-to-human transmission may lead to a pandemic of unknown magnitude. Preventing virus circulation in poultry addresses simultaneously the pandemic risk and the actual socio-economic impact of bird flu on the poultry industry and smallholders' livelihoods. A program of surveillance and control has substantially reduced the incidence of the virus in Thailand (Tiensin et al. 2007; Food and Agricultural Organization 2007). One aspect of surveillance and control measures is random sampling and testing of domestic poultry for H5N1 (viral sampling).

The risk of outbreaks of HPAI H5N1 is positively correlated in southeast Asia with the intensity of rice production, human population size and the abundance of ducks (Gilbert *et al.* 2008). We use this previously published map of the risk of HPAI H5N1 infection in Thai poultry flocks to represent the probability of an outbreak being present in a sub-district and remaining undetected in the absence of any viral sampling. We then sought a viral sampling protocol that minimizes the number of subdistricts with undetected outbreaks.

Our objective function was the expected number of subdistricts with undetected outbreaks of the virus, $L = \sum p_i \exp(-b_i x_i) = \sum p_i q_i^{x_i}$, which we aimed to minimize, subject to a budget B of 100 000 sampled flocks (Tiensin *et al.* 2005). The parameter q_i is the probability of failing to detect the virus when a single flock is sampled in sub-district *i* where H5N1 is present, p_i is the probability of H5N1 being present in the sub-district (Gilbert et al. 2008), and x_i is the number flocks sampled. This model essentially assumes that H5N1 occurs randomly in flocks within subdistricts where the virus is present. In the absence of knowledge about how prevalence of the virus in asymptomatic populations might vary among sub-districts, it is reasonable to assume that q_i is similar for all, in which case the optimal allocation (eqn 1) to minimize the expected value of L reduces to $x_i^* = B/n + (y_i - \overline{y})/b$, where $y_i = \ln p_i$ and $b = -\ln q$.

The parameter q was estimated to be 0.996 (b = 0.004) using data on the proportion of flocks that were infected in 2004 within each sub-district (888 out of 7410 sub-districts) where H5N1 was present (Tiensin *et al.* 2007; see Supporting Information). Variation in q was well represented by a beta distribution (Fig. 2). This low level of prevalence reflects that only a single flock was infected in most subdistricts where H5N1 was found present. The mean and variance of the probability of the virus being present in a



Figure 2 The probability that H5N1 highly pathogenic avian influenza was absent from a flock when present in a sub-district of Thailand during 2004 based on data in Tiensin *et al.* (2007). The black line is the observed frequency distribution of the proportion for the data (number of flocks free of H5N1 as a proportion of the number of flocks in the sub-district), and the grey line is the fitted beta distribution with parameters ($\alpha = 510$ and $\beta = 2$).

sub-district but remaining undetected when sampling x flocks can be determined (see Supporting Information). The performance of the surveillance system was assessed by predicting the number of sub-districts and districts in which H5N1 was present but the virus would have remained undetected during waves I, II and III in Thailand in 2004 and 2005 (see Supporting Information).

Surveillance should occur in sub-districts where the relative risk of HPAI H5N1 is greater than c. 0.56 to minimize the expected number of undetected outbreaks. In this case, up to 146 flocks are sampled in the highest risk sub-districts (Figs 3 and 4), which is predicted to reduce the expected number of undetected outbreaks by c. 10% below the level that would be expected without surveillance. This threshold occurs because the surveillance budget is not sufficiently large that the probability of occurrence of HPAI H5N1 in the higher risk sub-districts is reduced below this threshold by the viral sampling. If this optimal surveillance effort had applied during 2004 and 2005, the proportion of sub-districts with undetected outbreaks would have been reduced by 9, 18 and 15% in waves I, II and III respectively. These values compare with an expected reduction of 5% if surveillance effort were distributed equally across subdistricts. The proportion of infected districts (larger geographic areas than sub-districts) without detected outbreaks would have been reduced by 33, 49 and 71%. The relatively modest reduction in undetected outbreaks emphasizes the importance of passive surveillance (e.g., public awareness and participation) that is occurring in Thailand.

When considering uncertainty, the solution that maximizes the probability of reducing the number of outbreaks by at least 10% is almost identical to that obtained when minimizing the expected number of undetected outbreaks (result not shown). In contrast, a more even distribution of effort is optimal with a lower aspiration of reducing the number of outbreaks by at least 5% (Fig. 4). The solution based on a linear approximation of the reward functions provides a similar solution in this case.

Survey methods for Hemiptera

Invertebrates constitute a very large proportion of the world's biodiversity and have diverse functions in ecosystems (Gaston 1991; Moir *et al.* 2005). However, most groups of invertebrates are poorly known to science, with only a small fraction of species described. Designing efficient biodiversity surveys is important to be able to detect the range of species present in an area with the available resources. In this case study, we determine the most efficient use of different methods for collecting Hemiptera, one of the most speciose orders of insects (Gaston 1991). Its members are important herbivores and prey, and can be useful surrogates for the diversity of other taxonomic



Figure 3 Optimal number of poultry flocks to sample for highly pathogenic avian influenza (HPAI) H5N1 in each sub-district of Thailand, reflecting the relative risk of outbreaks as a function of the density of humans, ducks and rice paddies (Gilbert *et al.* 2008).

groups (Moir *et al.* 2005). We determined the allocation of resources between five methods for sampling insects that would maximize the number of hemipteran species collected in south-west Australia (Moir *et al.* 2005), a global biodiversity hotspot.

We used an additive model with hyperbolic reward functions to approximate the number of species that remain undetected when the time spent using survey method j at each site is x_{j} . In this case, the number of species that remain undetected, which is given by (see Supporting Information)

$$L = \sum_{i=1}^{s} \prod_{j=1}^{n} e^{-b_{i,j} x_j},$$
(3)

can be approximated by

$$L = \sum_{j=1}^{n} \frac{s_j}{(1 + \varphi_j x_j)^{\theta_j}},$$
(4)

where s_j is the number of species that are only collected using method *j*, and φ_j and θ_j depend on the mean and variance of the detection rates $b_{i,j}$. Equation 4 is the hyperbolic model, providing an analytical solution (eqn 2) that will approximately minimize eqn 3.

The data used here were a subset of those presented in the original paper (Moir *et al.* 2005), with methods applied only at the site level considered, i.e., methods: (1)



Figure 4 Optimal number of flocks to survey in each sub-district vs. the relative risk of H5N1 outbreak given in Gilbert *et al.* (2008). Curve (a) is obtained when the objective is to minimize the expected number of sub-districts with undetected outbreaks ignoring uncertainty in the detection rate (mapped in Fig. 3). This result is almost identical to those when uncertainty in the detection rate is included, and when the objective is to maximize the probability of reducing the number of sub-districts with undetected outbreaks by at least 10% (not shown). This is compared with the objective of maximizing the probability of reducing the number of sub-districts with undetected outbreaks by at least 5% (b), and a solution obtained using a linear approximation with this objective (c).

vacuuming, (2) beating of vegetation, (3) sweeping, (4) sticky traps and (5) hand collection. Values of φ_j and θ_j were estimated by fitting the hyperbolic function (4) using least squares to the observed detection function. An excellent fit



Figure 5 Expected number of species remaining undetected vs. the time spent surveying, sorting and identifying specimens for four different survey methods (vacuuming, beating of vegetation, use of sticky traps and sweeping). Dots and standard error bars represent the empirical detection data (Moir *et al.* 2005), and the lines are the fitted hyperbolic functions. These data are for species that were detected with only a single method.

(Fig. 5) was obtained when assuming that θ_j was the same for all methods ($\theta = 0.725$; see also Supporting Information). The parameters φ_j were estimated as 0.00335 for method 1 (vacuuming), 0.0105 for method 2 (beating), 0.0099 for method 3 (sweeping), and 0.0052 for method 4 (sticky traps). No species were solely collected using method 5 (hand collection).

With the estimated parameter values and for a budget of B = 10 h, the number of undetected species L is minimized when $x_1 = 7.1$ h, $x_2 = 2.3$ h, $x_3 = 0.6$ h, $x_4 = 0$ h and $x_5 = 0$ h, based on the analytical approximation (4). This result is similar to that obtained by numerically minimizing eqn 3, which gives the exact solution $x_1 = 5.6$ h, $x_2 = 3.0$ h, $x_3 = 0.6$ h, $x_4 = 0.4$ h and $x_5 = 0.4$ h. The outcome of numerical minimization is almost identical to that obtained analytically via the approximation; 47-49% of species (57-59% of those species detected using a single method) were expected to remain undetected with a budget of 10 h. We used a budget of B = 10 h for illustrative purposes. A small amount of sweeping is used in this case because the effort spent on vacuuming and beating is sufficiently large that the marginal efficiencies for these methods are reduced to a point where sweeping is equally

© 2010 Blackwell Publishing Ltd/CNRS

efficient. Larger budgets (e.g., B = 50 h) would lead to sticky traps being employed also.

When accounting for uncertainty in the efficiency of collection (represented by the standard error bars in Fig. 5), the distribution of effort would be slightly more even if we were content to sample fewer than the expected number of species. For example, if the minimally acceptable number of undetected species (T) is 25% more than the number expected, then the allocation that maximizes the probability of achieving this outcome is $x_1 = 7.0$ h, $x_2 = 2.4$ h, $x_3 = 0.6$ h, $x_4 = 0$ h and $x_5 = 0$ h. In this case, the allocation is similar regardless of the value of T, suggesting that the option that minimizes the expected number of undetected species is relatively robust to uncertainty in the efficiency of collection. Our results agree with the judgement in the original paper (Moir et al. 2005) that beating and vacuuming were the best complementary selection of survey methods. Our approach provides an objective basis for this judgement, and also determines the relative effort for each method.

DISCUSSION

This article makes two important advances. It shows that the question about how to allocate resources among options can often be approximated with a common mathematical structure for a range of environmental management problems; in the examples shown here, the benefits of management are additive or can be approximated as such. Note that multiplicative functions can be converted to an additive form (see Supporting Information). In addition to the examples shown here, additive management options apply to mitigating greenhouse gas emissions (Springer 2003), species management (Baxter et al. 2006), and, in particular cases, reserve design (Possingham et al. 2000; McCarthy et al. 2005). If ignoring uncertainty, the expected outcome is maximized by investing in options that have high expected returns, and to a level such that the marginal efficiency is equal.

The second advance is showing that uncertainty can be considered relatively easily because the mean and variance of the management outcome can be calculated from the means, variances and covariances of the management options. The additive benefits of management options simplify approaches to accounting for uncertainty because the probability distribution of the sum of random variables is relatively easy to calculate, particularly for a small number of options. When the number of options is large, the sum may be well approximated by a normal distribution, the mean and variance of which can be calculated.

Outcomes of investment in environmental management are not always additive, as we assumed in eqn 1. For example, if L were the population growth rate of a species as a function of the amount of money spent in different management options, the efficiency of each management option may depend on investments in other options; the benefits of reintroduction may depend on the control of exotic predators or the management of suitable breeding sites. Such interactions between options appeared in the Hemiptera example, with some species detected by multiple methods. This is mathematically equivalent to the issue of complementarity in reserve design (Possingham et al. 2000); the most important sites do not necessarily contain the most species. However, approaches that seek to select sites with many species that are found in few other places (i.e., concentrating on endemics as in the hotspots case study) may provide a useful heuristic. This approach is equivalent to restricting the Hemiptera analysis to species that are found with a single survey method. By doing this, the problem can be approximated by the additive function (eqn 1). Nevertheless, further extension of our approach to include interactions among options seems worthwhile.

The linear version of this problem is analogous to Markowitz's portfolio theory (Markowitz 1952, 1991), in which the investment decision involves a trade-off between the mean (expected) outcome and the uncertainty (variance) of the outcome, depending on the means, variances and covariances of the returns on individual assets. This linear version of the problem has been applied previously in environmental management (Springer 2003; Edwards et al. 2004). While the linear version is important and was the basis of Nobel-prize-winning research in economics, the prevalence of nonlinear responses in environmental management problems makes our novel solutions in these cases particularly important. One of the important outcomes of this article is to show that the same ideas of trading risk and reward can be applied in nonlinear problems, which are common in environmental management.

While linear relationships between investment and management outcomes are likely to be uncommon in environmental management, the linear form provides a useful approximation (Fig. 4), and has been used previously (Springer 2003; Edwards *et al.* 2004). Even in our hotspot example where the relationships are nonlinear due to the species–area effect, a linear approximation gives identical results because the level of investment is not sufficiently large, and the difference in costs among regions has the greatest influence on the results.

A benefit of using the linear form when possible is that analytical solutions are available, simplifying the calculations, and clarifying the basis of the solutions. In particular, when responses to management are approximately linear, incorporating uncertainty leads to a more uniform spread of investment among those options that are expected to perform better than the minimally required rate. This bet hedging is also seen in the case studies when the reward functions are convex.

There are several advantages of using our formal mathematical approach to allocating effort among management options, rather than subjective judgement. Our method demonstrates that the optimal solution depends on the particular objective, emphasizing that this requires careful thought and consideration by stakeholders. Our approach also emphasizes the complexity of some of the optimal management solutions. For example, the extent of extra effort spent on H5N1 surveillance of higher risk subdistricts depends on the objective, with some areas having almost the greatest effort under one objective, but none under another (e.g., consider when risk = 0.55 in Fig. 4). The difference arises because the two objectives weight the mean and variance of the outcome differently. Objectives that emphasize maximizing the expected outcome compared with minimizing the uncertainty of the outcome may have a greater concentration of investments. This can be seen in the solution of the linear version with the investment in option *i* proportional to $(\mu_i - T/B)/\sigma_i^2$. If values of $\mu_i - T/B$ are all substantially > 0, the optimal investment in each option will be similar. When some values of $\mu_i - T/B$ are close to 0 compared with others, then investment will be heavily weighted towards options with the larger values. Such sensitivity of the results, and the explicit or implicit weighting of the mean and variance, would be obscured if using subjective judgement. Finally, subjective judgements are prone to a range of human frailties (Tversky & Kahneman 1974), making them unreliable as the sole basis for environmental management decisions (Burgman 2005). While our mathematical approach to managing risks may be daunting to some, formal quantitative methods such as ours help to overcome problems of subjective judgement (Burgman 2005). These types of analyses are routine when designing financial investment portfolios that account for uncertainty; they should also be applied to investments for environmental management that are subject to at least the same level of uncertainty. We also note that these analyses should be used to support, not make, decisions, permitting investigation of different decisions.

By synthesizing previous efforts to optimize environmental investments, and extending these to account for uncertainty, our allocation theory can contribute to managing pressing environmental problems. The three case studies highlight the diversity of applications of our theory for environmental management. More generally, the theory can be applied to a range of instances in which management options provide approximately additive or multiplicative benefits to the environment. Further avenues for research include: (1) dealing with interactions among options, where the benefit ascribed to one management option depends on the performance of other options, (2) transaction costs (Brennan 1975), such as costs of travel between sub-districts in surveillance programs, for initiation of projects in biodiversity hotspots, and establishment of new survey methods and (3) different approaches to managing uncertainty.

ACKNOWLEDGEMENTS

We are grateful to Michael Bode for providing and discussing details of his data and analyses, and Rob Cannon, Tara Martin, Kirsten Parris, Peter Taylor and Kerrie Wilson for helpful comments. The work was supported by grants from the Australian Research Council (DP0774288, LP0884052), the Commonwealth Environmental Research Facility, and the Australian Centre of Excellence for Risk Analysis.

REFERENCES

- Ando, A., Camm, J., Polasky, S. & Solow, A. (1998). Species distributions, land values, and efficient conservation. *Science*, 279, 2126–2128.
- Bar-Shalom, Y. & Cohen, A.I. (1976). Optimal resource allocation for an environmental surveillance system. *IEEE Trans. Systems*, 6, 391–400.
- Baxter, P.W.J., McCarthy, M.A., Possingham, H.P., Menkhorst, P.W. & Mclean, N. (2006). Accounting for management costs in sensitivity analyses of matrix population models. *Conserv. Biol.*, 20, 893–905.
- Bode, M., Wilson, K.A., Brooks, T.M., Turner, W.R., Mittermeier, R.A., Mcbride, M.F. *et al.* (2008). Cost-effective global conservation spending is robust to taxonomic group. *Proc. Natl. Acad. Sci. USA*, 105, 6498–6501.
- Boyd, S. & Vandenberghe, L. (2004). *Convex Optimization*. Cambridge University Press, Cambridge, UK.
- Brennan, M. (1975). The optimal number of securities in a risky asset portfolio when there are fixed costs of transacting: theory and some empirical results. *J. Finan. Quant. Anal.*, 10, 483–496.
- Brooks, T.M., Mittermeier, R.A., Da Fonseca, G.A.B., Gerlach, J., Hoffmann, M., Lamoreux, J.F. *et al.* (2006). Global biodiversity conservation priorities. *Science*, 313, 58–61.
- Burgman, M.A. (2005). *Risks and Decisions in Environmental Management*. Cambridge University Press, Cambridge, UK.
- Cannon, R.M. (2009). Inspecting and monitoring on a restricted budget: where best to look? *Prev. Vet. Med.*, 92, 163–174.
- Drechsler, M. (2005). Probabilistic approaches to scheduling reserve selection. *Biol. Conserv.*, 122, 253–262.
- Edwards, S.F., Link, J.S. & Rountree, B.P. (2004). Portfolio management of wild fish stocks. *Ecol. Econ.*, 49, 317–329.
- Fenton, L.F. (1960). The sum of lognormal probability distributions in scatter transmission systems. *IRE Trans. Commun. Syst.*, 8, 57–67.
- Food and Agricultural Organization (2007). The Global Strategy for Prevention and Control of H5N1 Highly Pathogenic Avian Influenza. Food and Agriculture Organization, and World Organisation for Animal Health, Rome.
- French, S. (1986). Decision Theory: An Introduction to the Mathematics of Rationality. Horwood, Chichester, UK.

- Gaston, K.J. (1991). The magnitude of global insect species richness. *Conserv. Biol.*, 5, 283–296.
- Gilbert, M., Xiao, X., Pfeiffer, D.U., Epprecht, M., Boles, S., Czarnecki, C. *et al.* (2008). Mapping H5N1 highly pathogenic avian influenza risk in Southeast Asia. *Proc. Natl. Acad. Sci. USA*, 105, 4769–4774.
- Halpern, B.S., Regan, H.M., Possingham, H.P. & McCarthy, M.A. (2006). Accounting for uncertainty in marine reserve design. *Ecol. Lett.*, 9, 2–11.
- Hauser, C. & McCarthy, M.A. (2009). Streamlining 'search and destroy': cost-effective surveillance for invasive species management. *Ecol. Lett.*, 12, 683–692.
- Joseph, L.N., Maloney, R.F. & Possingham, H.P. (2009). Optimal allocation of resources among threatened species: a project prioritization protocol. *Conserv. Biol.*, 23, 328–338.
- Mace, G.M. & Lande, R. (1991). Assessing extinction threats: toward a reevaluation of IUCN threatened species categories. *Conserv. Biol.*, 5, 148–157.
- Markowitz, H. (1952). Portfolio selection. J. Finance, 7, 77-91.
- Markowitz, H. (1991). Portfolio Selection: Efficient Diversification of Investment. Blackwell, Cambridge, MA.
- Martin, T.G., Chadès, I., Arcese, P., Marra, P.P., Possingham, H.P. & Norris, D.R. (2007). Optimal conservation of migratory species. *PLoS ONE*, 2, e751.
- McCarthy, M.A., Thompson, C.J. & Possingham, H.P. (2005). Theory for designing nature reserves for single species. Am. Nat., 165, 250–257.
- McCarthy, M.A., Thompson, C.J. & Williams, N.S.G. (2006). Logic for designing nature reserves for multiple species. *Am. Nat.*, 167, 717–727.
- McCarthy, M.A., Thompson, C.J. & Garnett, S.T. (2008). Optimal investment in conservation of species. J Appl. Ecol., 45, 1428– 1435.
- Moir, M.L., Brennan, K.E.C., Majer, J.D., Fletcher, M.J. & Koch, J.M. (2005). Toward an optimal sampling protocol for Hemiptera on understorey plants. *J. Insect Conserv.*, 9, 3–20.
- Moore, J.L., Balmford, A., Allnutt, T. & Burgess, N. (2004). Integrating costs into conservation planning across Africa. *Biol. Conserv.*, 117, 343–350.
- Murdoch, W., Polasky, S., Wilson, K.A., Possingham, H.P., Kareiva, P. & Shaw, R. (2007). Maximizing return on investment in conservation. *Biol. Conserv.*, 139, 375–388.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A.B. & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858.
- Nocedal, J. & Wright, S.J. (1999). Numerical Optimization. Springer-Verlag, New York.
- Polasky, S., Camm, J.D., Solow, A.R., Csuti, B., White, D. & Ding, R. (2000). Choosing reserve networks with incomplete species information. *Biol. Conserv.*, 91, 1–10.
- Possingham, H., Ball, I. & Andelman, S. (2000). Mathematical methods for identifying representative reserve networks. In: *Quantitative Methods for Conservation Biology* (eds Ferson, S. & Burgman, M.). Springer, New York, pp. 291–306.
- Possingham, H.P., Andelman, S.J., Noon, B.R., Trombulak, S. & Pulliam, H.R. (2001). Making smart conservation decisions. In: *Conservation Biology: Research Priorities for the Next Decade* (eds Orians, G. & Soulé, M.). Island Press, Washington, DC, pp. 225–244.

- Ross, S.M. (2009). Introduction to Probability and Statistics for Engineers and Scientists. Academic Press/Elsevier, Burlington, MA.
- Simon, H.A. (1982). *Models of Bounded Rationality*. MIT Press, Cambridge, MA.
- Springer, U. (2003). International diversification of investments in climate change mitigation. *Ecol. Econ.*, 46, 181–193.
- Sundaram, R.K. (1996). A First Course in Optimization Theory. Cambridge University Press, Cambridge, UK.
- Tiensin, T., Chaitaweesub, P., Songserm, T., Chaisingh, A., Hoonsuwan, W., Buranathai, C. *et al.* (2005). Highly pathogenic avian influenza H5N1, Thailand 2004. *Emerg. Infect. Dis.*, 11, 1664–1672.
- Tiensin, T., Nielen, M., Songserm, T., Kalpravidh, W., Chaitaweesub, P., A. Amonsin, S. *et al.* (2007). Geographic and temporal distribution of highly pathogenic avian influenza A virus (H5N1) in Thailand, 2004-2005: an overview. *Avian Diseases*, 51, 182–188.
- Tversky, A. & Kahneman, D. (1974). Judgment under uncertainty: heuristics and biases. *Science*, 185, 1124–1131.
- Wilson, K.A., Mcbride, M.F., Bode, M. & Possingham, H.P. (2006). Prioritizing global conservation efforts. *Nature*, 440, 337–340.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Mathematical details.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

Editor, Stephen Polasky Manuscript received 4 March 2010 First decision made 8 April 2010 Second decision made 28 June 2010 Third decision made 13 July 2010 Manuscript accepted 13 July 2010