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Author

Wintle, Brendan A

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Adaptive Management, Population Modeling and Uncertainty Analysis for Assessing the Impacts of Noise on Cetacean Populations

Brendan A. Wintle
University of Melbourne, Australia

Population modeling is now widely used in threatened species management and for predicting the impacts and benefits of competing management options. However, some argue that the results of models must be used with caution, particularly when data are limited. This is important, as even the simplest models would generally require more data (and knowledge) than are available in order to have complete confidence in model predictions. In particular, population models often suffer from a lack of data on demographic rates, spatial distribution, dispersal, management responses, habitat correlations and the magnitude of temporal variations. A number of authors identify behavioral and physiological responses of animals to anthropogenic noise. Assessing population level impacts of noise on cetacean populations is essential to understanding how noise impacts on the future viability of marine mammal populations. This assessment will be particularly challenging due to the difficulties associated with identifying a clear link between behavioral responses of animals and physiological impacts, observing and measuring changes in cetacean population parameters and the long lag-times over which population changes manifest in long-lived species. The urgency of the conservation situation for many of these socially important species demands immediate action, despite pervasive uncertainty. Adaptive management provides a coherent framework for action and continuous improvement under uncertainty. I review the elements of adaptive management and discuss the role of population modeling in that context. I discuss Bayesian approaches to enhancing inferential power and reducing uncertainty in model parameter estimation. I then review approaches to characterizing irreducible uncertainty with Monte Carlo methods and sensitivity analysis and conclude with a brief discussion of formal decision tools available to assist with decision making under severe uncertainty. I propose that urgently needed action should not be postponed due to uncertainty and that adaptive management provides a coherent framework for instituting immediate action with a plan for learning.

Of primary interest to conservation practitioners is the degree to which human activities (such as anthropogenic noise) induce physiological and behavioral responses (e.g., a prolonged stress response) that ultimately manifest in changes to population dynamics such as reduced yearly survival and fecundity (collectively referred to as *vital rates*), and metapopulation dynamics such as immigration and emigration rates. More specifically, it is possible that anthropogenic noise may impact on marine mammal populations through direct physiological impacts leading to reduce survivorship and fecundity, or indirectly through changed behavior such as interrupted or altered foraging, mating or migration patterns (see Bateson, this issue; Beale, this issue; Deak, this issue; Lusseau, this issue; Romero & Butler, this issue; Wright et al., this issue, a. There

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(brendanw@unimelb.edu.au).

is mounting evidence that anthropogenic noise will result in population level impacts on marine mammal species, but substantial uncertainty about exactly how anthropogenic noise impacts will manifest. This is a common situation in conservation and natural resource management. In most situations we lack information about the magnitude of anthropogenic impacts and the efficacy of ameliorative actions on vital rates and metapopulation dynamics, as well as how they interact with environmental influences. Data on 'natural' demographic rates are also often lacking making inference about the population-level impacts of noise particularly challenging.

While such uncertainties are pervasive in conservation science, attempts at dealing with uncertainties in decision making have been largely ad-hoc and few applications utilize formal decision theory. However, some principles of decision making under uncertainty are articulated in the literature (Holling, 1978; Walters, 1986; Walters & Holling, 1990) and coherent approaches to management and decision making under uncertainty have recently emerged (Dorazio & Johnson, 2003; Nichols & Williams, 2006). Bayesian approaches to dealing with uncertainty due to imperfect knowledge and data have long been available but are only now becoming more widely used by ecologists and conservation biologists (Dorazio & Johnson, 2003; Ellison, 2004; McCarthy, 2007). There are a rising number of practical examples of formal decision making in conservation and natural resource management (Gerber et al., 2005; Hauser, Pople, & Possingham, 2006; Johnson & Williams, 1999; McCarthy & Possingham, 2007; Moilanen & Wintle, 2006; Regan et al., 2005), and the number of people trained to implement formal decision techniques is increasing. The synthesis of adaptive management principles, Bayesian approaches to characterizing and reducing uncertainty, and formal decision protocols may provide the basis for improved transparency, efficiency and robustness of conservation management under uncertainty. However, there are few examples of the successful integration of these approaches in practical applications of adaptive conservation management. Here I review aspects of uncertainty analysis and experimental management of threatened species populations and propose a framework for learning about the population-level impacts of noise-related stress effects.

Management under uncertainty: The adaptive management framework

Because uncertainty is pervasive in conservation management it is not appropriate to use uncertainty as an excuse for inaction (Bruntland, 1987), as inaction often results in deleterious environmental and biodiversity outcomes (Stern, 2007). Postponing decisions and changes to management because evidence for environmental harm is inconclusive or because impacts are not yet perfectly measured may be a highly sub-optimal strategy for conservation and should be weighed against the costs and benefits of various alternative actions. Adaptive management has been proposed as a paradigm for management under uncertainty and continuous improvement (Johnson et al., 1997; Linkov, Satterstrom, Kiker & Bridges, 2006a; Walters, 1986; Walters & Holling, 1990). Adaptive management can be loosely defined as management with a plan for learning. Under adaptive

management a range of management actions are prescribed at each time step that have the dual purpose of achieving management goals and facilitating learning about the system under management and the relative performance of management strategies. Adaptive management may be described in four steps (Figure 1);

- i) identification of management goals, constraints and performance measures;
- ii) specification of management options;
- iii) identification of competing system models and model weights; and
- iv) allocation of resources, implementation of management actions and monitoring of management performance.

The integration of ‘implementation of management actions’ and ‘monitoring’ emphasizes that monitoring is central to management and not an optional extra.

Modern interpretations of adaptive management based on adaptive optimization encourage an iterative approach to decision making (also known as ‘state-based’ decision making; Nichols & Williams, 2006). The act of determining management actions (strategies) for a discrete period of time that are optimal with respect to one’s belief and uncertainty about the state of the system, as well as one’s predictions about how the system will respond to management is intuitive though not always simple to achieve (see Allan and Curtis, 2005; Stankey et al., 2003, 2005). Indeed, it is not necessary that managers adopt formal optimization methods when implementing adaptive management as long as there is a plan for learning and a willingness to adapt management decisions in light of evidence that is collected through management experiments. Adaptive management is appealing in that it explicitly acknowledges that the decision being made is subject to substantial uncertainty and may change in the next time step depending on what is discovered (learnt) in the intervening period. It doesn’t require the completion of an experiment before a change to management can be instituted; rather it identifies the best decision to be taken now, based on what is believed about the state of the system and what has been discovered to date through previous monitoring and research. Adaptive management is well suited for managing systems in which changes take a long time to become apparent and definitive experiments are not possible in reasonable timeframes. Formal adaptive management helps to identify an immediate course of action despite substantial uncertainty. It also helps to clarify the role of monitoring as a process for reducing uncertainty and ranking the performance of management in ameliorating impacts.

One of the most challenging aspects of decision making in natural resource management is the process of identifying and setting management objectives, especially when multiple stakeholders hold conflicting or competing objectives (Step i in Figure 1). Environmental management requires decisions makers to integrate heterogeneous technical information with values and judgment. Methods for eliciting and reconciling competing objectives, such as multi-criteria decision analysis (MCDA; Figueira, Greco, Ehrgott, 2005) provide a basis for tackling this challenge. MCDA also provides a coherent way of integrating various forms of uncertainty (epistemic uncertainty, subjectivity, semantic ambiguity; Regan et al., 2001) with social preferences in the decision process. The methods and tools reviewed in the paper (adaptive management, Bayesian approaches, population modeling) are important tool for characterizing and reducing uncertainty that feed

into the decision making process. However, they do not make decisions *per se* because decision making is, necessarily, a social process that involves competing decision priorities. The common purpose of MCDA methods is to evaluate and choose among alternatives, based on multiple criteria using systematic analysis that overcomes the limitations of the unstructured individual or group decision making (Figueira et al., 2005). The aim of MCDA is to facilitate decision makers' learning about and understanding of the problem as well as about organizational preferences, values and objectives. MCDA can guide decision makers in identifying a preferred course of action through exploring these issues in the context of a structured decision analysis framework. MCDA framework may be integrated with adaptive management (Linkov et al., 2006a, b) as well as with Bayesian methods and population models. A detailed review of MCDA and associated methods is beyond the scope of this article. Here I focus primarily on approaches to characterizing and where possible, reducing uncertainty with efficient modeling and learning strategies. I recognize that these are aspects of the larger problem of dealing with uncertainty and social preferences in decision making.

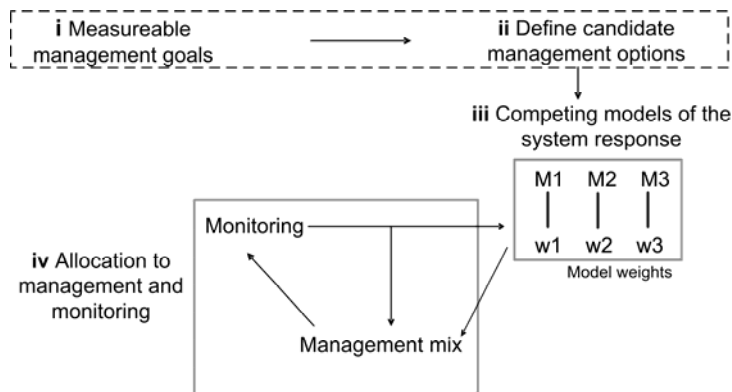


Figure 1. Adaptive management (reproduced from Figure 1, Duncan & Wintle, 2008, © with kind permission of Springer Science+Business Media); an approach to management under uncertainty with a plan for learning. The dashed-line box indicates steps that require elicitation of social preferences. Updating of models can include updating of individual model parameters (e.g. Dorazio & Johnson, 2003) and/or updating of model weights (e.g. Box 2, Johnson et al., 1997).

Population models, impact assessment and adaptive management

Adaptive management of threatened species requires the specification of a model (or competing models) of species' responses to impacts and management intervention. The role of models in adaptive management is twofold. Firstly, models help to characterize uncertainty and formalize competing views about population dynamics, and the manner in which populations respond to anthropogenic influence and interact with natural environmental processes. Secondly models are useful for making predictions about the likely impacts of future (or proposed) management actions, allowing managers and stakeholders to rank competing management options. Under adaptive management, competing

models are iteratively assigned credibility based on the observed response of species to management over time. Population models have been used in both terrestrial and marine systems to evaluate the long-term population consequences of competing management options (Box 1; Akcakaya, Radeloff, Mladenoff & He, 2004; Taylor & Plater, 2001; Wade, 1998; Wintle, Bekessy, Pearce, Veneir & Chisholm, 2005).

Box 1. The use of population modeling to rank management options: The wedge-tailed eagle and plantation conversion in northeastern Tasmania, Australia.

Bekessy et al. (in review) utilized dynamic landscape metapopulation models (DLMP: Akcakaya et al., 2004; Wintle et al., 2005) to assess the landscape-level impacts of plantation conversion on the viability of the wedge-tailed eagle in the north-east region of Tasmania. DLMP were fitted in the software package RAMAS Landscape (Akcakaya et al., 2004). The process of developing DLMP models may be broadly described in 4 steps (Wintle et al., 2005): (1) building a habitat model; (2) developing a model of population dynamics; (3) linking these models in a metapopulation model; and (4) building a forest-dynamics model and linking it to the metapopulation model to evaluate management options.

Bekessy et al. (in review) were able to use the DLMP framework to provide predictions about the future (160- year time horizon) wedge-tailed eagle population size in north eastern Tasmania under a range of forest management and plantation conversion scenarios including: (1) no logging (only 'natural fire disturbance'); (2) native forest harvesting only; and (3) native forest harvesting with extensive plantation conversion (~50% of total forest extent). Results of DLMP models were summarized using the expected minimum population size (EMP: see main text). The results of the DLMP risk assessment process indicated that all anthropogenic disturbance scenarios generated an EMP that was approximately half that of the no-logging scenarios (Fig. 1.1), but that there were no appreciable differences between native harvest-only and conversion scenarios for this particular species. This was thought to be because the primary limiting resource for the species was the availability of nesting habitat that only occurs in old, relatively undisturbed forest on sites with large trees, and that these conditions were approximately equally compromised by native forest harvesting and plantation conversion.

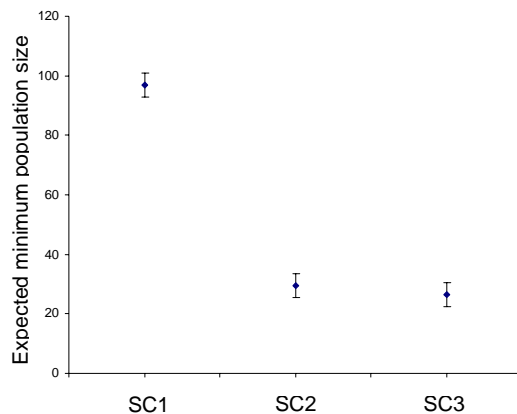


Figure 1.1. Expected minimum wedge-tailed eagle population sizes over a 160-year time horizon under three management scenarios (SC1 = no logging or plantation conversion, SC2 = only native forestry logging with natural regeneration, SC3 = native forestry with natural regeneration and approximately 30% plantation conversion). Error bars represent the 95% confidence interval on the mean EMP (this should not be confused with a 95% prediction interval for EMP). EMP may be interpreted as there being a 50% chance of the population falling below the stated level at some time over the next 160 years.

However, predictions of population models are subject to substantial uncertainty in parameter estimates (Ludwig, 1996). The standard approach to quantifying and representing such uncertainty is through Monte Carlo simulation. Monte Carlo methods are widely used for simulating the behavior of various physical and mathematical systems. Monte Carlo simulation of population models involves randomly sampling parameter values from a distribution of possible values over a number of ‘iterations’. For example, when conducting Monte Carlo simulations for a population model, the value of the adult yearly survival parameter at *each time step* might be selected from a beta distribution with a mean set at the best estimate of yearly survival and a variance determined by analyzing long-run variation in yearly survival of the species. Often it is the variance of such parameters that is hardest to determine. A single iteration of the model provides a single possible trajectory for the species. Over numerous iterations, a distribution of predictions is derived that represents the predictive uncertainty in expected population trajectory attributable to parameter uncertainty and the more general effects of environmental stochasticity. For more information about Monte Carlo sampling in population models, see Burgman, Ferson & Akçakaya (1993).

In order to test the sensitivity of model predictions to particular assumptions, one may conduct a sensitivity analysis. There are several different approaches to conducting a sensitivity analysis including random sampling or systematic perturbation of parameter values and analysis of how variation in a given parameter influences model predictions. A common approach to sensitivity analysis involves systematically adjusting individual parameters by a set amount (e.g. +/- 20%), while keeping all other parameters at their estimated mean value, and observing the magnitude of change in model predictions that arise. If the predicted change in expected population size is substantial for a small change in a particular parameter, then the model is said to be ‘sensitive’ to that parameter. Sensitivity analysis may be used to assess sensitivity of tail risks as well as expected population sizes. Sensitivity analysis may be used to prioritize research into vital rates or environmental parameters to which population projections are most sensitive.

McCarthy & Thompson (2001) proposed the now widely used metric ‘expected minimum population size’ (EMP) as an appropriate quantity of interest derived from population viability analysis. EMP is calculated by taking the mean of the smallest population size that occurred at over the simulation period for each Monte Carlo iteration of the model. The EMP is useful in ranking scenarios as it provides a good indication of the propensity for population decline but is less sensitive to model assumptions than the metrics *risks of decline* or *risk of extinction* (McCarthy & Thompson, 2001). One particularly useful property of EMP is that it can be used to delineate between management options for species that have almost no probability of going extinct under any option. The sensitivity of the model to a particular parameter, or the sensitivity of the species to a particular management option may be defined in terms of EMP (Wintle et al., 2005):

$$S_i = (EMP_i - EMP_b) / EMP_b \times 100,$$

where S_i is the sensitivity of model i (the model being investigated), EMP_i is the expected minimum population size of the model i , and EMP_b is the expected minimum population size of the base model. The base model usually represents the model for which parameter estimates are all ‘best’ estimates or the model representing the default (or current) management. Sensitivity calculated in this way provides an indication of both the magnitude and direction (positive or negative) of the change in EMP.

Despite the prevalence of substantial uncertainty, modeling may be useful in challenging stakeholders and managers to clearly state their belief about species population dynamics and the magnitude and mechanisms of anthropogenic impacts. Models represent testable hypotheses that may be improved and updated as new data or knowledge comes to hand. As data are gathered, updated models may begin to provide predictions that are more broadly trusted by managers and stakeholders. In data-poor situations, it is important to make the most of available expertise or ‘collateral’ data. That is the topic of the next section.

Bayesian approaches to inference

Ecological data are often expensive, time consuming and difficult to collect. Unlike in the physical sciences, the design of the definitive experiment that proves or disproves a theory can seldom be achieved in ecology and conservation. Ecological inference is largely a process of synthesizing disparate data and the results of inconclusive experiments to update knowledge and make the best possible decision. Ecological inference is primarily concerned with estimation of parameters and the weighting of competing hypotheses (models) rather than the rejection or acceptance of null-hypotheses (Anderson, Burnham & Thompson, 2000; Burnham & Anderson, 2002; Ellison, 2004; Johnson, 1999). Bayesian approaches to inference are particularly well suited to the synthesis of disparate information, parameter estimation and multi-model inference (Ellison, 2004; Harwood, 2000; McCarthy, 2007; Wintle, McCarthy, Volinsky & Kavanagh, 2003). Multi-model inference and iterative updating of knowledge (beliefs) are strengths of the Bayesian approach to inference. Ferson (2005) provides an excellent review of the criticisms of Bayesian approaches to inference and decision making, focusing on the use of prior information that is central to the Bayesian method. He identifies concerns about the contraction of uncertainty that arises when highly divergent distributions (i.e. prior and data) are combined with Bayes theorem. There are non-Bayesian alternatives to integrating multiple sources of information (e.g. meta-analysis; Sutton, Jones, Abrams, Sheldon & Song, 2000) and conducting multi-model inference (Burnham & Anderson, 2002), though they are regarded as theoretically less coherent by some authors (Link & Barker, 2006). A full review of the philosophical and practical differences between Bayesian and alternative analytical methods is beyond the scope of this paper. I also consider that the ‘controversy’ over Bayesian and non-Bayesian methods to be somewhat over-played and to be largely irrelevant here. However, warnings about Bayesian methods should not be ignored because, as is the case for all statistical methods, naïve applications of Bayes theorem can be dangerous. In the following two

sections I discuss two important functions of Bayesian inference in model-based management of threatened species. In the first section I discuss Bayesian approaches to reducing uncertainty through integration of alternative data sources and expert knowledge. In the second section I describe the role of Bayesian updating for iteratively assigning plausibility to competing management models under adaptive management.

Bayesian approaches to reducing uncertainty with prior data and expert opinion

Under adaptive management of noise-effects on cetaceans it is necessary to generate hypotheses and models that describe both the impacts of noise on cetacean population parameters as well as the value of proposed noise mitigation or management strategies. This can be particularly challenging in the absence of definitive studies or models that measure such processes, as is currently the situation with the case in point. McCarthy (2007; pg 134) provides an excellent example of how to develop informative prior information about the value of a poorly measured parameter (in this case, the yearly mortality rate of powerful owls in southeastern Australia). McCarthy utilized a regression of body mass on mortality rate using data for a range of (better studied) raptors from around the world. In his analysis McCarthy demonstrates the use and value of a model-based prior when making inference based on an extremely sparse data (in this case, one observed mortality in 35 observation years: Figure 2).

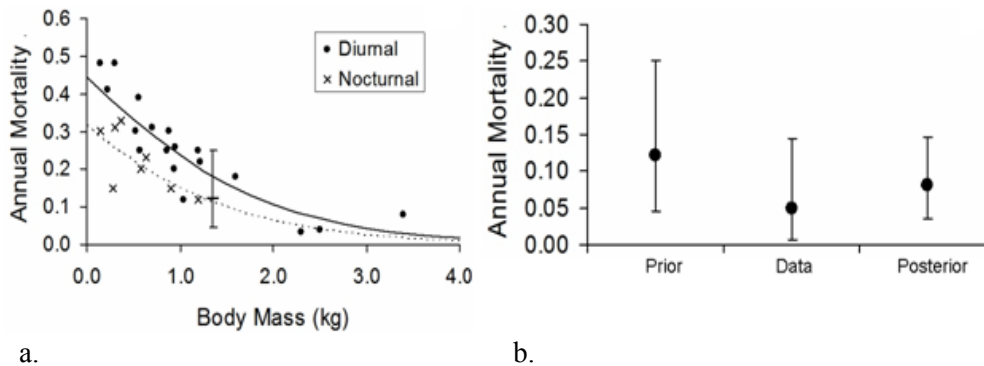


Figure 2. a) Annual mortality of raptors versus body mass for diurnal (solid line) and nocturnal (broken line) raptors. The prediction and prediction interval for the powerful owl, based on the regression for other owls, is shown as the dashes and vertical bar. b) Annual mortality of powerful owls showing the prior based on other species' mortality estimates (a), the data on powerful owls and the posterior estimate (circles are means and dashes delimit 95% CIs) [reproduced with permission of Michael McCarthy and Cambridge University Press].

Box 2. Using Bayes' theorem to assign credibility to competing models with monitoring data; the management of Mallard ducks.

Models that predict a system response to management actions are needed to optimize management decisions (Nichols & Williams, 2006). Typically, multiple competing views (opinions, hypotheses) about how a system will respond to management exist and these views can be formalized as competing models. The plausibility of competing models may be assessed by comparing their predictions to data obtained from monitoring. In developing an adaptive management strategy for Mallard duck harvest, Johnson *et al.* (1997) describe a process of updating belief about the plausibility of competing models based on Bayes' theorem, such that the plausibility of a given model given the newly observed data (D) is:

$$\Pr(M_i | D) = \frac{\Pr(D | M_i) \Pr(M_i)}{\sum_{j=1}^s \Pr(D | M_j) \Pr(M_j)}, \quad (\text{eq 1})$$

where $\Pr(M_i | D)$ is known as the 'posterior probability' or 'weight' of model M_i (i.e. the degree of belief in M_i after considering the available data). $\Pr(D|M_i)$ is the likelihood that a given set of data would be observed if M_i were true, $\Pr(M_i)$ is the prior probability assigned to model M_i and the denominator represents the sum across the products of prior probabilities and likelihoods for all competing models including model M_i .

Models describing duck population responses to hunting pressure are central to the sustainable management of duck harvests. Managers of Mallard ducks use equation 1 to iteratively update their belief in competing models as yearly monitoring data are collected (Johnson et al., 1997; Johnson & Williams, 1999; USFWS, 1999). Various scientists and stakeholders hold alternative views about how duck hunting impacts on duck population dynamics. Debate focused on whether population growth would compensate for harvest mortality (compensatory mortality vs. additive mortality) and whether reproductive success would be strongly or weakly linked to habitat availability (strong vs. weak density dependence). In developing an adaptive management system for duck hunting, competing views were summarized as four models of duck hunting population response: 1) additive mortality (am), strong density-dependent recruitment (sdd); 2) additive mortality, weak density-dependent recruitment (wdd); 3) compensatory mortality (cm), strongly density-dependent recruitment; and 4) compensatory mortality, weak density-dependent recruitment (USFWS, 1999).

The implication of strong density dependence and compensatory hunting mortality is that higher hunting quotas may be sustainable. More conservative harvesting may be warranted if density dependence is low and hunting mortality is not compensated by increased reproductive success and a reduction in other forms of mortality. Table 2.1 shows how model probabilities were updated with duck population monitoring data over the years 1995 - 1999. Note that prior to the collection of monitoring data in 1995, all models shared equal prior probability [i.e. $\Pr(M_i) = 0.25$]. As monitoring data were collected and compared against the predictions of the four competing models, it rapidly became apparent that the compensatory mortality hypothesis was not supported by the data as hunting had a substantial impact on overall survivorship estimates. The data provided slightly more support for strong density dependence than weak.

Table 2.1

Trends in probabilities for competing hypotheses of Mallard population dynamics taken from USFWS (1999) [model probabilities have been rounded to two decimal places].

Year	'95	'96	'97	'98	'99
Model (defined above)					
1 (am, sdd)	0.25	0.65	0.53	0.61	0.61
2 (am, wdd)	0.25	0.35	0.46	0.39	0.38
3 (cm, sdd)	0.25	0.00	0.00	0.00	0.00
4 (cm, wdd)	0.25	0.00	0.00	0.00	0.00

The above example illustrates how it is possible to derive parameter estimates where little or no data are available. Approaches to eliciting Bayesian estimates of parameters from experts where no data can be obtained are analogous to those described in this simple example (see Martin et al., 2005; McCarthy, 2007 on soliciting subjective priors). A similar analysis might be initiated to develop parameters that describe the survival and fecundity of species in other situations, such as whales under various noise exposure/management scenarios. The approach outlined above is a logically coherent approach to extrapolating, for example, noise-related impacts from other mammals to cetaceans. The degree to which this approach works depends on whether the responses in question (e.g., behavioral, physiological, psychological, etc.) are highly conserved between species. For example, stress response physiology does appear to be highly conserved between species (see Deak, this issue; Romero & Butler, this issue) and thus would be a good candidate for this approach.

Bayesian updating in adaptive management. Adaptive management encourages a formal process of iteratively updating degrees of belief in competing hypotheses (models) in light of evidence collected through monitoring. There is usually substantial uncertainty about how a species will respond to management intervention, or indeed, the ecological/biological processes that mediate that response. It is common for different experts to support qualitatively different models of ecological processes. Qualitatively different management strategies usually imply different views about how species and environmental processes interact with human and natural disturbances. When appropriate experts support qualitatively different models, it implies substantial uncertainty about the best approach for achieving desired management outcomes. When such uncertainty exists (and is acknowledged), there is value in implementing management options that will facilitate learning about the relative merits of competing models and ultimately the best long-term strategies for achieving management goals. In some instances, data and expert opinion may favor some models over others. When this is the case, formal methods for weighting competing models may be utilized (Box 2; Burnham & Anderson, 1998; Wintle et al., 2003). Competing model weights may be used to assist in the allocation of effort between competing management options. If there is no substantial evidence in favor of one model over another, then uninformative (equal) model weights may be appropriate until further evidence arises that provides support for one model over others (Box 2).

Conclusions

At first glance, the range of tools and the technical aspects of formal decision making may serve as a disincentive to engage in adaptive management. Here I have focused on techniques for making predictions, characterizing uncertainty, and learning about effective ways to manage threatened species. There are substantial components of the decision making process, such as reconciling competing objectives and social utilities that I have not dealt with in detail. While there are technical challenges to all decision analysis methods, the advantages gained in terms of transparency, repeatability and stakeholder trust far outweigh

the technical overheads. In short, dealing with uncertainty in conservation and natural resource management is a difficult challenge that necessitates sophisticated methods. The number of examples of adaptive management and formal decision theory applications occurring in conservation and environmental management are gradually increasing, though much un-chartered territory remains. A systematic method of combining quantitative and qualitative inputs from scientific studies of risk, cost and cost-benefit analyses, and stakeholder views has yet to be fully developed for environmental decision making (Linkov et al., 2006a). Management of threatened cetacean populations and the acute and chronic impacts of noise will involve numerous sources of uncertainty. This highlights the need for systematic approaches to learning and decision making. I encourage cetacean conservation managers to embrace the principles and tools of adaptive management as a means to efficient use of scarce conservation resources and better long-term conservation outcomes.

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