Decision analysis for threatened species management across the captive-wild spectrum

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ABSTRACT

Programs for the recovery of threatened species increasingly involve active management of variable intensity, such as captive breeding, reintroduction and translocation. Managers of such programs thus need to make decisions about whether and how to implement a given type of management, usually in the face of uncertainty and constraints. Structured decision making provides decision makers with a theoretical framework and practical methods to make rational decisions under uncertainty. In this thesis, I investigate how different principles and tools of structured decision making can assist decisions in threatened species management.

The fundamental decision problems in threatened species management concern whether and how to implement a given type of management for the target species. In Chapter 2, I examine the case of whether the conservation of a species should incorporate ex-situ management, using the recovery plan for an endangered frog species in south-eastern Australia as an example. I demonstrate that this question can only be answered rationally after determining how the ex-situ component will benefit the overarching objectives of the recovery plan. This logical sequence of decisions (how before whether) is however followed only infrequently in real-world conservation. I illustrate how managers can implement it with the aid of decision trees and multi-criteria decision analysis.

Since decisions are aimed at achieving objectives, they necessarily reflect the values and preferences of stakeholders. Using value functions, in Chapter 2 I demonstrate how the optimal decision depends on the relative importance attributed to different objectives (for example, maximising the probability of persistence of the target species and meeting budget limitations). In Chapter 3, I expand this analysis to demonstrate how to account for the attitude of decision makers towards the risk of negative outcomes. I use two case studies of recovery plans for threatened frog species to illustrate the application of stochastic dominance, a useful method to rank alternative actions in the face of uncertainty and risk.

Structured decision making provides methods to make decisions under uncertainty. However, in some instances reducing the existing uncertainty by collecting additional information can allow more robust decisions. As a result, managers of threatened species programs almost always advocate further research, in the expectation that it will improve the outcomes of management. In Chapter 4, I apply a formal method to calculate the expected benefit of additional information...
to two examples in threatened species management. I demonstrate how the value of information is a function of the current knowledge, by the potential to react to new information, and by the effectiveness of the learning process. Value of information analysis can help managers determine whether and how to implement experiments and monitoring programs to improve the ultimate outcomes of management.

For several threatened species programs, the scale and speed of the threatening processes often require decisions to be made immediately, leaving no time for formal experimental learning. Adaptive management describes a specific case of structured decision making in which managers learn by monitoring the outcomes of management and adjust actions accordingly. In Chapter 5, I analyse the conditions and challenges that exist to the application of adaptive management in threatened species programs. The temporal scale of such programs is often sufficient to allow managers to collect information and react by updating actions in subsequent time steps. Particularly for programs toward the captive end of the management spectrum, controlled conditions are also favourable for effective learning. Adaptive management requires the ability to clearly structure uncertainty into formal hypotheses, to allow effective and focused monitoring that addresses the most important sources of uncertainty. Most importantly, institutions and stakeholders must be committed and capable of implementing learning.

For clearly defined decision problems, structured decision making can draw upon a range of technical approaches to determine optimal management strategies. In Chapter 6, I consider a reintroduction program in which management decisions are complicated by the complex life history of the target species and budget constraints. I combine demographic modelling and cost-effectiveness analysis to identify the optimal rates of translocation between captive and wild populations.

This thesis illustrates how the iterative cycle of structured decision making can benefit all stages of the design of management strategies for threatened species conservation. First, it can help managers in thinking clearly about the decision problem, allowing a transparent assessment of subjective preferences and value. It can then ensure an objective evaluation of the available management alternatives, using qualitative or quantitative predictive approaches that explicitly recognise uncertainty. Finally, it can assist in finding solutions to trade-offs and incorporating additional knowledge to allow better decisions.
DECLARATION

This is to certify that

i) The thesis comprises only my original work towards the PhD except where indicated in the Preface;

ii) Due acknowledgement has been made in the text to all other material used;

iii) The thesis is less than 100,000 words in length, exclusive of tables, bibliographies and appendices.

Signed: …………………………………….

Date: ………………………

Stefano Canessa
This thesis is written as a series of independent publications. As such, there may be some repetition, primarily in the introductions to each of the chapters. Chapters Two to Six represent co-authored manuscripts that are either published or will be submitted following completion of this thesis. I am the primary author of all manuscripts that have been published, submitted or are in preparation for submission. I conceived the research questions, formulated and carried out the analysis, and wrote each draft. A number of the co-authors are my supervisors (Kirsten Parris, Michael McCarthy, Sarah Converse and Terry Walshe). In this case, co-authorship reflects assistance developing ideas and methodological structure.

A particular characteristic of this thesis is that some of the research presented was developed during workshops. Chapter Two arose from a workshop funded by the Australian Centre for Ecological Analysis and Synthesis. The workshop was carried out in 2013 in Brisbane, Australia. Chapters Three and Four arose from a workshop funded by the National Environmental Research Program, carried out in April 2014 in Melbourne, Australia. For both workshops I conceived the original ideas, wrote and managed the grant application, selected the participants and led the organization and execution of the workshops.

For all chapters, co-authors commented manuscript drafts. For Chapters Three and Four, Gurutzeta Guillera-Arroita, José Lahoz-Monfort and Darren Southwell provided assistance with statistical analyses. In Chapter Four, Bob Lacy and Doug Armstrong provided the original structure for the cheetah and hihi case studies respectively. All other help in the form of workshop participation and provision of expert knowledge is credited in the Acknowledgements.

This thesis is made up of the following chapters for publication.


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Chapter 1

INTRODUCTION
CHAPTER 1

Introduction

This thesis applies the principles and tools of decision analysis to problems in the direct management of threatened species. The managers of conservation efforts such as captive breeding, translocation and reintroduction programs must make many difficult decisions in the face of uncertainty and under multiple constraints. The principal motivation of this thesis is to understand whether decision-analytic tools can assist in determining if and how to manage species, and to provide guidance to practitioners in the implementation of those tools.

Managing threatened species along the captive-wild spectrum

The world is in the midst of a biodiversity crisis, with an unprecedented rate of loss and decline of species globally (Barnosky et al. 2011). Since 1500 AD, over 320 terrestrial vertebrate species have gone extinct, with an average rate of population decline of 25% among other species (Dirzo et al. 2014). The IUCN Red List of Threatened Species was established in 1994 to identify species undergoing or at risk of decline. It lists habitat loss, climate change, introduction of invasive species and a range of other processes, all associated with human activities, as the main drivers of species loss (IUCN 2014b). To slow and reverse the current crisis, the discipline of conservation biology aims to develop practical solutions to protect and restore natural systems and their functions (Soulé 1985). Its ultimate goal is the persistence of self-sustaining species and communities in representative environments without human intervention. However, given the extent and rate of species declines worldwide, active interventions of varying intensity are often required, such as the deliberate movement of animals between natural areas, possibly including temporary retention in controlled conditions such as captive environments (Seddon et al. 2014).

Attempts to manage and preserve threatened species through the movement of individuals date back to the late 19th century: for example, the earliest translocation
(Text Box 1) of a bird species in New Zealand was recorded in 1863 (Miskelly & Powlesland 2013). However, widespread adoption of such species management strategies did not occur until the 1970s and 80s, with high-profile programs for captive breeding and reintroduction of charismatic avian and mammal species. Prominent examples include the golden lion tamarin in Brazil (Kleiman & Mallinson 1998), the Arabian oryx in Oman (Stanley Price 1986) and the peregrine falcon in North America (Burnham 2003). The high visibility and apparent success of these translocations spurred an increase in the number of programs worldwide involving the active management of animals, including but not limited to ex-situ actions (Seddon, Armstrong & Maloney 2007 and references therein). However, early reviews soon highlighted the high rate of failure among such programs (Griffith et al. 1989; Wolf et al. 1996), and the actual complexity of reintroductions began to be realised. The attempts of scientists to pursue and apply ecological research to assist translocations led to the development of the discipline of reintroduction biology (Seddon, Armstrong & Maloney 2007).

**Definitions**

Throughout this introduction and the chapters that follow, I use different terms to describe different aspects of threatened species management. Where possible, I follow the official terminology used by the IUCN Reintroduction Specialist Group Guidelines (IUCN 2013), whereby translocations are all human-mediated movements of living organisms from one area to another; reintroduction involves the release of individuals of a species into areas of its range where it has disappeared; and reinforcement involves the release of individuals into an existing population of the same species. I also use the term ex-situ management to describe all management strategies that include (but are not necessarily limited to) management of individuals outside their natural habitat, for example in captive facilities. Captive breeding indicates ex-situ programs in which the reproduction of individuals in captivity is deliberately sought. Other definitions exist, such as repatriation or relocation (Dodd & Seigel 1991); these are acknowledged but not used in the interest of clarity. I use the phrase management across the wild-captive spectrum as an umbrella term to indicate conservation strategies that involve different combinations of in-situ and ex-situ actions.
Naturally, the biological sciences can provide information useful for managing the small and declining populations that are the focus of conservation management, for understanding and alleviating threatening processes, and for assessing the broader effects of species translocations on the recipient ecosystems (Armstrong & Seddon 2008). Knowledge can be generated through theoretical and experimental studies: for example, mathematical modelling and experiments with populations of *Drosophila melanogaster* have been used to explore the loss of fitness of individuals resulting from adaptation to captivity (e.g. Earnhardt 1999; McPhee 2004; Robert 2009). The analysis of actual conservation programs, both *a priori* (e.g., McCarthy 1994; Canessa et al. 2014) and *a posteriori* (e.g., by estimating survival of reintroduced individuals under different management settings: Ellis et al. 2000; Maschinski, Baggs & Sacchi 2004; Le Gouar et al. 2008; Aaltonen et al. 2009) also provides vital information for managers. Such research has been assisted by the creation of two dedicated Specialist Groups of the International Union for the Conservation of Nature (IUCN): the Conservation Breeding Specialist Group (CBSG, originally Captive Breeding Specialist group) in 1979 and the Reintroduction Specialist Group (RSG) in 1988. Both seek to inform and guide managers of threatened species, through guidelines for best-practice (IUCN 2013; IUCN 2014a) and direct assistance (Byers & Seal 2003) with particular focus on species restoration programs that involve translocations with or without ex-situ components.

In general, the definition of reintroduction *biology* highlights the aim of the discipline (the preservation of biological systems) and the main focus of the scientific research that seeks to support it. However, from a management perspective the conservation of threatened species involves more than just biological issues. First, the reasons *why* such conservation is carried out may reflect different values, although all ultimately related to the persistence of species, such as the preservation of cultural and economic capital or of ecological processes (Converse et al. 2013; Ewen, Soorae & Canessa 2014). Second, non-biological factors such as limited resources also influence *how* management is applied, and are possibly the most common cause of the difficulties encountered in reintroductions (Ewen, Soorae & Canessa 2014). For example, the reintroduction of wolves to Yellowstone National Park has been hampered at different stages of implementation by human-wildlife conflict (Williams, Ericsson & Heberlein 2002).
this sense, biological science is necessary but often not sufficient for the successful recovery of species.

The complex and multi-faceted nature of species translocations is increasingly recognised and reflected in the terminology and practical approaches used. In particular, the traditional dichotomy between captive and wild management is falling out of favour, and there is increasing recognition that recovery plans for threatened species require the integration of diverse management techniques along the captive-wild spectrum (IUCN 2008). Zookeepers need to manage captive populations not only for their long-term persistence, but also considering the post-release fitness of individuals (van Heezik, Seddon & Maloney 1999; Kraaijeveld-Smit et al. 2006). Even where the ultimate aim is to make human intervention unnecessary, the continued management of wild populations post-release is an integral part of the translocation process. For example, reintroduced individuals may require long-term provision of supplementary food, habitat restoration or predator control (Armstrong et al. 2002; Armstrong et al. 2006; Ewen et al. 2014). Adequate long-term monitoring is widely recognised as necessary for the assessment of trends and success, to detect conditions where additional management may be necessary, and to reduce uncertainties that hamper ongoing management (Lyons et al. 2008). Although increasingly implemented, such monitoring is still often insufficient or sub-optimal (Ewen & Armstrong 2007; Sutherland et al. 2010; Nichols & Armstrong 2012).

As the complexity of management actions increases, managers of programs are faced with an increasing range of decisions to be made (Converse, Moore & Armstrong 2013). What type and intensity of management should be implemented for a given species? Should it include ex-situ management? How should reintroductions be managed, i.e. how many individuals should be reintroduced, of which age(s), where and when? What type of research is needed to inform reintroductions, and what research can actually be carried out? How should outcomes (such as survival rates, breeding success and population persistence) be monitored? The purpose of this thesis is to explore how the discipline of decision analysis can assist managers in answering such questions.
Structured decision making

Structured decision making (also referred to as decision analysis throughout this thesis) encompasses both the theoretical framework and the ensemble of methods for approaching decisions under uncertainty (Gregory et al. 2012). It is not a novel discipline, having been developed from operations research and utility theory in the mid-20th century (Keeney 1982). Its potential applications in conservation have been recognised for nearly three decades, and successful implementation has already been achieved in various contexts (Ralls & Starfield 1995; McDaniels, Gregory & Fields 1999; Gregory, Failing & Harstone 2008; Martin et al. 2009). A structured approach to decision making consists of an iterative multi-step process: (1) carefully defining the decision problem, (2) formulating clear and measurable objectives, (2) identifying the available courses of action, (3) evaluating their expected outcomes, (4) acknowledging uncertainty, negotiating trade-offs and constraints, (5) making a decision and (6) implementing and reviewing it.

Most importantly, decision analysis explicitly recognises that decisions are value-based. The preferences and aspirations of decision makers, represented by objectives, underpin the reason for making a decision: if no objective existed, we would have no preferences regarding the outcomes of management, and it would not matter what action we chose (Keeney & Raiffa 1993). This is particularly relevant for threatened species management, which almost invariably involves multiple stakeholders with multiple objectives (Converse et al. 2013). Decision analysis seeks to separate the reasons why management is considered (which represent the values, objectives, or policy) and the objective assessment of how best to do it (which is the fundamental role of science).

Almost invariably, conservation decisions (and captive-wild management among those) must be made under uncertainty. Our understanding of natural systems is limited, often particularly so for threatened species of which small and declining populations remain. Besides our imperfect knowledge, uncertainty also arises from the intrinsic stochasticity of those systems: for example, the demographic fluctuations of populations, or natural variability in climate and weather patterns (Regan, Colyvan & Burgman 2002).
In some cases, a decision maker must accept the existing uncertainty, consider its implications in the decision problem, and proceed as effectively as possible: making decisions under uncertainty is the general motivation for structured decision making. On the other hand, it is sometimes possible to reduce uncertainty by collecting additional information. This is a common approach in threatened species management. For example, trial releases are often used to identify and improve management strategies for translocations (Kemp et al. 2015). Decision analysis provides an ideal platform to maximise the effectiveness of the learning process, particularly through the use of value of information analysis and adaptive management.

Value of information analysis (Schlaifer & Raiffa 1961) refers to the improvement in management outcomes that could be achieved by collecting additional information, eliminating or reducing uncertainty. In its different formulations, it provides quantitative answers to (1) whether additional information should be sought, (2) which uncertainties should be targeted first and (3) how the learning process can be structured to maximise its benefits. Value of information represents a key concept in the specific case of structured decision making known as adaptive management (Holling 1978; Walters 1986). The scale and speed of threatening processes often require immediate decisions, leaving little opportunity for delaying decisions and carrying out experimental research (Grantham et al. 2009). However, it is sometimes possible to integrate managing and learning, by implementing actions and monitoring their outcomes to improve future decisions. Adaptive management is an increasingly popular concept in conservation, including threatened species management (Armstrong, Castro & Griffiths 2007; McCarthy & Possingham 2007; McDonald-Madden et al. 2010; McCarthy, Armstrong & Runge 2012; Runge 2013). However, it is implemented only infrequently and often incorrectly (Allan & Curtis 2005; Allen & Gunderson 2011; Westgate, Likens & Lindenmayer 2013).

**Thesis aims and structure**

Significantly, translocations and other strategies for threatened species management have long been considered ripe for the application of decision-analytic tools (Maguire 1986; Maguire, Seal & Brussard 1987; Maguire et al. 1988; Maguire et al. 1990).
However, their application to real-world programs has only recently gained momentum (see for example Collazo et al. 2013; Gedir et al. 2013; Servanty, Converse & Bailey 2014) and a large implementation gap remains. Decision analysis is not part of the training of most conservation biologists and managers. Consequently, most published examples of conservation applications can be traced back to a small group of cross-trained researchers, many of whom feature in the list of references or collaborators of this thesis.

Conservation agencies at national and international levels can, and increasingly do, engage decision analysts to approach broad problems (e.g. Wilson et al. 2006; Joseph et al. 2008). However, the overwhelming majority of decisions in threatened species management fall to local practitioners with local concerns, such as the feeding regime of captive-bred individuals of a given species, or the release site for a small translocation. Structured decision making approaches are highly scalable, since they are based on the same, deliberative principles that can be adapted to a range of problems (Keeney 2004). Providing threatened species managers with the concepts and tools to structure their decisions can represent a cheap, effective way of improving decision making. This thesis was written with those local practitioners in mind.

The following chapters cover different steps of the decision making process in the conservation of threatened species. They seek to cover the why, whether and how to apply different types and intensities of captive and wild management. Each chapter includes a formal description of the principles and tools used, followed by an illustration of their application to threatened species management through a number of real or hypothetical case studies.

In Chapter 2, I use decision trees and multi-criteria decision analysis to assist the decision of whether ex-situ management should be implemented for a target species. I carry out a retrospective analysis of the recovery plan for the endangered spotted tree frog *Litoria spenceri* in south-eastern Australia. The results demonstrate that in rational decision making, the whether and how are linked decisions that must be approached together. In Chapter 3 I carry out the first application of stochastic dominance analysis to threatened species management. I demonstrate how stochastic dominance, a tool
mostly used for financial applications, can be used to evaluate conservation actions. I use the recovery plan for the Yellow-bellied toad *Bombina variegata* in Italy as a simplified case study to illustrate the calculation of stochastic dominance. I then expand the *Litoria spenceri* case study presented in Chapter 2 to illustrate how stochastic dominance can be combined with structured elicitation of expert judgment to express uncertainty when empirical information is limited. The results of both case studies highlight how different tolerances to uncertainty and risk can lead to the choice of different management actions.

In Chapter 4, I carry out a complete value of information analysis for two translocation problems for threatened species. I demonstrate how value of information assists decision makers in determining whether and to what extent additional information can make threatened species management more effective. In Chapter 5, I illustrate the application of adaptive management to threatened species management. First, I apply the principles and tools of adaptive management, in increasing levels of complexity (from conceptual problem framing to quantitative optimisation of trade-offs), to four case studies along the captive-wild management spectrum. I then discuss the conditions and challenges to the implementation of adaptive management to threatened species conservation.

Finally, in Chapter 6 I carry out a cost-effectiveness analysis of the reintroduction program for the critically endangered Corroboree frog *Pseudophryne corroboree*. I use a novel integration of demographic modelling and cost analysis to optimise the design a translocation strategy that meets conservation objectives and resource constraints.

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Chapter 2

PLANNING FOR EX-SITU CONSERVATION
IN THE FACE OF UNCERTAINTY
CHAPTER 2
Planning for ex-situ conservation in the face of uncertainty

Abstract
Ex-situ conservation strategies for threatened species can be challenging, often requiring long-term commitment and financial investment to achieve management objectives. In this chapter, I interpret the decision to adopt ex-situ management for a target species as the end point of several linked decisions. Logically, one must first decide which specific management actions are most likely to achieve the fundamental objectives of the recovery plan, with or without ex-situ populations. Once this first decision has been made, one can then decide whether to establish an ex-situ population, accounting for the probability of success in the initial phase. Approaching these decisions in the reverse order (attempting to establish an ex-situ population before its purpose is clearly defined) can lead to a poor allocation of resources. I use the recovery program for the threatened spotted tree frog (Litoria spenceri) in south-eastern Australia to illustrate the rational decision framework. Among a range of possible management actions, only those including ex-situ management were expected to provide > 50% probability of species’ persistence, but they came at a greater financial cost than in-situ-only alternatives. Ex-situ strategies were also never optimal if the probability of failure in the ex-situ program prior to release was greater than 60%. Naively implementing ex-situ conservation strategies can lead to inefficient management. I provide a framework to help managers explicitly evaluate objectives, management options and the probability of success prior to establishing a captive colony of any given species.
Introduction

Ex-situ conservation strategies, such as captive breeding for reintroduction and population augmentation, are considered useful tools to help recover threatened species (Bowkett 2009; Conde et al. 2011). However, ex-situ programs have often been criticised for their low success rates and high costs (Wolf et al. 1996; Fischer & Lindenmayer 2000). Additionally, many species that are considered for ex-situ programs may have poor prospects for in-situ conservation in the short term, due to continuing threats (as is the case for amphibian species threatened by disease; Zippel et al. 2011). For such species, a long-term ex-situ commitment may be necessary, which is likely to require a substantial financial investment. In these settings, conservation agencies face high-stakes decisions about whether to initiate ex-situ actions for species. These decisions are often complicated by considerable uncertainty and the need to evaluate trade-offs among multiple conservation objectives, such as the desire to conserve multiple species and habitats (Converse et al. 2013).

In accordance with IUCN guidelines (IUCN 2013), I assume conservation in the wild, rather than in a permanent captive population, is the ultimate management objective of ex-situ conservation programs. This chapter does not address other possible roles of ex-situ populations, such as providing individuals for research or to help assist fundraising or education to support in-situ conservation. Therefore, the ex-situ programs can be usually characterised by two steps: first, establishing an ex-situ population (such as a captive-breeding colony) and second, using individuals in that program to improve persistence of the species in the wild (for example, by establishing new populations or augmenting existing ones). Management decisions must account for both steps, because their combination determines the ultimate success of a program. In particular, the initial decision – whether to implement ex-situ actions for a target species, hereafter referred to as the “entry” decision – must also consider future actions that will use individuals generated from the ex-situ colony to support wild populations. In other words, to make defensible decisions, managers must formally consider how ex-situ populations will be integrated with in-situ conservation strategies before ex-situ populations are established. Unfortunately, such forethought may be the exception rather than the rule (Snyder et al. 1996).
Decision analysis is the logical structure and ensemble of methods to formally analyse decisions, deal with uncertainty, and account for trade-offs amongst multiple objectives (Raiffa 1968). Over the last three decades, the application of decision science has been advocated for solving conservation problems at various scales (McCarthy, Possingham & Gill 2001; Bottrill et al. 2008; Moilanen, Wilson & Possingham 2009). Significantly, ex-situ conservation programs have long been identified as ripe for the application of decision-analytic methods (Maguire 1986; Maguire, Seal & Brussard 1987; McCarthy 1994; Akçakaya, McCarthy & Pearce 1995). However, the implementation of decision analysis in ex-situ conservation programs has just started to gain momentum in recent years (Smith et al. 2011; Moore et al. 2012; Converse et al. 2013; Runge 2013).

In this chapter, I present a novel decision-analytic framework for the entry-decision problem faced by managers considering ex-situ actions as part of species recovery planning. I develop a simple and generalizable decision tree that captures the conditional nature of the two-step process. Applying the decision tree to an example species, I illustrate how it can be adapted to a specific planning scenario. My goal in presenting this framework is to provide a logical structure for managers facing the entry-decision problem. My key argument is that managers should decide whether to implement an ex-situ program by considering a series of linked decisions that account for how the resulting individuals will advance conservation in the wild. Otherwise, managers risk using resources – both money and individuals of the target species – inefficiently.

Decision framework

General decision tree for species-recovery decisions

A decision tree is a graphical representation of a decision process, which calculates the expected value of alternative choices, accounting for uncertainty (Behn & Vaupel 1982). In a decision tree, the problem is represented as a flow chart, where paths traced by connecting decision nodes (choices amongst decision alternatives, conventionally represented as squares) and chance nodes (possible outcomes of stochastic processes, represented as circles) lead to a series of discrete outcomes (represented as hexagons). When a specific decision (i.e., a branch of a decision node) leads to a stochastic node
with a number of possible discrete outcomes, the expected value for that decision is the average value of the outcomes weighted by their probability of occurrence:

\[ EV_a = \sum_{j=1}^{J} o(a, j)p_j(a) \]  \hspace{1cm} \text{Eq. 2.1}

where \( EV_a \) is the expected value of alternative \( a \). Alternative \( a \) may result in any of \( J \) stochastic outcomes (e.g., persistence or extinction of a reintroduced population), where each outcome \( j \) given action \( a \) has value \( o(a, j) \) and probability of occurring \( p_j(a) \). The optimal action, then, is

\[ a^* = \arg \max_a \sum_{j=1}^{J} o(a, j)p_j(a), \]  \hspace{1cm} \text{Eq. 2.2}

that is, the optimal action has the maximum expected value (note also that \( \sum_{j=1}^{J} p_j(a) = 1 \)). Because outcome nodes reflect management objectives, the values of \( o \) are expressed using relevant units (e.g., probability of persistence or extinction, number of individuals, monetary costs, etc.). Value functions are used to express the relative preferences of decision makers for certain outcomes: where the desirability of different outcomes is not a linear function of the natural units used to describe outcomes, a non-linear value function can be developed. For example, higher probabilities of persistence can be proportionally more desirable; in this case, value might be represented as an exponential function of the actual probability of persistence. Alternatively, if the objective is de-listing of the target species, and no value is ascribed if the reduced risk is insufficient to delist the species, a step-value function can be used, taking values of 0 or 1 when the conditions for de-listing are missed or met, respectively. Methods also exist to aggregate value functions to consider multiple objectives, such as persistence probability and cost (Keeney & Raiffa 1993).

The decision tree in Fig. 2.1 represents a general scenario of an existing wild population (source) of a target species, the recovery of which may or may not benefit from ex-situ actions. When read from left to right, the decision tree represents the temporal sequence. The first decision is whether to initiate the ex-situ program. At the second tier, there are two decisions: choosing the optimal strategy for reintroduction if the ex-situ population is established, or alternatively, choosing how to manage the original population in the absence of an ex-situ colony. This decision tree formally illustrates the linked nature of the decisions, in that decisions about managing the reintroduced population or source
population follow the decision to implement ex-situ actions. In order to solve a linked decision problem one begins by solving the second tier decisions first ("rollback" procedure; Smith 2010). Intuitively, this means that, to decide what to do at the initial decision node ("entry"), one must have already identified the best management alternatives available at the second tier decision nodes, and the expected value of those optimal alternatives, conditional on the alternatives available at the initial decision node.

In the decision tree, one begins by finding the solutions for the second-tier decision nodes given both the decision to establish an ex-situ program, and the decision not to establish an ex-situ program (hereafter, I define these as the ex-situ and no-ex-situ branches, respectively). When no-ex-situ management is chosen (lower branch in Fig. 2.1), because no other chance nodes exist in the no-ex-situ branch, no further solution is required, and the value of the entire no-ex-situ branch is equal to the value of the optimal no-ex-situ action available. Given $J$ possible outcomes for the actions in the no-ex-situ branch, $a^{NE}$, this is calculated as:

$$E_{NE} = \max_a \sum_{j=1}^{J} o(a^{NE}, j)p_j(a^{NE}).$$ 

Eq. 2.3

Similarly, the first step for the ex-situ branch (upper branch in Fig. 2.1) is to evaluate the expected outcome of the optimal ex-situ action. However, for this branch there is an additional source of uncertainty. The optimal reintroduction action can only be carried out if the captive program is established and maintained successfully: therefore, one should work backwards to incorporate the probability of success into the expected outcome. The expected value for the ex-situ branch is calculated as:

$$E_{ES} = p_s \max_a \sum_{j=1}^{J} o(a^{ES}, j, s)p_j(a^{ES}, s) + (1 - p_s) * o(a^{ES}, 1 - s)$$ 

Eq. 2.4

where $s$ represents success in setting up the captive population, and $p_s$ is the corresponding probability of success. Therefore, the first term in the summation represents the outcome of the best action among those that become available if the captive population is established successfully; the second term represents the outcome given failure in establishing the ex-situ population. The actual value of the latter will depend on the objectives: for example, $o(a^{ES}, 1-s)$ could be zero in terms of persistence, or a negative value if cost, for example, was part of the objective function (because money would have been spent to initiate the unsuccessful captive program).
Thus, the solution to the “entry” problem is to initiate ex-situ conservation when the expected value of the optimal ex-situ course of action is greater than that of the best of the no-ex-situ alternatives ($EV_{ES} > EV_{NE}$). This direct comparison can usefully analyse the sensitivity of the decision to uncertainty in the parameters. For example, one could determine – given values for $o(a^{ES}, j, s)$, $p_j(a^{SE}, s)$, $o(a^{NE}, j)$, and $p_j(a^{NE})$ – what values of $p$ will result in $EV_{ES} > EV_{NE}$. There may or may not be any direct empirical measures of the required parameters for a situation of interest. When such empirical information is not available, expert judgment can help develop plausible estimates that most effectively inform these high-stakes decisions (Runge, Converse & Lyons 2011; Martin et al. 2012).

**Ex-situ management as a component of recovery plans**

Normally, ex-situ programs are initiated by removing individuals from the source population. In a mutually exclusive formulation, the ex-situ option would involve removing the entire source population and transferring it to captivity, and the no-ex-situ option removing no individuals. However, a realistic program might fall somewhere in between, with only a partial removal of the source population. In these circumstances, the smaller remaining source population may be subject to elevated risks arising from demographic and genetic stochasticity (McCarthy 1994; Akçakaya, McCarthy & Pearce 1995; Dimond & Armstrong 2007); these risks may or may not be adequately offset by the benefits of a successful ex-situ program. Managers planning the recovery strategy will need to consider the expected benefits of managing an ex-situ population, and eventually a reintroduced or augmented population, and those of managing the remaining source population. In this case, the overall expected outcome might be composed of expected outcomes for both the source and reintroduced populations, depending on the value function used. One additional possibility is that the ex-situ population is only used to supplement the original source population, resulting in a single population. For the sake of brevity, I do not take up this last possibility in detail here, but in the illustrative case study I show how to integrate it into the general framework.
Figure 2.1. Decision tree for the choice between implementing or not ex-situ actions for a candidate species. After decision nodes (rectangles), labels on arrows indicate the decision alternatives. After chance nodes (circles), labels indicate the possible outcomes of the event (here success/failure), with probability of success in brackets. Hexagons represent the rewards for successes or failures (e.g., $p_A$ and $p_A'$ respectively). The equations show the expected outcome of either branch (Eqs. 2.1-2.3). Note that here I assume “Additional feeding” and “Predator control” are the optimal ex-situ and no-ex-situ actions respectively; for clarity, I only show equations for their expected outcomes.
Figure 2.2. This figure expands the decision tree in Fig. 2.1 to account for combined strategies. When only part of the source population is removed, managers have the option of combining management of the reintroduced and source populations. Outcomes change accordingly. Here, I assume the outcome can be 0 (extinction) or 1 (persistence), and the probability of success is the cumulative probability of persistence over both populations. I also assume the no-ex-situ actions for a residual source population are the same, regardless of the ex-situ component, but their effectiveness can be modified (e.g., from $p_c$ to $p'_c$), to reflect the influence of attempting an ex-situ program regardless of its success.
Under the partial-removal scenario, if the ex-situ population fails, it will still be possible to manage the source population to avoid extinction. Figure 2.2 is an expansion of Fig. 2.1 and illustrates two additional scenarios: first, where the ex-situ component succeeds, a new set of actions becomes available, in which management can be carried out on both populations; second, where the ex-situ population is not established successfully, a set of actions will still be available to manage the remaining source population (these may correspond at least in part to the original no-ex-situ alternatives). Assuming the optimal action will be chosen in each respective set, the expected value of this “partial ex-situ” strategy can be expressed by modifying Eq. 2.4 as follows:

\[ EV_{(\text{partial ES})} = \sum_{s} \sum_{max}^{l} o(a^{\text{partial ES}},j,s)p_j(a^{\text{partial ES}},s) \] 

Eq. 2.5

The magnitude of the expected values will depend on the value functions used. In the simplest scenario, the respective outcomes in the source and reintroduced populations can be considered independent, and value can be realised in both, one, or neither of the two. For example, if the outcomes \( o \) are measured in units such as the number of individuals, the outcome of a combined strategy, involving management of both reintroduced and source populations, can be calculated as the sum of the respective outcomes (i.e., the sum of both population sizes). If persistence is the outcome of interest, this could be expressed as the cumulative probability of persistence over all existing populations. Alternatively, if the objective is to maximise the number of populations, this can be described by a step function with three levels, where \( o = 0 \) if both populations fail, \( o = 1 \) if a single population persists, and \( o = 2 \) if both populations persist.

Of course, in a realistic recovery plan with limited resources and biological constraints, the process of setting up the ex-situ population may change the effectiveness or feasibility of in-situ management of the source population. In addition to the aforementioned demographic and genetic impacts of harvesting existing populations, the financial costs of the ex-situ program might need to be covered by diverting resources from in-situ management. Synergies can occur: for example a captive program could leverage additional resources for in-situ management, or provide new knowledge that improves management of the original population. Scenarios of this type are represented in Fig. 2.2 with different probabilities of success for management of the
source population in the ex-situ branch compared to the no-ex-situ branch ($p'_j$ versus $p_j$). The ratio of $p'_j$ to $p_j$ may be greater or less than 1, depending on the particular situation.

**Illustrative example**

I illustrate the application of the decision framework using the ongoing recovery plan for the spotted tree frog (*Litoria spenceri* Dubois 1984; Anura: Hylidae). *Litoria spenceri* is endemic to south-eastern Australia and is listed as critically endangered in the IUCN Red List (Hero *et al.* 2004). Severe declines have been observed in the recent past, initially attributed to predation by introduced trout (Gillespie 2001) and habitat degradation (Gillespie 2002). Chytridiomycosis has also been implicated in the species’ decline (Gillespie & Hines 1999). A recovery plan has been developed for the species, with the objective of increasing the abundance of the wild population so its status can be downgraded to a less severe threat category (Gillespie & Clemann *in press*). As part of the species’ recovery plan, a captive breeding program was initiated at two institutions in Melbourne, Australia in 1990. One of these institutions successfully produced offspring for a trial reintroduction in 2005 at a site where local extinction had occurred (D. Hunter, *pers. comm.*).

While the entry decision for *L. spenceri* has already been made, the recovery plan provides a realistic and convenient case study for the proposed decision framework. First, the range of possible threats presents managers with a variety of available management strategies, the outcomes of which are uncertain. Second, having already achieved success in establishing an ex-situ population, it is possible to isolate the expected outcomes for the second decision node (the optimal action under both no-ex-situ and ex-situ branches) from the probability of success in establishing the ex-situ population, treating the latter as a hypothetical parameter. Therefore, a semi-retrospective assessment can be made, simulating the entry decision at the beginning of a recovery effort.

I assumed two fundamental objectives: first, maximizing the probability of persistence of the species in the wild after 20 years, and second, minimizing management costs.
These objectives were aggregated in an additive multi-attribute function (Keeney & Raiffa 1993) as:

\[ EV_{Total(i)} = EV(C)_i w_C + EV(p)_i w_P \]  

Eq. 2.6

where \( EV_i \) is the aggregate expected value of action \( i \), \( C \) and \( p \) are the expected cost and probability of persistence respectively, rescaled to the interval \([0,1]\) and \( w_C \) and \( w_P \) are weights between 0 and 1 reflecting the preference for either objective (such that \( w_C = 1 - w_P \)).

During a dedicated workshop, I asked a panel of 12 experts in amphibian conservation biology to define a range of possible management strategies for \( L. \ spenceri \), on the basis of various combinations of ex-situ and in-situ actions. The panel defined a final set of 32 alternative strategies: one “do nothing” option; three in-situ-only strategies involving in-situ management of the existing wild population alone; four strategies involving in-situ management of the existing wild population and its supplementation with captive-bred individuals; and 24 combined strategies involving management of both the existing wild population (source) and of one reintroduced population (Table 2.1). I elicited the probability of persistence and the expected cost under each strategy from the experts. It should be noted that all figures for the expected outcomes are simply indicative values for illustrative purposes. A more rigorous assessment of the recovery plan is currently being undertaken to inform specific management decisions; the set of actions considered here is not necessarily exhaustive (for example, the translocation of individuals between extant wild populations could represent another cost-effective management option).

I assessed the problem retrospectively, and investigated how variable weights on persistence of the species and management costs, different value functions and an imperfect probability of success for the ex-situ component (\( p_S \) in Eq. 2.3) would influence the choice of ex-situ or no-ex-situ actions. For each possible combination of weights on persistence and cost (\( w_P \) and \( p_S \), each between 0 and 1), I used the elicited persistence and cost to assign parameters to Eqs. 2.3-2.4, and used Eq. 2.6 to calculate the aggregate expected value of all actions. I then solved the decision tree and identified the optimal action under that parameter combination, and whether it involved ex-situ management. I carried out all analyses in R (R Development Core Team 2014).
Table 2.1. Selection of alternative management strategies for the recovery of *Litoria spenceri*, involving a range of available actions.

<table>
<thead>
<tr>
<th>Alternatives&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Do nothing</th>
<th>Habitat management</th>
<th>Trout eradication</th>
<th>Supplement source</th>
<th>Reintroduction to new site</th>
<th>Identify and maintain chytrid-free site</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Do nothing</td>
<td>✓</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2. In-situ 1</td>
<td></td>
<td>✓</td>
<td>✓</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3. In-situ 2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4. In-situ 3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5. Supplementation 1</td>
<td></td>
<td></td>
<td></td>
<td>✓</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6. Supplementation 2</td>
<td>✓</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7. Supplementation 3</td>
<td></td>
<td>✓</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8. Supplementation 4</td>
<td></td>
<td>✓</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>9. Reintroduction 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>✓</td>
<td></td>
</tr>
<tr>
<td>10. Reintroduction 2</td>
<td>✓</td>
<td></td>
<td></td>
<td></td>
<td>✓</td>
<td></td>
</tr>
<tr>
<td>11. Reintroduction 3</td>
<td></td>
<td>✓</td>
<td></td>
<td></td>
<td>✓</td>
<td></td>
</tr>
<tr>
<td>12. Reintroduction 4</td>
<td>✓</td>
<td></td>
<td></td>
<td></td>
<td>✓</td>
<td></td>
</tr>
<tr>
<td>13. Reintroduction 5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>✓</td>
<td></td>
</tr>
<tr>
<td>14. Reintroduction 6</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>15. Reintroduction 7</td>
<td></td>
<td>✓</td>
<td></td>
<td></td>
<td>✓</td>
<td>✓</td>
</tr>
</tbody>
</table>

<sup>a</sup> Alternatives 1-4 refer to management of the existing population (source). Alternatives 5 to 8 refer to management of the source, plus its supplementation with captive-bred individuals. Alternatives 9 to 15 refer to available alternatives for a new (reintroduced) population: in the analysis, I considered these as part of combined alternatives for the source and reintroduced populations. For example, alternative 2 + 12 would entail doing nothing to the source population, and carrying out habitat management and trout eradication in support of the reintroduced population.
In addition to the weights on the objectives, I also considered the possibility that managers could have a non-linear preference for increases in probability of persistence. For example, managers might be willing to allocate more resources to increasing the probability of persistence from 0 to 0.05 (a minor improvement for a population under extreme threat) than to increasing it from 0.95 to 1 (fully securing a population that is already relatively safe), all other things being equal. I modelled this attitude by repeating the full analysis described above for three different exponential value functions, indicating diminishing, linear, and increasing returns for higher probabilities of persistence, respectively. I defined the exponential value functions as:

\[ EV(p)_i = \frac{1-e^{-((p_i-\min_i p)/k)}}{1-e^{-((\max_i p-\min_i p)/k)}} \]  

Eq. 2.7

where \( p_i \) is the predicted probability of persistence for action \( i \) and \( k \) is an exponential constant used to indicate returns (Kirkwood 1997). I evaluated three possible values of \( k \): \( k = 0.2 \) (indicating diminishing returns), \( k = 100 \) (a large value used to approximate a linear value function) and \( k = -0.2 \) to indicate exponentially increasing values (illustrated in Fig. 2.3b). I assumed the value function for cost was always linearly decreasing, reflecting a situation in which the cost of a single recovery plan is a relatively minor component of the total budget of an organisation (such as a government department).

Results

On the basis of the elicited outcomes and costs for all possible actions, some ex-situ strategies were expected to result in a greater probability of persistence of \( L. \) spenceri than no-ex-situ alternatives, but this always came at a greater financial cost. For example, the best available no-ex-situ strategy (habitat management and eradication of trout) was expected to yield on average a 40% probability of persistence. In comparison, the best available ex-situ strategy (reintroduction of frogs to a chytrid-free site annually for 20 years, supported by habitat recovery and trout eradication) would lead to an average probability of persistence of 85%, but the expected cost was almost three times greater than the best available no-ex-situ action.
Figure 2.3. Solution to the decision tree for *Litoria spenceri*, across the range of weights for persistence ($w_p$) and all possible probabilities of ex-situ success ($p_S$). For each combination of these two parameters, plot (a) indicates whether the optimal choice is to implement ex-situ actions or not (ex-situ and no-ex-situ, above and below the solid lines, respectively). Note that here no-ex-situ also includes a “do nothing” option. The three solid lines reflect three possible value functions for probability of persistence, illustrated by plot (b): a linear relationship (approximated by $k = 100$ in Eq. 2.7), diminishing returns (i.e., there is less satisfaction in going from high to very high persistence; $k = 0.2$) and increasing returns (i.e., there is greater preference for very high persistence; $k = -0.2$).

When I analysed different weights in Eq. 2.6 to reflect different preferences, under the current situation of an ex-situ population of known success ($p_S = 1$), ex-situ strategies were optimal when persistence was considered more important than cost (Fig. 2.3a). Strategies involving ex-situ actions were also preferred when greater value was placed on high persistence outcomes, as opposed to improvements in the lower part of the persistence range (Fig. 2.3a). However, if the probability of success in the ex-situ establishment phase was assumed to be less than perfect ($p_S < 1$), this additional stochasticity is offset the greater persistence expected from ex-situ strategies and made them sub-optimal. In general, managers for which improving persistence has diminishing value as the species becomes more secure should avoid ex-situ strategies except under high values of $p_S$ and a strong preference for persistence over management costs (Fig. 2.3a). Conversely, if managers valued very high probabilities of persistence,
ex-situ strategies would be preferred more often in spite of their high cost (Figs. 2.3, 2.4). Doing nothing was always the preferred action when very strong emphasis was placed on costs (weight on persistence $w_P < 0.15 - 0.3$, depending on the value function used; Fig. 2.4), but this would necessarily entail a higher risk of species extinction.

**Figure 2.4.** Optimal choice between ex-situ, in-situ and do-nothing strategies for *Litoria spenceri*, assuming a linear value function for both persistence and costs ($k = 100$ in Eq. 2.7), and under all possible combinations of objective weights ($w_P$) and probability of successful ex-situ establishment ($\rho_S$).

**Discussion**

The emerging science of reintroduction biology is increasingly embracing decision-analytic methods to improve the management of captive breeding and reintroduction. However, previous studies have mostly focused on decisions about how to use ex-situ
programs to effect recovery in the wild (Rout, Hauser & Possingham 2009; Smith et al. 2011; Converse, Moore & Armstrong 2013; Runge 2013). To my knowledge, the question of whether to implement ex-situ conservation in the first instance has received little attention (Maguire 1986). The present study clearly demonstrates that these two problems cannot be considered in isolation. In the simulated retrospective decision, one could determine whether bringing *L. spenceri* into captivity would be the optimal decision only after having decided how to utilise the resulting propagules. The latter decision could only be made after comparing the expected outcomes of specific management strategies under a given set of objectives.

In the *L. spenceri* case study, with a captive program of known success and individuals available for reintroduction, all ex-situ strategies available for *L. spenceri* were expected to increase the probability of persistence of the species more effectively than any of the in-situ-only alternatives. If the problem is assessed in the current state, with the ex-situ population already established, the optimal decision is, not surprisingly, to use the captive individuals for reintroduction. However, if we consider the entry problem retrospectively, it is easy to see how different attitudes by decision makers towards the persistence and cost objectives and the possibility of failure in the ex-situ establishment phase might have changed the optimal decision. For *L. spenceri*, the analysis only serves as an example. Since the expected outcomes of alternative actions are the first driver of the optimal decision, more robust estimates of such outcomes would be required to make actual management recommendations for this species. However, the factors that influenced the optimal decision in the example are also likely to be relevant for ex-situ programs for other species. Failure to account for such dynamics can lead to sub-optimal decisions, misplaced long-term investment of limited resources, and elevated extinction risks for threatened species.

As illustrated in the case study, the optimal strategy depends on the values and preferences of managers. The definition of preferences includes a variety of possible factors affecting managers’ priorities, from personal moral values to legislation that requires the achievement of specific performance targets. In the *L. spenceri* example, ex-situ strategies did incur a greater cost than in-situ-only alternatives, but they were the only options expected to achieve persistence probabilities of 50% or higher. In contrast, strategies that did not involve ex-situ actions were predicted to achieve a lower
probability of persistence (<40%), but the estimated financial cost of implementing them was also substantially lower. This is likely to be a common situation for ex-situ programs (Snyder et al. 1996). Decision makers facing this typical conundrum should carefully consider the balance of objectives and the preference for alternative outcomes. The assessment of different value functions highlighted that ex-situ actions would be chosen only when placing proportionally greater value on high probability of persistence. Ex-situ actions would become less optimal in the case of diminishing returns for higher persistence. It is now generally accepted that reintroductions are unlikely to work unless integrated into a broader recovery plan (IUCN 2013). In support of this, the _L. spenceri_ example showed that reintroduction or supplementation were never optimal unless combined with in-situ management of the reintroduced population. The results highlight the real strength of ex-situ programs as components of broad recovery plans, aimed at securing species that cannot otherwise be recovered by in-situ management alone.

The selection of ex-situ strategies was also driven by the expectations about the establishment of the ex-situ population. Even a moderate probability of failure would have reduced the expected return for choosing strategies involving an ex-situ population. This further highlights the need to consider the sequence of linked decisions, accounting for stochasticity and uncertainty at every step in the decision process. In this case study, I simplified most outcomes as binary (success/failure). For example, I defined success in establishing an ex-situ population as the ability to produce propagules in numbers adequate to carry out a given reintroduction or supplementation action, with a binary outcome (success or failure). I particularly emphasised the importance of failures in the ex-situ phase itself. The definition of ex-situ failure may of course differ between specific management actions. Programs that rely on translocation of wild individuals might not require a stochastic node for success of a captive program, but may introduce a stochastic node to reflect the expected risk to animals during the movement phase (capture and release). At the same time, modified metrics of success might reflect more complex dependencies. For example, the number of individuals released drives reintroduction success (Sarrazin & Barbault 1996; Green 1997; Earnhardt 1999). In this case, success of the ex-situ program could be measured as the
number of captive individuals made available for release, influencing the probability of success and the expected outcomes in the release and post-release phases.

The probabilities of a given outcome (e.g., a given number of individuals is available for release) can then be assigned parameters using the available evidence. Previous studies have highlighted several drivers of success for ex-situ programs, including the size and genetic structure of the founder stock (Earnhardt 1999), available knowledge of ex-situ management and the existence of model species and adequate processes for learning (Fischer & Lindenmayer 2000), the duration of the ex-situ program (Robert 2009), the resources available (Fischer & Lindenmayer 2000) and the captive experience of individuals (Jule, Leaver & Lea 2008). Assessing all relevant knowledge transparently could help identify requirements for additional information. Research and consultations with experts could then focus on areas where additional knowledge is likely to influence the optimal decision. In this sense, ex-situ programs represent ideal candidates for adaptive management approaches (Runge 2013). The framework presented here provides a sound platform for adaptive management, in which collected data can be used to update the nodes in the decision tree and the surrounding uncertainty.

In the *L. spenceri* example, I assumed the effectiveness of in-situ management would not be reduced when the ex-situ program was in place. However, there may be both biological and financial trade-offs which mean that the probability of positive outcomes for the in-situ population may be reduced if an ex-situ population is established. Biological effects may reflect, for example, the removal of individuals from the source population. In financial terms, investing in an ex-situ program can divert resources from in-situ efforts. On the other hand, ex-situ programs that fund themselves (via exhibits, donations or other activities) might be independent of resource availability for in-situ actions, or even provide additional benefits. For example, Zoos Victoria’s Fighting Extinction program (which involves *L. spenceri*) has provided resources for both ex-situ and in-situ actions for threatened species. In many cases, captive individuals may also provide additional research opportunities, ultimately improving the effectiveness of in-situ actions (Griffiths & Pavajeau 2008). In this case, the implementation of management actions, including in-situ management of the existing populations, may
become even more effective in the presence of an ex-situ program. Such considerations can easily be incorporated into the decision making process.

Further conflicts over resource allocation may emerge in a multi-species scheme, where ex-situ management of a given species may involve opportunity costs arising from the inability to dedicate resources to the recovery of another species under a limited budget. The decision tree I have presented can also form the basis for a multi-species prioritization. Any prioritization should account for the trade-offs, opportunity costs, and synergies between species, where different taxa might co-benefit, for example, from sharing fixed costs of captive breeding and reintroduction. The complexity of such management issues can make it difficult to decide whether to initiate ex-situ strategies for candidate species. A rational approach to decision making can promote the efficient use of resources by facilitating constructive collaborations between different researchers and agencies involved in ex-situ and in-situ management decisions.

References


Chapter 3

STOCHASTIC DOMINANCE TO ACCOUNT FOR UNCERTAINTY AND RISK ATTITUDE IN MANAGEMENT DECISIONS RELATING TO THREATENED SPECIES
CHAPTER 3

Stochastic dominance to account for uncertainty and risk attitude in management decisions relating to threatened species

Abstract

Practical conservation of threatened species normally requires decision making in the face of uncertainty. Our preference for particular outcomes, such as a high probability of species persistence, and the risk we are willing to accept to achieve those outcomes, shape the way conservation decisions are made. In this chapter, I illustrate the application of stochastic dominance in conservation decision making. First, I use a frog conservation problem in Italy as a case study to show how first-order stochastic dominance can identify the optimal action when outcomes are uncertain, and second-order stochastic dominance can account for risk-averse or risk-seeking attitudes by decision makers. I then re-evaluate the recovery plan for the spotted tree frog *Litoria spenceri*, illustrated in Chapter 2, to show how stochastic dominance can be combined with structured elicitation of expert judgment to account for uncertainty. Stochastic dominance has been widely studied in economic decision making. Its broader application in threatened species management, and conservation biology in general, may encourage a transparent assessment of probabilistic uncertainty and of the preferences and attitudes of decision makers. These in turn may help ensure rational decision making and remove potential causes of stakeholder conflict.
Introduction

Conservation biology aims to develop practical solutions to protect and restore natural systems and their functions (Soulé 1985) in a setting where the predicted outcomes of actions are typically uncertain, reflecting the variability of natural systems, incomplete knowledge or vagueness in problem definition (Regan, Colyvan & Burgman 2002). For some actions, success can protect systems but failure can accelerate their demise. In the context of threatened species management, consider for example the risk of introducing new diseases during the translocation of individuals, (Cunningham 1996) or the potential damage from trophic cascades following eradication of invasive species (Bergstrom et al. 2009).

Expected utility theory (EUT: Von Neumann & Morgenstern 1944) deals with decision making under probabilistic uncertainty. In EUT, such decisions are represented as lotteries, in which a decision can result in a series of outcomes, each with a given probability of occurring (with probabilities summing to 1 for any action). Consider an example in which managers need to choose between three conservation actions: action A will preserve either two or six species with equal probability ($p=0.5$); action B will preserve either twenty or zero species with a probability of 0.2 and 0.8 respectively; action C is certain to preserve four species (Fig. 3.1a). In general, any conservation decision maker faced with such a problem will seek to maximise the number of species preserved; however, their risk attitude will also inform their choice of action (Pratt 1964). A risk-neutral decision maker will rate all actions equally: the expected outcome (the average of the possible outcomes weighted by their probabilities) is the same (four species). A risk-averse decision maker may prefer action C: for them, avoiding a poor outcome is most important. A risk-seeking decision maker may choose action B, preferring a chance of achieving the best possible outcome.

Within EUT, the attitudes of any rational decision maker can be represented by a utility function, which describes the satisfaction resulting from probabilistically uncertain outcomes of the available actions (Von Neumann & Morgenstern 1944). Rational decision makers will seek to maximise the utility of their decisions. In the above example, a risk-neutral decision maker may obtain the same utility from all actions,
since they have the same expected value. The utility function of the risk-neutral decision maker is linear (Fig. 3.1b). A risk-averse decision maker will obtain greater utility by avoiding poor outcomes, so their utility function will be concave. Conversely, a risk-seeking decision maker will have a convex utility function, reflecting the greater preference for highly positive outcomes (Fig. 3.1b). Although stakeholders may share the same broad conservation objective, failure to openly recognise differences in risk attitude might lead to conflict and hence undermine conservation efforts. Note the difference between utility functions and the value functions expressed in Chapter 2 (Eq. 2.7). Utility functions represent attitudes towards different possible outcomes; value functions represent attitudes towards different levels of expected outcomes. The former address uncertainty explicitly, while for the latter uncertainty is hidden in the calculation of expected outcomes.

![Figure 3.1](image)

**Figure 3.1.** Panel (a) represents a hypothetical lottery with a decision between three alternative actions with different outcomes (numbers of species preserved) depending on success (with probabilities indicated by branch labels). Expected outcomes are calculated as the mean of possible outcomes weighted by their respective probabilities (e.g., for action A $6 \times 0.5 + 2 \times 0.5 = 4$). Panel (b) represents the utility functions of risk-averse, risk-neutral and risk-seeking decision makers as indicated by labels.
The potential influence of risk attitudes on conservation decisions, including those pertaining to threatened species management, is widely recognised (Mace & Hudson 1999; Akçakaya et al. 2000; Finnoff et al. 2007; Duncan & Wintle 2008); however, they are rarely openly addressed in real-world conservation decision making (Greiner, Patterson & Miller 2009). This may reflect difficulties in eliciting the utility functions of decision makers (Durbach & Stewart 2009). The definition of utility can be problematic for complex outcomes and non-monetary values; moreover, since utilities represent the preferences of individuals, the extent to which they can be compared and aggregated has long been debated in decision science (Eisenberg 1961). This can present a problem for conservation, where decisions often involve multiple stakeholders. Such difficulties may deter managers unfamiliar with decision theoretic methods from formally articulating uncertainty and risk attitudes.

Stochastic dominance analysis (SD; Levy 1998) can facilitate the explicit evaluation of risk in conservation decisions, as it does not require a full elicitation of the utility function, but only a progressive definition of its parameters. It has been widely applied in economics (Levy 1992), but has had very limited application in conservation, in spite of its potential value (Benítez et al. 2006; Knoke et al. 2008; Yemshanov et al. 2012).

In this chapter, I illustrate the use of SD to assist decisions in the management of threatened species. First, I use a hypothetical example to explain the concepts and calculation of SD. I then use SD to expand the analysis of the recovery plan for the spotted tree frog *Litoria spenceri* presented in Chapter 2. Finally, I discuss the advantages and limitations of this method when compared to other approaches to decision making under uncertainty.

**Stochastic dominance**

Stochastic dominance is a decision-analytic tool that allows the ordering of decisions with different probabilistic outcomes (the lotteries described in the previous example). To explain the basic concepts of stochastic dominance, I consider the case of the Apennine yellow-bellied toad *Bombina variegata* in the northern Italian region of Liguria as an illustrative example. This species has undergone a marked decline in the region, possibly as a result of habitat loss (Canessa et al. 2013). A range of conservation
actions for this species are underway (Arillo et al. 2011); here, I present a simplified version of the decision problem for illustrative purposes. I assume the objective is to maximise the probability of persistence by the subspecies over the next 100 years. To achieve this objective, I consider three possible actions: (1) do nothing; (2) carry out in-situ management on the extant population only, for example by reducing vegetation to increase insolation and improve larval survival; (3) carry out a translocation of some individuals from extant populations to restored sites to establish new populations. The expected outcomes of the three actions could be assessed quantitatively, for example through population viability analysis; hypothetical results are presented in Fig. 3.2a. Choosing no action might result in a relatively high probability of extinction. In-situ management alone may be effective locally, but less so at the regional scale, due to the small size of extant populations and their isolation. Although translocations could increase the probability of persistence, they also entail potential risk such as the introduction and spread of the pathogenic fungus *Batrachochytrium dendrobatidis* throughout the region, including to extant sites where it has not so far been detected (Canessa, Martel & Pasmans 2013). Indeed, the first report of mortality in *B. variegata* by *B. dendrobatidis* concerned wild-caught individuals within a reintroduction effort (Stagni et al. 2004). As a result, the potential outcomes of translocation are more uncertain than those of the other actions (Fig. 3.2a).

**First-order stochastic dominance**

We can assess the outcomes of candidate actions by comparing their cumulative distribution functions (CDFs). For any value $y$ over the interval $[a,b]$, the CDF of a function $f(x)$ is the cumulative probability that the value of $f(x)$ is not greater than $y$. In other words, the CDF of the outcomes of an action for a given value of the objective represents the probability that the outcomes of that action will be equal or worse than that value. For example, the CDF at 0.5 is 0.02 for translocation and 0.2 for no action (Figure 3.2b). In other words, if we choose translocation, there is a 2% chance that the resulting probability of persistence will be smaller or equal to 0.5; if we choose no action, there is a 20% chance that the probability of persistence will be smaller or equal to 0.5. Therefore, the probability of persistence is more likely to be greater than 0.5 when translocating than when taking no action. When the objective is to maximise the
value of $y$ (in this case persistence), the rational choice is to select the action with the smallest CDF for a given value of $y$. Assuming that greater utilities will always be preferred (more is better) implies that the utility function is non-decreasing and its first derivative $u'$ is always positive. Under this assumption, Action A has first-order stochastic dominance (FSD) over Action B if:

$$F_A(x) \leq F_B(x) \text{ for all } x,$$  
Eq. 3.1

$$F_A(x) < F_B(x) \text{ for at least one value of } x$$

where $F_A(x)$ and $F_B(x)$ are the CDFs of the utility functions for actions A and B respectively, calculated as $F(x) = \int_a^x f(x) \, dx$ (Levy 1998). In other words, A dominates B at the first order when it has a smaller or equal CDF for any value of the objective $x$ (in this case persistence), meaning that the CDFs of A and B do not cross.

![Figure 3.2](image)

**Figure 3.2.** Panel (a) shows the distribution of hypothetical expected outcomes for no action (NA, red), in-situ management (IS, green) and translocation (T, blue) for *B. variegata*. Outcomes are expressed as the probability of persistence of the species. Panel (b) shows the cumulative density function of the distributions in panel (a). Where CDFs do not cross first-order stochastic dominance exists: here, NA is dominated by both IS and T, which in turn are non-dominant to each other.
In the case of *B. variegata*, the preference assumption is valid, since the recovery objectives for the species is to maximise the probability of persistence. We can then calculate the CDFs of the distributions of outcomes for the three actions and compare them. Across all values, the CDFs of translocation and no action do not cross: translocation has at least the same probability of persistence as no action at every point along the x-axis, and a greater probability at one or more points (Fig. 3.2b). Therefore, Eq. 3.1 is verified, and translocation first-order stochastically dominates no action. Translocation is the optimal decision for any rational decision maker, so there is no need to elicit their risk attitude. Similarly, in-situ management first-order stochastically dominates no action. Since no action is dominated by all other actions, we do not consider it further.

However, the CDFs for in-situ management and translocation cross; therefore, Eq. 3.1 is not verified and neither action stochastically dominates the other at the first order (Fig. 3.2b). In this case, we need to take into account risk attitudes: are managers willing to take the gamble of the translocation, or would they choose the less risky, but potentially less rewarding option of in-situ management? Note that a risk-neutral decision maker in this case would be indifferent to the level of risk, and would simply select the strategy with the highest expected return (the highest mean persistence). Here, translocation has a mean persistence of 0.61, compared to 0.55 for in-situ management alone. Consideration of additional objectives (such as the cost of each action) may also influence the decision; in this case, the utility function might reflect multiple objectives rather than persistence only.

*Second-order stochastic dominance*

Second-order stochastic dominance (SSD) requires knowledge of the general risk attitude of the decision maker; that is, whether they are risk-averse or risk-seeking.

A risk-averse decision maker, when given two lotteries with the same expected outcomes and different ranges of outcomes (as in Fig. 3.1a), will choose the action that is less likely to result in a poor outcome. This preference for minimizing risk implies a concave utility function with a second derivative that is always negative (Fig. 3.1b). Under this assumption of risk aversion, we can compare actions using the ascending
integral of the CDF, $\int_a^x F(x)\,dx$. Action A has *ascending second-order stochastic dominance* over Action B if

$$\int_a^x F_A(x)\,dx \leq \int_a^x F_B(x)\,dx \quad \text{for all } x,$$

Eq. 3.2

and

$$\int_a^x F_A(x)\,dx < \int_a^x F_B(x)\,dx \quad \text{for at least one value of } x \text{ (Levy 1998)}.$$

In this example, the integrals of the CDFs for in-situ management and translocation cross (Fig. 3.3a). Therefore, Eq.3.2 is not verified and a risk-averse decision maker could not use SSD to discriminate between these two actions.

Conversely, a risk-seeking decision maker will prefer higher outcomes (in this case, a higher probability of persistence) even if these involve risks: this attitude implies a convex utility function with a second derivative that is always positive. Under this condition, we can compare actions using the ascending integral of the complementary CDF ($\int_x^b F(x)\,dx$; Wong & Li, 1999), representing the integral of the cumulative probability that the outcome of an action is greater than a value $x$. Action A has *descending second-order stochastic dominance* over Action B if

$$\int_x^b F_A(x)\,dx \leq \int_x^b F_B(x)\,dx \quad \text{for all } x,$$

Eq. 3.3

and

$$\int_x^b F_A(x)\,dx < \int_x^b F_B(x)\,dx \quad \text{for at least one value of } x.$$

For this example, the descending integral of the CDFs for translocation is always at least equal to that of in-situ management, and is greater for some values of persistence (Fig. 3.3b). The integrals of the CDFs do not cross: therefore, translocation has descending SSD over in-situ management, and a risk-seeking decision maker would choose it as the preferred action.

In this case, I was able to identify dominating actions at the second order for a risk-seeking decision maker but not for a risk-averse one. If we knew the decision maker was risk-averse, a rational choice between in-situ management and translocation could be sought by exploring third-order SD (Whitmore 1970). This would require us to elicit
the shape of the marginal utility function of the decision makers (Von Winterfeldt & Edwards 1986). This corresponds to making assumptions about the third derivative of the utility function (Whitmore 1970). Such assumptions, and those for higher-order SD, may be more difficult to interpret and apply to conservation decisions.

**Figure 3.3.** Second-order stochastic dominance for the outcomes of no action (NA, red), in-situ management (IS, green) and translocation (T, blue) for *B. variegata*. Curves represent the integrals of the CDFs depicted in Fig. 3.2b. Panel (a) shows ascending SSD for a risk-averse decision maker: IS and T are non-dominant to each other at SSD, since their curves cross. Panel (b) shows descending SSD for a risk-seeking decision maker, where translocation is the dominant action, since its curve does not cross the others.

**Stochastic dominance and formal expert elicitation**

This second case study illustrates how stochastic dominance can be paired with structured methods for the elicitation of uncertainty from experts to provide a comprehensive assessment of probabilistic uncertainty and risk attitude. In Chapter 2, I used expected outcomes to identify the best management strategy for the spotted tree frog *Litoria spenceri* in south-eastern Australia. The analysis relied on the average expectations elicited from a panel of experts during a workshop. In addition to the best
estimates used in Chapter 2, I elicited from experts an assessment of uncertainty through the use of a modified Delphi technique (McBride et al. 2012). For the expected outcomes and costs of each management strategy, experts were asked to provide their best estimates (i.e., the values presented in Chapter 2), as well as realistic minimum and maximum values for the estimates, and a level of confidence that the true value of the estimate was included in the interval. For example, for action A an expert may estimate the probability of persistence as 0.5, with a minimum of 0.4 and a maximum of 0.65, and be 80% confident that the true probability of persistence falls between 0.4 and 0.65.

The four-point estimates provided by each expert were then normalised to allow comparison, using linear extrapolation (McBride et al. 2012). I calculated 100% confidence intervals $\alpha_{abs}$ and $\beta_{abs}$, containing all possible values of the estimates, as

$$\alpha_{abs} = \gamma - (\gamma - \alpha)\left(\frac{c}{\rho}\right)$$

$$\beta_{abs} = \gamma + (\beta - \gamma)\left(\frac{c}{\rho}\right)$$

where $\gamma$, $\alpha$, $\beta$ and $\rho$ are the elicited values for best estimates, lower and upper bounds and confidence respectively, and $c$ is the confidence desired (here $c=100\%$). I characterised the uncertainty surrounding the estimates for each expert by fitting a beta-PERT distribution to the normalised estimates. The beta-PERT is an extension of the beta distribution developed specifically for treatment of elicited expert opinion (Vose 1996). I truncated the distributions as necessary (to the interval $[0, 1]$ for probabilities, and to non-negative values for costs). After assessing the presence of outliers, I then used linear pooling (McBride et al. 2012) to aggregate the best estimates and 100% intervals across experts for each action. The adoption of linear pooling was justified by the two-stage elicitation process, in which the group discussion ensured no divergence of interpretation and facilitated sharing of expert knowledge. The final outcome of the elicitation process consisted of two full distributions, describing the expected probability of persistence and cost respectively for each alternative strategy.

Stochastic dominance can then be used to compare those distributions and identify the best decision under uncertainty (first-order SD) and for a given risk attitude (second-order SD). For clarity, here I restricted the application of stochastic dominance to a
representative subset of five strategies: (i) doing nothing, (ii) full in-situ management of the existing population only, (iii) supplementation of the existing population with full in-situ management, (iv) reintroduction to a new site with no further management and (v) reintroduction to a new site and full in-situ management of both populations. I considered the probability of persistence as the only outcome. I repeated the analysis for the current state of the recovery plan, in which the ex-situ component has already achieved success ($p_s=1$ in Eq. 2.5), and for a retrospective example where the ex-situ component has equal probability of failing or succeeding ($p_s=0.5$). I considered value as a linear function of persistence (Eq. 2.7), and compared the best choice for both risk-averse and risk-seeking attitudes.

When the success of ex-situ establishment is known ($p_s=1$), the outcomes of actions can be discriminated easily. The cumulative distribution functions of all actions do not cross (Fig. 3.4b), indicating first-order dominance between all pairs. Among the selected set of management strategies, reintroduction paired with in-situ management of both the existing and source populations has first-order dominance over all other actions (Fig. 3.4b). Therefore, it represents the best action regardless of the risk attitude of the decision maker (Fig. 3.4c-d).

Conversely, the possibility of failure in the phase of ex-situ establishment ($p_s=0.5$) increases risk. The cumulative distribution functions for the selected actions now cross in two cases: between in-situ management with and without supplementation, and between reintroduction with and without in-situ management (Figure 3.5b). However, the latter actions still dominate the others at the first order of SD (Figure 3.5b), so the choice is restricted to this pair. For a risk-averse decision maker, reintroduction with in-situ management of both source and reintroduced population is the best action, since it has second-order dominance (Figure 3.5c). Conversely, a risk-seeking decision maker cannot distinguish between the two actions at the second order of SD, since the descending integrals of the CDFs cross (Figure 3.5d). However, the absolute difference between the two actions is marginal, suggesting the decision maker may be indifferent to the choice, or discriminate based on cost preferences instead.
Figure 3.4. Stochastic dominance analysis for the *Litoria spenceri* example, assuming known success of the ex-situ establishment phase \( (p_s = 1 \text{ in Eq. 2.5}) \). Outcomes are expressed as the probability of persistence of the species. Panel (b) shows the cumulative density function of the distributions in panel (a). Panels (c) and (d) show the ascending and descending integrals of the CDFs in panel (b), indicating stochastic dominance for risk-averse and risk-seeking decision makers, respectively. Actions indicate doing nothing (1), full in-situ management of the existing population only (2), supplementation of the existing population with full in-situ management (3), reintroduction to a new site with no further management (4) and reintroduction to a new site and full in-situ management of both populations (5).
Figure 3.5. Stochastic dominance analysis for the Litoria spenceri example, assuming equal probability of success or failure of the ex-situ establishment phase ($p_s = 0.5$ in Eq 2.5). Outcomes are expressed as the probability of persistence of the species. Panel (b) shows the cumulative density function of the distributions in panel (a). Panels (c) and (d) show the ascending and descending integrals of the CDFs in panel (b), indicating stochastic dominance for risk-averse and risk-seeking decision makers, respectively. Actions indicate doing nothing (1), full in-situ management of the existing population only (2), supplementation of the existing population with full in-situ management (3), reintroduction to a new site with no further management (4) and reintroduction to a new site and full in-situ management of both populations (5).
Discussion

Stochastic dominance provides a relatively simple tool to assist conservation decisions in the face of uncertainty and risk. Its potential for environmental management has been recognised by previous studies regarding invasive species (Yemshanov et al. 2012), fisheries management (Baldrsson & Magnússon 1997) and compensation schemes for farming (Benítez et al. 2006) and forestry (Knoke et al. 2008). Stochastic dominance could prove a valuable tool for a range of decision problems in the conservation of threatened species. Virtually all decisions regarding the choice of management actions will be surrounded by uncertainty, as illustrated in the recovery plan for L. spenceri. Risk attitudes may be particularly important for particular types of management, such as translocations, as illustrated in the B. variegata example, assisted colonization (Seddon 2010) and the prioritization of conservation actions (Joseph, Maloney & Possingham 2008).

Expected outcomes are often used to assess conservation decisions in the face of uncertainty (Burgman 2005), as they provide an intuitive method to account for probabilistic outcomes. In Chapter 2, I used expected outcomes to evaluate management actions for L. spenceri with multiple objectives and sources of uncertainty. However, expected outcomes do not immediately convey information about uncertainty or risk attitude: as highlighted by the example lottery in Fig. 3.1a, mean outcomes assume risk neutrality. An alternative approach in economics is to take the variance or standard deviation as a measure of risk, evaluating the mean-variance relationship over a defined degree of risk-aversion (Markowitz, 1987; see Leskinen et al. 2006 for a conservation application). However, the variance is an adequate measure of risk only for normal or symmetric distributions, which are less likely to be encountered in many conservation outcomes. Conversely, stochastic dominance uses the full distributions of outcomes instead of one or two moments of the distribution.

In addition, a mean-variance analysis still requires a complete formulation of utility functions through indifference curves (Markowitz 1987). In this sense, possibly the greatest benefit of applying a non-parametric method such as SD to conservation decisions is in encouraging an explicit treatment of uncertainty and risk attitude by
reducing the elicitation burden. Increasing orders of SD can be tested by progressively eliciting only limited information about the attitudes of decision makers (Hildebrandt & Knoke 2011). Testing for FSD only requires an assumption of non-decreasing utility, and the calculation of CDFs for predicted outcomes. Full probability distributions can be obtained from a wide range of quantitative analyses, as suggested in the hypothetical example for B. variegata, or from formal methods for the elicitation of expert judgment as illustrated by the four-point elicitation used for the L. spenceri problem.

For those actions that are not dominated at the first order, SSD adds an assumption about the general shape of the utility function (concave or convex). For example, there may be little meaning in comparing the utility functions elicited from a group of stakeholders; however, the same group might reach a consensus about general risk-aversion, and such a simple definition is sufficient for a test of SSD. A general definition of risk aversion may also intuitively represent situations in which the preferences of decision makers are dictated by mandates (such as institutional commitments to the precautionary principle). The practical implementation of SD reflects this process of pairwise comparisons at increasing orders of SD (Porter, Wart & Ferguson 1973; Levy 1998). Comparisons first identify a set of non-dominated actions for FSD, then exclude actions dominated for SSD, and so on (e.g. Yemshanov et al., 2012). The main limitations are computational, for large-dimensional problems, and the difficulty of interpreting the assumptions of higher-order SD.

The specification of utilities and risk attitudes might be seen as an unnecessary complication in the context of specific decision problems (Durbach & Stewart 2009). Pannell (2006) found “flat payoffs” to be predominant in agricultural production; the outcomes of different actions are similar enough that deviating from the optimal action will have little effect on utility, and risk attitudes will be irrelevant. This was verified in the L. spenceri example, where close similarity between the expected outcomes of actions 5 and 6 suggested decision makers may be indifferent as to which of the two is chosen. However, more marked differences may result from considering additional objectives (such as management costs). Moreover, even where flat payoffs are verified for all objectives, the appeal of SD as a simple decision support tool remains. Rather than discovering the irrelevance of uncertainty after undertaking the onerous task of
eliciting utility functions, FSD can discriminate actions by simply comparing their cumulative distributions.

In the examples presented, risk-averse and risk-seeking decision makers may choose different actions, yet both are rational under their respective preferences and attitudes. Unless the uncertainty surrounding outcomes is expressed and risk attitudes are approached transparently, such conflicts may not be resolved. Consider for example the debate concerning “triage” of threatened species (Joseph et al., 2008). Proponents of triage apply rational decision making to find the set of management actions that maximise the number of species conserved: this might imply that species with little chance of recovery may be less likely to be allocated resources (Bottrill et al. 2009). Critics of triage argue that allocation of resources should account for currently unforeseen breakthroughs that may eventually allow recovery (Jachowski & Kesler 2009; Parr et al. 2009), even if this means a greater chance of poorer overall returns by spreading resources over a larger set of species. It is possible that both sides consider different objectives (overall conservation and species-specific conservation respectively); that they differ in the predicted outcomes of actions (such as the probability and effectiveness of undetermined breakthroughs); or that they differ in their risk attitude (for example, risk aversion may differ when managing endangered or common species). Tulloch et al. (2014) found that lower risk tolerance would reduce the total number of species protected, since efforts would concentrate on the higher-risk and more expensive species. Future research could investigate risk attitudes in other areas of conservation, and explore violations of the assumption of rational decision making that is fundamental to expected utility theory and stochastic dominance. For example, conservationists are unlikely to be immune to irrational decision making behavior, such as variable risk attitudes depending on how problems are framed (Tversky & Kahneman 1981) or a tendency to overvalue certain outcomes compared to uncertain ones (Kahneman & Tversky 1979).

Moreover, recognizing that decisions reflect utility rather than expected outcomes alone reveals that the definition of risk depends on preferences, and does not simply coincide with predicted outcomes. The use of decision analysis can help by promoting a clear separation between preferences and predictive science (Gregory et al. 2012). If policy
can be defined explicitly and transparently through utilities and risk attitudes, managers can take full advantage of quantitative predictive tools that incorporate the full range of probabilistic uncertainty.

**References**


Chapter 4

CALCULATING THE VALUE OF INFORMATION IN TRANSLOCATION PROGRAMS
CHAPTER 4

Calculating the value of information in translocation programs

Abstract

The managers of threatened species programs continually seek and advocate further research, under the assumption that obtaining more information will reduce uncertainty and lead to better decisions. Value of information (VoI) analysis can be used to quantify how additional information may improve management outcomes: in spite of its potential, this method is still underused in environmental decision making. In this chapter, I calculate the value of information for two common problems in the translocation of threatened species: (i) translocating a frog species when there is uncertainty about the presence of disease at the destination site and (ii) learning about post-release survival in the reintroduction of an endangered turtle.

In each case study I present two measures of the VoI. The expected value of perfect information is a calculation of the expected improvement in management outcomes that would result from access to perfect knowledge. The expected value of sample information calculates the improvement in outcomes expected by collecting a given sample of new data. I place particular emphasis on the use of Bayesian updating to incorporate new information. Calculating the VoI requires an explicit formulation of management objectives and actions. Uncertainty must be clearly structured and its effects on management outcomes assessed. The VoI depends on our current knowledge, the quality of the information collected, and the expected outcomes of the available management actions. Threatened species programs may benefit from additional information, but the collection of information can require significant investments of resources. VoI analysis assists managers in deciding whether these investments are justified.
**Introduction**

Our knowledge of the ecology of threatened species is almost invariably limited by the complexity and variability of the species themselves and of the natural systems in which they occur. As a result, uncertainty affects decision making at every level of threatened species conservation, from global protection planning (Wilson *et al.* 2006) to species-level recovery plans (Chadès, Curtis & Martin 2012). It is natural, then, that conservation biologists and managers continually advocate further research, assuming that learning will reduce uncertainty and result in better decisions. However, the speed and magnitude of threatening processes often require immediate decisions with limited time and resources to gather information (Martin *et al.* 2012). The learning process itself may be expensive, and the information collected may be of limited utility. So when is the collection of further information actually warranted?

Value of information (VoI) analysis (Schlaifer & Raiffa 1961) can provide a rigorous answer to this question. This method has been applied to health and economic problems (Yokota & Thompson 2004; Bratvold, Bickel & Lohne 2007). A typical example is the decision of whether to adopt widespread screening for certain types of cancer, trading off the benefits of increased screening levels and their economic costs and discomfort for patients (Hassan *et al.* 2009). The environmental management literature is increasingly exploring the concept of VoI (Mäntyniemi *et al.* 2009; Runge, Converse & Lyons 2011; Johnson *et al.* 2014; Williams & Johnson 2014). However, as a management tool VoI remains underused, possibly because managers are not familiar with the decision-theoretic principles and notation used in the existing studies, or because they find the calculations technically challenging. In this chapter, I calculate the VoI in two examples of active threatened species management. I first provide the formal definitions of the metrics. I then use two examples to illustrate the concepts and calculations of two VoI metrics, the expected value of perfect information and of sample information. I detail in particular the use of Bayesian updating, to illustrate how the learning process in a real-world context influences the actual value of information.
Definitions

Value of information analysis is a component of structured decision making, the ensemble of theory and methods for rational decision making under uncertainty (Raiffa 1968). In particular, VoI relies on the concept of the expected outcome of actions. Making a decision implies choosing one of a set of candidate actions to achieve one or more specified objectives. The expected outcomes of each action will be affected by uncertainty about the system. This uncertainty can be represented as alternative hypotheses about the system, each with a given probability of being true (prior belief). Hypotheses might be different states of the system (e.g. the number of individuals in a population at a given time), competing models of a system (e.g., the type of density-dependence in a population), or competing values for a given parameter of a model (e.g., sampling uncertainty on an estimated survival rate). Hereafter I use $V(a, s)$ to refer to the value (or outcome) of taking action $a$ under state $s$. These values are measured in units compatible with management objectives (for example, probability of extinction).

The expected value of an action under uncertainty is calculated as:

$$\mathbb{E}_s[V(a, s)] = \sum_{s=1}^{N} [V(a, s) \cdot p_s]$$  \hspace{1cm} \text{Eq. 4.1}

where $\mathbb{E}_s$ indicates that the expected value $\mathbb{E}$ is the sum of the possible $V(a, s)$ for action $a$ across the variable $s$ (i.e., across all $N$ states of the system), each weighted by the respective probability $p_s$ of each state $s$ being true. A rational decision maker will choose the action with the highest expected value. Therefore, the value of the decision under uncertainty is calculated as:

$$EV_{\text{uncertainty}} = \max_a \mathbb{E}_s[V(a, s)]$$  \hspace{1cm} \text{Eq. 4.2}

where $\max_a$ indicates that the action $a$ with the highest expected value under uncertainty is chosen (again, the subscript $a$ indicates that the maximum is selected across the variable $a$, that is, all possible actions).

The VoI represents the difference between the expected management outcomes when a decision is made only on the basis of the original (prior) information, and when new information is gained (Yokota 2004). The expected value of perfect information (EVPI)
is the expected benefit of eliminating uncertainty entirely. Assuming that the true state of the system was known, the optimal action could be identified immediately as the one with the highest value. In this case, the choice would not be made on the expected value $\mathbb{E}$ under uncertainty, but by choosing the action $a$ with the maximum value $V$ for the known state of the system: i.e., $\max_a V(a,s)$. Since the true state is unknown prior to resolving the uncertainty, the \textit{expected} value of a decision made under certainty is calculated as

$$EV_{\text{certainty}} = \mathbb{E}_s [\max_a V(a,s)] = \sum_{s=1}^{N} [\{\max_a V(a,s)\} \cdot p_s] \, . \quad \text{Eq. 4.3}$$

Conceptually, one calculates the value of the best action, conditional on each hypothesis being true, then calculates the weighted sum of those values, where the weight is the prior belief in the respective hypotheses. EVPI is then calculated as the difference between the expected values under certainty and uncertainty (Raiffa 1961):

$$EVPI = EV_{\text{certainty}} - EV_{\text{uncertainty}} = \mathbb{E}_s [\max_a V(a,s)] - \max_a \mathbb{E}_s [V(a,s)] =$$

$$= \sum_{s=1}^{N} [\{\max_a V(a,s)\} \cdot p_s] - \max_a \sum_{s=1}^{N} [V(a,s) \cdot p_s] \quad \text{Eq. 4.4}$$

The respective positions of $\max_a$ and $\mathbb{E}_s$ in $EV_{\text{uncertainty}}$ and $EV_{\text{certainty}}$ highlight how the action with the maximum outcome ($\max_a$) is taken respectively before and after uncertainty has been resolved ($\mathbb{E}_s$).

While EVPI provides a useful measure of the maximum possible benefit of resolving uncertainty, achieving perfect information is seldom possible. The expected value of sample information (EVSI) calculates the expected improvement in management outcomes that could be obtained by gaining access to a given amount of additional information before making a decision. EVSI is calculated as:

$$EVSI = \mathbb{E}_x \{\max_a \mathbb{E}_{s|x} [V(a,s)]\} - \max_a \mathbb{E}_s [V(a,s)] \quad \text{Eq. 4.5}$$

where $x$ represents the sample information and the first expectation $\mathbb{E}_x \{ . \}$ averages over all the possible values that the sample $x$ can take. Note that the second term of Eqn. 5 is the same as in Eqn. 4: the expected outcome in the current state of knowledge is the
reference term for any formulation of VoI. To calculate EVSI, we need to perform a Bayesian pre-posterior analysis (Berger 1985). I explain this procedure in detail in the following case studies.

**Value of information for wildlife disease risk assessments**

First, I demonstrate the concepts and application of VoI using a simple example in which uncertainty is clearly defined as mutually exclusive states of the system: in this case, the presence or absence of disease when managing a threatened species. The amphibian chytrid fungus *Batrachochytrium dendrobatidis* has been implicated in the decline and extinction of several amphibian species worldwide (Skerratt *et al.* 2007). In the absence of effective methods for removing the threat in-situ, several captive breeding and wild-to-wild translocation programs have been initiated worldwide, to prevent immediate extinction and eventually re-establish and reinforce declining or extinct populations (Zippel *et al.* 2011). However, decisions concerning such active movement of individuals must account for the risk of disease outbreaks that may nullify or reduce the effectiveness of reintroductions.

I consider the hypothetical case of a threatened frog species that occurs in one location within a protected area. Managers aim to maximise the overall number of individuals of the species within the protected area at the end of a 10-year period. To achieve this objective, they might seek to establish a new population within the protected area by translocating some individuals to a new site. However, chytrid might be present at the new site, so any potential management action must be evaluated in light of two possible states of the system: chytrid presence or absence. The managers’ prior belief of the disease being present at the new site is 0.5, reflecting the background infection rate of sites in the region of interest.

For simplicity, here I consider two actions: translocating 50 individuals or doing nothing (in practice, we could do the calculation for any number of actions). Prior to VoI calculations, managers need to determine the value $V$ (here the total number of individuals) predicted for each action under each scenario (Table 4.1). When doing nothing, they expect the existing population to remain at its current size (with a mean expectation of $V=100$ individuals). When translocating, if chytrid is absent from the
new site, then the released individuals will establish and population model predictions indicate that we can expect to have 135 individuals over the whole protected area at year 10, reflecting the high suitability of the new site ($V=135$). Conversely, if chytrid is present at the new site, the new population will fail to establish. Due to the removal of individuals for the translocation, the existing population will also decrease; here I assume that model predictions indicate a total of 55 individuals by year 10 ($V=55$).

Based on the values of $V$ for each action, and the prior belief in chytrid presence, managers can identify the best decision under uncertainty. Using Eq. 4.1, the expected outcome for the translocation is $55 \times 0.5 + 135 \times 0.5 = 95$ individuals. This is less than what is expected if no animals are translocated ($V=100$ individuals), so the optimal decision under the current state of uncertainty would be not to translocate ($EV_{\text{uncertainty}}=100$; Table 4.1).

**Expected value of perfect information**

If managers could know whether chytrid is present or not at the new site, they would be sure of choosing the best action. If chytrid were absent, they would choose to translocate, since this action leads to 135 individuals, compared to 100 for no translocation. If chytrid were present, they would do nothing and maintain 100 individuals at the source site. Assuming a method to obtain such perfect information were available, the prior belief suggests a 0.5 chance that it would indicate chytrid presence, and a 0.5 chance that it would indicate its absence. Therefore, making this decision under perfect information has an expected outcome of $EV_{\text{certainty}}=135 \times 0.5 + 100 \times 0.5 = 117.5$. This is greater than the expected outcome of the optimal action under uncertainty (doing nothing, giving $EV_{\text{uncertainty}}=100$). Using Eq. 4.4, the expected value of perfect information is $EVPI = 117.5 - 100 = 17.5$ individuals. That is, perfect information would lead to an expected gain of 17.5 individuals at the end of the 10 year period (Table 4.1). But what if, instead of perfect information, one considers the actual process of collecting data?
Expected value of sample information

Managers might seek to test for the presence of chytrid in the skin secretions of other amphibians present at the prospective site using quantitative polymerase chain reaction (qPCR). However, the qPCR test for chytrid is imperfect. On the basis of published information (Skerratt et al. 2008), managers define the mean sensitivity of the standard qPCR for chytrid described by Boyle et al. (2004) as 0.73 and its mean specificity as 0.94 (i.e., approximately a 27% chance of a false positive and a 6% chance of a false negative for a single test on a single individual; Table 4.2).

The managers’ belief about chytrid presence will change after each test. To evaluate how running such a test might influence our management decisions and outcomes, a Bayesian pre-posterior analysis must be performed (Berger 1985). For this, managers need to consider the possible results of the test (positive or negative) and compute how obtaining either result would change their belief about the system. This can be calculated using Bayes theorem:

\[
P(\text{hypothesis}|\text{data}) = \frac{P(\text{data}|\text{hypothesis})P(\text{hypothesis})}{P(\text{data})}.
\]  
Eq. 4.6

For instance, if the test returns positive, the updated belief about chytrid presence at the new site is calculated as

\[
P(\text{chytrid}|\text{test}^+) = \frac{P(\text{test}^+|\text{chytrid})P(\text{chytrid})}{P(\text{test}^+)}.
\]  
Eq. 4.7

The terms of Eq. 4.7 are interpreted as follows. \(P(\text{chytrid}|\text{test}^+)\) is the updated belief after a positive test result (i.e. the probability of chytrid presence, given a positive test). \(P(\text{chytrid})\) is the prior belief about the probability of chytrid presence, which was initially assumed to be 0.5. \(P(\text{test}^+|\text{chytrid})\) is the probability of the test returning positive if chytrid is present, that is, the test sensitivity (0.73). The denominator \(P(\text{test}^+)\) is the overall probability of observing a positive test result, which includes the probability of a true positive (if chytrid is present and the test correctly detects it) and of a false positive (if chytrid is absent, but the test incorrectly returns positive): \(P(\text{test}^+) = 0.73 \times 0.5 + 0.06 \times 0.5 = 0.4\). By substituting these values in Eq. 4.7, after a positive test
result the managers’ belief about chytrid presence will change from the prior value of 0.5 to \( P(\text{chytrid}|\text{test}^+) = 0.73 \times 0.5 / 0.4 = 0.92 \), and consequently their new belief about chytrid absence will be \( P(\text{no chytrid}|\text{test}^+) = 1 - 0.92 = 0.08 \). Similarly, Bayes theorem can be used to compute updated beliefs assuming a negative test result:

\[
P(\text{chytrid}|\text{test}^-) = \frac{P(\text{test}^-|\text{chytrid})P(\text{chytrid})}{P(\text{test}^-)}
\]

Eq. 4.8

Here \( P(\text{test}^-|\text{chytrid}) = 1 - \text{specificity} = 0.06 \) and \( P(\text{test}^-) \) is the total probability of a test returning negative, i.e. the sum of the probabilities of a false negative and of a true negative (0.27 \times 0.5 + 0.94 \times 0.5 = 0.6). Here the managers’ belief will change to \( P(\text{chytrid}|\text{test}^-) = 0.27 \times 0.5 / 0.6 = 0.22 \) and thus \( P(\text{no chytrid}|\text{test}^-) = 0.78 \) (Table 4.2).

For each of these two possible sets of new beliefs, Eq. 4.1 can be used to calculate the expected value of translocating or not translocating. If the test returns positive, the expected value of translocating will change to \( V = 55 \times 0.92 + 135 \times 0.08 = 61.4 \) individuals; if it returns negative, it will be \( V = 55 \times 0.22 + 135 \times 0.78 = 117.4 \). The expected outcome for not translocating is not affected by the test result and is thus again \( V = 100 \). The optimal decision, then, would be to translocate after a negative test (giving 117.4 individuals), and not to translocate after a positive test (giving 100 individuals).

To complete the Bayesian pre-posterior analysis, these expected values must be weighted by the overall probability of either test result (including correct and incorrect results, as calculated above). This gives the overall expected value given the test is carried out: \( 100 \times 0.4 + 117.4 \times 0.6 = 110.4 \) (Table 4.2). Comparing this to the expected value of making the decision without carrying out the test (not translocating, with \( EV_{\text{uncertainty}} = 100 \)), it results that the expected value of acquiring the sample information (here testing 1 individual) is \( EVSI = 110.4 - 100 = 10.4 \) individuals (Eq. 4.5; Table 4.2). It is also possible to explore VoI for different initial priors (Fig. 4.1). Information would be most valuable for a prior belief in chytrid presence of 0.43, whereas sample information would have no value if \( P(\text{chytrid}) < 0.06 \) or \( P(\text{chytrid}) > 0.74 \).
Figure 4.1. Relationship between the value of perfect and sample information (EVPI and EVSI respectively, expressed as the total number of individuals at the end of a 10-year period) and the prior belief that chytrid is present at the destination site for the frog translocation example.

Value of information for learning about demographic rates

In the previous example, clearly defined uncertainty about the state of the system (the absence or presence of disease) was linked to discrete actions (translocation or no translocation). However, the managers of threatened species programs will often face less clearly defined structural uncertainty. For example, demographic rates such as survival and fecundity are a common source of uncertainty in the research and management of threatened species; since they are continuous parameters, uncertainty could be formulated as infinite possible hypotheses. However, VoI can still be applied in such situations. In this example, I estimate the VoI when learning about demographic rates.

The European pond terrapin *Emys orbicularis* occurs throughout the European continent: however, habitat loss has led to local declines and extinctions (IUCN 2013). In the northern Italian region of Liguria, *E. orbicularis* was considered locally extinct until the re-discovery of small populations in the 1990s, and a captive breeding centre was set up in 2000 to produce individuals for reintroduction (Ottonello *et al.* 2010). As
part of a LIFE/EU project (www.lifeemys.eu), three consecutive years of releases will be implemented between 2014 and 2016. The age of individuals released ranges between three years (the minimum age of release that avoids the high mortality hatchlings and juveniles experience in the wild) and five years (the year before the earliest onset of reproduction in this subspecies). The captive breeding centre is expected to produce approximately 50 turtles every year: these can be released as soon as they reach three years of age, or held in captivity longer and then released (in numbers that are then smaller than 50 due to mortality) at age four or age five. The decision problem is which age class to release.

The objective is to maximise the survival of released individuals: all other things being equal, greater survival will improve population persistence. The value of the alternative actions can be quantified in terms of the cumulative probability of surviving from three to six years of age:

\[ S_6 = \phi_{3l}\phi_{4l}\phi_{5l} \quad \text{Eq. 4.9} \]

where \( \phi_{ai} \) describes the survival of individuals of age class \( a \) in stage \( i \) of the release process: in captivity, in the year after release, or in the wild. This formulation can incorporate differences in captive and wild survival, and the possibility that the survival in the first year after release is affected by post-release effects. Several studies have highlighted reductions in survival following release (Jule, Leaver & Lea 2008; Le Gouar et al. 2008). This may reflect adaptation to captive conditions, leading to inefficient foraging behaviour (Stoinski et al. 2003) or inadequate predator avoidance (Griffin, Blumstein & Evans 2000). Translocated individuals may also be more likely to disperse permanently from the release site (Tweed et al. 2003).
Table 4.1. Step-by-step calculation of the expected value of perfect information for the frog translocation in Case Study 1. The outcome of each action is expressed as the total number of individuals in the protected area at the end of a 10-year period.

<table>
<thead>
<tr>
<th>True state at new site</th>
<th>Prior belief</th>
<th>Decision under uncertainty</th>
<th>Expected value under uncertainty (Eq. 4.2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chytrid</td>
<td>0.5</td>
<td>Predicted outcome (number of individuals)</td>
<td>55×0.5 + 135×0.5 = 95</td>
</tr>
<tr>
<td>No chytrid</td>
<td>0.5</td>
<td>Translocation</td>
<td>55</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Do nothing</td>
<td>100</td>
</tr>
</tbody>
</table>

Decision under certainty (perfect information)

<table>
<thead>
<tr>
<th>Predicted outcome under certainty (optimal action always chosen)</th>
<th>Expected value under certainty (Eq. 4.3)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Outcome of optimal action</td>
<td></td>
</tr>
<tr>
<td>100 (no translocation)</td>
<td>100×0.5 + 135×0.5 = 117.5</td>
</tr>
<tr>
<td>135 (translocation)</td>
<td></td>
</tr>
</tbody>
</table>

Expected value of *perfect* information (Eq. 4.4)

117.5 - 100 = 17.5
Table 4.2. Step-by-step calculation of the expected value of sample information for the frog translocation in Case Study 1.

<table>
<thead>
<tr>
<th>Test result</th>
<th>Expected test performance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Test +</td>
<td>0.73 0.06</td>
</tr>
<tr>
<td>Test -</td>
<td>0.27 0.94</td>
</tr>
</tbody>
</table>

Updating prior belief depending on test results

<table>
<thead>
<tr>
<th>Test result</th>
<th>Chytrid</th>
<th>No chytrid</th>
</tr>
</thead>
<tbody>
<tr>
<td>Test +</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>P(chytrid</td>
<td>test +) = P(test +</td>
</tr>
<tr>
<td>Test -</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>P(chytrid</td>
<td>test -) = P(test -</td>
</tr>
</tbody>
</table>

Updated consequence table after test positive

<table>
<thead>
<tr>
<th>Action</th>
<th>Translocation</th>
<th>No translocation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Updated belief after test +</td>
<td>0.92</td>
<td>0.08</td>
</tr>
<tr>
<td>Expected value under uncertainty</td>
<td>55 × 0.92 + 135 × 0.08 = 61.4</td>
<td></td>
</tr>
</tbody>
</table>

Updated consequence table after test negative

<table>
<thead>
<tr>
<th>Action</th>
<th>Translocation</th>
<th>No translocation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Updated belief after test -</td>
<td>0.22</td>
<td>0.78</td>
</tr>
<tr>
<td>Expected value under uncertainty</td>
<td>55 × 0.22 + 135 × 0.78 = 117.4</td>
<td></td>
</tr>
</tbody>
</table>

Outcome of optimal action after test result

<table>
<thead>
<tr>
<th>Probability of test result</th>
<th>Test positive</th>
<th>Test negative</th>
<th>Expected value under uncertainty</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0.73×0.5 + 0.06×0.5 = 0.4</td>
<td>0.27×0.5 + 0.94×0.5 = 0.6</td>
<td></td>
</tr>
<tr>
<td>Outcome of optimal action</td>
<td>100 (no translocation)</td>
<td>117.4 (translocation)</td>
<td>100×0.4 + 117.4×0.6 = 110.4</td>
</tr>
</tbody>
</table>

Expected value of sample information | 110.4 – 100 = 10.4 |
For *E. orbicularis*, I assume that the post-release effect acts only in the first year after release, after which surviving turtles share the same rates as wild-born individuals. For individuals released as 4-yr-olds, Eq. 4.9 then takes the form \( S_6 = \phi_{3c}\phi_{4p}\phi_{5w} \), where survival between three and four years of age is that of a captive individual (\( \phi_{3c} \)), survival between four and five is that of a newly-released individual (\( \phi_{4p} \)) and survival between five and six is that of a “wild” individual (\( \phi_{5w} \)). For individuals released as 3-yr-olds, \( S_6 = \phi_{3p}\phi_{4w}\phi_{5w} \); for individuals released as 5-yr-olds, \( S_6 = \phi_{3c}\phi_{4c}\phi_{5p} \). Since \( \phi_{ac} \) and \( \phi_{aw} \) are known for all ages \( a \), respectively by observation of captive individuals and by existing information (Canessa, Ottonello & Salvidio 2014; Table 4.3), the most important uncertainty affecting the decision is in the post-release survival rates (\( \phi_{ap} \)).

If there is no post-release effect on survival, the release of 5-yr-old turtles is expected to lead to better survival than releasing 4- or 3-yr-olds, since it involves a longer stay in captivity where survival is greater. If survival in the first year after release is reduced compared to wild-born individuals of the same age, its specific effect depends on which age class is most affected. If this post-release effect (additional mortality compared to wild individuals) is higher in younger individuals, for example due to greater vulnerability to predation, releases of older turtles may be the best action. Alternatively, the post-release effect may be stronger in older turtles, due to a stronger dispersal instinct or to greater adaptation to captivity reflecting their longer captive life. In this case, releasing younger individuals may become the best action.

I articulate these three hypotheses about uncertainty as three sets of alternative parameters values within the same model (Eq. 4.9), reflecting the proportional difference between the survival rate of individuals in the first year after release and that of wild individuals of the same age (i.e., \( \Delta \phi_a = \phi_{ap} / \phi_{aw} \) in Eq. 4.9). I calculate how the value of \( S_6 \) for individual actions changes under each hypothesis (Table 4.3): (1) no post-release effect, with post-release survival equal to that of wild individuals of the same age (\( \Delta \phi_a = 0 \), i.e. \( \phi_{ap} = \phi_{aw} \) in Eq. 4.9); (2) a post-release effect that decreases with age: i.e., younger individuals have proportionally greater post-release mortality (\( \phi_{ap} < \phi_{aw} \) and \( \Delta \phi_3 > \Delta \phi_4 > \Delta \phi_5 \)); (3) a post-release effect that increases with age: older individuals have greater post-release mortality (\( \phi_{ap} < \phi_{aw} \) in Eq. 4.9, and \( \phi_{3p} < \phi_{4p} < \phi_{5p} \)).
I assume priors of 0.4, 0.2 and 0.4 for the three hypotheses, on the basis of preliminary data analysis of past releases in the area (Table 4.3).

**Expected value of perfect information**

Following the same procedure described in the previous example, the action with the maximum expected value ($EV$) of $S_6$ across all three hypotheses is to release 4-yr-old turtles, with $EV_{\text{uncertainty}} = 0.620$ (Eqs. 4.1-4.2), whereas the expected value of making the decision under perfect knowledge is $EV_{\text{certainty}} = 0.659$ (Eq. 4.3). Therefore, the expected value of acquiring perfect information is an increase of 0.039 in the survival between 3 and 6 years of age (EVPI=0.039; Eq. 4.4).

**Expected value of sample information**

Information about post-release survival could be collected through a trial release, a common approach in reintroduction projects (Batson, Abbott & Richardson 2015). Managers could release a number of turtles, assess their survival in the first year after release and then update the prior belief in the hypotheses about post-release survival. However, the observed survival rate will be the result of a stochastic process, and the statistical inference that can be drawn from this observation is limited by the size of the trial release: the smaller the sample, the more uncertain the inference. Here I assume the fate of each turtle released in the trial can be observed perfectly (e.g., by use of radio-telemetry). To determine the value of information of a trial release, I again carry out a Bayesian pre-posterior analysis.

I begin by considering a release of ten 3-yr-old turtles. In this case, Bayes theorem can be interpreted as follows:

$$P(\text{hypothesis}|\text{data}) = \frac{P(\text{data}|\text{hypothesis})P(\text{hypothesis})}{P(\text{data})} = \frac{P(N|h)P(h)}{P(N)}$$  \hspace{1cm} \text{Eq. 4.10}

where $N$ is the number of individuals released in the trial that would survive after the first year, if hypothesis $h$ were true. Here I model this number as the result of a binomial process:
\[ N|h \sim \text{Bin}(n, \phi_{ap}^{[h]}) \]

where \( n \) is the number of individuals released of a given age \( a \) (here, \( n=10 \) 3-yr-old turtles) and \( \phi_{ap}^{[h]} \) is the predicted post-release survival of those individuals under hypothesis \( h \) (Table 4.3). Hence, the probability of observing a given number of survivors \( N \) under hypothesis \( h \) is:

\[
P(N|h) = \binom{n}{N} \left( \phi_{ap}^{[h]} \right)^N \left( 1 - \phi_{ap}^{[h]} \right)^{n-N}. \tag{4.11}
\]

For each value of \( N \) between 0 and 10, there is one value of \( P(N|h) \) under each hypothesis (that is, three values in total). For example, the probability of observing 7 survivors is 0.27 if there is no post-release effect, 0.20 if there is a post-release effect that decreases with age and 0.16 if there is a post-release effect that increases with age (Fig. 4.2). Since each hypothesis has a given probability \( P(h) \) of being true (prior belief), the probability of observing \( N \) survivors across all hypotheses is calculated as:

\[
P(N) = \sum_{h=1}^{H} P(N|h)P(h). \tag{4.12}
\]

Based on Eqs. 11-12, I can now apply Bayes theorem (Eq. 4.10) to calculate the belief in each hypothesis after running the experiment and observing a given number of survivors. Every observed number of survivors would lead to a different posterior belief. For example, observing 7 survivors would lead to beliefs of 0.5, 0.19 and 0.31 (for post-release effects absent, increasing with age and decreasing with age respectively). On the basis of the updated belief, managers would choose the optimal action under the updated uncertainty (I refer to the uncertainty remaining after the test as “updated uncertainty” to distinguish it from the initial uncertainty in \( EV_{\text{uncertainty}} \)). I use Eq. 4.1 to calculate the expected value of a decision: since there are eleven possible outcomes of the trial (0 to 10 survivors), there are eleven possible sets of posteriors and correspondingly eleven possible expected outcomes of making a decision after the trial.

To calculate the expected value of making a decision over all possible trial results (\( E_x \) in Eq. 4.5), I sum the expected values for all possible trial results, weighted by the respective probabilities. This is calculated as:
\[ EV_{\text{uncertainty}}^{\text{updated}} = \sum_{N=1}^{n} \left\{ EV_{\text{uncertainty}}^{[N]} P(N) \right\}, \quad \text{Eq. 4.13} \]

where \( EV_{\text{uncertainty}}^{[N]} \) is the expected value of making a decision after observing \( N \) survivors, and \( P(N) \) is the probability of observing \( N \) survivors (Eq. 4.12).

**Figure 4.2.** Probability of observing a given number of survivors one year after a release of ten individuals, under the three hypotheses of how post-release survival changes with age.

Here, where the test is to release ten 3-yr-old turtles, I obtain a value of \( EV_{\text{uncertainty}}^{\text{updated}} = 0.622 \). This is the expected value of management when the decision is made after running a trial and corresponds to the first term in Eq. 4.5. Since \( EV_{\text{uncertainty}} \) before the test (i.e. based on prior beliefs) is 0.620, it results that this sample information has an
expected value of 0.002 (EVSI = 0.002). The same procedure can be repeated for a trial release of ten 4-yr-old turtles to obtain \( \mathbb{E}_x \left[ \max_\alpha \mathbb{E}_{x|s} [V(\alpha, s)] \right] = 0.634 \) and EVSI = 0.014; and for a trial release of ten 5-yr-old turtles, obtaining EVSI=0.028. A trial release of 5-yr-olds is thus expected to produce greater improvement in management outcomes than trials focusing on 3- or 4-yr-olds. It is also possible to explore how EVSI increases for larger trial releases (Fig. 4.3).

Table 4.3. Survival rates and expected outcomes for the reintroduction of turtles of different ages. Post-release effect refers to additional mortality in the first year after release. The outcome of each reintroduction strategy is expressed as the cumulative survival of released individuals to six years of age.

<table>
<thead>
<tr>
<th>Age class</th>
<th>Captive</th>
<th>Wild</th>
<th>Post-release effect decreasing with age</th>
<th>Post-release effect increasing with age</th>
</tr>
</thead>
<tbody>
<tr>
<td>3-yr-olds</td>
<td>0.9</td>
<td>0.85</td>
<td>0.72</td>
<td>0.68</td>
</tr>
<tr>
<td>4-yr-olds</td>
<td>0.92</td>
<td>0.90</td>
<td>0.83</td>
<td>0.60</td>
</tr>
<tr>
<td>5-yr-olds</td>
<td>0.95</td>
<td>0.90</td>
<td>0.86</td>
<td>0.40</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Combined survival from 3 to 6 years as outcome of reintroduction strategy</th>
</tr>
</thead>
<tbody>
<tr>
<td>Post-release effect</td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td>Prior belief</td>
</tr>
<tr>
<td>Action</td>
</tr>
<tr>
<td>(age class to release)</td>
</tr>
<tr>
<td></td>
</tr>
</tbody>
</table>

Decision under certainty (perfect information)

<table>
<thead>
<tr>
<th>Predicted outcome under certainty</th>
</tr>
</thead>
<tbody>
<tr>
<td>No change</td>
</tr>
<tr>
<td>Outcome of optimal action</td>
</tr>
</tbody>
</table>

Expected value of perfect information 0.659 - 0.620 = 0.039
Figure 4.3. Increase in the expected value of sample information (EVSI) with increasing numbers of turtles released in the trial. EVSI is expressed as the proportion of the expected value of perfect information (EVPI) calculated for this decision problem (where EVPI=0.039).

Discussion

Value of information provides the quantitative answer to a fundamental question of threatened species conservation: when is the collection of further information warranted? As illustrated in the examples, VoI highlights the three key factors that determine this answer: (1) the initial state of knowledge, (2) the quality of the information collected (i.e. the extent to which it reduces uncertainty) and (3) the available management actions and their expected outcomes.

Prior beliefs represent our state of knowledge before any additional information is collected, and may reflect inference drawn from available data (such as weights assigned to competing models of a system: Maxwell et al. 2014), existing literature (for example through meta-analyses: Ades, Lu & Claxton 2004) or expert judgment (Runge, Converse & Lyons 2011). In general, more informative priors will lead to smaller VoI: the more we already know about the system, the less additional information can be expected to modify our decisions (Maxwell et al. 2014). However, as highlighted in the
frog example (Fig. 4.1), the maximum VoI does not always correspond with the point of maximum uncertainty (e.g., a prior of 0.5 for two competing hypotheses). Rather, the maximum VoI corresponds with the point where the effects of uncertainty are greatest, and those effects are defined by both prior beliefs and expected outcomes. In the frog example (Fig 1), EVSI was greater than 0 only for prior belief in chytrid presence between 0.06 and 0.74: outside this interval, the sample of information considered (a single test for chytrid with the reported test performance) was insufficient to change the optimal action.

Prior information is also important in clearly structuring uncertainty. In the frog example uncertainty was naturally defined as two states, with chytrid either present or absent. In the turtle example, the choice of the three hypotheses was, to a degree, still arbitrary: I could have specified different hypotheses to explore additional scenarios. However, careful evaluation of prior information allowed me to exclude biologically implausible hypotheses such as extreme differences in survival among individuals of similar age. Conversely, in the frog example uncertainty was clearly defined as two states, with chytrid being either present or absent. I could have also incorporated additional uncertainty by defining probability distributions for the uncertain parameters, and using Monte Carlo methods and numerical integration for the pre-posterior analysis (Ades, Lu & Claxton 2004).

The VoI is also limited by the quality of the information collected. In trial reintroductions such as that described in the turtle example, the quality of the information obtained depends on the size of the release cohort. Unfortunately, the status of threatened species often limits the number of individuals available for trials and experiments (Kemp et al. 2015). A priori calculation of VoI can assist in evaluating whether the risk of losing individuals is compensated by the improvements afforded by increased knowledge. In the frog example, the value of information was influenced by the performance of the diagnostic test: increasing the sample size by testing more individuals might improve the chances of correctly determining the presence or absence of chytrid fungus. The test is already relatively accurate: therefore, EVSI corresponds to a large proportion of the maximum improvement achievable (EVPI; here, EVSI/EVPI=0.59). For increasing sample sizes, EVSI will approximate EVPI (see also
Fig. 4.3). In this sense, EVPI provides a benchmark for any experimental/monitoring program under consideration. The value of partial perfect information (EVPXI) is a possible formulation of EVPI, representing how much management could improve if we could eliminate or confirm perfectly only one or some of our hypotheses (Runge, Converse & Lyons 2011; Maxwell et al. 2014; Williams & Johnson 2014). Where different learning actions are required to learn about different hypotheses, EVPXI allows for prioritization of those actions.

From a management perspective focused on the decision problem at hand, if information has no influence over our actions there is no benefit in collecting it. In the frog example, if we expected the source population to return to its initial size of 100 individuals regardless of the fate of the reintroduced population, the translocation should always be done, and information would have no value (EVPI=EVSI=0). However, for values of Vi >0 the decision of whether to collect information can become less intuitive, since there is no universal rule to decide whether the value of information is “high enough”. For example, in the frog translocation problem EVSI suggested a 10% improvement in management outcomes, which may or may not be considered sufficient by the relevant managers to justify the cost of setting up an experimental or monitoring program. Low Vi does not imply uncertainty is unimportant and information not required, since learning may still be necessary, for example to assess management success: rather, Vi represents the expected benefit of collecting additional information (Williams & Johnson 2014). Moreover, in a decision-analytic context alternative actions are evaluated in terms of management objectives; therefore, the Vi is expressed in the same units and it may change with different specifications of objectives.

This consideration becomes especially important for managers with multiple objectives. In particular, information will usually come at a cost, generating a trade-off where the benefits of resolving uncertainty may need to be considered against its cost. If the objective is monetary, this trade-off can be addressed directly since Vi itself will be a monetary value (Yokota & Thompson 2004; Bratvold, Bickel & Lohne 2007; Mäntyniemi et al. 2009; Maxwell et al. 2014). Alternatively, the cost of information can be assessed as an opportunity cost, where the resources allocated for learning might
have been used for other purposes. Finally, decisions might need to be delayed for the
time necessary to collect information, and the delay can have a negative effect on
outcomes, particularly when dealing with threatened species that are already undergoing
declines (Martin et al. 2012).

On the other hand, if decisions are iterated and uncertainty concerns the dynamics of the
system rather than a transient state (as in the turtle and frog examples respectively), it is
possible to learn from the outcomes of management and use the resulting knowledge to
inform future decisions, using an adaptive management approach (Holling 1978). In this
sense, VoI analysis is a necessary condition for adaptive management: if the expected
value of information is low, then the use of adaptive management might not be
warranted (Williams, Szaro & Shapiro 2009; Williams & Johnson 2014). More
generally, opportunity costs and constraints make it unlikely that every source of
uncertainty can be resolved. In such cases, VoI highlights the key uncertainties which
have the greatest effect on our management actions and which can be most effectively
reduced, particularly in the partial value of information (EVPXI) formulation (Runge,
Converse & Lyons 2011; Williams & Johnson 2014). Research and monitoring can then
be focused on these key uncertainties, ensuring a rational and cost-efficient allocation of
resources.

Finally, I have focused on how additional information can modify beliefs, and therefore
the expected values of actions. However, learning can further modify the decision
problem. For example, the trial release of turtles could lead to estimates of survival
which deviate from the expected values I used to populate the consequence table (e.g.,
recaptures of released turtles may indicate post-release survival increases with age more
markedly than expected; or additional information could change the initial estimates of
captive and wild survival). This in turn can modify the expected values of actions from
initial predictions. Again, carefully structuring uncertainty and prior beliefs will assist in
addressing these issues. In general, VoI is part of the framework of structured decision
making (Gregory et al. 2012). Within this framework, decision making should be seen
as an iterative process, any stage of which can be repeated and revised once the new
information is collected. In adaptive management, where the management decisions are
themselves iterated, this process is frequently referred to as double-loop learning (Williams, Szaro & Shapiro 2009).

In summary, VoI analysis is an intuitively useful tool for threatened species management. Where a desire for additional information is expressed, VoI can assist in determining whether it is actually warranted (which benefit it will provide), where it should be directed (the key uncertainties we should focus on) and how much needs to be done (the required study design). I have provided a reference guide species biologists and managers interested in the application of value of information.

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Chapter 5

**ADAPTIVE MANAGEMENT OF THREATENED SPECIES ACROSS THE CAPTIVE-WILD SPECTRUM**
CHAPTER 5

Adaptive management of threatened species across the captive-wild spectrum

Abstract

Conservation of threatened species is moving towards a greater integration of captive and wild management efforts. Managing threatened species in these complex management contexts requires making decisions in the face of uncertainty, often with limited resources available to collect information. Adaptive management (AM) provides a framework in which management is coupled with monitoring, with the aim of updating models of system function and improving decision making. Here I aim to provide a guide for managers who may be intrigued by the potential of AM, but are unsure where to start. Along the captive-wild spectrum, managers implementing AM can encounter specific opportunities and challenges. The urgent need for continuous management decisions, the existence of uncertainty, and the opportunity for learning offered by often highly-controlled environments create conditions for AM. However, low sample sizes may generate difficulties for learning; planning and implementing experiments and monitoring may be especially challenging for programs involving multiple institutions; and low risk tolerance sometimes discourages the implementation of new management strategies. I present four case studies based on common decisions encountered in threatened species programs that illustrate how AM can be applied to different stages along the captive-wild spectrum, with different levels of technical complexity. I focus on the practical steps needed to get AM programs underway in managing threatened species across the captive-wild spectrum.
**Introduction**

Conservation biologists increasingly recognise that successful management of threatened species requires the integration of diverse management techniques, involving a broad range of scientific expertise (IUCN/SSC 2008). While conservation approaches are often categorised as focusing on the “wild” or *in situ* environment versus its “captive” or *ex situ* counterpart, conservation methodologies in reality span a spectrum of management intensity; few programs involve completely unmanaged wild populations or complete control over captive populations (Redford, Jensen & Breheny 2012). For simplicity, in this paper I refer to this spectrum as the captive-wild spectrum.

Along this spectrum, conservation management requires making difficult decisions about the best actions to apply. Decisions range from whether to establish new populations in breeding centers or via direct translocations among wild populations, to the specific methods used to establish new populations or manage existing ones. These decisions must be made under incomplete knowledge of the biological system, resulting in uncertainty about how to manage most effectively (Burgman 2005). For many complex programs, decision making must also be coordinated between different points along the captive-wild spectrum (for example managing captive and reintroduced populations as a linked system). The number of uncertainties may thus increase and create even greater challenges for decision makers.

Managers might seek to reduce uncertainty via traditional research, assuming it will lead to better decision making in the future. However, threatened species management often requires immediate decisions, limiting the time available for traditional research (Martin *et al.* 2012b). Still, management itself can provide opportunities to learn. By monitoring the outcomes of implemented actions, managers can improve their understanding of the system, and inform future decisions. The process of using learning to update understanding of the system for use in subsequent decisions represents the essence of adaptive management (AM; Holling 1978; Walters 1986), which has been increasingly advocated for conservation in recent years (McCarthy & Possingham 2007; McDonald-Madden *et al.* 2010; Runge 2011; McCarthy, Armstrong & Runge 2012). AM has been explicitly highlighted as an important tool in comprehensive species
conservation strategies (IUCN/SSC 2008), as well as in guidelines for reintroductions (IUCN/SSC 2013) and ex situ programs (IUCN/SSC 2014).

With its focus on objectives and uncertainty, AM lies within the more general framework of structured decision making (Gregory et al. 2012). Structured decision making is the process of rationally analyzing decisions, wherein decision makers clearly state the decision problem, define objectives and available actions, predict the expected outcomes of different actions, and use analytical methods to determine which action is optimal. Within structured decision making, AM specifically reflects the desire and capacity to improve management outcomes by learning about them, thus reducing uncertainty (Runge 2011).

Despite offering numerous potential advantages, the implementation of AM in conservation is infrequent and often incorrect (Allan & Curtis 2005; Westgate, Likens & Lindenmayer 2013). Several authors have suggested this implementation gap may result from confusion surrounding key concepts and definitions, misunderstanding of the practical barriers to implementation, and lack of adequate institutional structures and support (Gregory, Ohlson & Arvai 2006; Allen & Gunderson 2011; Rist, Campbell & Frost 2013). Rather than reviewing these challenges again, with this contribution I seek to assist managers of threatened species programs who understand the potential benefits of AM but are unsure of how to apply it to their specific decision problems. Using four case studies along the captive-wild spectrum, I explain the key concepts of AM, highlight the steps of the implementation process as well as the necessary conditions and the potential challenges in the context of threatened species management.

**How to get started in adaptive management**

Management is adaptive when it explicitly recognises the effect of uncertainty on decisions, and it seeks to reduce that uncertainty to improve management outcomes. This reduction can be “passive”, where managers make the decision that is considered best under the current knowledge, but apply adequate monitoring to collect specific information that will allow a subsequent re-evaluation of the decision (Williams 2011). Alternatively, “active” AM seeks to solve a dual-control problem, where managers seek to simultaneously maximise learning in order to maximise management outcomes.
(Williams 2011). Actions that are not deemed optimal in the short-term may be taken because they accelerate learning, which has value in the long term. Both active and passive AM differ from “reactive” or “trial-and-error” approaches, where managers may react to new knowledge, but do not clearly specify what uncertainty exists, how it can be reduced and how decisions will change in response to new information (Runge 2011).

In implementing AM, a sequence of steps should be followed: (1) formulate the decision problem, (2) define objectives, (3) define management actions, (4) articulate uncertainty in explicit hypotheses, (5) predict the outcomes of actions in terms of the management objectives and conditional on the hypotheses, (6) assess the expected benefits of learning, (7) identify a method of collecting new information, (8) define how this information will be used to update knowledge and influence decisions, and (9) implement and revise the process.

First, we need to clarify the decision problem. For AM to be useful, choosing one action over another should have a real influence on management outcomes, and it must be possible to apply learning: in this sense, AM is only suitable where decisions are recursive, or where new information can be used in subsequent decisions (Williams, Szaro & Shapiro 2009). It must be possible to adapt actions in response to new information: this requires institutional support and stability (Williams, Szaro & Shapiro 2009). Second, we must clearly articulate the fundamental management objectives, acknowledging multiple and possibly conflicting objectives (Converse et al. 2013). Third, we need to identify a set of alternative actions that can be used to achieve those objectives (Gregory & Long 2009).

Fourth, we articulate our uncertainty about the system. Uncertainty in natural resource management arises from different sources, including environmental and demographic stochasticity as well as partial observability and partial controllability (respectively, the ability to observe the state of the system, and the ability to implement the action in practice as planned; Williams et al. 2009). However, AM focuses in particular on uncertainty that arises from an incomplete understanding of the dynamics of a natural system. This can take the form of uncertainty about which of a set of competing models best describes the structure of the system (model uncertainty), and uncertainty about the
true parameter values within a given model (parametric uncertainty). It must be possible to articulate uncertainty as a set of alternative, testable hypotheses (for example, different models of the system, or different values of key parameters in a given model). This step is the key to AM.

Fourth, we need to predict the expected outcomes of those actions in terms of the management objectives, and conditional on the various hypotheses, using quantitative models based on empirical data, or expert judgment elicited using methods to minimise bias and semantic uncertainty (Martin et al. 2012a; see Chapter 3). The relationship between hypotheses and the outcomes of alternative actions must be clear and explicit: we need to make predictions of the expected outcomes of actions under each hypothesis. On the basis of those predictions, in the sixth step we need to evaluate the benefit of collecting additional knowledge. The concept of value of information refers to the improvement in management outcomes that could be expected by reducing or eliminating all or part of the existing uncertainty (Runge, Converse & Lyons 2011; Williams, Eaton & Breininger 2011; Johnson et al. 2014). Again, the application of AM is conditional on the existence of non-negligible value of information. If resolving a given uncertainty is not possible, or it is not expected to improve management outcomes, then additional information has no value and the use of AM is not warranted (Williams, Szaro & Shapiro 2009). Basic value of information calculations, applied to a reintroduction program, are described in Runge, Converse and Lyons (2011).

In the seventh step, we need to define a monitoring system which allows the collection of the required information. Monitoring should allow us to assess management outcomes, to determine the state of the system where this influences our decision, and to update our knowledge of the system to be able to revise actions (Williams & Johnson 2014). Useful monitoring implies both an adequate experimental design and sufficient resources to sustain the monitoring effort (Gregory, Ohlson & Arvai 2006). In the eighth step, we need to define how the results of monitoring will be used to update the support for competing models, or to update parametric distributions. Poorly implemented AM programs often lack such an explicit definition (Westgate, Likens & Lindenmayer 2013). We can simply collate new and existing data and re-analyze them to obtain new model rankings or parameter distributions. More usefully, AM can be approached in a Bayesian framework, where existing information is represented as
priors, and new information is used to update beliefs in models or parameters (McCarthy & Possingham 2007). Optimization techniques such as stochastic dynamic programming (SDP; Walters 1986) can be used to find the optimal action in the face of model or parametric uncertainty (McCarthy & Possingham 2007). Alternatively, simulations can provide sub-optimal but acceptable solutions that are less demanding in terms of technical skills and computational capacity (Walters 1986).

As part of the structured decision making framework, AM is an iterative process which may involve the repetition of all or part of the above steps. In “single-loop” learning, actions are implemented and outcomes monitored to improve existing practices (Tosey, Visser & Saunders 2012). Where necessary, any step of the entire decision problem can be revisited, including redefining objectives and alternative actions, reformulating hypotheses, and redesigning the monitoring system ("double-loop" learning; Tosey, Visser & Saunders 2012).

**Adaptive management in practice**

I illustrate the application of AM using four case studies across the captive-wild spectrum, ranging from captive management for reintroduction to the release process itself and to ongoing management of reintroduced populations in the wild. For each case study, I describe the AM process, assess whether the key conditions for AM are met, and identify potential challenges to its implementation. The varied set of examples allows us to focus on different steps, illustrating problem definition, technical solutions for updating knowledge, and the iterative process of AM.

**Choosing breeding pairs in captive management of cheetahs**

The first example focuses on captive breeding to maintain a captive population. Cheetahs (*Acinonyx jubatus*) have never bred prolifically in zoos. For cheetahs in North American zoos, only about 20% of pairs reproduce: as a result, the captive population is currently projected to decline by 5% per year unless sustained by imports (Marker-Kraus & Grisham 1993). Such low breeding rates may result from managers choosing incompatible pairs (animals are usually not allowed to choose mates). I explore the
potential application of AM to the pairing process in captive cheetahs, through a conceptual description of the AM steps and the challenges that may be encountered.

First, the decision problem is to choose a pairing protocol that will allow the population to be sustained demographically and genetically without further imports. Second, the management objective is to increase the proportion of pairs that produce litters. Since pairs can be selected anew every year (i.e., cheetahs do not maintain pair bonds), the decision is recursive and thus potentially suitable for AM; the long-term management horizon would allow sufficient time for information to be collected and applied. Third, we could consider the following management alternatives: (1) continue to pair cheetahs according to managers’ assessments of optimal genetic mates, then transfer cheetahs to different facilities to try with new partners if the first pairing does not succeed; (2) move cheetahs to larger facilities where females can choose amongst males; (3) test female preferences by exposing them to urine from multiple males, then pair them with the male whose urine elicited the most interest; (4) expose females to urine of genetically optimal males to improve their acceptance.

The outcomes of these alternative actions are likely to reflect at least in part structural uncertainty about cheetah behavior. In the fourth step, we need to articulate this structural uncertainty via competing models of the system. For example, we might identify four drivers of breeding success: (1) the number of possible mates in physical proximity; (2) transferring animals may affect their receptivity to mate; (3) genetic similarity may determine mate acceptance; (4) mate choice may be driven by olfactory cues. We could then predict the outcomes of the management alternatives under each hypothesis; we could build four competing models of breeding success and use model weights to express our beliefs (Hauser & Possingham 2008). The fundamental challenge here is that explicit hypotheses of breeding dynamics have not yet been developed, hindered perhaps by different assumptions about the importance and direction of drivers. Collaboration among experts and elicitation of initial estimates from currently scattered data and divergent expert opinion may allow this gap to be filled.

In the sixth step, we determine whether information would have any value in terms of management outcomes. If experiments are carried out in isolation by individual institutions, sample sizes may be too low to allow reliable statistical conclusions: this
can reduce the value of information, since uncertainty may not be resolved to any meaningful degree. Again, inter-institutional collaboration may increase sample sizes for experimentation. Deciding how to implement learning (seventh step) may be even more challenging in this case. In general, monitoring breeding success should be facilitated by the high observability and controllability of the captive environment. However, facilities with at least moderate breeding success are often reluctant to test alternative methods and to subject highly-valued animals to experimentation: in this case, passive AM may be more acceptable than active AM for risk-averse managers. Simulations of the outcomes of a possible AM plan would allow institutions to assess the expected short-term costs (in terms of predicted breeding success) of placing some animals under protocols that are judged currently to be less likely to succeed, for example through a loss of breeding opportunities. Institutions can then assess these short-term costs in view of the expected long-term gains of experimentation. In summary, the choice of breeding pairs in captive cheetahs meets several conditions for AM. The main challenges to AM implementation reflect the need for collaboration and commitment by multiple institutions, to allow a clear formulation of objectives and uncertainty, an informed prediction of the outcomes of management actions, and to overcome limitations in the capacity for learning.

Choosing between parent-rearing and costume-rearing in whooping cranes

The second example also focuses on captive-rearing, but with the aim of maximizing population growth after reintroduction. I illustrate how to use a quantitative model to structure uncertainty and compare alternative actions. Endangered whooping cranes (Grus americana) are hatched in captivity, from captive breeding stock, and trained for release before their first birthday. Two reintroduced populations are currently receiving annual releases: the Eastern Migratory Population (EMP; Servanty et al. 2014) and the Louisiana Non-Migratory Population (LNMP; Zimorski, Perkins & Selman 2013). Two general rearing methods are used: costume-rearing (CR), where birds are reared by costumed handlers and puppets, and parent-rearing (PR), where captive pairs raise their own chicks. Managers know relatively little about PR, as it is a lesser-used method. While currently being tested in the EMP, it has not yet been tested in the LNMP. The LNMP has been established with annual releases of CR birds from 2011 to present.
Managers of the LNMP have an opportunity to learn about rearing methods, and respond adaptively to that learning.

The decision problem, then, is what type of rearing method to use for cranes in the LNMP: parent-rearing or costume-rearing. The decision is recursive, since chicks are reared every year, and there is capacity for adapting actions to reflect additional knowledge. PR cranes may have different survival and breeding success than do CR cranes, so it seems reasonable to consider an objective of maximizing lifetime reproductive contribution of each release cohort. The alternative actions are the two rearing methods (CR and PR). Their outcomes can be predicted through a quantitative model of the system. We can identify four parameters contributing to lifetime reproductive contribution: annual survival of pre-breeders (Sj), age of breeding onset (M), annual fecundity after onset (f), and annual survival of breeders (Sb). We can calculate the expected longevity after the onset of breeding as 

\[ S_B = -\frac{1}{\ln(S_b)} \]

and then can calculate the expected population lifetime reproductive contribution of a rearing method (a) as:

\[ PLRC(a) = R(a) \times S_j(a)^{M(a)-1} \times \left( -\frac{1}{\ln(S_p(a))} \right) \times f(a) \]  

Eq. 5.1

where R is the number of birds released under that action, and where the model parameters are a function of the action, a. There is likely to be greater complexity in survival as a function of age than is suggested by Eq. 5.1, but the division into two stages (pre-breeders and breeders) is a reasonable simplification for the purpose of this example.

Currently, uncertainty surrounds the four parameters in Eq. 5.1 for CR and PR. We could work with experts, and use empirical information from the EMP (Converse et al. 2011, Servanty et al. 2014) and from a previous non-migratory release in Florida (Folk et al. 2008, Moore et al. 2012) to develop prior distributions for each of the four parameters, under each release method. For example, it is expected that on average about twice as many chicks could be produced annually for CR compared to PR (based on egg fertility rates, the expected number of pairs that could successfully rear a chick of their own, and staff hours available for costume-rearing; GH Olsen, US Geological Survey, personal communication). Therefore, we could assume \( R = 1 \) for CR and 0.5 for
There is some evidence from other reintroductions that survival of PR cranes is lower, at least initially (Ellis et al. 2000a; Ellis et al. 2000b) though this information is highly uncertain. However, it is also hypothesised that the CR method may result in poor reproductive behaviors (Runge et al. 2011) which may reduce age at first breeding and annual fecundity.

Once priors were established, and Eq. 5.1 used to make predictions of PLRC under each action, the system could be managed via passive AM, beginning by releasing all birds according to the rearing method with the best PLRC under the priors. Challenges to learning may include the difficulty of monitoring birds after release, where observability is lower, and the cost of direct monitoring methods such as radio-tracking, which may in turn reduce the sample size available. We could use the collected data to update prior beliefs using Bayes’ theorem. This would allow us to detect whether the observed population lifetime reproductive contribution for the initially-preferred alternative is lower than that expected for the non-preferred alternative. In this event, managers could switch to the (initially) non-preferred alternative, and monitor the parameters for that alternative. Although the long-term reintroduction program for cranes would be sufficient to allow the application of new information, there would be a significant delay between the implementation of actions and learning about their outcomes, due to the relatively late onset of breeding in cranes (3-5 years). Again, institutional commitment to monitoring and AM over time is the key to addressing this challenge.

Choice of reintroduction site for Arizona cliffroses

In this example I compare different technical approaches to the evaluation of whether and how to implement AM. I focus on the choice of reintroduction sites, a fundamental problem in reintroduction management (Osborne & Seddon 2012). I consider a hypothetical translocation program for the endangered Arizona cliffrose *Purshia subintegra* in the south-western United States. Previous reintroductions of this evergreen shrub have demonstrated a positive relationship between germination success and the characteristics of release sites, such as soil moisture (Maschinski, Baggs & Sacchi 2004; Maschinski *et al.* 2006). I describe a translocation plan in which managers can translocate a fixed number of 16 seedlings every year over a 10-year period, with the objective of maximising the number $N$ of seedlings surviving over their first year.
(establishing). A decision must be made every year and there is the potential to apply learning given the duration of the program.

I assume there are two potential sites for reintroduction. Each year, managers must decide what proportion of the 16 seedlings should be translocated to site 1 and site 2 respectively. Ultimately, managers expect to release all the seedlings in a given year at the most suitable site. However, at the start of the management program there is uncertainty about which site is best: that is, about the survival of seedlings in the first year after release at each site. I express this probability of survival as a beta distribution: \( \phi_1 \) for site 1 (mean=0.18, s.d. 0.09) and \( \phi_2 \) for site 2 (mean=0.22, s.d. 0.09). The 95% CIs overlap substantially, reflecting uncertainty about which site will be better.

I now imagine that a manager must decide how, if at all, to learn about survival rates at the two reintroduction sites. I compare five different approaches to learning which allow us to develop an understanding of the trade-offs between learning and managing under different time frames. First, no AM: all seedlings are translocated to the site with the highest mean survival rate (in this case site 2) and no monitoring is carried out to learn about their fate. Second, passive AM: every year 16 seedlings are reintroduced to the site with the highest mean survival; the number of survivors is then monitored, the estimate of survival at the reintroduction site is updated, and the decision revised if necessary. Third, active AM: in the first year each site receives eight seedlings, the number of survivors is monitored and used to update survival estimates and choose the release site for subsequent years. The fourth and fifth approaches are variations of the previous active AM approach, in which the experimentation is carried out for four and eight years respectively. I use simulations to evaluate approaches one to five, by iterating the decision process 10,000 times and drawing the “true” values of \( \phi_1 \) and \( \phi_2 \) randomly from the prior beta distributions.

For the sixth approach, I use an optimization tool called stochastic dynamic programming (SDP) to find the optimal active AM strategy. SDP optimises the trade-off between the short-term losses of experimentation and the long term benefits of learning by finding the optimal decision for every possible state of knowledge while accounting for the possible outcomes of future events. In this example, a state of knowledge is defined by the number of seedlings that survive at each site.
Figure 5.1. Guide to the interpretation of the optimal active adaptive management output from stochastic dynamic programming (SDP). Each cell of each table corresponds to a state of knowledge, defined by the number of previous observations of surviving and dead seedlings at each site ($\alpha_1$, $\beta_1$ respectively for site 1, $\alpha_2$, $\beta_2$ for site 2). For each combination of these four values, the SDP returns the optimal number of seedlings to allocate to each site in the current time step to maximise long-term outcomes. For example, “16” indicates all seedlings should be planted at site 1, “0” indicates all should be planted at site 2 and “8” indicates an equal allocation of seedlings for maximum learning.
Figure 5.1 illustrates how results of the SDP can inform the optimal active AM strategy: each point in the graph represents a unique combination of the two parameters (i.e., survival of seedlings at each site), and it indicates the optimal allocation of individuals to each site that we should choose if we were in that state of knowledge.

The results of the five learning approaches highlight some key properties of AM, particularly regarding the trade-off between learning and management. A non-adaptive approach of simply translocating to the site with the highest estimated mean survival gave \( N = 35.4 \pm 16.1 \) s.d. seedlings establishing over the 10-year period, with a similar survival rate between years (Fig. 5.2). Passive AM improved the expected (mean) outcome, although the overall distribution of outcomes changed only marginally (\( N = 38.0 \pm 15.2 \)). When using active AM, longer experimental releases provided better expected outcomes (increasing mean) and less risk (decreasing standard deviations), but only once the best site was selected. Longer experimental releases also meant lower mean and overall survival, since they involved releases at the less suitable site, and less time to reap the benefits of learning (Fig. 5.2). As a result, the mean overall number of established seedlings decreased with the length of the experimental period and was always lower than when adopting passive AM (respectively \( N = 36.8 \pm 15.7 \), \( N = 36.1 \pm 13.7 \) and \( N = 33.4 \pm 12.0 \) for one, four and eight years of experiments). As expected, optimal adaptive management based on the SDP strategy provided a compromise between managing and learning. The total number of seedlings produced was slightly lower than that expected from passive AM, but uncertainty was reduced more effectively (\( N = 37.6 \pm 14.7 \)). As a result, optimal AM provided better outcomes than passive AM in later years of releases, suggesting it might provide greater benefits for longer programs or larger sample sizes (Fig. 5.2).

In this example, I have chosen a hypothetical decision problem with a clear link between uncertainty and management actions (reintroduction sites), and scope to apply the results of learning. The observability of results is facilitated by the nature of the target species, although I ignored environmental stochasticity which may confound survival estimates in different years. The limited number of individuals available for translocation provides only limited opportunities to apply the results of learning, especially given the management horizon is short relative to the speed of learning.
I also focused on the difference in seedling survival, which can be assessed in the first year after release; possible effects on adult survival or germination rates would only be observed after a significant time lag, making it difficult or impossible to apply learning.

Due to practical constraints, simulations may allow only a comparison of sub-optimal strategies. Conversely, SDP can identify the optimal AM solution. Although its application requires more specialised skills, toolboxes are now freely available in different platforms to help in applying SDP (Chadès et al. 2014; Marescot et al. 2013). SDP is also computationally intensive, so complex problems with large dimensions (i.e. large numbers of trials and longer time horizons) may become intractable. In this case, simulations may again provide a useful alternative.

**Figure 5.2.** Simulated outcomes of different strategies for the translocation of *Purshia subintegra*. Lines indicate the number of reintroduced seedlings that survive the first year after release, averaged over 10000 simulation runs to reflect uncertainty. Labels indicate the choice of no AM (“none”), “passive” AM, “active” AM with an experimental phase of 1, 4 or 8 years respectively, or the optimal AM identified by stochastic dynamic programming. Longer experimental phases provide better outcomes once learning is applied, traded off with lower survival during the experimental phase. The total number of survivors over the 10-yr period is $N=35.4$ (no AM), $N=38$ (passive AM), $N=36.8$ (active 1-yr), $N=36.1$ (active 4-yr), $N=33.4$ (active 8-yr) and $N=37.6$ (optimal active AM).
Choosing on-going management regimes after reintroduction

In the previous examples I have described the potential application and challenges for AM in current or prospective threatened species programs. In the final example I illustrate how the process was implemented in a past program, and how meeting those challenges led to improved management outcomes. I focus on the ongoing management of a population after reintroduction. Ongoing investment in reintroduced populations may range from low- to high-intensity management such as different levels of supplementary feeding or continuous control of exotic predators. AM can be used to optimise this investment, for example by stopping management actions that are ineffective or resource-demanding but unnecessary for population persistence.

The hihi (Notiomystis cincta), an endangered nectar-feeding forest bird, was reintroduced in 1994 to Mokoia Island, New Zealand (Armstrong et al. 2007; McCarthy et al. 2012). Although it had been hypothesised that survival or reproduction may be food limited at reintroduction sites, no data had been collected on these rates before the start of the program, leading to uncertainty regarding the effectiveness of supplementary feeding. In this case, the decision problem was to choose a supplementary feeding regime that would achieve the objectives of maximizing population persistence given the available budget. The decision was recursive both for the specific target population, and in that new information would be later applied to other reintroduction sites.

A complete description of this case study is provided in Armstrong, Castro and Griffiths (2007). Eight alternative management regimes were devised, consisting of different availabilities, distributions and quality of supplementary food. These attempted to balance the need to learn about food limitation with the aims of maintaining the population and avoiding unnecessary starvation of birds. A population model was used to predict the expected outcomes of alternative management regimes. This model consisted of a combination of sub-models, selected from a larger candidate set using information-theoretic criteria: therefore, uncertainty was formalised as competing sub-models, and prior beliefs represented by information-criterion model weights, as well as parametric uncertainty surrounding vital rates (Armstrong, Castro & Griffiths 2007).
In this case, the large number of treatments and the complexity of the system prevented the use of a formal optimization such as SDP, given the available resources and skills. Instead, actions were applied sequentially over eight years. The monitoring system in place relied on assessing population parameters by surveying adult and juvenile birds, and assessing the level of use of feeder stations by individual birds. The data collected were used to update the population model annually, accounting for partial observability in the estimation of vital rates (Armstrong, Castro & Griffiths 2007). Results suggested that reproduction (but not survival) was greatly increased by providing 3-4 sugar-water feeders on the island, but that there was negligible additional gain from providing a full food supplement (including protein as well as sugar-water) or providing feeders to individual females.

Again, institutional commitment was fundamental to meeting the challenges to AM in this program. First, the structure of the recovery group allowed the successful collaboration of a diverse set of stakeholders and ensured the necessary skills were available for the experimental set up and the analysis of monitoring data (Ewen, Adams & Renwick 2013). Adequate support for monitoring was also maintained throughout the duration of the program. Second, the trade-off between persistence and cost was openly recognised, and the long-term benefits of learning were considered superior to the short-term risk of population decline or unnecessary spending that could result from testing sub-optimal regimes. This basic supplementation regime has subsequently been applied to six other reintroduced hihi populations. Institutional commitment also allowed double-loop learning to be undertaken in this case. In this specific decision problem, the outcomes of different strategies were used to improve existing practices on Mokoia. In a double-loop reiteration of the whole decision process, the Hihi Recovery Group is currently developing a formal AM program for simultaneously optimizing decisions at all current and prospective reintroduction sites.

Conditions and challenges for adaptive management across the captive-wild spectrum

Each of the above examples highlighted specific strengths and weaknesses that may facilitate or hinder the application of AM. Indeed, not all management decisions are well suited for AM; the basic conditions that warrant the formulation of an adaptive
management program should be considered before resources are committed to it. Williams, Szaro and Shapiro (2009) list the following conditions: (1) the need for an immediate action in the face of uncertainty; (2) explicit and measurable objectives; (3) a real choice between alternative actions, which have the ability to influence management outcomes; (4) the ability to formulate uncertainty as a set of testable hypotheses; (5) adequate stakeholder support and institutional capacity to sustain an AM program; (6) a sufficiently high value of information (that is, a measurable benefit in reducing uncertainty); (7) a monitoring program that can provide such information; and (8) the flexibility to apply learning by modifying or updating management actions. In this section, I consider them in light of the characteristics of threatened species management across the captive-wild spectrum that may represent challenges and limitations to the implementation of AM.

Figure 5.3 highlights the most common decision problems along the captive-wild spectrum. Most are likely to meet the first condition of AM, given the typical need for immediate decisions in managing poorly-known species. Decisions are usually recursive: increasingly, continuous, long-term population management is becoming the norm, as illustrated in the cheetah and whooping crane examples. However, the ability to formulate clear objectives can present a challenge. Particularly for complex programs, although conservation objectives (such as species persistence) are likely to be shared by different stakeholders, different attitudes may exist in regard to non-biological objectives such as management costs or advocacy. In the hihi example, the agreement on the need to maximise persistence and minimise cost ensured AM could be focused on those objectives. Striving to address stakeholder preferences is key to structured decision making (and thus to AM), and can prove beneficial if it allows agreement on a common strategy, and increases confidence in its reasonableness and transparency (Gregory, Ohlson & Arvai 2006).
Figure 5.3. Types of management decisions along the captive – wild spectrum, contrasting in-situ and ex-situ populations (round and square boxes respectively) and physical movement (arrows: capture from the wild, release to the wild and movement between captive breeding facilities). Typical management decisions that may be hindered by uncertainty are listed under each type in the grey boxes. Icons represent the six main sources of uncertainty (in black when they are typically dominant).
The examples illustrate the model and parametric uncertainty that is the focus of AM; however, threatened species management is also likely to be affected by other sources of uncertainty, such as environmental and demographic stochasticity, and partial observability and controllability (Williams, Szaro & Shapiro 2009). Their relative importance may change along the captive-wild spectrum (Fig. 5.3). All sources are common in management at the wild end of the spectrum, where management does not typically target individual animals directly, instead acting at the habitat (e.g. vegetation restoration or supplementary feeding) or population level (e.g., harvest management). Conversely, populations toward the captive end of the spectrum live under more controlled conditions and their management is typically not affected to the same extent by environmental stochasticity (Fig. 5.3). Furthermore, their management normally targets (or can target when needed) each individual through individualised provision of food, health care, chances for reproduction, and so on. Under such conditions, partial controllability and partial observability are usually less of a problem. Management towards the captive end of the spectrum, allowing more direct and intensive interventions, can also provide greater opportunities to compensate for the effects of demographic stochasticity. However, our knowledge of the response to management actions can still be incomplete, reflecting structural uncertainty (for example in the survival of individuals of different age classes under different levels of feeding). Most importantly, within integrated programs that span the captive-wild spectrum, the same source of uncertainty at one point along the spectrum affects management at other points (Fig. 5.3). For example, the captive population of whooping cranes must be managed in the face of uncertainty about reproductive success in the wild, and delays in learning about outcomes in the wild may affect decisions in captivity.

The relevance of such sources of uncertainty also has implications for the capacity to establish an adequate monitoring system. Several challenges to this condition can arise in threatened species management. Given the status of the managed species, low sample sizes (i.e., few individuals) may be a significant challenge to learning. For example, captive populations may be scattered across multiple institutions and different management settings, introducing confounding variables. It may be difficult to determine hypotheses and prior beliefs for little-known systems, although meta-analyses of shared data may assist in this sense (such as the ZIMS database for zoos; Cohn
In wild populations, environmental stochasticity and partial observability may decrease the effectiveness of monitoring and reduce the value of information. Explicit evaluation of the value of information can help determine the benefits of AM. Quantitative methods, such as the simulations I presented for the *Purshia subintegra* translocation, can highlight the trade-offs between managing and learning and assist in evaluating the strengths and weaknesses of alternative approaches.

All the case studies highlight the importance of institutional capacity and commitment to undertake and sustain AM, including long-term monitoring and re-evaluation. The cheetah example highlights how coordinated efforts from multiple institutions may be needed and how different levels of commitment among those may jeopardise the implementation of AM. Resource constraints are also likely to influence the capacity to carry out long-term experimentation and monitoring; however, AM can also increase cost-effectiveness by allowing managers to focus monitoring on key uncertainties rather than applying vaguely-defined surveillance monitoring (Nichols & Williams 2006). The risk attitudes of stakeholders may also influence the application of AM. Individuals of threatened species may be perceived as too valuable to be subject to experimentation; in some cases, members of the public or other stakeholders may legally challenge agencies if perceived as ‘compromising’ protected species. On the other hand, the hihi example again represents a successful case in which the long-term commitment of multiple stakeholders committed to learning eventually led to improved management outcomes.

**Conclusions**

The concept of learning while managing and then using new information to improve outcomes is intuitively appealing for threatened species management, where immediate decisions are often required in the face of incomplete knowledge. This appeal is reflected by the increasingly large number of conservation programs that nominally adopt “adaptive management” (Westgate, Likens & Lindenmayer 2013). However, there is more to AM than just “learning by doing”; I have illustrated how the full benefits of AM can only be obtained by approaching it within a broader structured decision making process. Failure to do so may result in poor allocation of resources. This can occur if attempting to apply AM where the necessary conditions do not exist,
for example where the management horizon does not allow for the application of new information. On the other hand, where the conditions exist and the challenges can be met, AM holds great potential for threatened species management.

I have provided a guide for managers interested in AM for conservation programs along the captive-wild spectrum; the examples also illustrate how AM can be applied with different levels of technical complexity. While some complex, high-stakes, and publicly visible problems may benefit substantially from the assistance of a skilled practitioner in structured decision making, outside expertise is not required for every problem. There is an increasingly comprehensive and accessible body of literature that can help a group to get started with structuring their decisions (Hammond, Keeney & Raiffa 1999 is particularly notable for its accessibility), and much of this literature focuses on natural resource management problems (e.g., Possingham et al. 2001; Runge 2011; Gregory et al. 2012). Managers interested in making more deliberative and transparent decisions should familiarise themselves with some of this basic literature, sit down with colleagues, and work through development of a first decision sketch.

References


Chapter 6

OPTIMAL RELEASE STRATEGIES
FOR COST-EFFECTIVE REINTRODUCTIONS
CHAPTER 6

Optimal release strategies for cost-effective reintroductions

Abstract

Ex-situ programs for endangered species commonly focus on two main objectives: insurance against immediate risk of extinction and reintroduction. Decisions about whether to release individuals from captivity into the wild may present managers with a trade-off between the two objectives. This can be further complicated when considering the costs of the captive population and the possible release of different life stages. In this chapter, I approached this decision problem by combining population models and decision-analytic methods, using the reintroduction program for the southern corroboree frog *Pseudophryne corroboree* in Australia as an example. I identified the optimal release rates of eggs and sub-adults which maximised the size of the captive and reintroduced populations whilst meeting budget constraints. Assuming a stable age distribution, large proportions of individuals could be released without decreasing the captive population below its initial size. The optimal strategy was sensitive to the post-release survival of both life stages, but sub-adult releases were generally most cost-effective, producing a large wild population and requiring a cheaper captive population. Egg releases were optimal for high expected juvenile survival, whereas mixed releases of both life stages were never optimal. In the short-term realistic scenario, sub-adult releases also produced the largest wild population, but they required a large increase in the size and cost of the captive population that exceeded the available budget. Egg releases were cheaper but yielded smaller numbers in the wild, whereas joint releases of both life stages provided more wild individuals, meeting budget constraints without depleting the captive population. Optimal release strategies for the reintroduction of threatened species reflect the trade-offs between insurance and reintroduction objectives, and depend on the vital rates of the released individuals. Although focusing on a single life stage may have practical advantages, mixed strategies can maximise cost-effectiveness by combining the relative advantages of releasing early and late life stages.
Introduction

Reintroductions from captive breeding programs for endangered species have been criticised for their low success rates and high resource requirements (Snyder et al. 1996). However, they may be effective when species cannot be recovered by in-situ conservation alone (Balmford, Mace & Leader-Williams 1996; Bowkett 2009). Captive programs can have multiple objectives, including education and research (Converse et al. 2013); however, the main focus is usually the long-term viability of the target species (IUCN 2013). This is usually achieved by establishing captive insurance populations to minimise the short-term extinction risk, and by reintroducing individuals into the wild to re-establish self-sustaining populations (Armstrong & Seddon 2008). In the short term, large captive populations can provide greater insurance value; in the long term, they will allow larger releases, which can improve the chances of a successful reintroduction (Griffith et al. 1989; Wolf et al. 1996; Fischer & Lindenmayer 2000).

However, releases deplete the captive population and can reduce its viability, generating a trade-off between the “insurance” and “reintroduction” objectives. Both aspects need to be considered, even though their relative importance can vary among programs. Indeed, for several species the decision to retain individuals in captivity after releases had started has ensured that eventual reintroduction failure did not result in their overall extinctions (Odum & Corn 2003; Winnard & Coulson 2008). Even for captive populations with no immediate prospect of reintroduction, releases can help in evaluating management actions and understanding threats (Rodriguez, Barrios & Delibes 1995; Letty et al. 2000). Here, larger releases can provide more information, but at the cost of reducing the viability of the captive population and negatively affecting eventual reintroductions. The biological aspects of the trade-off between reintroduction and insurance have previously been recognised (McCarthy 1994). However, the implications for cost–effectiveness have not been considered: larger captive populations can provide better insurance value, but can be more expensive to maintain. Given limited conservation resources, this aspect of the trade-off must be explicitly addressed.
The cost of the captive population can also vary depending on the length of time that individuals spend in captivity, which in turn may affect reintroduction success. Releasing early life stages may be cheaper because of reduced husbandry requirements per individual: however, younger animals generally have lower survival (Sarrazin & Legendre 2000). Therefore, the survival and fecundity of the respective life stages will influence the trade-offs associated with the choice of actions (which life stage to release) and the importance of fundamental objectives (insurance and reintroduction). Longer periods in captivity may also imply a lack of exposure to natural selection, which can reduce survival following release, as observed for several taxa (hereafter, I refer to such reductions simply as “post-release effects”; see for example Jule, Leaver & Lea 2008). Later life stages may incur greater post-release effects in species in which selection affects mainly early stages, such as amphibians (Wells 2007). Again, previous analyses of this trade-off have not included cost as an important decision making criterion (Burgman, Ferson & Lindenmayer 1994; Sarrazin & Legendre 2000).

In this study, I use population models to assess the cost-effectiveness of alternative release strategies for species with complex life histories. For an on-going program for a critically endangered amphibian, I identified the optimal release rates for eggs or sub-adults, in regard to both insurance and reintroduction objectives and management costs. Under a long-term program, assuming a captive population with a stable age distribution, large releases of sub-adults were the optimal choice. Conversely, for a short-term release plan, mixed releases of variable proportions of both eggs and sub-adults provided larger and cheaper wild and captive populations.

**Materials and methods**

*Matrix population model*

In a stage-structured population model, the vector $N_{(t+1)}$ of stage-specific abundances at time $t+1$ is the product of the abundances in the previous time step ($N_{(t)}$) and the transition matrix $L$:
\[ N_{(t+1)} = L \cdot N_{(t)} \]

where \( f_i \) is the reproductive output of individuals in age class \( i \), and \( s_{ij} \) is the probability of transitioning (survival) from stage \( i \) to stage \( j \) (Caswell 1989). For a matrix \( L_c \) associated with a captive population, the transition rates apply to individuals that have not been released. Therefore, release rates can be interpreted as another matrix \( R \) of the same dimensions, whose elements are multiplied by the respective elements of \( L_c \) (Hadamard product):

\[ N_{(t+1)} = \left[ L_c \circ R_{(t)} \right] \cdot N_{(t)} = L_c \circ \begin{bmatrix} r_{1(t)} & r_{2(t)} & \cdots & r_{n(t)} \\ r_{1(t)} & r_{2(t)} & \cdots & r_{n(t)} \\ \vdots & \vdots & \ddots & \vdots \\ r_{1(t)} & r_{2(t)} & \cdots & r_{n(t)} \end{bmatrix} \cdot N_{(t)} \]

where \( r_{n(t)} \) is the proportion of individuals in age class \( i \) that are retained (not released) in the captive population in year \( t \). Note that here I assume releases are carried out after reproduction: therefore, in captivity multipliers for fecundities are equal to 1, and the release rate of the first captive life stage changes the probability of transitioning to the second stage. The right eigenvector of \( L \) provides the stable age distribution, the proportion of individuals within each age class in the population when this is growing at the rate \( \lambda \) (the dominant eigenvalue of \( L \): Caswell 1989).

The “insurance” objective ultimately describes the viability of the captive population. Translating this to a target number of individuals can facilitate interpretation and measurement of this objective for management purposes. The exact target may depend, for example, on the population size required to retain genetic diversity (Lande & Barrowclough 1987). In a stable-age-distributed population, the insurance objective can be expressed in terms of the growth rate for the captive population. For example, the objective of maintaining at least the initial population size can be stated as \( \lambda \geq 1 \).
Similarly, the “reintroduction” objective might reflect the size of the recipient population. Here, the vector $W$ of age-structured abundances at time $t+1$ can also be represented as the product of the abundances at time $t$ and the vital rates of that population ($L_w$), augmented at any given time by releases from the captive population:

$$W_{(t+1)} = L_w(t)W(t) + \left[(1-R)(t) \circ L_r\right]N(t)$$  \hspace{1cm} \text{Eq. 6.3}$$

where $(1-R)(t)$ is the matrix of release rates (the proportion of individuals that are not retained at year $t$), and $L_r$ is the matrix that describes the vital rates of individuals post-release. These can correspond to the rates of the wild population if no post-release effects are assumed ($L_r=L_w$), or can be represented as another matrix of estimated vital rates that describe any post-release effects such as increased mortalities or decreased fecundities. The optimal release strategy corresponds to the values of $R$ that maximise success for the chosen objectives.

Given a sufficiently long time frame (damping ratio of $L$: Caswell 1989) with constant vital rates, all populations will reach an asymptotic stable age distribution. However, in actual reintroduction programs initial numbers may deviate from the stable age distribution, which may not be achieved within short time frames. In this case, the discrete growth rate might be an unsuitable measure of success; however, the matrix framework (Eqs. 6.1-6.3) can still be used to identify the optimal release rates after adapting the objectives.

**Study species**

I applied the approach described above to the on-going release program for the southern corroboree frog *Pseudophryne corroboree* Moore (Anura: Myobatrachidae). This species, endemic to south-eastern Australia, has declined since the late 1980s (Osborne 1989) and is listed as critically endangered on the IUCN Red List (IUCN 2011). A captive breeding program was advocated since the initial recovery plan (Hunter *et al.* 1999; NSW National Parks and Wildlife Service 2001), particularly after the discovery of the fungal disease chytridiomycosis in wild populations (Hunter *et al.* 2010). *P. corroboree* is now being bred in captivity at several Australian institutions (McFadden *et al.* 2013). The project currently aims to maintain a presence of individuals in the wild
to improve knowledge of the dynamics of disease spread and induced mortality, and to allow the possible development of tolerance to the pathogen. At the same time, it is necessary not to deplete the captive population to the extent of reducing its viability, to allow future full-scale reintroductions.

I represented the reintroduction program for *P. corroboree* as a combination of two populations (one wild and one captive). I modelled only females, assuming equal sex ratio (as observed in the captive population: M. McFadden, *unpubl. data*) and defined six age classes: eggs (*N*₀), one-, two- and three-year-old juveniles (*N*₁, *N*₂, *N*₃), four-year-old sub-adults (*N*₄) and sexually mature adults (*N*₅) five or more years old (Hunter 2000). I parameterised the transition matrices *L*ₖ and *L*₉ₖ, for the captive and wild population respectively (Eqs. 6.1-6.3), using values elicited from experts, relying on their knowledge and on published information (Hunter *et al.* 1999; Hunter 2000). I defined a most-likely, a worst-case and a best-case estimate for every parameter (Table 6.1). To fully characterise uncertainty, for each parameter I then fit a beta-PERT distribution to the estimates, a modified beta distribution specifically developed for the treatment of expert-elicited information (Vose 1996). I carried out the optimisation using the Solver and MCSimSolver add-ins in MS Excel.

*Stable age distribution*

Initially, I assumed a stable age distribution and identified the maximum release rate of either eggs or sub-adults that could be sustained indefinitely without reducing the captive population below its initial size (*λ*ₖ ≥1). I used simulations to account for parametric uncertainty in the parameters of *L*ₖ and *L*₉ₖ. For each of 10,000 iterations, I parameterised *L*ₖ drawing the value of each parameter from its distribution and identified the maximum release rate (1-*r*ₖ) of the chosen life stage, constraining for *λ*ₖ ≥1. I calculated mean and 95% confidence intervals of the maximum release rate across all iterations. I repeated the analysis three times, calculating the maximum release rate for either eggs or sub-adults when retaining all the other life stages, and the maximum rate for each stage when releasing both eggs and sub-adults.
Table 6.1. Parameter estimates for the three considered scenarios (best-, worst- and most likely case). Parameters: $s_0$ indicates the survival of eggs to one-year old froglets, $s_1$ to $s_5$ indicate survival for the corresponding age class post-metamorphosis, $f$ indicates the fecundity of adult frogs; $b$ indicates the proportion of individuals breeding in a given year.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Captive population</th>
<th>Wild population</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Best</td>
<td>Likely</td>
</tr>
<tr>
<td>$s_0$</td>
<td>0.82</td>
<td>0.7</td>
</tr>
<tr>
<td>$s_1$</td>
<td>0.85</td>
<td>0.85</td>
</tr>
<tr>
<td>$s_2$</td>
<td>0.9</td>
<td>0.85</td>
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<tr>
<td>$s_3$</td>
<td>0.95</td>
<td>0.9</td>
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<tr>
<td>$s_4$</td>
<td>0.95</td>
<td>0.9</td>
</tr>
<tr>
<td>$s_5$</td>
<td>0.95</td>
<td>0.9</td>
</tr>
<tr>
<td>$f$</td>
<td>15</td>
<td>12</td>
</tr>
<tr>
<td>$b$</td>
<td>1</td>
<td>0.75</td>
</tr>
</tbody>
</table>

To evaluate the consequences of these release rates for the reintroduction objective, I simulated the trajectories of a system of two populations when the maximum rates were used to populate $R$ (Eqs 6.2-6.3). For the captive population, I assumed a stable age distribution from $t=0$, as inferred from the dominant eigenvector of the matrix $L_c \circ R$ (Eq. 6.3). I also calculated the trajectory of a wild population, with initial size set to zero, which received the corresponding number of released individuals at every time step. I expanded the simulation to account for parametric uncertainty in the wild population. I expressed the result in terms of the ratio of individuals in the wild per individual in the captive population; assuming the captive population remains stable, its size can be easily translated into resource requirements for any given time step. I then repeated the analysis for a different objective function, the ratio between the wild population size and the yearly cost of maintaining the captive population. I estimated costs based on expert opinion, with yearly figures of A$ 58 for the first year (from egg to metamorphosis), and of A$ 50 for every year in the life of a post-metamorphic individual. These figures include all costs of food, housing, disease screening,
equipment maintenance and staffing, based on records for the two main captive populations of *P. corroboree*. I did not include the cost of releases, assuming they would be equal for different life stages. All costs were borne after breeding and before any reintroduction.

Initially, I ran all analyses assuming no post-release reduction in vital rates. I then assessed the sensitivity of outcomes to the post-release survival of released individuals in both life stages and to the fecundity of released sub-adults (I assumed no change in the fecundity of individuals released as eggs, after being exposed to four years of natural selection). For all possible combinations of tadpole and sub-adult survival (over the [0, 1] interval) and sub-adult fecundity (over the realistic estimated range [6, 15]: Table 6.1), I calculated the expected outcome of each strategy as the number of adults in the wild for every A$ 1,000 spent. For clarity, I ignored parametric uncertainty by setting all remaining parameters equal to the mean values of their distributions, and applied the average optimal release rates identified for those values.

**Variable initial values and demographic stochasticity**

I then simulated a more realistic scenario in which the stable age assumption was violated and the time frame shortened. I set the initial values for the captive population as $N_{0(0)}=300$, $N_{1(0)}=150$, $N_{2(0)}=250$, $N_{3(0)}=900$, $N_{4(0)}=300$ and $N_{5(0)}=340$, based on actual numbers held in captivity at the beginning of this study. I identified the release rates that maximised the average number of adult individuals in the wild ($W_5$) over a 10-year period. I compared the optimal release rates for eggs only, sub-adults only and a mixture of the two age classes. Again, I used simulations to represent parametric uncertainty, reporting means and confidence intervals of the optimal release rates. I set two constraints to the optimisation. First, the number of captive breeding adults at any given time should not be smaller than that at the beginning of the program ($N_{5(t)} \geq N_{5(0)}$), again reflecting a simplified “insurance” objective as previously discussed. Second, the total cost of the captive population at any time step should not exceed A$ 250,000, reflecting the actual yearly budget in the years 2008–2012.

Finally, I compared the outcomes of each strategy when incorporating demographic stochasticity. Using the mean values for $L_e$ and $L_w$, I re-fitted the models in RAMAS
Metapop (Akçakaya & Root 2002) assuming that fecundity and individual survival followed Poisson and binomial distributions respectively (Akçakaya 1991). I ran 10,000 simulations for each strategy over ten years, using the optimal release rates. I assumed no density-dependence, allowing the populations to grow exponentially. I then compared the mean number of adults in the wild and the cost of the resulting captive population.

**Results**

**Stable age distribution**

Assuming a stable age distribution, the mean growth rate of the captive population was $\lambda_c=1.64$ (95% CI: 1.57, 1.69). The maximum sustainable release rate of either eggs or sub-adults was on average $r=0.98$ (95% CI: 0.97, 0.99; Table 6.2). When releasing equal proportions of eggs and sub-adults, the maximum sustainable release rate for each stage averaged $r=0.86$ (95% CI: 0.85, 0.91; Table 6.2). The stable age distribution in the captive population was also influenced by the release strategy. For egg and joint releases, adults represented more than half the population, whereas for sub-adult releases they were only 2% of all individuals (Table 6.2). On the other hand, sub-adult releases produced a more diverse stable age distribution, with similar proportions of the first four stages.

The discrete growth rate for the wild population was $\lambda_w=0.75$ (95% CI: 0.71, 0.80), suggesting that without continuous releases the population would not persist. When releasing 98% of eggs, the wild population became stable at a constant size equal to 41% of the stable captive population (31%, 54%; Table 6.2). When releasing sub-adults, the ratio increased to 249% (191%, 325%; Table 6.2). Finally, when releasing both eggs and sub-adults at $r=86\%$, the stable wild population was 102% the size of the captive one (80%, 131%; Table 6.2). Population trajectories are described in Fig. 6.1. The cost of the captive population was slightly higher for sub-adult releases (A$ 57 per individual, compared to A$ 51 for egg and joint releases), since they implied retaining eggs. However, this difference was marginal and the cost of the captive population at
stability was similar under all scenarios: therefore, the optimal choice did not change when including costs in the objective function.

**Table 6.2.** Outcomes of applying the maximum release rates to a captive population with stable-age distribution.

<table>
<thead>
<tr>
<th>Stable age distribution of captive population</th>
<th>Release strategy</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Eggs only</td>
<td>Sub-adults only</td>
<td>Joint and equal releases</td>
</tr>
<tr>
<td>Maximum release rate(^1)</td>
<td></td>
<td>0.98</td>
<td>0.98</td>
<td>0.86</td>
</tr>
<tr>
<td>Eggs</td>
<td></td>
<td>0.14</td>
<td>0.30</td>
<td>0.13</td>
</tr>
<tr>
<td>1-yr</td>
<td></td>
<td>0.10</td>
<td>0.21</td>
<td>0.10</td>
</tr>
<tr>
<td>2-yr</td>
<td></td>
<td>0.08</td>
<td>0.18</td>
<td>0.09</td>
</tr>
<tr>
<td>3-yr</td>
<td></td>
<td>0.07</td>
<td>0.15</td>
<td>0.09</td>
</tr>
<tr>
<td>Sub-adults</td>
<td></td>
<td>0.06</td>
<td>0.14</td>
<td>0.08</td>
</tr>
<tr>
<td>Adults</td>
<td></td>
<td>0.56</td>
<td>0.02</td>
<td>0.50</td>
</tr>
<tr>
<td>Yearly cost of captive population(^2)</td>
<td></td>
<td>51.1</td>
<td>57.1</td>
<td>51.1</td>
</tr>
<tr>
<td>Wild/captive ratio(^3)</td>
<td></td>
<td>0.41</td>
<td>2.41</td>
<td>1.80</td>
</tr>
</tbody>
</table>

1 Maximum release rate for \(\lambda_c \geq 1\).

2 Calculated by multiplying the stable-age proportion for each class by its respective cost (A$ 58 for eggs, A$ 51 for post-metamorphic individuals).

3 Number of wild individuals for every individual maintained in captivity.
Figure 6.1. Outcomes of optimal release strategies under the stable age distribution assumption. Y-axis values correspond to the number of wild individuals for every individual existing in captivity at a given time. Maximum release rates calculated for a captive population with $\lambda=1$, for each scenario (eggs or adults only: 98%; joint releases: 86% each). The shaded areas correspond to 95% confidence intervals over 10,000 simulations across the parametric uncertainty of vital rates.

Figure 6.2 shows the sensitivity of the optimal choice and its outcome to the post-release survival of tadpoles and sub-adults. For any combination of these rates, the joint release strategy was always worse than at least one of the single-stage ones. Egg releases were only optimal for low sub-adult survival rates and unrealistically high tadpole survival ($s_0>0.75; s_4<0.2$). Even where they were the optimal choice, their outcome was poor, yielding less than one wild adult every A$ 1,000 spent (Fig. 6.2). Outcomes were largely insensitive to the fecundity of individuals in the year post-release: even assuming that released sub-adults would not breed in the first year ($f=0$), the wild/captive population ratio at stability varied by less than 0.01, and the optimal strategy did not change.
Figure 6.2. Changes in the effectiveness of releasing either eggs or sub-adults, depending on the respective vital rates in the year after release. For every combination of tadpole and sub-adult post-release survival (x- and y-axis respectively), the plot indicates (a) which strategy is most effective: egg releases below the solid line, sub-adult releases above; (b) the outcome of the optimal strategy, indicated by the background colour, and expressed as the number of adult individuals in the wild for every A$ 1,000 spent. For example, if the post-release survival is 0.2 for tadpoles and 0.4 for sub-adults, sub-adult releases are the optimal strategy, and they result in 2 wild adults every A$ 1,000 spent. All outcomes were calculated assuming maximum release rates under a stable age distribution, with average vital rates for all other stages.

Variable initial values and demographic stochasticity

Under a more realistic scenario with different initial abundances in captivity, budget constraints and short-term objectives, the optimal release rates differed for every year. Over a 10-year period, a strategy focusing on egg releases required large releases (>98% in years 1–9 and 65% in year 10). This strategy was generally cheaper than the available budget, but it never produced more than 150 breeding adults in the wild (Fig. 6.3). A strategy focusing on sub-adult releases also required high release rates (>90% every year), and was expected to provide the highest number of wild individuals (Fig.
6.3). However, this strategy required a very large captive population, and it was not possible to satisfy both constraints: when aiming not to deplete the captive population, the yearly budget was exceeded (Fig. 6.3). The optimal strategy using joint releases of both stages required partial retention of eggs (averaging 20 to 70%) in the first two years, to reach capacity and maximise production in the following years, partial retention of sub-adults in years three and four (39% and 40%) to ensure that the desired number of adults was maintained, and finally large releases of both stages in years 5–9 (>80%). This strategy provided better outcomes than egg releases alone, and although in the last five years it produced fewer individuals than a sub-adult-only strategy, its total cost was 68% lower, without exceeding the yearly budget (Fig. 6.3).

**Discussion**

The first objective of ex-situ programs for critically endangered species is often the establishment of a viable captive population as insurance in the event of extinction in the wild (Conway 2011). The growth rate of the captive population will determine whether this objective can be met, and how it can be balanced with future reintroduction efforts. Populations with high predicted growth are more likely to be able to sustain large release rates and still maintain viability. For *P. corroboree*, long-term persistence of the captive population could be ensured even when releasing a large proportion (0.98 on average) of either eggs or sub-adults, due to high survivorship and productivity in captivity.

Releasing different life stages will also change the stable age distribution of the captive population and may affect specific objectives regarding its structure (for example, representation of genetic diversity). The cost of a stable and constant captive population depends on the maintenance requirements of different stages. In the stable age distribution scenario for *P. corroboree*, the difference between maintenance costs for eggs and other life stages was not sufficient to change the optimal strategy. However, if differences are significant (for example when breeding adults need large individual enclosures), different release strategies may have different costs, influencing the optimal decision when cost is an objective.
In the stable age distribution scenario, the insurance objective for the captive *P. corroboree* population was to maintain $\lambda_c \geq 1$, as a simple approximation of viability. Managers may initially seek a higher growth rate, to increase the size of the captive population and release greater absolute numbers in the future; however, resource constraints are likely to impose an upper limit to the captive population size. Once this carrying capacity is reached, then the “insurance” objective may simply shift to $\lambda_c = 1$. Similarly, initial releases in excess of the maximum sustainable rate will result in a
population reduction ($\lambda_c < 1$) until a lower bound is reached. In this case, I assumed this bound was equal to the initial population size $N_0$, although the exact relationship may differ among projects. In a theoretical study, Tenhumberg et al. (2004) suggested that it is generally optimal to increase the size of the captive population as rapidly as possible, and to start releases once this approaches its carrying capacity. In real programs, the practical challenge for managers lies in estimating the optimal duration of this “build-up” phase and the subsequent proportion of individuals to release. Framing population models in a clear decision-analytic framework can help in assessing the optimal decision.

In regard to the reintroduction objective, the trajectory of the wild population depends on its intrinsic growth rate. If $\lambda_w > 1$, then the population will grow accordingly after the initial releases, and assuming exponential growth, constant releases from a stable and constant captive population will become progressively less important in the long term. On the other hand, if $\lambda_w < 1$, as it was for *P. corroboree* in this study, continuous releases are needed to prevent the wild population from declining to extinction. Whether such an approach is justified depends on the objectives of the specific program. In the case of *P. corroboree*, where the wild population depended on continuous releases, egg releases were less effective than sub-adult releases, yielding a smaller number of individuals in the wild for every individual maintained in captivity. If cost is an objective, it is therefore necessary to consider that when releasing eggs a greater population will need to be maintained to provide the same absolute numbers of individuals in the wild.

The effectiveness of releasing different life stages will depend on their expected vital rates. In general, individuals that are released later in life will have better survival than those released early, and thus provide a greater wild-to-captive ratio. Within the matrix population model framework, the effects of this increase in survival can be summarised, for example, using reproductive values (the expected number of offspring an individual will produce over its lifetime: see for example Sarrazin & Legendre 2000). However, newly released individuals can suffer abnormally high mortality or low fecundity, reflecting a lack of natural selection during the captive phase or adaptation to captivity (McCarthy, Armstrong & Runge 2012). Reintroduced adults can also exhibit abnormally high dispersal, a behavioural aspect observed in several taxa (Le Gouar,
The use of environmental cues for dispersal has been demonstrated for amphibians, particularly for juveniles learning dispersal routes post-metamorphosis (Ferguson 1971). In this case, the effects of post-release dispersal on the establishment of a reintroduced population may be higher for late-age-class release strategies, in which individuals have had no opportunity to learn dispersal routes. Although no information is available in this sense for *P. corroboree*, post-release dispersal could be considered as additional mortality.

Although such post-release effects can reduce the relative benefit of releasing later life stages, these may still be advantageous where the better survival of older individuals compensates the incidence of post-release effects. For example, Sarrazin & Legendre (2000) modelled releases of Griffon vultures *Gyps fulvus* in Europe, suggesting that where post-release effects remain small, releases of adults should indeed prove more effective for long-lived species. In this sense, the average longevity of *P. corroboree* (six to ten years in the wild: Hunter 2007) makes it a comparable case study for several amphibians, mammals and birds targeted by captive breeding efforts (see for example the species listed in Short *et al.* 1992; Griffiths & Pavajeau 2008; Graham *et al.* 2013). Additionally, for amphibians and other *r*-selected taxa, mortality in early life stages can naturally be an order of magnitude higher than for adults, potentially offsetting post-release mortality of older individuals. Amphibians are also less reliant on learnt behaviour than mammals or birds, further reducing the potential for adaptation to captivity (Griffiths & Pavajeau 2008). Finally, for many amphibian species it might be possible to compensate mortality by releasing thousands of individuals, especially for juvenile stages, as shown for example by the results for *P. corroboree*. Such numbers may not be practical for other taxa, reducing the scope for a solution of the trade-offs in vital rates.

In this case study, results were also generally insensitive to the short-term fecundity of released sub-adults. This was a result of the longevity of adults and of the assumption of no long-term variation in fecundity (from the second year after release all individuals would have the same reproductive output). Greater sensitivity might be expected in the case of long-term variations in fecundity that differed between life stages (for example, if early-age releases achieved full reproductive potential, and late-age releases never
did). In this sense, the results are consistent with those of Sarrazin & Legendre (2000), who found greater sensitivity of reintroduction success to post-release survival than to fecundity for *Gyps fulvus* in Europe (for reductions both in the short and long term).

Environmental stochasticity can also have life stage-specific effects that will influence the relative effectiveness of release strategies (Sarrazin & Legendre 2000). In *P. corroboree*, egg survival can be affected by environmental stochasticity: since eggs are laid in nests on the ground, they need sufficient precipitation to be flushed to a water body that must retain water throughout the period of tadpole development (Hunter *et al.* 2009). High mortality of eggs and low recruitment have been observed in drought years (Osborne 1989). On the other hand, wet years can facilitate the spread and virulence of chytrid fungus, again with potential age-specific effects (Kriger 2009). In light of this complexity, currently not entirely understood for *P. corroboree*, I chose not to explicitly model environmental stochasticity in this study; however, it may affect the efficiency of egg releases in particular, and monitoring is being carried out to evaluate this possibility.

When the size of the captive population is not constant, retaining individuals in captivity for a longer period will increase the overall financial cost of a program and may generate conflicts where limited resources are available (such as space or human resources at zoo institutions). In this case, strategies that envisage releases of a single life stage releases inevitably bear the consequences of this trade-off. Focusing only on releases of early life stages might be appealing to risk-seeking managers with strict budget constraints. This was clearly reflected in the realistic short-term example for *P. corroboree* with multiple objectives (insurance, reintroduction and costs). Across the full range of parametric uncertainty, mixed strategies including joint releases of eggs and sub-adults provided the most cost-effective solution. Although egg releases allowed the lowest costs, they were also less effective towards the reintroduction objective. The reduction of age-class diversity in the captive population might be another concern. Conversely, releasing sub-adults was predicted to produce a greater presence in the wild. This potential risk-averse solution, however, led to high and increasing costs, making it impossible to meet both cost and insurance objectives. In this sense, mixed strategies allow managers to combine the advantages of releasing different life stages,
for example releasing sub-adults to improve viability and managing egg releases to control the size and cost of the captive population.

Ultimately, the evaluation of the trade-off between additional costs and the predicted improvements in viability associated with releasing later life stages must be solved on the basis of the importance given to each objective. For example, Martínez-Abraín et al. (2011) used population viability analysis to assess translocation options for crested coots *Fulica atra* in Spain: they found that releasing adults improved viability, but this remained generally poor. They concluded that a 160% increase in costs “outweighed” the marginal conservation benefits of releasing adults rather than juveniles. However, the definition of the threshold above which benefits are outweighed by costs will differ among programs. Adopting an explicit decision-analytic approach may help define priorities and consequently the optimal decision.

The definition of clear objectives is the key to a rigorous approach to decision making (Possingham *et al.* 2001). In the realistic scenario, I chose a short time frame to reflect the current requirement of the release program for *P. corroboree* and used the number of breeding adults as a metric of success; longer programs may focus on growth rates or probability of extinction. Those choices are influenced by the current difficulty in mitigating threats for this species, reflected by the expected negative growth rate of the wild population. Reintroduction programs aimed at establishing self-sustaining populations, or involving species with longer generation times, may need to consider longer time-frames, which can be easily accommodated in the approach presented.

Finally, I recognise that legislative or funding constraints can create additional objectives, for example requiring managers to report some metric of success within a given deadline. If such additional objectives can be stated explicitly, the decision framework can be modified to accommodate them.

Additional aspects would also need to be considered in a more realistic analysis. For example, the assumption of exponential growth may be violated, for example by small-population dysfunctions such as Allee effects. I did not model the genetic viability of the species either in captivity or in the wild, although the management of captive populations to minimise inbreeding is recognised as a key component of recovery.
efforts for *P. corroboree* (Lees, McFadden & Hunter 2013). Again, different components of the decision process for this problem could be modified to account for these aspects.

The ex-situ conservation program for *P. corroboree* shows characteristics common to most similar efforts worldwide; the rapid and seemingly irreversible decline of the target species, the unknown feasibility and time frame of threat abatement, the need to minimise time in captivity and maximise production of release candidates, while containing costs. Population models can provide useful information for managing a captive insurance population, while life stage-specific release plans can help in addressing trade-offs between numbers of releases, the probability of establishing a wild population and management costs. Framing models in an explicit decision-analytic framework can assist in evaluating key objectives, uncertainty and trade-offs.

**References**


Chapter 7

GENERAL DISCUSSION AND CONCLUSIONS


CHAPTER 7

General discussion and conclusions

Discussion of findings

The conservation of threatened species is likely to require different types and intensities of active management, such as establishment and maintenance of captive populations, translocation of individuals within and between captive and wild populations, and short- and long-term support of reintroduced populations. Managers of such conservation programs face difficult decisions in the face of multiple objectives, constraints and uncertainties. Structured decision making provides a range of principles and methods for approaching difficult decisions under uncertainty. This thesis demonstrates the application of those principles and methods to decisions about whether and how to carry out different types and intensities of active management.

Intuitively, the first decision faced by conservation managers is whether a given type of management should be implemented at all. I addressed such a decision problem in Chapter 2, through the use of decision trees and multi-criteria decision analysis. I demonstrated how the question of whether an ex-situ population should be established can only be answered rationally by deciding how that population will be used; that is, how it will contribute to the fundamental management objectives for a species. However, real-world ex-situ programs often follow the inverse decision process, whereby individuals of a species are brought into captivity, often as a last resort against imminent demise, before detailed consideration of future strategies for reintroduction (Snyder et al. 1996; Lacy 2013). This inversion of the rational decision process can lead to poor decisions and inefficient resource allocation. Highlighting this discrepancy is important for two reasons. First, it reinforces the need for integrated management across the spectrum, where ex-situ and in-situ management are approached as connected components of the same species recovery plan (IUCN 2008; IUCN 2013). Second, the choice of whether to choose a given type of management depends on why it is being considered: that is, the management objectives and the preferences of managers.
In Chapter 2, I used value functions and multi-attribute utility theory to describe the preferences of managers towards two objectives (persistence of populations and species and management costs) and different levels of expected outcomes. When trade-offs must be made, the solution depends on the relative importance of the objectives. In the *Litoria spenceri* example, this corresponds to how much managers are willing to pay for a given increase in species persistence. The presence of multiple objectives, and the use of multi-criteria decision analysis, has been previously discussed for reintroduction programs (Converse *et al.* 2013; Ewen *et al.* 2014). However, the study presented in Chapter 2 is the first to demonstrate how the solution to the same trade-offs may also vary in response to different expectations about outcomes. For example, reducing the risk of extinction from 100% to 90% may be considered more worthy of resources than a reduction from 20% to 10%. Explicit recognition of such nonlinear preferences is important for addressing multiple objectives rationally.

Furthermore, preferences (and consequently decisions) may also be influenced by uncertainty. In Chapter 3, I demonstrated how different decision makers may choose different management options from the same set, because the decision makers diverge in their attitude toward uncertainty and risk. The relevance of risk attitude in the active management of threatened species is demonstrated by the ongoing debate around assisted colonisation (Ricciardi & Simberloff 2009; Schlaepfer *et al.* 2009; Seddon *et al.* 2009; Seddon 2010) and conservation “triage” (Bottrill *et al.* 2008; Jachowski & Kesler 2009; Part *et al.* 2009). Decision analysis cannot reconcile fundamentally different attitudes or preferences; it can, however, assist in identifying and formally expressing those attitudes and preferences and their implications for rational choice. This in turn can facilitate discussions and promote clarity and transparency. In Chapter 3 I presented the first application of stochastic dominance analysis to threatened species management. This method provides an excellent starting point for incorporating considerations of risk attitude in translocation decision making. Its advantage is in the progressive application of higher orders of dominance only where needed. At least for first- and second-order dominance, both the calculations and the elicitation process required are simple, facilitating application in group settings and for practitioners who are not familiar with decision-analytic tools.

In Chapters 4 and 5, I explored in greater detail how uncertainty can be treated in the decision making process. Threatened species programs are affected by several sources of uncertainty,
usually recognised and approached analytically. Population models for translocations normally incorporate demographic and environmental stochasticity (Armstrong & Reynolds 2012; Converse, Moore & Armstrong 2013), while experimental studies and reintroduction trials are used to reduce uncertainty about management outcomes (Kemp et al. 2015). In Chapters 4 and 5, I illustrated how structured decision making can improve the link between the analytical treatment of uncertainty and the choice of management actions.

First, value of information analysis can help in determining whether learning will improve management, which sources of uncertainty should be targeted, and how experiments and monitoring should be designed. In Chapter 4 I calculated the value of information for two common decision problems in current threatened species management: a translocation under risk of disease and a trial reintroduction where there is uncertainty about demographic rates. Second, learning can occur through experimental work carried out independently from management, or as a component of the management itself under the definition of adaptive management (AM). Although the concept of AM is increasingly advocated for conservation, it is often applied with limited effectiveness (Westgate, Likens & Lindenmayer 2013). In Chapter 5, I analysed the characteristics of threatened species management that influence whether it meets the conditions necessary for the fruitful application of AM. Many threatened species problems may lend themselves to the application of AM, since they require recursive decisions in the face of structural uncertainty and active management can provide opportunities to learn. The most significant challenges often occur at the institutional level and reflect the attitudes of stakeholders, for example toward experimentation with small and valued populations.

Once a problem has been adequately defined, objectives stated and management alternatives identified, structured decision making can draw upon a range of methods to identify the optimal decision. In Chapter 6, I solved a reintroduction problem in which the life history of the target species leads to a trade-off between management effectiveness and costs. In this case, I used a simple optimisation tool to link the biology of the species (described by a population model) and the associated management costs. I then identified the optimal release rates of different age classes that best fulfilled the objectives of maintaining viable ex- and in-situ populations and of meeting budget constraints. Demographic models are commonly used in threatened species management: the simple method I presented in Chapter 6 can reinforce an explicit connection between modelling and management objectives.
Future directions

Reintroductions and other active threatened species management were among the first examples brought forward by early advocates of structured decision making in conservation (e.g. Maguire 1986; Maguire et al. 1988). It may therefore appear surprising that over three decades later, only a restricted sample of real-world applications exist, and this thesis is still concerned with setting the foundations for a greater penetration of SDM in practice. Much remains to be learned, and a large implementation gap must be filled.

Many of the difficulties, and future opportunities for research, stem directly from our limited knowledge of threatened species, and their environment, as natural systems. The ecology of species that exist in small and declining populations is naturally challenging for researchers. The idiosyncrasies of species and ecosystems also mean that general rules for conservation are hard to develop: a theoretical question of whether captive breeding and reintroduction are more effective than in-situ management only does not have a rational answer. In this sense, the research gaps for decision making in threatened species programs reflect the knowledge gaps about the species themselves.

However, even in the face of such knowledge gaps conservation is continually happening. This implies that difficulties do not prevent decisions being made, and therefore in most cases should not prevent the application of SDM. Technical solutions for well-defined decision problems are increasingly available. Chapter 6 is representative of most implementations of decision analysis in conservation to date; it provides a technical solution to an already clearly formulated decision problem. In a broader sense, all chapters in this thesis explore tools that are well-known in other fields such as economics or health management, but have been underused in threatened species management to date. Certainly future research can help shed light on difficult management decisions, and make such solutions more technically advanced and robust. For example, the importance of genetic processes (such as inbreeding and outbreeding depressions) in threatened species programs has long been a major focus of research, yet the application of decision analysis to genetic management remains largely unexplored (Smith et al. 2011; Weeks et al. 2011). Similarly, the risk of disease transmission and spread in active species management has been widely recognised (Viggers, Lindenmayer & Spratt 1993; Cunningham 1996), but veterinary and epidemiological research have only
infrequently been integrated in decision making frameworks (Sainsbury & Vaughan-Higgins 2012; Ewen et al. 2015).

However, perhaps the most important implication of structured decision making is that rational choices only exist in relation to the objectives we seek to achieve. Without a clearly structured problem, defined objectives and realistic alternatives, even sophisticated ecological analyses may fail to provide guidance to decision makers. In other words, there is no good answer to whether and how if the why is not defined. Further research on methods that provide guidance on defining the “value” components of decision problems, such as the value functions or stochastic dominance illustrated in this thesis, may prove particularly helpful in this sense. Researchers and conservation organizations can assist practitioners by providing frameworks and guidelines for selection of objectives and metrics that accurately reflect the fundamental values of a reintroduction.

Concurrently, future research and application should proceed in close connection: only advancing the former would simply widen the existing implementation gap. Many of the methods presented in this thesis are still absent from most conservationists’ toolboxes. However, I have demonstrated how they are often intuitive in principle and application. Complex specialist skills are only required for a minority of problems, and most of the benefits of decision analysis can be accrued early in the process. For example, Keeney (2004) argues that over 99% of decision problems might be resolved simply by better structuring the decision problem or by clarifying objectives. Ultimately, it should not be forgotten that decision-analytic methods do not provide fixed and unquestionable solutions, but only guidance for more informed and transparent decision making.

On the other hand, structured decision making may be unsuitable for some decision problems, particularly where objectives are hidden or science is disputed (Gregory et al. 2012). Concerns about the risk of “paralysis by analysis” have also been raised by some authors, whereby the iterative process leads to a lack of action while objectives, actions and predictions are continually updated (Conroy & Peterson 2013). However, most threatened species programs represent long-term commitments, for which a small initial investment in refining decisions can avoid later frustrations and the poor allocation of resources. The process and methods I have illustrated are also scalable: they do not require standard
investments in time and resources, but can be tailored to the needs and conditions of specific programs.

Decision-analytic methods are now well established in the conservation literature, and increasingly adopted in practice. However, the management of threatened species would benefit from a broader penetration of the concepts and tools of structured decision making in medium and small-scale decision making. Clearly, structured decision making will not remove uncertainty or variability: decisions will remain difficult, and failures possible even when choosing the best available actions. However, rational decisions can have better outcomes in the long run, both in terms of species and population persistence and of efficient use of resources. The scale and speed of species declines and threatening processes will not abate in the near future, while resources remain limited and knowledge incomplete. It is my hope that this thesis has provided useful tools to preserve species under such conditions.

References


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