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Adaptive management for improving species conservation across the captive-wild spectrum

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ABSTRACT

Conservation of endangered species increasingly envisages complex strategies that integrate captive and wild management actions. Management decisions in this context must be made in the face of uncertainty, often with limited capacity to collect information. Adaptive management (AM) combines management and monitoring, with the aim of updating knowledge and improving decision-making over time. We provide a guide for managers who may realize the potential of AM, but are unsure where to start. The urgent need for iterative management decisions, the existence of uncertainty, and the opportunity for learning offered by often highly-controlled captive environments create favorable conditions for AM. However, experiments and monitoring may be complicated by small sample sizes, and the ability to control the system, including stochasticity and observability, may be limited toward the wild end of the spectrum. We illustrate the key steps to implementing AM in threatened species management using four case studies, including the management of captive programs for cheetah (*Acinonyx jubatus*) and whooping cranes (*Grus americana*), of a translocation protocol for Arizona cliffroses *Purshia subintegra* and of ongoing supplementary feeding of reintroduced hihi (*Notiomystis cincta*) populations. For each case study, we explain (1) how to clarify whether the decision can be improved by learning (i.e. it is iterative and complicated by uncertainty) and what the management objectives are; (2) how to articulate uncertainty via alternative, testable hypotheses such as competing models or parameter distributions; (3) how to formally define how additional information can be collected and incorporated in future management decisions.

1. Introduction

Conservation biologists increasingly recognize that successful management of threatened species requires the integration of diverse management techniques (IUCN/SSC, 2008). While conservation approaches are often categorized as focusing on the "wild" or in situ environment versus its "captive" or ex situ counterpart, in reality they span a spectrum of management intensity; few programs involve completely unmanaged wild populations or complete control over captive populations (Redford et al., 2012). For simplicity, in this paper we refer to this spectrum as the captive-wild spectrum.

Along this spectrum, conservation management requires making decisions about which actions to apply. Decisions include whether to establish new populations in breeding centers or via translocations among wild populations, how and when to translocate individuals, and which methods to use to manage wild populations. Incomplete knowledge of the biological system results in uncertainty about how to manage most effectively (Burgman, 2005). On the other hand, 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. This process represents the essence of adaptive management (AM; Holling, 1978; Walters, 1986), which has been increasingly advocated for conservation in recent years (McCarthy and Possingham, 2007; Runge, 2011). With its focus on objectives and uncertainty, AM lies within the more general framework of structured decision making, the process of rationally analyzing decisions (Gregory et al., 2012). AM has been explicitly highlighted as an important tool in comprehensive species

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conservation strategies (IUCN/SSC, 2008), as well as in guidelines for reintroductions (IUCN/SSC, 2013) and ex situ programs (IUCN/SSC, 2014).

Despite its potential advantages, implementation of AM in conservation is infrequent and often incomplete or unsatisfactory (Westgate et al., 2013). This implementation gap may result from confusion surrounding key concepts and definitions, misunderstanding of the practical barriers to implementation, and inadequate institutional structures and support (Allen and Gunderson, 2011; Gregory et al., 2006). Rather than reviewing those challenges again, with this contribution we 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. We interpret the conditions and challenges to AM implementation identified by previous studies in the practical context of threatened species management. We then illustrate the process of AM implementation using four case studies along the captive-wild spectrum.

2. How to get started in adaptive management

Management is adaptive when it explicitly recognizes 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 management decision (Walters, 1986). Alternatively, "active" AM seeks to solve a "dual control" problem, where managers seek to use the learning process to maximize management outcomes; in other words, to control both their knowledge of the system and the system itself (Gregory et al., 2006; McCarthy and Possingham, 2007; 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).

The implementation of AM follows a sequence of steps (see also Runge, 2011; Walters, 1986; Williams et al., 2009):

(1) Formulate the decision problem. For AM to be useful, it must be possible to apply learning: in this sense, AM is only suitable where decisions are iterative, or where new information can be used in subsequent decisions (Williams et al., 2009).
(2) Specify the fundamental management objectives, acknowledging multiple and possibly conflicting objectives (Converse et al., 2013b).
(3) Identify a set of alternative actions that can be used to achieve those objectives (Gregory and Long, 2009).
(4) Articulate uncertainty about the system. This step is the key to AM. Uncertainty can arise from different sources, including environmental and demographic stochasticity, partial observability, and partial controllability (respectively, the ability to observe the state of the system, and the ability to implement the action as planned; Williams et al., 2009). In particular, AM focuses on uncertainty resulting from incomplete understanding of the system of interest. 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). Hypotheses can be intuitively discrete (e.g. presence or absence of disease), continuous (e.g. distributions of survival probabilities) or discrete partitions of a continuous parameter space that are biologically plausible and relevant for management. The belief in a given hypothesis is expressed through the corresponding probability distribution, or using weights to describe support, such as information-criterion scores (Hauser and Possingham, 2008) or formal expert judgment (Runge et al., 2011). Where no initial information exists, this can be reflected by a uniform distribution, or by equal weights for all hypotheses (e.g. Nichols et al., 2007).
(5) Predict the expected outcomes of actions in terms of the management objectives using empirical data or formally-elicited expert judgment (Martin et al., 2012a). The relationship between hypotheses and the outcomes of alternative actions must be explicit, allowing predictions of the expected outcomes of actions under each hypothesis.
(6) On the basis of the above predictions, select the best action and implement it. The decision may require solving the stochastic dynamic trade-off between short-term learning and long-term outcomes (passive/active AM; see Section 4.3). The selection may be based on probabilistic criteria, such as expected (mean) outcomes, or non-probabilistic criteria such as minimum regret (McCarthy, 2014). Where uncertainty is expressed as discrete hypotheses, the optimal decision may be identified using a multi-attribute additive function, where the predicted outcomes of each action under different hypotheses are aggregated, weighted by the respective belief or model weight (Goodwin and Wright, 2004).
(7) Monitor outcomes and update knowledge about key uncertainties. 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 (Lyons et al., 2008). Useful monitoring implies an adequate experimental design and sufficient resources to sustain the monitoring effort (Gregory et al., 2006). If resolving a given uncertainty is not expected to improve management outcomes, then additional information has no value and AM is not warranted; learning is only pursued if necessary to maximize management outcomes (Williams et al., 2009). Value of information analysis can provide this information (Canessa et al., 2015; Johnson et al., 2014; Runge et al., 2011).
(8) Re-evaluate the best action, using the information collected to update the support for competing models, or to update parametric distributions. 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 belief in models or parameters (McCarthy and Possingham, 2007).

Steps 1–5 represent the "set-up" phase common to any structured decision making process, whereas steps 6–8 represent the "iterative" phase of monitoring and decision making that is specific of AM (Williams et al., 2009). Where necessary, any step of the entire decision problem, including steps in the "set-up" phase, can be revisited, including redefining objectives and alternative actions, reformulating hypotheses, and redesigning monitoring. This broader iteration is sometimes referred to as "double-loop" learning, as opposed to "single-loop" in which only the iterative phase is repeated (Tosey et al., 2012).

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

In spite of its intuitive appeal, AM is not suitable for every type of decision problem. Williams et al. (2009) listed the following conditions for the application of AM: (1) the need for immediate action under uncertainty; (2) explicit and measurable objectives; (3) a real choice between alternative actions, which can 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 (i.e., a measureable 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. Other studies have highlighted similar conditions and challenges (Keith et al., 2011; Rist et al., 2013; Runge, 2011). Below, we briefly consider them in the practical context of threatened species management across the captive-wild spectrum.

3.1. Immediate need for decisions

Fig. 1 highlights several common decision problems along the captive-wild spectrum (for fundamental references, see Armstrong et al., 2015; Converse et al., 2013a; Ewen et al., 2012; IUCN/SSC, 2013, 2014). Decisions concern the management of captive and wild populations, of the transfer processes between and within wild and captive populations, and of on-going management prior to and after those movements. Most such decisions are likely to meet the first condition of AM, given the typical need for immediate decisions in managing poorly-known species (Martin et al., 2012b).

3.2. Explicit and measurable objectives

Although broad conservation objectives (such as species persistence) are likely to be shared among stakeholders, different attitudes may exist toward multiple objectives, including non-biological ones such as management costs (Converse et al., 2013b). The conflicts arising from such divergences can represent a major challenge to the implementation of AM (Keith et al., 2011). However, AM can still go forward in the face of multiple and potentially competing objectives, as long as stakeholders and decision-makers can agree on a process by which the multiple objectives will be accommodated.

3.3. Ability to formulate uncertainty as a set of testable hypotheses

Most of the decisions in Fig. 1 are affected by uncertainty (Armstrong and Seddon, 2008). Research traditionally focuses on model and parametric uncertainty, for example comparing the suitability of different reintroduction sites (Osborne and Seddon, 2012), release methods (Batson et al., 2015) and post-release management (Armstrong et al., 2007). 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 et al., 2009). Their relative importance may change along the captive-wild spectrum (Fig. 1). For example, imperfect detection (i.e., partial observability) is likely to affect monitoring of wild populations to a greater extent than for captive populations. At the captive end of the spectrum, environmental stochasticity can be controlled by addressing individual needs in the provision of food, health treatment, chances for reproduction and so on. Conversely, in the wild control is limited because management mostly acts at the population level, typically through habitat modifications (e.g. vegetation restoration or supplementary feeding; Oro et al., 2008; Webb et al., 2005). Nevertheless, our knowledge of the response to management actions in captivity can still be structurally uncertain (for example in the response of individuals to different feeding regimes; e.g. Bloomsmith et al., 1988). Within integrated programs that span the captive-wild spectrum, one source of uncertainty at one point along the spectrum also affects management at other points; for example, captive experience can influence the post-release fitness of individuals (Jule et al., 2008). For most sources of uncertainty, it may also

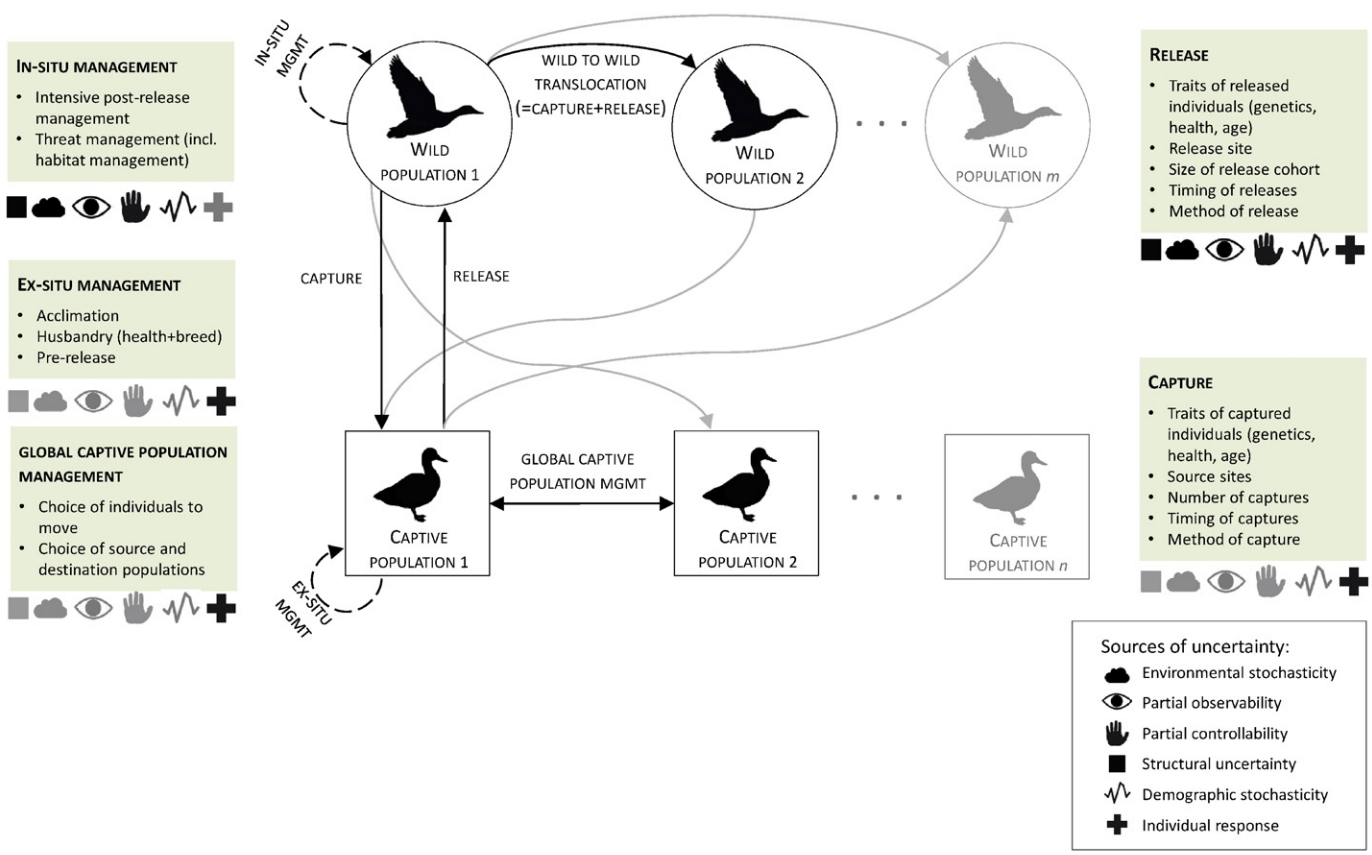

Fig. 1. Types of management decisions along the captive-wild spectrum, contrasting in situ and ex situ populations (round and square boxes respectively) and physical movement (arrows: capture from the wild, release to the wild and movement between captive breeding facilities). Typical management decisions that may be hindered by uncertainty are listed under each type in the gray boxes. Icons represent the six main sources of uncertainty (in black when they are typically dominant).

be difficult to determine hypotheses and prior beliefs for little-known systems, although meta-analyses of shared data may assist (such as the ZIMS database for zoos).

3.4. High value of information and effective monitoring program

Determining whether the benefit of learning is high enough requires a value judgment and it is difficult to infer a universal rule for all threatened species management problems (Canessa et al., 2015). In general, however, both in captive and wild settings the ability to learn may be limited by small sample sizes when dealing with remnant populations of critically endangered species. The type of uncertainty faced also determines the capacity for adequate monitoring, which may be reduced by partial observability and stochasticity, particularly in wild populations (Nichols and Armstrong, 2012).

3.5. Adequate stakeholder support and institutional stability

Several authors have highlighted the importance of institutional capacity and commitment to undertake and sustain AM (Gregory et al., 2006; Williams et al., 2009). Monitoring and experiments can be expensive and require long-term planning capacities (Allen and Gunderson, 2011; Walters, 1997), and multi-stakeholder problems may require the ability and will to resolve conflicts (Keith et al., 2011). However, such difficulties are not necessarily specific to AM, and may reflect more general management failures (Rist et al., 2013). Monitoring reintroductions is difficult and often poorly implemented regardless of whether it serves an adaptive purpose (Nichols and Armstrong, 2012); resource constraints are common to most conservation problems (Ewen et al., 2014). A more specific institutional challenge to AM in threatened species management may lie in the risk attitudes of stakeholders, particularly where individuals of threatened species may be perceived as too valuable to be subject to experimentation (Allen and Gunderson, 2011; Ludwig and Walters, 2002). However, Runge (2011) suggests this perceived challenge is in fact a misconception. Optimal active AM can account for risk attitudes, ensuring experimentation only occurs if it is expected to improve management outcomes.

3.6. Ability to apply learning

Continuous, long-term population management is increasingly becoming the norm in threatened species management (Redford et al., 2012). As a result, most decisions summarized in Fig. 1 are iterative and should provide opportunities to revise and adjust management actions in response to new information.

4. Adaptive management in practice

In this section, we illustrate the application of AM using four case studies across the captive-wild spectrum, ranging from captive management for reintroduction to ongoing management of reintroduced populations in the wild. The case studies were selected for their illustrative potential, and reflect the experiences of the co-authors. As such, they do not represent an exhaustive review of the conditions and challenges in implementation of AM. Rather, we use them as a basis to describe the possible development of an AM process and comment on the key conditions and challenges to AM implementation.

4.1. 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. In North American zoos, only about 20% of pairs reproduce: as a result, the captive population was projected to decline by 5% per year unless sustained by imports (Marker-Kraus and Grisham, 1993). Such low breeding rates may result from managers choosing incompatible pairs (animals are usually not allowed to choose). We explore the potential application of AM to the pairing process of captive cheetahs.

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 maximize the proportion of pairs that produce litters. The decision is iterative, because the management horizon will require multiple pairings to be made, both for future and extant individuals (cheetahs do not maintain pair bonds, which are formed anew every year). Therefore, the decision problem is potentially suitable for AM; the long-term management horizon would allow sufficient time for information to be collected and applied. Third, management alternatives would be identified by the managers. These might, for example, include the following: (A1) continue to pair cheetahs based on pedigree calculations of optimal mates; (A2) move cheetahs to larger facilities where females can choose among males, and base pairings on the greatest expressed interest by females toward individual males when presented to each one; (A3) expose females to urine from multiple males, then pair them with the male whose urine elicited the most interest; (A4) continue to pair cheetahs based on pedigree calculations but also expose females to urine of genetically optimal males prior to pairing to improve acceptance.

In the fourth step, we need to articulate structural uncertainty via competing models of the system; this requires the identification of potential drivers of breeding success, their direction and magnitude. This step is challenged by the wide range of potential drivers, and by the fact that managers have not yet enumerated a set of explicit hypotheses about the importance and direction of drivers. Possible hypotheses might include: (H1) there are mating preferences based on male phenotype, such that some males are unacceptable to each female; (H2) an increase in the number of possible mates in physical proximity increases receptivity; (H3) mate choice is driven by olfactory cues. The hypotheses are not all mutually exclusive, as several drivers of breeding success may be important, but the combination of factors that are primary determinants of breeding will consequently determine which management alternative(s) can achieve the objective of increasing litter production. Based on the hypotheses, in the fifth step we could work with experts to make predictions of management outcomes under the various actions and conditional on the competing hypotheses (Table 1). Collaboration among experts and elicitation of initial estimates from data that are currently scattered among different institutions and from divergent expert opinion may allow this gap to be filled.

In the sixth step, an experimental approach (active AM) could be chosen to maximize success by actively learning more about the hypotheses. However, if experiments are carried out in isolation by individual institutions, sample sizes may be too low to allow reliable statistical conclusions. In general, monitoring breeding success to update knowledge (seventh step) 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. Simulations of a possible AM plan would allow institutions to assess the expected short-term costs (e.g. the predicted loss of breeding success when experimenting with sub-optimal pairing methods) against the expected long-term gains of experimentation.

In summary, the choice of breeding pairs in captive cheetahs meets several conditions for AM implementation. Challenges 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.

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

Our second example also focuses on captive rearing, but with the aim of maximizing reintroduction success. Endangered whooping cranes

Table 1
A possible consequence table for adaptive management of captive cheetah. Columns indicate hypotheses about structural uncertainty; rows indicate possible management actions. Structural uncertainty has an effect on decisions, as indicated by the fact that some actions may be more or less successful than others depending on which hypotheses are true (represented by + and − signs in individual cells).

Action	Hypothesis		
	There exist phenotypic preferences, such that some males are unacceptable to a female	Exposure to more potential mates increases receptivity	Olfactory cues are used
Pair based on pedigree; re-pair if 1st fails	−	−	−
Move cheetahs to a few large facilities	−	+	−
Test preferences with urine	+	−	+
Pair based on pedigree and condition with urine to increase acceptability	−	−	+

(*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 et al., 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. 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 and respond adaptively to that learning.

The decision problem is what type of rearing method to use for cranes in the LNMP: parent-rearing or costume-rearing. The decision is iterative, since chicks are reared every year, and there is capacity for adapting actions to additional knowledge. PR cranes may have different survival and breeding success than CR cranes, so a realistic objective may be to maximize lifetime reproductive contribution of each release cohort. The alternative actions are the two rearing methods (CR and PR; we assume that, due to logistical constraints, all birds will be reared using the same method in a given year). 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 (S_j), age of breeding onset (M), annual fecundity after onset (f), and annual survival of breeders (S_b). We can approximate the mean life span after the onset of breeding as $-\frac{1}{\ln(S_b)}$ (Brownie et al., 1985), and then approximate the expected population lifetime reproductive contribution (PLRC) of a rearing method (a) as:

$$PLRC(a) = R(a) * S_j(a)^{M(a)} * \left(-\frac{1}{\ln(S_b(a))}\right) * f(a) \qquad (1)$$

where R is the number of birds released under method a, and the other model parameter values are a function of that method. Intuitively, the offspring produced by a given cohort will be a function of the size of that cohort (the first term in Eq. (1)), the individual probability of reaching sexual maturity (the second term), the expected number of years spent in the breeding state (the third term) and the annual fecundity in the breeding state (the fourth term). Survival might be a more complex function of age than is suggested by Eq. (1), but the division into two stages (pre-breeders and breeders) is a reasonable simplification for our purposes.

Currently, uncertainty surrounds the four parameters in Eq. (1) for CR and PR. Adaptive management could be used to reduce this parametric uncertainty, giving a stronger indication of which rearing method is best. We could initially use data from the EMP (e.g. Servanty et al., 2014) and from a previous non-migratory release in Florida (e.g. Folk et al., 2008) 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 PR. 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 hypothesized that the CR method may result in poor reproductive behaviors (Runge et al., 2011) which may increase age at first breeding and reduce annual fecundity.

The system could then be managed via either passive or active AM. In this case, given the cost and difficulty of raising birds, managers might be especially reluctant to trial approaches that are believed to be sub-optimal. The design of an active AM approach could incorporate such risk attitude (Runge, 2011), but strong risk aversion would likely favor the action with the highest expected value. This effectively corresponds to a passive AM approach, suggesting there might be little benefit in pursuing active AM in this case. Under passive AM we would begin 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 and the cost of direct monitoring methods such as radio-tracking. We could use the collected data to update prior beliefs using Bayes' theorem. This would allow us to detect whether our observed PLRC 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 long enough to allow the application of new information, there would be a significant delay between implementation of actions and observation of their outcomes, due to the relatively late onset of breeding in cranes (3–5 years). Some uncertainties might be resolved within a shorter timeframe than others; for example, survival of pre-breeders could be investigated without the need to wait for breeding onset. We could calculate the partial value of perfect information to identify the relative importance of different sources of uncertainty, and prioritize the collection of further information (Runge et al., 2011).

4.3. Choice of reintroduction site for Arizona cliffroses

In this example we compare different technical approaches to evaluate whether and how to implement AM. We focus on the choice of reintroduction sites, a fundamental problem in reintroduction management (Osborne and Seddon, 2012). We consider a hypothetical translocation program for the endangered Arizona cliffrose *Purshia subintegra* in the southwestern United States. Previous reintroductions of this evergreen shrub have demonstrated a relationship between germination success and the characteristics of release sites, such as soil moisture (Maschinski et al., 2006; Maschinski et al., 2004). We imagine 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 maximizing the number N of seedlings surviving over their first year (establishing).

We 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. We express this probability of survival as a beta distribution: φ_1 for site 1 (mean = 0.18, s.d. 0.09) and φ_2 for site 2 (mean = 0.22, s.d. 0.09). These hypothetical values are presented here for illustrative purposes, reflecting published information about survival of caged translocated seedlings of *P. subintegra* (Maschinski et al., 2004). The two distributions overlap substantially, reflecting uncertainty about which site is better.

We compare six different approaches that highlight the trade-offs between learning and managing that are characteristic of AM programs. First, no AM: all seedlings are translocated to the site with the highest mean survival (in this case site 2) and no monitoring is carried out. Second, passive AM: every year 16 seedlings are reintroduced to the site with the highest expected mean survival; the number of survivors is then monitored, the estimated survival at the reintroduction site is updated, and the decision revised if necessary. Third, active AM; to solve the trade-off between the short-term losses of experimentation and the long-term benefits of learning, we use an optimization tool called stochastic dynamic programming (SDP; Bellman, 1957). SDP finds the optimal decision for every possible state of knowledge, 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. Fig. 2 illustrates how to interpret the SDP results; the analysis presented here was implemented in Matlab® using custom-written code (any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government). Fourth, we evaluate three strategies in which experimentation is carried out to accelerate learning and improve long-term outcomes. In an initial experimental phase, each site receives eight seedlings and the number of survivors is monitored. After the end of this experimental phase, the updated estimates are used to choose the release site, switching to passive AM for the remaining years. We evaluate formulations of this approach where the experimental phase lasts one, four, and eight years respectively. We use simulations to evaluate these experimental approaches, iterating the decision process 10,000 times drawing the "true" values of φ_1 and φ_2 randomly from the prior beta distributions (this set of "true" values was the same across all simulations and the SDP). These approaches simply represent simulations of possible learning strategies, and as such do not optimize the dual control trade-off, providing only sub-optimal strategies. However, we interpret them as "intuitive" active AM here since they actively seek to reduce uncertainty in the short term to improve long-term outcomes. This "management by experiment" is in contrast to a passive AM approach. Passive AM accepts the current state of knowledge (i.e. what is known at the moment of making the decision) as best; it admits future corrections, but the decision does not take into account possible future states of knowledge (i.e., what might be learned in the future; Williams, 2011).

The results highlight some key properties of AM, particularly regarding the trade-off between learning and management. A non-adaptive approach gave $N = 35.4 \pm 16.2$ s.d. seedlings establishing over the 10-year period, with a similar proportion of surviving seedlings between years (Fig. 3). Passive AM improved the expected (mean) outcome ($N = 38.2 \pm 15.1$). When using active AM, longer experimental releases provided better expected outcomes (increasing mean) and less risk (decreasing standard deviations) after the best site was selected. However, 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. 3). As a result, the mean *total* number of established seedlings decreased with the length of the experimental period and was always lower than when adopting passive AM (respectively $N = 38.2 \pm 15.1$, $N = 36.6 \pm 13.7$ and $N = 33.6 \pm 12.2$ for one, four and eight years of experiments). As expected, the active AM based on the SDP strategy provided the optimal compromise between managing and learning, with the highest total number of

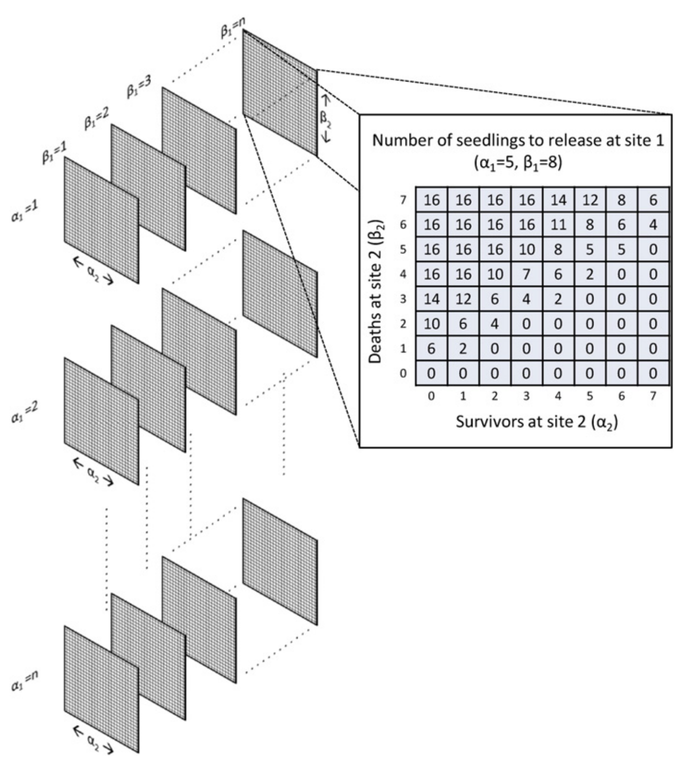

Fig. 2. Guide to the interpretation of the optimal active adaptive management output from stochastic dynamic programming (SDP). Each cell of each table corresponds to a state of knowledge, defined by the number of previous observations of surviving and dead seedlings at each site (α_1, β_1 respectively for site 1, α_2, β_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 maximize 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. The magnified section illustrates how to read the SDP results. Assuming that, from past attempts, 5 seedlings survived and 8 died at site 1, and 5 seedlings survived and 4 died at site 2, then the optimal strategy is to allocate 2 seedlings to site 1 and the rest to site 2. Note that the numbers of past seedlings do not necessarily need to sum to multiples of 16 (the yearly release cohort for this example), since it could also incorporate the results of previous studies, or a prior belief expressed as the sufficient statistics of a beta distribution.

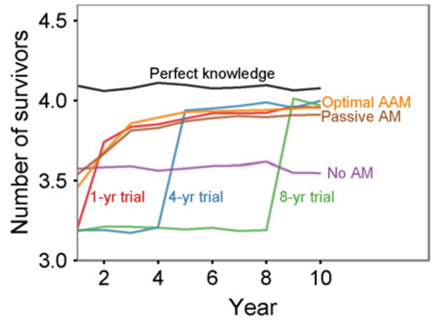

Fig. 3. Simulated outcomes of different strategies for the translocation of *Purshia subintegra*. Lines indicate the number of reintroduced seedlings that survive the first year after release, averaged over 10,000 simulation runs to reflect uncertainty. Labels indicate the choice of no AM ("none"), passive AM, "intuitive" active AM with a trial (splitting seedlings equally between sites) of 1, 4 or 8 years respectively, or the optimal active 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-year period is $N = 35.8$ (no AM), $N = 38.2$ (passive AM), $N = 38.2$ (1-year trial), $N = 36.6$ (4-year trial), $N = 33.6$ (8-year trial) and $N = 38.5$ (optimal active AM). The black line indicates the simulated results in a state of perfect knowledge, where seedlings are always allocated to the truly better site (total $N = 40.8$).

survivors among all approaches ($N = 38.5 \pm 14.7$). The optimal active AM performed worse than the passive AM in the first year, but this allowed better outcomes in following years; on the other hand, the short-term loss was only pursued where required by the state of knowledge, ensuring its impact on long-term outcomes was less marked than in the experimental AM approaches (Fig. 3).

In general, the overall distribution of outcomes changed only marginally among strategies. Differences mostly resulted from demographic stochasticity in the simulations, with standard deviations largely overlapping. Simulating a state of perfect knowledge (i.e. where the "true" values were known and seedlings were thus always released at the best site) yielded an expected outcome of $N = 40.8 \pm 15.2$ s.d., suggesting the value of information is small in this case study. This is largely due to the small number of individuals available for translocation, which provides only limited opportunities to apply the results of learning, especially given the management horizon is short relative to the speed of learning (Hauser and Possingham, 2008).Using AM does not guarantee better results in a single realization: however it represents a safer choice on average, as reflected by the higher mean results. We used our prior beliefs to simulate "true" survival based our expectation about the true values. In a planning phase, this represents a rational use of the available information. In practice, the initial priors might be altogether wrong; in this case, using AM can ensure the error is quickly identified and rectified.

In this example, simulations of possible learning strategies provided useful information. However, in more complex examples (e.g. longer time frames, larger sample sizes or several actions) it may not be feasible to simulate all possible strategies. Conversely, SDP can identify the optimal AM strategy over the range available. Although its application requires more specialized skills, toolboxes and primers are available in different platforms (Chadès et al., 2014; Fackler, 2011; 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 (the "curse of dimensionality"; Bellman, 1957). In this case, simulations may again provide a useful alternative.

4.4. Choosing on-going management regimes after reintroduction

Finally, we focus on the wild (post-reintroduction) end of the spectrum to illustrate a retrospective example in which AM helped improve management outcomes. Ongoing management of reintroduced populations ranges from low to high intensity, such as different levels of supplementary feeding or predator control. AM can be used to optimize this investment, for example by stopping management actions that are 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). Although it had been hypothesized that survival or reproduction might 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 maximize population persistence while meeting budget constraints. The decision was iterative, informing future decisions both for the Mokoia population and for reintroductions at other sites.

A complete description of this case study is provided in Armstrong et al. (2007); here, we present a summary as an example of a complete AM process in which conditions and challenges were met successfully. Eight alternative management regimes were devised, consisting of different 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. To predict the expected outcomes of alternative management regimes, a set of candidate population models were built and compared using information-theoretic criteria. Uncertainty was therefore formalized as competing models, with prior beliefs represented by information-criterion model weights, as well as parametric uncertainty surrounding vital rates (Armstrong et al., 2007).

The complex system and large number of treatments prevented the use of optimization tools such as SDP; instead, actions were applied sequentially over eight years. This approach was similar to the "intuitive" experimental AM described in the previous case study, in that no optimal solution to the active AM trade-off was sought, and a sub-optimal experimental learning strategy was used instead. Monitoring 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 et al., 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 benefit 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. Collaboration among diverse stakeholders provided the necessary skills for the experimental set-up and the analysis of monitoring data (Ewen et al., 2013). Adequate support for monitoring was also maintained throughout the program. The trade-off between persistence and cost was openly recognized, 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. Institutional commitment also allowed double-loop learning. The outcomes of different strategies were used to improve existing practices on Mokoia and six other hihi populations, and the hihi Recovery Group is currently developing a formal AM program for simultaneously optimizing decisions at all current and prospective reintroduction sites.

5. 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. However, there is more to AM than just "learning by doing". Attempting to apply AM where the necessary conditions do not exist, for example where the time horizon does not allow for the application of new information, can represent a poor allocation of resources. On the other hand, where the conditions exist and the challenges can be met, AM holds great potential for threatened species management.

Our 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 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 (e.g., Gregory et al., 2012; Possingham et al., 2001; Runge, 2011). Managers interested in making more deliberative and transparent decisions should familiarize themselves with some of this basic literature, sit down with colleagues, and start framing the decision problem following the process we have described.

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