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Perspective

A call for structured decision making in conservation programs considering wild egg collection

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ABSTRACT

Wild egg collection can be a powerful tool in avian conservation management. It can be used to establish and augment captive breeding programs for conservation translocations, mitigate low productivity during incubation in wild populations, and further research on reproductive and environmental biology. Such benefits need to be balanced against potential risks, like detrimental demographic effects on source populations and disease transfer. A lack of thorough consideration and evaluation of associated benefits, risks, and trade-offs may prevent conservation managers from effectively utilising this powerful conservation tool, and may lead to poor management outcomes for wild populations. Structured decision making (SDM) can offer a framework for making decisions in the presence of uncertainty about how a system will respond to different management alternatives. We therefore advocate for the use of SDM to explore whether an egg collection program is a desirable management tool and, if so, to assess how new data iteratively informs decisions throughout all stages of the recovery program. Here, we review the current literature evaluating the practice of wild egg collection, provide an overview of the SDM process, and then use the whooping crane (*Grus americana*) as an example of how to conduct such an evaluation. Our overall aim is to provide guidance on how SDM can help develop best practice for responsible egg collection from wild populations to enable efficient and effective recovery of endangered avian species.

1. The risks and benefits of wild egg collection

Collecting eggs from wild populations can be a powerful tool to help recover endangered avian species. Wild eggs can be used to establish and manage captive populations for release (Kuehler and Witman, 1988; Powell et al., 1997), aid wild recruitment by rearing vulnerable young in captivity for subsequent release (Powell et al., 1997; Robertson et al., 2006), and help to answer questions that enhance conservation management decisions (e.g. Hickey and Anderson, 1968). Yet, collecting eggs from wild populations can incur serious risks, such as compromising source population abundance and persistence (e.g. Claassen et al., 2014), spreading disease (IUCN/SSC, 2018), and causing financial loss if recovery is ineffective (IUCN/SSC, 2013, 2018). The decision to use wild egg collection in a conservation program must therefore be informed to maximise the benefits gained by this tool.

A fundamental objective of a wild egg collection program is often to increase the viability of a population or species. This can be quantified and evaluated by population models that predict population-level outcomes under differing management actions (Converse et al., 2013a). However, even conservation programs of increasingly endangered species are often resource limited (James et al., 1999), involve multiple stakeholders, and manage species that are understudied (Runge et al., 2011). In the presence of such uncertainties, integrating population model predictions into a formal decision analytic framework, such as structured decision making (SDM), can facilitate optimal decision making on whether to collect wild eggs or not.

Despite the availability of decision making tools and the increased use of translocations (Seddon et al., 2014) and head-starting in avian conservation management, conservation programs rarely evaluate wild egg collection (Heinrichs et al., 2019) and to our knowledge no study has employed a SDM approach. Here, our aim is to highlight this issue, and provide guidance on how SDM can be used to evaluate wild egg collection as a management action and promote better practice in endangered avian species management.

2. Wild egg collection in avian conservation

Wild egg collection has been predominately used for captive breeding and release programmes, spanning the avian orders: Falconiformes (Jone et al., 1995); Accipitriformes (Toone and Risser,

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1988; Wood and Collopy, 1993); Galliformes (Apa and Wiechman, 2015; Thompson et al., 2015); Gruiformes (Link et al., 2003; Boyce et al., 2005; Villers et al., 2010; Butler et al., 2013; Wilson et al., 2016); Apterygiformes (Robertson et al., 2006); Rheiformes (Navarro et al., 1998); Passeriformes (Tweed et al., 2003; Lobo and Ângelo Marini, 2012); and Charadriiformes (Powell et al., 1997; Keedwell et al., 2002; Roche et al., 2008; Claassen et al., 2014; Collins et al., 2016). These species often have life-history traits that mitigate the effects of wild egg collection on the source population. For example, species may be able to compensate for such losses if they produce surplus offspring (Roche et al., 2008) or are long-lived as population growth in longer-lived species tends to be less sensitive to variation in reproductive rates and juvenile survival (Saether and Bakke, 2000; Stahl and Oli, 2006; Clark and Martin, 2007). Source population vital rates may also mitigate the impact of wild egg collection if, for instance, egg mortality rate is high during incubation (Lobo and Ângelo Marini, 2012).

Despite the wide use of wild egg collection in conservation programs few have evaluated its use in the peer-reviewed literature. Of those that have, most have looked at source population individual-level effects. In the Greater sage-grouse (*Centrocercus urophasianus*), nest survival was lower on average for nests with 50% egg removal than control nests. It was concluded that negative effects to the source population could be mitigated if entire clutches were removed at the beginning of incubation to encourage re-nesting (Thompson et al., 2015). American oystercatcher (*Haematopus palliatus*) daily nest survival rates were higher, but chick survival rates were lower, for nests where egg collection (all eggs taken, but one) had occurred compared to control nests. Thus egg collection for a head-starting program from American oystercatcher nests was deemed appropriate if productivity loss in the population was predominately during incubation (Collins et al., 2016). Finally, the modelled number of one-year-old Great Lakes piping plovers (*Charadrius melodus*) recruited into the population was lower for nests where 100% hypothetical egg collection had occurred compared to control nests. The authors concluded that protecting nests in situ rather than relying on collection of eggs for captive rearing was the preferred management action (Claassen et al., 2014).

A less explored, but crucial and relevant avenue is to look at source population-level effects, as this predicts how population growth is affected and whether wild egg collection will aid in species recovery. In a study by Wood and Collopy (1993) the growth rates in a bald eagle population (*Haliaeetus leucocephalus*) in Northern Florida after a five- and ten-year egg collection program were modelled using a matrix population model. It was predicted that the population size after 25 years was lower, but not significantly, than the non-manipulated population. The authors concluded that egg collection could be a viable tool for future conservation management. The population-level effects of egg collection are therefore the most relevant to evaluate due to their long-term predictions on the probability of extinction and recovery of the source population.

Ultimately a wild egg collection program should compare its effectiveness to other management actions to understand whether it will increase population viability. In a novel study, Dolman et al. (2015) investigated the efficacy of a captive breeding and release program for the Vigors great Indian bustard (*Ardeotis nigriceps*) under different egg harvesting levels. Sampling parameters reported for bustard captive-breeding programs predicted that only collecting five to ten eggs per year for five years would result in a 73 to 88% chance of captive population extirpation in 50 years. It was also found that when eggs were not collected to create a captive population, habitat improvements alone over the course of a decade were predicted to yield a larger number of wild adult female birds after 50 years than an above-average captive breeding and release program. More recently, Heinrichs et al. (2019) investigated the efficacy of a captive breeding and release program for the Greater sage-grouse. No long-term effects on the source populations were inferred under the various egg collection scenarios for multiple populations. Maximal juvenile releases from a captive population best improved near-term (10 years) population abundance and extinction risk projections. However, it was noted that to improve long-term population abundance and avoid extirpation, successful improvements to in situ conditions were required. This emphasises the importance of modelling to make predictions about the systems response to alternative management actions and in turn prevent the misuse of valuable conservation resources.

Overall, the discrepancy between the number of studies that have evaluated wild egg collection and its wide and often undocumented use in conservation management (Runge et al., 2011) highlights that predictive modelling is often overlooked. Furthermore, no study formally considered uncertainty in the modelling step, which can lead to poor management outcomes. We therefore advocate for the use of a SDM process, which we explicate below, to help achieve optimal decision making around the choice to embark upon a wild egg collection program and to inform every stage of the program once it has begun.

3. Decision analysis and wild egg collection

The outcomes of management actions in conservation, such as wild egg collection, are often riddled with uncertainty (Runge et al., 2011). However, delaying action until uncertainty is resolved is not practical for species at risk. SDM can offer a framework for making decisions about wild egg collection in the presence of uncertainty by defining management objectives, potential management alternatives, modelling outcomes to such alternatives, and identifying optimal solutions (Fig. 1 Williams et al., 2002, Dorazio and Johnson, 2003, Gregory et al., 2012, Nichols and Armstrong, 2012). Below we illustrate this SDM process as a simplified flow chart (Fig. 1).

Objectives are developed by key stakeholders, incorporating values such as species persistence, and financial implications, and are used to manage the conservation program and to judge its success or failure. Formal statements of these objectives are known as objective functions and can incorporate how the stakeholders respond to the risk of different possible outcomes made in the presence of uncertainties, such as socio-political factors (Converse et al., 2013a).

Once objectives are defined, alternative management actions can then be identified (Nichols and Armstrong, 2012). For a wild egg collection program, fundamental objectives might be to increase the demographic, genetic or ecological viability of a population or species whilst minimising cost. Management alternatives to achieve these objectives may include differing egg harvesting levels, time frames and management actions. Models are then used to make predictions about the objectives over time under the different management alternatives. At this point, uncertainty in the systems response can be incorporated either in a key parameter or as multiple discrete models that act as different hypotheses (Nichols, 2001; Williams et al., 2002; Nichols and Armstrong, 2012).

The final component of SDM is to evaluate the management alternatives on the objectives. This can be done with consequence tables, that estimate the predicted consequences of various alternatives in relation to each measurable objective (Gregory et al., 2012), or by an optimisation technique, such as stochastic dynamic programming (Marescot et al., 2013). Here, the distribution of potential outcomes for each alternative are used to choose the one that best matches the risk tolerance of the key stakeholders (Williams et al., 2002; Nichols and Armstrong, 2012; Marescot et al., 2013; Converse et al., 2013a).

If the wild egg collection program is sourcing eggs over multiple years it will also be important to resolve uncertainty about the systems response to the action by using an adaptive management approach (Runge et al., 2011; Converse et al., 2013a). This is a subset of SDM designed to resolve uncertainty (environmental variation, partial observability, partial controllability and structural uncertainty, Williams, 1997) in reoccurring decisions using monitoring data. For instance, deciding on the number of eggs that can be harvested each year without causing the population to decline below a critical threshold. Monitoring

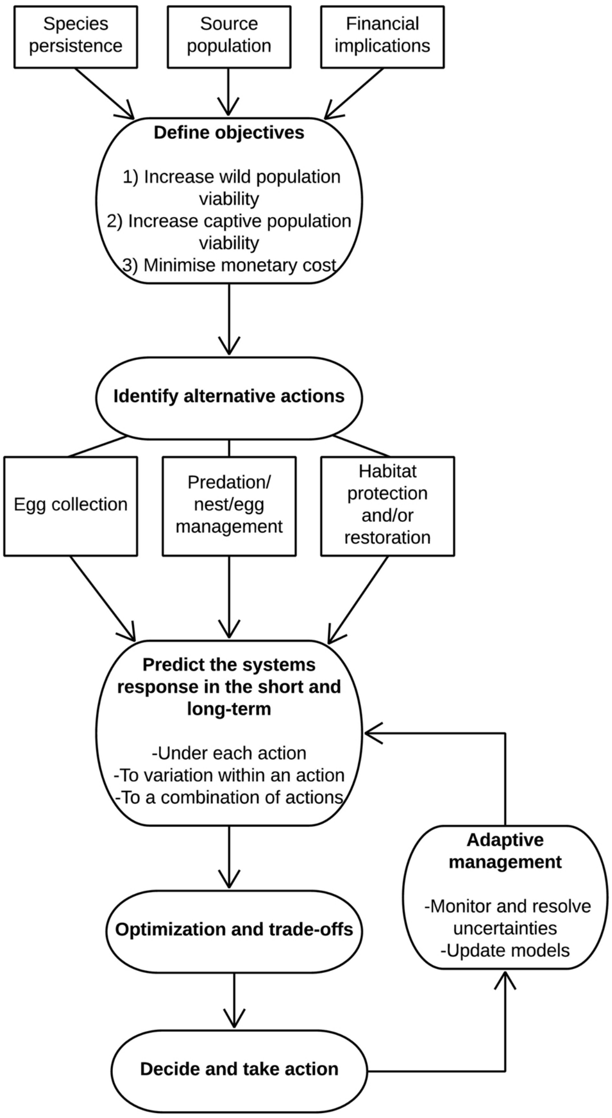

Fig. 1. A simplified flow chart of the structured decision making process, adapted from Converse et al. (2013a). The process begins by defining management objectives, then identifying alternate management actions, modelling the populations' response to the management action, and using an optimisation technique to identify the best action and final decision. Adaptive management is a subset of SDM where monitoring data are used to update model predictions to inform future decisions.

data provide estimates of the current state of the system and improve knowledge about the systems dynamics (Conroy and Peterson, 2013). The updating and comparison of model predictions that incorporate structural uncertainty with the monitoring data erode uncertainty, and allow for better future decision making (Converse et al., 2013a).

4. The whooping crane case study

The whooping crane suffered major population declines in the early 20th century due to over-hunting and habitat loss (Doughty, 1989), reaching a low of 16 individuals in the remnant Aransas-Wood Buffalo population (AWBP) in the 1940s (Boyce, 1986; French Jr et al., 2018). In a bid to conserve the species, one out of two eggs were removed from nests in Canada's Wood Buffalo National Park during 1967–1996, totalling to 496 eggs (Boyce et al., 2005; Converse et al., 2018a), in order to establish several captive breeding and release programs. However, reintroduction has been challenging, due to poor demographic performance, with two failed attempts in Idaho and Florida (Converse et al., 2018b), and two current attempts in the Eastern United States (Urbanek et al., 2005) and Louisiana (Gomez, 2014). Consequently, SDM has been used to support management decisions around release strategies and resolving poor reproductive performance (Moore et al., 2012; Converse et al., 2013b, 2014; Servanty et al., 2014; Converse et al., 2018a, 2018b). Here, and in the following section, we use whooping cranes as a case study. We review the past evaluation of egg collection in AWBP and the use of SDM in the reintroductions, and provide recommendations for the evaluation of egg collection in the future.

4.1. *Wild egg collection*

Egg collection in the AWBP was deemed a viable conservation action for a number of demographic and life-history reasons. Young were mainly produced by a stable cohort of long-lived adults (expected maximum lifespan of 30 years, Mirande et al., 1993, C.W.S and U.S.F.W.S., 2007), mortality was highest in the subadult cohort which limited recruitment into the breeding population, and clutches often contained two eggs but fledged one chick (Novakowski, 1966; Bergeson et al., 2001; C.W.S and U.S.F.W.S., 2007). Egg collection was ceased in 1996 due to the establishment of a productive captive population, and monetary and philosophical concerns (Lewis, 2001). Subsequently, the effects of egg collection on recruitment and population growth in the AWBP have been retroactively evaluated (Link et al., 2003; Butler et al., 2013; Wilson et al., 2016).

Two studies have investigated the effects of egg collection on individual-level recruitment. Link et al. (2003), using a matrix population model, estimated that the number of one-year-old individuals produced by a breeding individual was lower in years with egg collection than years without. However, Boyce et al. (2005) found that the probability of producing an individual that survived before or after migration was highest for nests from which eggs had been collected. These contradictory findings may be because Link et al.'s (2003) analyses were based on winter population data and so the number of breeding pairs was unknown, which can affect recruitment estimates.

Similarly, the studies looking at the effects of egg collection on population-level recruitment have been contradictory. Cannon et al. (2001) using a two-sample *t*-test, found that the proportion of young in the total population was lower in years with egg collection compared to years without. However, Cannon et al. (2001) did not account for annual variation in adult survival, and when Lewis, 2001 adjusted for this, it was found the proportion of young in the total population was higher in years with egg collection than years without. These findings, however, may be undermined by the fact that data amongst years was compared, which can introduce confounding year-effects.

In contrast, population-level analyses looking at the effects of egg collection on the source population have yielded similar conclusions. Using an integrated population model, Wilson et al. (2016) found no difference between mean annual fledgling rates in years with and without egg collection (see also Ellis and Gee, 2001). Butler et al. (2013) using a time series analysis to examine the population growth rate after egg collection, also did not find a difference between years with and without egg collection. Despite both studies excluding observation errors from the nest and territory counts, it is believed that survey counts correlate strongly with abundance (Boyce and Miller, 1985, Boyce, 1986, Dinsmore and Johnson, 2005, C.W.S. & U.S.F.W.S., 2007, Stehn and Taylor, 2008).

Overall, the population-level analyses coupled with the life-history of the whooping crane suggest egg collection did not have a significant positive or negative effect on the AWBP. Criticisms of past data collection, such as non-random nest selection (Ellis and Gee, 2001, Mark Bradley, Parks Canada, pers. comm.) and lack of data on unmanipulated nests (Mark Bradley, Parks Canada, pers. comm.), and of past analyses, highlight the importance of robust experimental design and analyses to

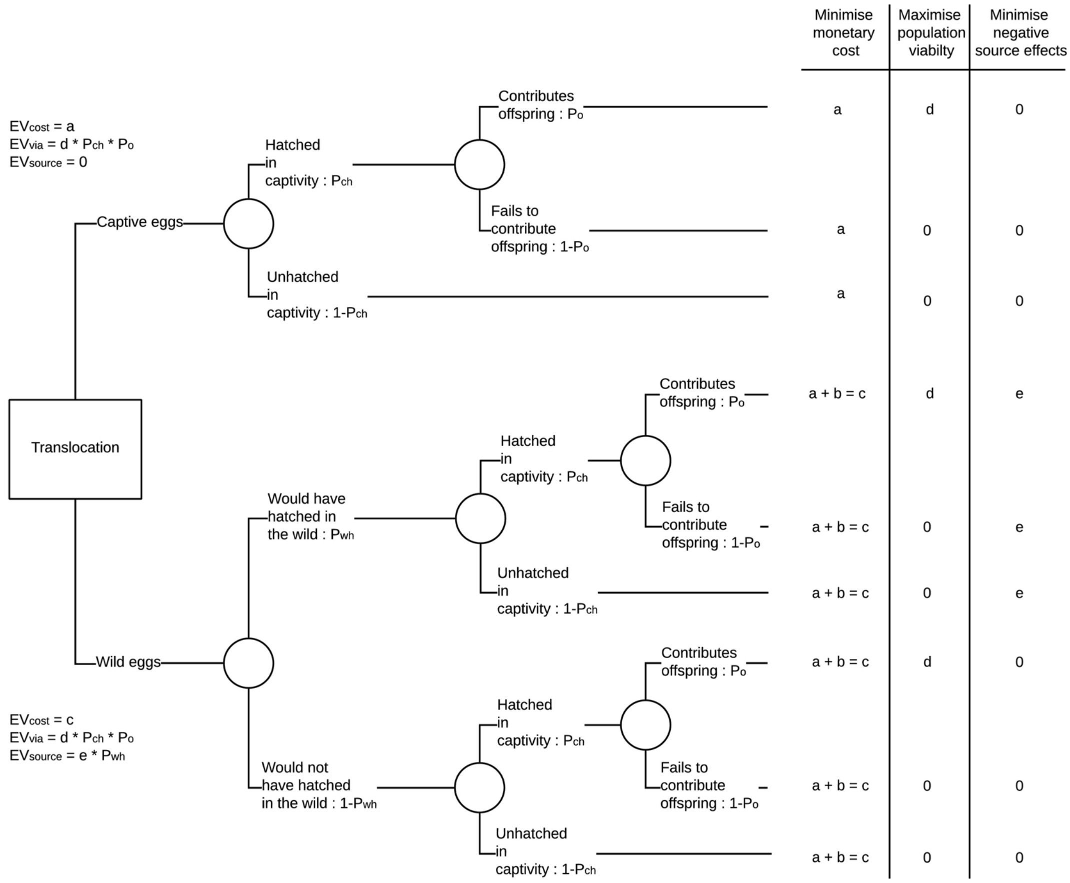

Fig. 2. A decision tree showing the choice to source eggs from the wild or from captivity for a translocation management action. The rectangle depicts the decision with two alternatives and the circles depict uncertainties. The table shows the outcomes associated with each endpoint for each of the three objectives: minimising monetary cost, maximising population viability and minimising negative source population effects. The decision tree can be used to calculate the expected value (EV) for each alternative by summing the product of each endpoint and their associated probability. EV_{cost} = the expected value of monetary cost, EV_{via} = the expected value of an increase in population viability, EV_{source} = the expected value of negative source population effects. P_o = the probability of contributing offspring, P_{ch} = the probability of a captive hatch, P_{wh} = the probability of a wild hatch. a = the monetary costs associated with hatching eggs in captivity, b = the monetary costs associated with sourcing eggs from the wild, d = the increase in population viability, e = the increase in negative source population effects, 0 = no cost or benefit. In this example we have assumed that the probabilities of an egg hatching and reproduction do not differ between alternatives.

Table 1
Potential variables to monitor for adaptive management in a wild egg collection program. Cited references provide an example of the approach needed to test each hypothesis.

Variables to monitor	Specific question	Reference
Population-level	Does egg collection or alternative management action affect	
	-Growth rate?	Butler et al., 2013
	-Recruitment?	Boyce et al., 2005
Individual-level	Does egg collection affect	
	-Hatching rate?	NA
	-Daily nest survival?	Collins et al., 2016
	-Nest success?	Lobo and Ângelo Marini, 2012, Thompson et al., 2015
	-Fledgling productivity?	Claassen et al., 2014, Collins et al., 2016
Confounding	Are population-level outcomes affected by	
	-Predator/prey abundance?	Wilson et al., 2016
	-Weather conditions (e.g. precipitation)?	Bolger et al., 2004
	-Nest location (e.g. territory quality)?	Haché et al., 2014
	-Parental experience?	Bouwhuis et al., 2009
Cost-effectiveness	Is egg collection the most cost-effective management action?	Lobo and Ângelo Marini, 2012

understand individual-level and population-level effects. There is still uncertainty about whether egg collection is a viable future management action amongst other alternatives, and how the AWBP and stakeholders (i.e. agencies responsible for wildlife management, local and indigenous communities) would respond to the resumption of egg collection. We therefore advocate for this decision to be made in an SDM framework.

4.2. *Applying SDM*

In order to make management decisions in the presence of uncertainty, SDM has been used in the whooping crane reintroductions in both the Florida non-migratory population (FNMP) and the Eastern migratory population (EMP, Runge et al., 2011, Moore et al., 2012, Converse et al., 2013b, 2014, Servanty et al., 2014, Converse et al., 2018a, 2018b). In the FNMP high mortality and low recruitment plagued the population. Consequently, a demographic model was developed and used to frame and analyse release strategies that aimed to establish a viable population. The analysis recommended ongoing reintroductions of three cohorts per year for 10 years, but this recommendation was not adopted by federal agencies responsible for whooping crane management and so releases into the FNMP were stopped (Moore et al., 2012; Converse et al., 2013b, 2018b). In the EMP, hypotheses for poor reproductive success were captured in structurally distinct demographic models (Servanty et al., 2014) and used to evaluate release strategies aimed at establishing a viable population (Converse et al., 2018a). The results of this analysis were used by the Whooping Crane Eastern Partnership to continue ongoing ultralight and direct autumn releases in eastern Wisconsin (Converse et al., 2018a). SDM was then further used in the EMP to evaluate management strategies aimed at increasing reproductive performance (Runge et al., 2011; Converse et al., 2018b). Building on Runge et al.'s (2011) expert elicitation, Converse et al. (2018a, 2018b) showed that optimal strategies in the short-term were forced re-nesting and predator training for juveniles, and in the long-term were forced re-nesting and parent rearing of chicks. These management actions are under continued evaluation and are being used to inform future management decisions in an iterative process.

This body of SDM work has been vital in enabling research and management to work together to improve long-term outcomes. However, the SDMs in the EMP did not consider the costs of wild egg collection, which may have altered its ranking amongst alternative management actions. For example, in Fig. 2 we show a simplified example of a decision tree outlining the choice to source eggs from the wild or from captivity for a translocation management action. Incorporating monetary cost, source population effects as well as population viability directly into the decision making process allows the decision maker to explicitly weigh the trade-offs associated with these values. In this example, since the expected value (i.e. probability-weighted average) of the population viability objective does not differ between alternatives, the decision is reliant on the trade-off between the increased cost associated with captive egg collection and the larger source population effect associated with wild egg collection. Overall, incorporating monetary cost and source population effects into the decision making process may result in a different recommendation to use egg collection as a management action than if only population viability was considered.

5. Future guidance for wild egg collection

To guide conservation managers on egg collection in avian recovery programs, we outline a conceptual SDM framework and illustrate potential applications for the whooping crane. In the first step, we define a problem statement that describes how our objectives will be fulfilled by the predicted outcomes of the actions we propose (Conroy and Peterson, 2013). An example problem statement for whooping crane would be which management action or combination of actions (e.g. egg collection for translocations or augment captive population, predator/nest/egg management, habitat management), best increases the viability of the wild and captive populations in the short and long-term.

In the second step, we define the values that are important to the recovery program. This may include species persistence, impacts on the source population and financial implications. The fundamental objectives are then defined incorporating these values. Objectives for the whooping crane as stated by the International Whooping Crane Recovery Team are to establish wild self-sustaining populations and to maintain a genetically and demographically stable captive population, while minimising cost (Fig. 1, C.W.S. & U.S.F.W.S., 2007).

Third, we identify the alternative management actions that achieve our objectives. For the whooping crane these could include wild egg collection for translocations into existing or new populations to improve recruitment, predation/nest/egg management in the reintroduced populations to improve fledgling success (Traylor-Holzer, 2018), and extended habitat protection/restoration to reduce adult mortality (Butler et al., 2017, Traylor-Holzer, 2018, Fig. 1).

In the fourth step, we predict the effects of the alternative management actions on each of the fundamental objectives. For instance, by modelling population-level outcomes in the short and long-term (e.g. recruitment, population growth rate) under each management action or combination of actions, and modelling variation within these actions (e.g. varying the egg harvesting level; Fig. 1, Table 1).

Fifth, we evaluate the management alternatives on the objectives by using an optimisation technique, such as stochastic dynamic programming, or a consequence table to identify the most optimal action, or combinations of actions, to take given the fundamental objectives and the risk tolerance of the key stakeholders (Fig. 1).

In the sixth step, we decide and act, whilst also implementing an adaptive management approach to resolve uncertainties that are identified in the initial analyses using high quality monitoring data (Fig. 1). For example, if a wild egg collection program is deemed beneficial for recovery, nests should be assigned randomly to a control and treatment group and monitored for their reproductive outcomes to assess individual-level effects (e.g. fledgling productivity, Table 1). It will also be important to record variables that may confound analyses such as year effects and individual differences between nests (e.g. nest location, Table 1), and record financial costs to ensure the program's cost-effectiveness is monitored (Table 1).

Overall, we hope to encourage the use of SDM when making decisions around wild egg collection to ensure it is the most optimal management action to take and to inform future stages within the program. By incorporating uncertainty and understanding the risks and benefits, SDM improves our ability to make transparent and robust management decisions, and ultimatelyhelps prevent damage to endangered source populations and improves the the use of valuable conservation resources.

Declaration of competing interest

The authors declare that they have no conflict of interest.

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