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Lessons from 30 years of population viability analysis of wildlife populations

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Population viability analysis (PVA) has been used for three decades to assess threats and evaluate conservation options for wildlife populations. What has been learned from PVA on in situ populations are valuable lessons also for assessing and managing viability and sustainability of ex situ populations. The dynamics of individual populations are unpredictable, due to limited knowledge about important factors, variability in the environment, and the probabilistic nature of demographic events. PVA considers such uncertainty within simulations that generate the distribution of likely fates for a population; management of ex situ populations should also take into consideration the uncertainty in our data and in the trajectories of populations. The processes affecting wildlife populations interact, with feedbacks often leading to amplified threats to viability; projections of ex situ populations should include such feedbacks to allow for management that foresees and responds to the cumulative and synergistic threats. PVA is useful for evaluating conservation options only if the goals for each population and measures of success are first clearly identified; similarly, for ex situ populations to contribute maximally to species conservation, the purposes for the population and definitions of sustainability in terms of acceptable risk must be documented. PVA requires a lot of data, knowledge of many processes affecting the populations, modeling expertize, and understanding of management goals and constraints. Therefore, to be useful in guiding conservation it must be a collaborative, trans-disciplinary, and social process. PVA can help integrate management of in situ and ex situ populations within comprehensive species conservation plans.

KEYWORDS
conservation planning, ex situ, extinction, in situ, simulation, threat assessment, uncertainty

1 | INTRODUCTION

Population Viability Analysis (PVA) encompasses methods of quantitative analysis for assessing threats to wildlife populations (Beissinger & McCullough, 2002; Morris & Doak, 2002). PVA usually employs simulation models to project population trajectories, but more generally PVA is any synthesis of knowledge about a species, its environment, and human actions in a model of population dynamics to assess status, threats, and management options. Although PVA models are quantitative and require a lot of data, the model structure, inputs, scenarios assessed, and interpretation of results rely also on assumptions, expert opinion about unmeasured variables, and even our values. In the 30 years that PVA has been a core methodology in conservation science, a lot has been learned about the factors determining the dynamics of wildlife populations and about techniques for assessing viability. In this paper, I describe some of the lessons learned from the use of PVA in wildlife conservation, and discuss how those lessons can benefit also long-term management of ex situ populations.

PVA was developed to guide management of in situ populations, where threats are many, uncertainties abound, and rigorous control of individual animals is difficult. Never are data adequate to allow confidence that an accurate prediction for a given population can be generated from a simulation. Rather than making a single prediction of viability, PVA usually involves exploration of multiple scenarios. The focus is on the impacts of uncertainties in our knowledge, range of plausible outcomes, and probabilities of success under different management strategies.

In contrast to the use of PVA simulations of alternative scenarios to inform management of in situ populations, management of ex situ populations—in zoos, aquariums, and other centers that strive to sustain wildlife populations outside of their natural habitats (hereafter encompassed by the term "zoos" for simplicity)—has generally focused on precise, analytical calculations based on the history of the population, leading to management decisions at both the population and individual animal level. For example, at the population level, a target population size is often calculated that will achieve, as the mean expectation, retention of 90% of the gene diversity of the source population. Specific breeding recommendations are then made for each individual, following calculation of the expected genetic benefit to be obtained from each planned mating. It has always been recognized that we do not have total knowledge and control even of animals in zoos, and we account for some of this uncertainty by making adjustments to calculations. For example, genetic decisions are based on the known part of a pedigree (Willis & Lacy, 2016), effective population size is used as an adjustment factor to account for our inability to control breeding completely, and calculation of the number of pairings needed is based on the proportion of pairs that are typically successful (Ballou et al., 2010). However, ex situ population management rarely includes full consideration of uncertainty in the input data and the distribution of outcomes (see section 2.1). The probability of achieving management goals and the consequences of failure are rarely explicitly addressed.

Increasingly, it has been recognized that our rigorous management of ex situ populations is often not ensuring that populations will sustain the desired numbers, preserve species-typical characteristics, or perhaps even persist (Lees & Wilcken, 2009; Leus et al., 2011; Long, Dorsey, & Boyle, 2011). The challenges to long-term management of populations are many, and they include: inadequate resources to carry out plans prescribed to meet goals; goals consequently being scaled back, with inadequate regard for long-term consequences; unwillingness to prioritize so as to maximize effectiveness of resources; and difficulty in managing for an unpredictable future.

These challenges are not unique to ex situ populations, and PVA was developed to address these kinds of challenges in wildlife management. It has long been recognized that PVA has relevance also to ex situ population management (Foose, deBoer, Seal, & Lande, 1995), and the recent efforts by the AZA to assess the viability of its SSP populations (Che-Castaldo et al., this issue) is a notable use of PVA. However, zoos globally have not yet fully embraced either the application of PVA methods for estimating likelihood of reaching goals or concepts from PVA for guiding how we think about population management. PVA of ex situ populations can be conducted with generic PVA models, such as Vortex (Lacy & Pollak, 2014), or with the ZooRisk software customized for analysis of zoo populations (Earnhardt et al., 2008). Recent examples of PVA being used to guide management of ex situ populations include the Tasmanian devil conservation plan (CBSG, 2008), assessment of extinction risk for the Bali mynah Species Survival Plan (SSP) (Earnhardt, Thompson, & Faust, 2009), the ex situ breeding program for Puerto Rican parrots (Earnhardt et al., 2014), and the Amur Tiger SSP (Harris & Traylor-Holzer, 2016). In the Tasmanian devil program, PVA is used to assess the efficacy of strategies for selecting animals to be moved between subpopulations. The PVA of the Puerto Rican parrot evaluated the potential for the breeding program to sustain releases to the wild. For the Amur Tiger SSP, a detailed PVA allowed more rigorous assessment of the prospects for attaining population goals.

Throughout this paper, I will focus on "viability" rather than "sustainability," even though the terms are nearly synonymous when applied to in situ population management. However, the goal of most ex situ cooperative breeding programs is not actually sustainability in the sense of preventing any degradation of the resources (Lacy, 2013). Instead, the goals are to keep the risk of demographic or genetic collapse to an acceptably low level for a finite period of time. This matches the concept of population viability in conservation science.

2 | LESSONS ABOUT THREATS TO WILDLIFE POPULATIONS

2.1 | Life is unpredictable

Shaffer (1981) identified stochastic processes that can threaten the persistence of a population. He categorized these into demographic stochasticity, environmental variability, catastrophes, and genetic drift and inbreeding, and he noted that they all are more threatening in small populations. Assessing population viability requires probabilistic analysis of these processes, layered on top of analysis of mean demographic rates and the environmental changes that are usually the original cause of population decline (Caughley, 1994). PVA must also deal with scientific uncertainty due to small sample sizes, confounding effects of multiple factors impinging on the populations, and lack of reliable extrapolation from past to future conditions. The development of methodologies for dealing with such unpredictability in a risk assessment framework was a fundamental advance in wildlife conservation.

Ex situ population management similarly would benefit from accepting uncertainty—in both the inputs and outputs of our assessments—as the context within which we work. Breeding program decisions are generally based on point estimates of input values, rather than on upper and lower plausible bounds as would be necessary in a more precautionary approach. As one example, we generally assume that the impact of inbreeding will be similar to the mean effect reported for species that have been studied. Yet, the severity of inbreeding depression is known to vary widely among species (Frankham et al., 2017). While it is tempting to assume that any population we manage will be one of the lucky ones with little inbreeding impact, it might be more prudent to assume that a potentially irreplaceable population will fall in the upper quartile of inbreeding depression.

Even with parameters that are estimated from direct observation of the population, we know that our estimates are imprecise. Current ex situ population management tends to assume that each population will follow the calculated average trajectory, whereas we should determine also the likelihood of doing worse than expected, and then assess that against our risk tolerance. Consideration of uncertain parameters is generally limited to exploration of alternative scenarios for a few parameters rather than full compounding of uncertainty across the many imprecisely known values. PVAs for in situ populations have also been criticized for under-appreciating the types and scales of uncertainty, and recent work has focused on efficient methods for more complete sensitivity analyses (Prowse et al., 2016).

Variability in outcomes can lead to false hope. It is often claimed that successes of some small populations contradict the dire warnings of PVAs. However, some successes are always to be expected when chance is involved, and some failures are expected even when there is a high probability of success. Consider a strategy in which management plans are sufficient so that, on average, they address the risks just adequately to avert failure. By following such a strategy we should expect to fail to meet our conservation goals for almost 50% of the species. Is this adequate? Or should we use a standard for acceptable management more comparable to the benchmarks typical in PVAs—such as an expectation of failure no more than 10%, 5%, or 1% of the time? If we want to succeed most of the time, then we need to aim higher than what is required for success in the average case.

Resources are limited, and this makes decisions about acceptable levels of risk and, consequently, what size populations and intensity of management are necessary very difficult. Spreading resources too thin can lead to most populations failing; concentrating resources to achieve high probabilities of success can forego opportunities to conserve other populations. The need for optimal allocation of limited space for breeding programs is a reason why PVAs for ex situ populations are now of interest to the zoo community. PVAs are, by definition, the approach that allows us to assess the trade-offs, because they project the probability that we will have success under each analyzed scenario. However, it should also be acknowledged that a mathematical solution to protecting the most populations does not obviate the fact that the allocation decision is ultimately a consideration of our values. Eliciting views of stakeholders on what level of risk is acceptable for each population can be part of the broader collection planning process (McCann & Powell, this issue).

We cannot assess population viability if we do not consider the components of variation that cause instability. An essential part of PVA is estimation of the variation in demographic rates, including the statistical separation of sampling error, variance due to temporal fluctuations in the environment, and individual variation. Princée (2016) describes methods for calculating measurement error and distributions of demographic parameters. Yet, although the detailed, individual data available on many zoo populations would make such analyses possible, rarely is this partitioning of variation done, and such information is not yet used to guide management of zoo populations. To deal adequately with uncertainty will require changes in our methodologies: including calculations of measurement error; projecting distributions of outcomes; and defining acceptable risk. One set of metrics of acceptable risk have been proposed and incorporated into Zoo Risk.

2.2 | It's not demography or genetics; it's both

The original concept of PVA centered on the synergies of genetic and demographic instability (Gilpin & Soulé, 1986; Shaffer, 1981, 1987), and soon debates raged over the relative importance of genetic threats, demographic threats, and the feedbacks between them (Caughley, 1994; Hedrick, Lacy, Allendorf, & Soulé, 1996; Lande, 1988). However, in spite of that initial attention, it remains the case that many PVAs exclude consideration of genetics, and few recovery plans for endangered species include any genetic management (Whitely, Fitzpatrick, Funk, & Tallmon, 2015). In this regard, ex situ population management has been ahead of most other wildlife management in the emphasis on both genetic and demographic stability as components of viability.

Unfortunately, both PVA of in situ populations and management of ex situ populations still often treat demography and genetics as independent, rather than as tightly coupled processes. For example, demographic and genetic projections are made independently in the PMx software (Lacy, Ballou, & Pollak, 2012) without consideration of the impact that accumulating inbreeding will have on demography. This gap persists even though field studies (Frankham, 1998), experimental research (Reed, 2010), and simulation analyses (O'Grady et al., 2006) have reinforced the importance of feedbacks between genetics and demography to population viability. It might be difficult to project accurately the full effects of genetic decay on demographic rates, because inbreeding depression has traditionally been measured for very few aspects of demography (often, only infant survival), but increasingly data are becoming available on the impacts on other components of fitness (O'Grady et al., 2006; Ryan, Lacy, & Margulis, 2002).

The other direction of feedback—the effect of demographic fluctuations on genetic decay—would be easier to project, because Mendelian inheritance can be simulated for any defined population demography. PVA simulations that include genetic sub-models, such as Vortex and ZooRisk, can provide projections of the impacts of demography on genetics. However, the demographic data required for such analyses are not often available. Genetic decay is driven by variation in breeding success among individuals and across generations (Lande & Barrowclough, 1987), but to date the demographic analyses of ex situ populations have dealt almost exclusively with estimating mean, age-specific rates rather than variation in rates across years and among individuals. However, because we have lifetime data on individual animals, analyses of amounts and causes of variation in demography are possible. The determinants of reproductive success have been investigated recently for lions (Daigle et al., 2015) and tigers (Saunders, Harris, Traylor-Holzer, & Goodrowe Beck, 2013). Even explorations of just some of the determinants of reproductive success and survival (using methods like Reproductive Viability Analyses [Bauman et al., this issue] and survival analysis [Princée, 2016]) could provide insights into whether individual variation, genetic diversity, spatial (institutional) differences, and temporal trends are typically large determinants of demographic success. If not, then simpler PVA models that assume constant, age-specific probabilities of reproduction and survival are probably adequate.

There are other feedbacks that can stabilize or destabilize a population, only a few of which will be mentioned here. Loss of genetic diversity increases susceptibility to infectious disease (Spielman, Brook, Briscoe, & Frankham, 2004) and cancers (Ujvari et al., 2018). Evolutionary adaptation to ex situ conditions can also occur (Frankham, 2008; Lacy, Alaks, & Walsh, 2013; Williams & Hoffman, 2009), including some purging of deleterious alleles that cause inbreeding depression (Hedrick & Garcia-Dorado, 2016). If the mechanisms of feedbacks are known, they can be included in flexible PVA models so that their consequences can be foreseen.

2.3 | We need a lot of data

As an endeavor to assess the multiple, interacting factors that determine population fates, PVA requires data on a large number of population demographic and environmental variables. The lack of sufficient data on population demography and environmental determinants of demography is often the stumbling block that prevents reliable population projections and management decisions based on PVA (Ralls, Beissinger, & Cochrane, 2002). Some of the parameters required for a comprehensive PVA can be calculated only if there are data across a number of years, including: lifetime variance in individual reproductive success (Lande & Barrowclough, 1987), annual variation in demographic rates (Shaffer, 1987), and frequency of catastrophes (Reed, O'Grady, Ballou, & Frankham, 2003). In this regard, PVA of ex situ populations potentially has an advantage over PVA of in situ populations. Studbooks are kept for more than 1,000 zoo populations (Oberwemmer, Bingaman Lackey, & Gusset, 2011), and these databases of individual animal births, parentage, location transfers, and deaths provide the opportunity to calculate demographic rates precisely. This also provides the opportunity to subset the data by time periods encompassing different management regimes (e.g., attempted growth, sustained desired size, or purposeful reductions in numbers), allowing assessment of the malleability of demographic rates to management practices. However, although calculation of mean birth and death rates (the "life table") is standard practice, many of the parameters needed for PVA—including the three levels of variation in rates mentioned above—are rarely estimated from studbook data.

2.4 | Long-term effects and time lags

Conservation often requires urgent action, based on whatever information is available, and management involves decisions on an annual basis. However, population viability is a long-term concept. An often-hidden assumption in most PVAs and in demographic projections made from life tables is that past demographic rates predict the future accurately—that is, that neither the environment nor management is changing over time (Coulson, Mace, Hudson, & Possingham, 2001). If there are trends in rates over time, data of sufficient duration to distinguish trends from random environmental fluctuations are needed. Demographic analysis often emphasizes calculation of equilibrium or long-term population outcomes, such as stable age distributions and exponential rates of increase that arise from temporally consistent demography (Caswell, 2001). However, PVA simulation modeling demonstrates that there is a several-generation delay to approaching equilibrium. Short-term instability can affect long-term population sizes and even threaten populations.

One cause of delayed impacts in population dynamics is the time it takes for a population to become sufficiently inbred so as to cause noticeable depression of survival or reproduction. PVA of Florida panthers, after the reversal of inbreeding via genetic rescue with released Texas cougars, suggested that the population had become demographically viable. However, when models were projected out further, the resumption of inbreeding was predicted to cause later collapse if the population could not expand into additional habitat or receive periodic genetic supplementation (Maehr, Lacy, Land, Bass, & Hoctor, 2002).

The existence of time lags in population dynamics has several implications for maintaining ex situ as well as in situ populations of wildlife. As was the case with the projected fates for Florida panthers, deleterious genetic impacts will be delayed for several generations. The projections for ex situ populations made with the Goals component of PMx assist with identification of population sizes adequate to avoid eventual genetic damage. However, those calculations do not include projected demographic decline as genetic diversity decays, so they will likely over-estimate how long a population will stay genetically and demographically robust. Use of PVA models that include feedbacks between demography and genetics would more accurately predict the time to loss of viability.

We need to be skeptical of any projections made from data based on only a few years of observations. Even if a population is intensively monitored, by the time that effects become statistically significant, the damaging process might be too far along to be reversed. We also should be wary of interpreting short-term trends as being biologically meaningful. Many aspects of wildlife populations are highly stochastic. Even a statistically significant pattern could have been driven by a short-term fluctuation in the population (e.g., changing age structure, sex ratio, or social structure) or environment (e.g., climate, diet, or husbandry). Estimates of long-term means and trends are unreliable when data span less than one generation.

Thus, a population increase or decrease for a few years should not engender undue optimism or pessimism. Bad luck, and good luck, happens; populations can undergo substantial short-term changes in growth due to population structure; and the consequences of feedbacks can be slow to be realized. A primary advantage of PVA simulation modeling is that it reveals the range of long-term trajectories that can arise from current or forecast conditions.

2.5 | There are no lost causes, only difficult ones

A "minimum viable population" (MVP) was defined as a probability, not a certainty. Shaffer (1981) proposed that an MVP could be the population size above which a population had greater than 99% chance of survival for 1000 years, although subsequently most practitioners use much less stringent criteria. The development of PVA as a methodology to examine probability of extinction arose in part as a counter to the incorrect interpretation of an MVP being a size below which extinction is inevitable. That interpretation was incorrect both because an MVP is a probability statement that does not delineate a sharp boundary between viable and not viable, and because the purpose is to identify populations at risk and therefore in need of conservation action, rather than to flag some populations as being doomed (Soulé, 1987). Perhaps because most ex situ populations are below any reasonable estimate of their MVPs, zoos have been less susceptible to the invalid assumption that populations below MVP cannot be deserving of resources.

2.6 | One size does not fit all

PVA also directly counters another misconception about MVPs—the view that there is a single standard that applies to all species. This view has led to simplistic generalizations about required population sizes for conservation, including ongoing debates as to whether a "standard" long-term MVP is 500 (Franklin, Allendorf, & Jamieson, 2014) or 1,000 (Frankham, Bradshaw, & Brook, 2014). PVA is a class of methods for determining viability, based on the biological characteristics of the population, the specific threats, and the expected consequences of human activities. Thus, PVA provides a methodology for estimating an MVP appropriate to each population.

The cooperative breeding programs of zoo associations were attuned to the uniqueness of each species from the start, with population goals based on the number of founders, population growth rate, generation time, and proportion of animals breeding (Ballou et al., 2010; Soulé, Gilpin, Conway, & Foose, 1986). Thus, zoos have long been estimating the equivalent of an MVP for managed populations. The recent effort by AZA to conduct PVAs on many species using ZooRisk (Che-Castaldo et al., this issue) extends this approach, and the evolving PVA methods should increasingly be exploited to identify safe population sizes.

Some recovery plans for in situ populations have been criticized for misinterpreting both the meaning of an MVP and the precision with which it can be estimated from PVA. For example, the recent Mexican Wolf Recovery Plan (U.S. Fish & Wildlife Service, 2017) functionally used the MVP estimated from a PVA as an upper limit, above which the population would not be allowed to grow, rather than as a minimum threshold below which a recovered population should not be allowed to fall. A common practice in ex situ population management, in which spaces are allocated sufficient only to reach target sizes that are projected to sustain genetic diversity at the specified goal, can be seen as making the same mistake. It is necessary to partition resources so as to maximize the number of species that can be protected, but it is also risky to leave no margin for error or unexpected events.

Given the considerable uncertainties in PVA projections, a precautionary approach would set the management threshold far enough above the estimated MVP to protect against possibly overly optimistic model estimates. Sensitivity analyses that explore ranges of plausible parameter values should be used to determine what confidence should be placed in PVA predictions (Mills & Lindberg, 2002). When setting management targets, we should be wary of assuming more precision and accuracy than is warranted.

2.7 | There is no one best method

Different PVA models are suitable for different species, threats, and questions. Models that include genetics are required if goals include maintenance of genetic diversity. Individual-based models are necessary to capture the stochastic threats to small populations (Lacy, 2000), but population-based models are adequate for larger populations. Spatially structured models, such as HexSim (Schumaker, 2016) and RAMAS GIS (Akçakaya & Root, 2005), are needed for analyses of habitat fragmentation and connectivity. Spatially structured models are probably less often useful for ex situ populations, because husbandry methods can be standardized and managers can move animals between zoos as needed. However, regional variation can be important when demographic success is dependent on climate or other conditions that vary among sites. The development of Global Species Management Plans as a means to help achieve sustainability of ex situ populations (Lees & Wilcken, 2011) should use PVA models that allow examination of the stability of metapopulations (such as RAMAS or Vortex) under various strategies for managed movements.

Data requirements for some models are less than for others, because they omit some factors that can influence population fates. For example, PVA models that do not require or allow estimates of inbreeding depression, frequencies of catastrophes, or initial age structure assume, respectively, no inbreeding effects, no catastrophes, and a stable age distribution. If important processes are omitted from the analysis, then projections will not be reliable. However, the relative viability under various scenarios can still inform conservation planning (McCarthy, Andelman, & Possingham, 2003), and sensitivity testing can reveal which uncertain variables are likely to have large effects on results (Mills & Lindberg, 2002). More complex PVA models can reveal dynamics that are otherwise unanticipated (Lacy, Miller, et al., 2013), but unnecessarily complex models often depend on parameters that cannot be estimated (Fieberg & Ellner, 2000). It is often instructive to compare projections with vs. without added complexity to help assess how much complexity is necessary to provide reliable results for the purposes of the PVA. Even after a modeling platform is chosen, the specific PVA methods to be used should depend on the purpose. For example, different sensitivity tests are appropriate if the intent is to compare relative effects of the same proportional change in each parameter, or to assess which factors are currently most threatening the population, or to evaluate which conservation options will have largest positive impact (Manlik, Lacy, & Sherwin, 2018).

Two PVA packages currently used for ex situ populations, Vortex (user's manual: Lacy, Miller, & Traylor-Holzer, 2018) and ZooRisk (user's manual: Faust, Earnhardt, Schloss, & Bergstrom, 2008), are individual-based models that project loss of genetic diversity, can use a studbook as the starting population, and can model imports and exports, inbreeding depression, genetic management, and carrying capacity, but they implement these processes differently. For example, the default Vortex model imposes carrying capacity by removing excess individuals, while ZooRisk reduces breeding; Vortex models inbreeding depression with an exponential function, while ZooRisk uses a threshold model; and Vortex can apply either static or dynamic mean kinships for selecting pairs, while ZooRisk uses static mean kinships. The programs each include some features not available in the other: Vortex includes annual fluctuations in demographic rates, models fates of alleles, and can model metapopulations that exchange individuals; ZooRisk extracts demographic rates from the studbook and can assess space trade-offs between species programs. Overall, Vortex provides more flexibility (allowing input parameters to be functions of individual, population, or environmental characteristics), and Vortex would be the PVA model of choice when the data, expertise, and time permit exploration of complex models that include individual variation, subpopulation structure, or complex feedbacks between demography and genetics. When a standardized approach is appropriate, ZooRisk facilitates more rapid analysis of ex situ populations.

3 | LESSONS ABOUT PROCESSES FOR ASSESSING VIABILITY

Many of the lessons learned from applying PVA to wildlife conservation relate not primarily to wildlife population biology, but instead to human values and effective social processes.

3.1 | Viability is a human value, not a biological truth

There is no absolute viability, as every population has some risk of extinction. Therefore, we must identify the acceptable risk that we want as our definition of viable. In both the history of the PVA approach and, in my experience, in many cases of the application of PVA to specific conservation challenges, participants start with an ambitious criterion for success (such as less than 1% probability of extinction), but then back down to weaker criteria (such as a 10% chance of failure) after seeing how difficult it will be to achieve the higher goal. This relaxing of standards is made more palatable by the admission that PVA methodology rarely provides confidence that we can estimate probabilities of extinction within 5%. Similarly, the Regional Collection Plans of AZA Taxon Advisory Groups often scale back ambitions and settle on target sizes that will sustain less than 90% of original gene diversity. While adjusting goals in the face of reality can be a useful part of the planning process, we need to be explicit and document what criteria we accept.

In assessing viability of wildlife populations, the same standard might be applied to all species, or instead the definition of viability might be customized based on our perceptions of value of the species or the difficulty in securing its viability. For some purposes, such as the IUCN Red List that provides a repeatable categorization of threat that allows comparison across species, a common standard is required. In contrast, the US Endangered Species Act (ESA) does not define an objective standard ("Endangered means a species is in danger of extinction [how much danger?] throughout all or a significant portion of its range"), and leaves the Threatened category even more vaguely defined as "any species which is likely [how likely?] to become an endangered species within the foreseeable future [how soon?]" (16 U.S.C. §1532). If we are to be scientific, transparent, and accountable in our species conservation programs, we cannot leave our criteria as poorly defined as are the endangerment categories in the ESA.

In assessing ex situ populations, we will need also to decide whether to apply the same definition of viability to all species, as in the standardized approach in ZooRisk, or instead allow each program to define its own goals for viability, as is being done in the restructuring of species programs in the European Association of Zoos and Aquaria (DeMan, Leus, & Holst, 2016). The former approach allows consistent measurement across species; the latter approach measures success against the purposes for each program.

A necessary part of our definition of viability is the specification of the time frame for management. The seminal paper by Soulé et al. (1986) directly addressed this issue, and the intended duration of ex situ programs has been revisited occasionally since (Ballou et al., 2010; Foose et al., 1995). The time frame for measuring viability can be standardized for comparative analysis, left flexible to respond to individual program goals, or both in different contexts.

3.2 | Viability means many things

Although population viability was first defined in terms of probability of extinction, viability can be expressed by any measure of performance that is of interest. Different species recovery plans define their goals as achieving a desired number of individuals, number of populations, or population growth rate. Population size criteria are often intended to be indices of extinction probabilities, and size goals are often based on PVA modeling (e.g., Florida panther [U.S. Fish & Wildlife Service, 2008], and Fender's blue butterfly [Schultz & Hammond, 2003]). Sometimes it is the population size itself that is of primary interest: The goal for beluga whales in the St Lawrence estuary is a return to 70% of the historic size (DFO Canada, 2012). One measure of viability combines size and persistence criteria: The quasi-extinction rate is the probability of declining below a lower limit that delineates functional extinction, a threshold below which the population would be unlikely to recover or would fail to fulfill valued roles. Concepts of viability can be even further removed from simple biological persistence, such as goals related to ecological, economic, or cultural values (IUCN/SSC, 2008).

There are implications of how we choose to define viability of ex situ populations. For example, programs often define viability in terms of genetic variation, and target sizes are often based on what is necessary to retain 90% of gene diversity for 100 years. However, it has never been clear if that criterion is intended to protect individual animal fitness and well-being, or is an indicator of high likelihood of population persistence, or reflects a desire to protect the gene pool as a fundamental property that defines the population, or instead is aimed at ensuring evolutionary adaptability. The reason that underlies the genetic viability criterion can make a difference to how we manage populations. For example, if a population falls below 90% of original gene diversity, but has adequate fitness even under that level of inbreeding, then we might be comfortable adjusting our viability definition downward if the goal is animal well-being or population persistence, but not if a goal is genetic representation of the species or future adaptability.

3.3 | Don't do this alone

A PVA that is sufficient to guide management involves consideration of many factors. These include not only basic demographic rates, but also —depending on the situation—fluctuations in rates, social behavior, disease, genetics, environmental change, species relationships, and evolutionary change. Indeed, the reason for the development of PVA simulation models was that the multitude of interacting processes that can influence wildlife population dynamics precludes analytical solutions in all but the simplest cases. Consequently, model construction, parameter estimation, interpretation of PVA results, and application to management decisions require trans-disciplinary collaboration (Westley & Miller, 2003). A PVA technician who runs the simulation model might need to be assisted by experts in genetics, reproduction, disease, behavior, ecology, taxonomy, and evolution, as well as the managers who determine the program goals, what resources are allocated, and what external constraints are placed on options. Moreover, the data, modeling, and interpretation of PVA are complex and to an extent species-specific. Thus, it is imperative that PVAs be reviewed by others who can question assumptions, identify gaps in documentation, provide additional data, and offer alternative interpretations (Ralls et al., 2002).

In PVAs, where there was inadequate flow of ideas and information between the population modelers and other experts, the PVA results have not been accepted by managers. For example, conclusions of a Steller Sea Lion PVA (National Marine Fisheries Service, 2008) were rejected and replaced with vaguely defined "weight of evidence" because managers later questioned assumptions made in the modeling. Recommendations arising from a PVA on the Mexican wolf (Carroll, Frederickson, & Lacy, 2014) were rejected by state and federal wildlife agencies that made alternative assumptions about biological parameters and imposed different limits on what conservation actions could be considered (U.S. Fish & Wildlife Service, 2017). Consequently, the Population and Habitat Viability Assessment (PHVA) workshop process of the IUCN Conservation Planning Specialist Group relies on participation of stakeholders with various kinds of expertise (Westley & Byers, 2003). In workshops with active exchange among diverse experts, often participants have identified the cross-disciplinary discussions as being even more valuable than the specific results from the PVA modeling (Westley & Miller, 2003). Out of the need to attend to the management of many species, increasingly the process of producing Breeding and Transfer Plans for SSPs relies mostly on a few participants (e.g., SSP Coordinator, Studbook Keeper, and Population Management Center advisor) rather than actively involving many SSP members and outside advisors. However, if population management is to be based on more than standardized genetic and demographic analyses, it might be valuable to invest in the broader process that was characteristic previously in the SSP Master Plans—at least once every few planning cycles.

3.4 | We will never know enough, but we can know more

It could be argued that PVA should not be done if there are not extensive data on the population. However, if we waited for complete information, no conservation action would ever be taken. The alternative of using only intuition or rules of thumb, rather than PVA, foregoes the opportunity to use the information that is currently available to inform decisions, paradoxically discarding data that are available because of a concern that the data are fewer than desired.

The common lack of important data, coupled with the imperative to take action, leads to the need to use PVA for wildlife management within an Adaptive Management framework (Runge, 2011). Adaptive Management is not as simple as trial-and-error, in which a strategy is tried, and if it fails, then we try something else. Instead, it is a multi-step methodology for integrating research and management. Adaptive Management starts with clear specification of the management problem, goals, and measures of success. It then requires enumeration of two or more management options, and identification of uncertainties (stated as alternative hypotheses) that preclude determination of which action is best. Analysis of the distribution of outcomes expected for each possible management action under each alternative hypothesis is then used to identify which management choice will achieve both high probability of success and improved understanding of the critical uncertainties. Through repeating cycles of analysis-decision-action-monitoring-updating, knowledge is gained so that successive actions can become more optimal with respect to the expected success toward defined goals.

PVA can be a powerful tool within Adaptive Management (Ludwig & Walters, 2002), because PVA provides distributions of success projected under scenarios that can describe both uncertain parameter values and alternative management actions. Vortex Adaptive Manager (included in the Vortex installation) is a program that implements calculations for Adaptive Management using Vortex as the simulation to project distributions of outcomes. Vortex Adaptive Manager also provides calculations of the "value of information" (Canessa et al., 2015), the improvement in management success that would be expected if we can obtain more information about currently uncertain parameters.

Although we often have more detailed data on ex situ than in situ populations, successful management of ex situ populations is also challenged by the lack of sufficient information—about environmental requirements, social needs, behavioral flexibility, genetic effects, and more. However, the long time horizon of most ex situ conservation programs together with the ability to monitor populations closely provide the opportunity for learning. Thus, Adaptive Management could assist with achieving viable ex situ populations and ensuring that they fulfill their conservation purposes (Canessa et al., 2016).

3.5 | Integrated population management

PVA can be a powerful tool for the integration of in situ and ex situ conservation efforts. A "One Plan Approach" has been defined as "integrated species conservation planning, which considers all populations of the species, inside and outside their natural range, under all conditions of management, engaging all responsible parties and all available resources from the very start of any species conservation planning initiative" (Byers, Lees, Wilcken, & Schwitzer, 2013). When PVAs have been conducted previously on both in situ and ex situ populations of a species, those analyses provide background data needed for integrated conservation planning, such as the Integrated Collection Assessment and Planning (ICAP) process described by Traylor-Holzer, Leus, and Bauman (this issue). When the ICAP must rely instead on coarser status assessments, such as the IUCN Red List, species designated for further conservation attention would often benefit from subsequent PVA that provides the quantitative analyses to inform detailed and comprehensive species conservation plans. Even when the conservation role of an ex situ population is determined not to require a self-sustaining, long-term population, PVA can provide documentation that any reliance on wild captures to sustain the ex situ population does not jeopardize the future of in situ populations, and that the ex situ conservation actions will enhance the overall species viability.

Thus, all components of integrated planning would benefit from comprehensive PVA that evaluates threats and estimates likelihood of success of in situ and ex situ actions aimed at countering those threats. For example, PVA of the in situ population would reveal if its persistence could not be assured, thereby indicating a potential need for an ex situ assurance population. PVA of the ex situ population would reveal if the breeding program was adequate to meet the short or long-term needs for supporting the in situ population. This would include assessment not only of the viability of the population as a self-sustaining entity, but its ability to produce also animals required for releases (Dolman, Collar, Scotland, & Burnside, 2015; Earnhardt et al., 2014), research, education, or other roles. To most effectively answer these questions, a comprehensive PVA should be conducted on the metapopulation consisting of the in situ and ex situ populations. Such a meta PVA would inform us about the viability of each population, the resilience of each to removals needed to support other populations, the necessary movements of animals between populations to stabilize each demographically and genetically, and the prospects for success of the overall conservation strategy. Recent examples of such uses of metapopulation PVA to guide management of both ex situ and in situ populations include conservation plans for the Cat Ba langur (Lees, Rawson, Behie, Hendershott, & Leonard, 2014), and takahe (Lees, Greaves, Joustra, Eason, & Jamieson, 2014).

4 | CONCLUSIONS

With the evolution of PVA, methods exist to address the challenges of inadequate data, delayed effects, synergistic threats, resource limitations, and an uncertain future. However, much of what has been learned over the past three decades about drivers of population viability, robust methods to assess viability, and the effective use of PVA in guiding management has not yet been fully incorporated into ex situ population management. The application of PVA to ex situ populations could help reveal the long-term consequences of current management and which management options will allow us to reach our goals. Indeed, it is hard to see how progress can be made toward sustainability if we do not both look at where our populations are heading at present and evaluate what it will take to achieve sustainability of populations for the conservation purposes that they serve. Thus, the methodology of PVA could be important to improving the *sustainability* of ex situ populations, just as PVA has become an essential tool in species recovery planning for in situ populations. Even without the direct application of PVA to all cooperative breeding programs, lessons learned from PVA on in situ populations raise important questions and provide some answers regarding the challenges of securing a future for ex situ populations as well.

At the outset of the field of conservation biology, detailed pedigrees of ex situ populations allowed studies of inbreeding depression that had large impact on understanding of the role of genetic diversity in the viability of wildlife populations much more broadly (e.g., Ralls, Ballou, & Templeton, 1988). Subsequently, methods developed for managing cooperative breeding programs are being applied to in situ populations (Frankham et al., 2017; Jamieson & Lacy, 2012). There is now an opportunity for technology transfer in the other direction—from in situ wildlife management to help sustain viable ex situ populations.

Only relatively recently has PVA software been customized for ex situ populations, starting with the release of ZooRisk in 2004. As PVA is applied to many more ex situ populations and management scenarios, methods that would further facilitate the use of PVA for these populations will become apparent. The availability of improved tools and methods will in turn lead to the need for additional data on the demographic, genetic, behavioral, and husbandry factors that influence population dynamics.

The application of PVA will be essential to the further integration of ex situ programs with in situ conservation. Ex situ populations are often necessary as a source of animals for reintroductions and supplementation of in situ populations, for research, for education, or as insurance against irreversible loss of species. PVA provides a powerful methodology for determining the prospects for the ex situ populations to be able to fulfill those roles, the effectiveness of the ex situ efforts to enhance species conservation, and the integrated management of all populations of the species.

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