Population Viability Analysis: A review

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4/26/13

As habitat disruption, fragmentation, climate change, and gratuitous sources of anthropogenic pollution infiltrate the global environment, many terrestrial and aquatic species are at risk of extinction. In the rapidly changing climate of the 21st century, an estimated 10,000 to 15,000 species are projected to go extinct every year (Primack 2010). Because the biosphere has become so fragmented and local conditions exert considerable influences on the fate of populations and subpopulations of species, models are desperately needed in order to make reliable predictions on the minimal habitat requirements of species at risk of extinction as well as the minimum population size needed to sustain a viable population. An ideal form of risk assessment would take into account metapopulations, local extinction events, migration patterns, as well as the economic aspect of species, which incorporates willingness to pay; admittedly, these are difficult and constantly changing variables, but they must be addressed in order for conservation biologists to accomplish management goals and protection measures for vulnerable and threatened species.

Population viability analysis (PVA) is a type of risk assessment on the ecological level, and with the aid of mathematical and statistical methods, can predict whether a species has the ability to persist in a given environment (Primack 2010). PVA is an extension of demographic analysis, which follows known individuals of different ages and sizes in a population to determine their rates of growth, reproduction, and survival (Primack 2010). In PVA, the risk assessment aspect arises from the predictions of the probability that a population or a species will go extinct at some point in the future (Primack 2010). The process of identifying the requirements of and threats faced by rare and threatened species consists of the short-term objective to minimize extinction and the long-term objective to promote ideal conditions under which the species can continue on with its evolutionary potential (Akģakaya and Sjögren-Gulve 2000). By taking into account whatever available information exists about the natural histories of certain species, the effects of local and large-scale human activities on a species, and dispersal patterns of many species, PVA can be expressed as extinction risk, time to decline, chance for recovery, persistence time, and local and regional occupancy rate (Akćakaya and Sjögren-Gulve 2000).

For species that are at risk of extinction but are not necessarily on the brink of extinction, PVA according to one study can serve three useful functions. First, PVA can indicate how urgently recovery efforts need to be for certain populations, which can be done simply through estimating the probability of extinction within a specified time (Morris et al. 2002). A second function of PVA involves synthesizing monitoring data into an assessment of the effectiveness of recovery plans, such as tracking the birth rate of a population over a period of time (Morris et al. 2002). Thirdly, PVA can identify particular life stages that should be primary targets of management (Morris et al. 2002). In addition to these three basic functions, PVA can be divided into four general approaches: count-based, structured, metapopulation, and spatially-explicit (Morris et al. 2002). Count-based is the simplest approach to monitoring populations, as it uses time series data on total population size to parameterize models that predict extinction risk; this method requires data on both current population size and trends in population size over time (Morris et al. 2002). The next type of PVA class is the structured approach, which uses life tables in order to track changes in the numbers of individuals in different stages in a population. Structured models allow for more detailed analysis of "critical life stages or demographic processes that are potential targets for management," but they require highly detailed data on mortality and fecundity rates (Morris et al. 2002). Metapopulation PVAs take into account the colonization and dispersal rates of different subpopulations. The purpose of this approach is, by tracking the fates of several subpopulations within a matrix, to determine whether the rate of establishment of new subpopulations is enough to offset the rates of extinction in existing subpopulations (Morris et al. 2002). This approach requires more information than the previous two classes, but is not as data-intensive as the fourth class, which is the spatially-explicit PVA. Spatially-explicit models simulate the behaviors of individual organisms on detailed landscapes, and on these landscapes the sizes and locations of suitable habitat patches are mapped (Morris et al. 2002). This class also requires data on individual birth rates, death rates, and movement patterns, as well as information on the degree of isolation or fragmentation of suitable habitat patches (Morris et al. 2002). With the fourth approach being the most detailed and extensive one to use, it would be the ideal model for monitoring the viability of endemic species with several habitat patches that could be separated from each other and thus reduce the movement of individuals between patches.

Although PVA can provide plausible effectiveness or ineffectiveness of alternative management strategies, there is always an underlying degree of uncertainty in determining the priorities for conservation action (Neri-Arboleda 2010). Accurate extinction risk predictions and minimum viable habitat requirements of species requires extensive data collection, which can take several years of field research. The power of the PVA model is only as strong as the quantity and quality of the data that is input into the various software programs that generate the models. Recent applications of PVA include projecting risk of extinction for butterflies, tarsiers, caribou, and threatened northern map turtles. All of these illustrate how different models of PVA can be tailored to different species based on available data, level of concern, and influence of anthropogenic threats to population viability of the species of interest.

A recent example of the application of PVA to metapopulation conservation took place in the Netherlands, with the species of interest being the butterfly *Maculinea alcon* (Radchuk et al. 2012). This study focused the potential of PVA on this particular butterfly species because it is listed as Endangered in Europe as well as the fact that the complicated life history, which includes part of the life cycle being spent within an ant nest, makes them an ideal model for the emerging field of preserving species interactions (Radchuk et al. 2012). Dispersal capabilities of *M. alcon* within different patch networks are important for population viability, which is often the case for scores of other species; using this context of dispersal, the researchers developed a spatially-explicit PVA model for this species in the northern region of the Netherlands. Collected data was put into RAMAS/GIS software and subsequent sensitivity analysis was conducted for the entire metapopulation and for each habitat patch by altering carrying capacity, maximum growth rate, initial abundances, and dispersal rates (Radchuk et al. 2012).

After distinguishing between four habitat patch networks, the researchers came up with four management options that could be used to enhance population viability:

enlargement of existing habitat patches; improvement of habitat quality; increasing connectivity through the creation of new habitat patches; and raising population size by introducing reared butterflies (Radchuk et al. 2012). In order to determine the best management option, a Structured Population Model took into account local demography, which involves carrying capacity, maximum growth rate, and density-dependent processes including intraspecific competition during the larval stages on the host plant and in the ant host nests (Radchuk et al. 2012). These parameters exemplify the rigorous need for the collection of as much field data as possible. After running the collected data through RAMAS/GIS software, the results from the baseline scenario model predicted a decline in population size over the next 200 years, with only 17 patches being occupied at the end of the 200 year period, which is a drastic decrease from the starting point of 27 occupied patches in 2003 (Radchuk et al. 2012). In addition, sensitivity analysis indicated that model predictions at the regional and local levels were highly sensitive to carrying capacity and environmental stochasticity. With the finding that population viability increases with carrying capacity, the best management option was found to be habitat enlargement (Radchuk et al. 2012).

PVA has also been used for threatened primate species, including howlers, Northern woolly spider monkeys, and western Hoolock gibbons. In the Philippines, a PVA was applied to the tarsier *Tarsius syrichta*, a species susceptible to extinction due to several factors, including high infant mortality rates in the wild and in captivity, a highly specialized diet, limited geographical range, high population density, and extensive habitat destruction (Neri-Arboleda 2010). Not only are these species at risk of extinction, but also of conservation concern is the Philippines in general; the existing protected areas suffer from lack of funding, resources, and lack of support from local governments (Neri-Arboleda 2010). As a conservation tool, PVA could provide the guidance for identifying areas that require improvement and could lead to the push for active and sustainable conservation programs.

Methods for this tarsier PVA study included using the island of Bohol as a study area, and life history data of *Tarsius syrichta* and *T. bancanus* was collected for the PVA model. The PVA model used was ALEX, which is a Monte Carlo simulation model that takes into account home range size, environmental stochasticity, age classes, litter size and sex ratio, mortality, and lifespan (Neri-Arboleda 2010). The purpose of performing a PVA for this species was to determine the minimum viable habitat area for a population of tarsiers when the probability of extinction was less than 5% within 100 years. To do this, different simulations for different habitat areas were run; these ranged from 20 ha to 70 ha. The results from this PVA showed that 60 ha was the minimum habitat area that showed less than 5% probability of extinction within 100 years (Neri-Arboleda 2010).

Aquatic species may prove to be the more abstract and difficult organisms on which to model a PVA. For instance, the northern map turtle of Ontario, Canada is federally listed as a species of special concern, and one of the major threats to this turtle is recreational boating (Butlé et al. 2010). A PVA was conducted to quantify mortality rate and demographic impact of boat injury-induced mortality, and the study was based on field data collected from the St. Lawrence River and Lake Opinicon in Ontario (Butlé et al. 2010). For this PVA, Vortex 9.93 software was implemented, and the data input into this model quantified the annual probability of being hit by a boat and surviving for male and female turtles (Butlé et al. 2010). The output from this software showed that males have 0.3% chance of being hit by a boat and surviving, while for females this probability was 0.14%. Information required to generate these figures included the number of hours spent basking in the sun by females and males, location of the turtles in the river and lake which would influence their probability of being hit and relative sizes of the two sexes. One of the major findings from this study included that even low mortality rates in females can lead to a high probability of extinction over 500 years (Butlé et al. 2010). According to the PVA, if the percentage of females killed from boat-induced injuries is 10%, then the probability of extinction in Lake Opinicon goes from 0% to 63%. Although the risk of extinction is in the time frame of 500 years, the PVA of this study shows how even small changes in mortality rates can have significant long term consequences on the viability of the population. To that end, the risks of extinction could be actively reduced in the present decade; there could be conservation management that calls for lowered boat speeds in this species' habitat, or recreational boating could be prohibited all together in areas that are considered especially vulnerable.

Especially with metapopulation studies, PVA can be useful in conservation efforts where species have a patchy distribution and limited dispersal (Radchuk et al 2012). This aspect of PVA is critical in areas where the community or population is fragmented as a result of human activities such as deforestation. More recently, however, a culmination of human influenced effects such as climate change and habitat destruction is having adverse consequences on woodland caribou in boreal forests of Ontario, Canada (Dybas 2012). This boreal forest-dwelling ungulate is listed as *threatened* under Ontario's Endangered Species Act, and several threats to woodland caribou such as habitat loss, fragmentation, and degradation due to forestry and mining developments demand a province-wide caribou conservation policy (Dybas 2012). In order to determine the best conservation management plan to protect this vulnerable species, researchers are employing the use of PVA. In this case, there are a plethora of environmental factors imposing on the fate of caribou: global climate change, wolf predation rates, the quality and quantity of caribou food, and the effects of massive hordes of black flies (Dybas 2012). In order for any population viability analysis to be effective in generating probabilities of extinction, which could influence conservation management plans, a surfeit of field data is necessary. This need for ample field data can be the one factor that makes PVA less powerful as statistical tool and more theoretical and lacking in concrete conservation management plans.

Global climate change should be regarded as a high priority global change in the distribution and ultimate survival of species on this planet. As global changes bring about alarm for the possible extinction of iconic species, conservation biologists are constantly seeking innovative tools for modeling risks for extinction and survival. According to Fryxell, a researcher collecting caribou data, "PVA indicates how urgent conservation efforts need to be and identifies important life stages or processes that should be the focus" (Dybas 2012). In the case of the caribou, which are at risk of extinction by 2100, information on the diets of moose, caribou, and wolves is needed in order to develop a powerful PVA model. Caribou prefer reindeer lichen as their winter energy source, but as climate change progresses, the lichens' ranges may be pushed further north; this potential change in the distribution of a primary energy source could also limit the viability of caribou. As a result of these anticipated changes, the projected range of lichens as well as the ability of lichens to spread northward as its current climate zone inches to the north should be included in the PVA of caribou populations. In addition to the large amount of field data needed for the PVA to be as accurate as possible, anthropogenic land disruption of the Boreal also needs to be quantified in terms of moose populations, predator populations, and abundance of winter foods such as lichen (Dybas 2012). A thorough PVA on woodland caribou would have to be done over a period of several years in order to collect sufficient data on the movement of lichen, wolves, moose, and caribou into higher latitudes. To that end, the most thorough PVA may not be complete for many years, and sufficient data may be difficult to obtain when only computer simulation models are used to project the effects of predation on caribou populations. With climate change in the equation, concrete probabilities seem to have less definitive power in projecting the future viability of species most susceptible to the effects of climate change.

The previous case studies on extinction risks presented to species with different habitat requirements used PVA methods that focused mostly on static, discrete variables such as age and sizes of habitat patches. However, there is a unique opportunity for elements of landscape ecology and PVA to work together to project possibly more accurate extinction probabilities. It is important for PVA to incorporate environmental and landscape change since climate change and habitat fragmentation have contributed and will continue to contribute to extinction of species (Chisholm and Wintle 2007). Accurate PVA predictions based on the use of dynamic landscape metapopulation models (DLMP) take into account landscape and population stochasticity; however, these landscape model repetitions are computationally intensive and must be done manually, and the repetitions for the population model are generally less intense and can be automated (Chisholm and Wintle 2007). As a result, temptation exists for researchers to use a higher number of the population models than the landscape models (Chisholm and Wintle 2007). It would be advantageous to incorporate landscape ecology into PVA, but people must be willing to put in more time and effort to make the PVA worthwhile.

When considering how to implement PVA into species restoration and conservation plans, the software must be compatible with the intended goals. For instance, the PVA model used in the tarsiers study was ALEX. While the model can simulate the dynamics of spatially structured populations and allows for independent environmental stochasticity modeling at the subpopulation level, ALEX takes into account only one sex, which is usually the female (Neri-Arboleda 2010). Using only females and their life history for generating extinction risks may be useful in the sense that reproductive rates are the major limiting factor for most populations, but at the same time, ignoring the other sex also ignores the effects of genetic structure on population viability (Neri-Arboleda 2010). In addition, focusing only on females or males for generating a model would leave out important data on sex ratios and mortality rates of the two sexes for side-by-side comparison. Another important consideration for the ALEX model is that it only allows for three classes of individuals: newborn, juvenile, and adult (Neri-Arboleda 2010). Another type of PVA software is Vortex 9.99, has a plethora of data entries ranging from species description, dispersal, reproductive system, reproductive rates, and carrying capacity. In the reproductive system scenario, researchers can choose to include whether or not their species of interest is polygynous, monogamous, or hermaphroditic (Vortex 9.99). There is even an option to add more scenarios, so that researchers can make this program simulate whatever aspect of the species they deem important in predicting extinction probabilities.

There is an inherent risk of population viability models being biased as overly optimistic and overly pessimistic. These biases stem from the amount and types of data being input into different computer software models, but they have their own unique outcomes on conservation efforts. In the optimistic predictions, the extinction risk of a species may be underestimated. This can happen when not all of the potential threats to an endangered species are included in the model (Brook 2000). Optimistic predictions can be the outcome of analyses that lack comprehensive data collection and field studies of wildlife populations that are too short of a duration which results in the lack of the ability to detect rare events and environmental stochasticities (Brook 2000). Shortened field studies can also reduce the ability to quantify the importance of density-dependent factors such as disease and the recognition of long-term trends (Brook 2000). Without taking into consideration the real and forthcoming future changes in land use, human population growth, and climate change, optimistic predictions in population viability carry with it the danger of overlooking the conservation needs of species that may truly be on the verge of extinction. On the other side of this bias, pessimistic predictions can oftentimes overestimate the risk of species extinction. For instance, data collected from field studies, such as fecundity rates and mortality rates, are kept as separate entities from other factors such as habitat fragmentation and deforestation. However, the raw data collected in the field over a period of several generations could contain the hidden effects of habitat destruction, but if researchers input the collected data plus the extrinsic environmental factors, "double dipping" can occur (Brooks 2000). In double dipping, certain software programs for PVA may already have catastrophes, inbreeding depression, and demographic stochasticity incorporated within PVA parameter estimates, and these factors become duplicated when field data such as mortality is included in the simulation (Brooks 2000). In this situation, extinction risks may be presented as superficially high. Although it might seem better for extinction risks to be presented artificially higher rather than low, it is important that PVA models realistically reflect the dynamics of endangered species by accounting for all factors that could contribute to extinction risks. In order for PVA models to be portrayed as realistically as possible, underlying bias and errors must be eliminated so that conservation management plans can operate to suit the present needs of the species and protect the species from decline.

Although PVA has been incorporated into a wide range of species management plans, recovery plans do not make a significant use of PVA. In fact, as of 2002, a survey found that only 14.4% of recovery plans used information that could be incorporated into a PVA, such as the data collected for count-based or structured PVAs; another 6.8% stated that information needed to construct a complete PVA did not exist (Morris et al. 2002). In the past, prior to 1991, less than 20% of recovery plans used PVA, and almost 20% of plans thought that PVA would be beneficial for recovery efforts (Morris et al. 2002). What is promising is that post-1991, significantly more recovery plans have used information to make PVAs and have expressed a desire for increased use of information to construct a PVA to benefit future recovery efforts (Morris et al. 2002). Despite the slow increase in incorporating PVA into endangered species conservation efforts, less than 50% of plans in the early 2000's assigned recovery tasks to collect information about PVA (Morris et al. 2002). A major cause for concern here is the growing need for recovery plans for endemic species and scores more that will be adversely impacted by climate change and habitat destruction. Although there is an increased desire of recovery managers to utilize PVA, recovery plans rarely collect and synthesize complete sets of field data, which could result in inevitable biases in PVA simulations as well as the underutilization of PVA in future recovery planning for endangered and threatened species (Morris et al. 2002).

Population viability analysis, although it has only a limited capacity for accurate extinction predictions, can be used proactively as a conservation management tool in the protection of endangered and threatened species. As conservation biology is a crisis discipline with the ultimate goal of preserving the evolutionary integrity of all species, no matter their inherent, ecological, or economic value, conservationists can use this tool to monitor several populations of species over a long term. In order for PVA to be most effective, data collection for accurate and unbiased PVAs should be a continual process, and should be considered as preliminary measures in the conservation plans for all species. As the case studies for tarsiers, northern map turtles, butterflies, and caribou have shown, PVA shows promising results for accurate predictions if the field data is collected and put into various simulation programs that can portray extinction and viability risks. While PVA alone is powerful as a prediction tool, the numbers that are obtained from the simulations need to be known to conservation management organizers, researchers, and the general public. Knowledge that a particular species, especially a flagship species or keystone species, is at a high risk of extinction should serve as the impetus for the continued preservation of the species.

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