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Population Viability Analysis of jaguar populations in Brazil

Population viability analysis (PVA) was used during the workshop for the Jaguar National Action Plan to better understand jaguar population dynamics and simulate different scenarios to understand the impact of threats and projected outcome of potential conservation strategies. The method is explicitly designed to broaden stakeholder involvement and enhance information sharing across disparate scientific and social domains. During the Jaguar National Action Plan workshop a base model was built for jaguars, a sensitivity analysis was run, and theoretical case studies of questions and situations raised by the participants were developed. The focus of this work was to examine concepts of jaguar population dynamics, stimulate discussions on jaguar life history parameters, fuel discussion on different threats, evaluate potential impact of these threats, and introduce participants to concepts of population viability analysis and its value as conservation planning tool.

Small populations of animals are at risk of extinction not only due to threats such as habitat loss and poaching, but are also particularly vulnerable to the impacts of stochastic (chance) processes that can lead to extinction. During the Jaguar National Action Plan workshop the simulation software program Vortex (v9.96) was used to examine the viability of jaguar populations. Vortex simulates the effects of deterministic forces as well as demographic, environmental, and genetic stochastic events on wild or managed populations, making it well suited to assess the viability of small populations. Vortex models population dynamics as discrete sequential events that occur according to defined probabilities. The program begins by creating individuals to form the starting population and then steps through life history events (e.g., births, deaths, dispersal, catastrophic events), typically on an annual basis. Population attributes such as breeding success, litter size, sex ratio at birth, and survival rates are determined based upon designated probabilities that are established during the workshop based on the literature and participant expert knowledge. Specific events that occur in the lifetime of an individual are uncertain, so probabilities are used to determine what happens to each animal in each simulated future. Consequently, each run (iteration) of the model gives a different result. By running the model hundreds of times, it is possible to examine the probable outcome and range of possibilities for the future of a population.

For a more detailed explanation of Vortex and its use in population viability analysis, see Lacy (1993, 2000) and Miller & Lacy (2005).

Population viability analysis (PVA) enables workshop participants to better understand jaguar population dynamics and simulate different scenarios to understand the impact of threats and projected outcome of potential conservation strategies. The method is explicitly designed to broaden stakeholder involvement and enhance information sharing across disparate scientific and social domains. Each participant is encouraged to add his or her knowledge of the species and its situation, potential actions, and additional questions to develop scenarios to be examined through modeling.

During the Jaguar National Action Plan workshop a base model was built for jaguars, a sensitivity analysis was run, and theoretical case studies of questions and situations raised by the participants were developed. The focus of this work was to examine concepts of jaguar population dynamics, stimulate discussions on jaguar life history parameters, fuel discussion on different threats, evaluate potential impact of these threats, and introduce participants to concepts of population viability analysis and its value as conservation planning tool. During the workshop the viability of jaguar populations from the different biomes was NOT examined, but will be investigated in the near future based on this initial work and the maps developed during the workshop (Ferraz et al. 2012, this issue).

Base model

Due to the potential variation of several parameters among the different biomes it was decided to construct a general base model for jaguars that could then be tailored to specific Brazilian biomes and specific jaguar populations. The base population model was designed to investigate the viability of a non-specific but biologically accurate jaguar population. Details of the parameters used in the base model are available in Table 1.

Some parameters were debated at length by workshop participants. For example some participants felt that females could have their first litter at 2 years of age and males at 3, while others insisted females on average would have their first litter at 3 years of age, as they need to have an established territory and be in good physical condition. There was also considerable debate about whether jaguar reproduction is density dependent. At high densities some participants thought that animals will compete for prey, territories and mates, limiting reproduction. However, others felt that in solitary living carnivores reproduction is not necessarily density dependent. A value of the PVA modeling approach is that it helps to identify such different perspectives, and then allows sensitivity testing of the effects of alternative values without prejudging which is closer to the truth.

After some discussion, maximum age was set at 15 years; however mortality rates after 10 years were increased in the model so that very few individuals (~5%) actually reach such an old age. By comparing observed population growth rates to those calculated for different plausible values of age-specific mortality, the workshop participants were able to come to consensus around the best estimates of mortality to use in the models. Mortality rates were set highest for the first year of life, moderate during years when cubs are with the mother or dispersing, and lowest for prime age adults, with increasing mortality after 10 years of age.

The base model represents the biological potential of jaguars: no harvest, no increase in mortality due to road kill, disease or fire, and no catastrophes are included. This does not represent a realistic situation, but provides the basis upon which future models that include these and others threats can be constructed.

The demographic rates (reproduction and mortality) included in the base model can be used to calculate deterministic characteristics of the model population. These values

Table 1. Summary of parameter input values used in the base model; EV = environmental variation, expressed as a standard deviation. Details for these values are given in the action plan (de Paula et al. 2010).

Parameter	Base value
Breeding system	Polygyny
Age of first reproduction (λ/ λ) in years	3 / 4
Maximum age (in years)	15
% adult males in breeding pool	90
Density dependent reproduction?	debated
Annual % adult females reproducing (EV)	50 (5)
Average litter size	2
Maximum litter size	4
Overall offspring sex ratio	50:50
% mortality from age 0-1 (EV) (λ/ λ)	42(7)/ 42(7)
% mortality from age 1-2 (EV) (λ/ λ)	17(3.5)/ 17(3.5)
% mortality from age 2-3 (EV) (λ/ λ)	20(5)/ 20 (5)
% mortality from age 3-4 (EV) (λ/ λ)	6(1.5)/ 25 (6)
% mortality from age 4-10 (EV) (λ/ λ)	8(1.5) / 10(2)
% mortality from age 10-15 (EV) (λ/ λ)	Add'l 5 % mort. ea. yr.
Inbreeding depression	6 lethal equivalents
% of inbreeding effect due to recessive lethal alleles	50

are a good initial summary of the population characteristics, as they reflect the biology of the population in the absence of stochastic fluctuations (both demographic and environmental variation), inbreeding depression, limitation of mates, and immigration/emigration. The base model results in a deterministic growth rate for females of (rdet) of 0.060 (λ= 1.058). This represents an annual potential growth rate of almost 6%. Adult sex ratio is female biased and the sex ratio of adult males to adult females is 1:2.7. Adult individuals (sexually mature individuals) represent 51% of the population (SOM Table 2 at www.catsg.org/catnews).

Results from the base model (500 iterations) project that a population of 200 jaguars in the absence of threats is likely to persist over the next 100 years. When N=100 and K=200 the stochastic growth rate (r-stoc, the mean rate in the simulated populations, subjected to all the demographic, genetic, and environmental uncertainty in the model) is 0.027, representing an annual population growth of almost 3%, enabling the population to grow when below carrying capacity. There is zero probability of extinction (PE) in 100 years, and the mean population size at 100 years is 187 jaguars with 91.28% gene diversity remaining (Supporting Online Material SOM Fig. 1).

Sensitivity analysis of demographic rates

Sensitivity analysis is a tool used to evaluate the robustness of a model to variations in parameter values. The most sensitive parameters require greater certainty in the input values to produce more confident results. This also helps to identify where further research is needed. Sensitivity analyses using highest and lowest values for each demographic rate were compared to evaluate the effect of model parameters on the stochastic growth rate (r-stoc) of jaguar populations. Mortality rates were increased and decreased by 25%, 1 year was either added or subtracted to age of first reproduction, 4 years were added/subtracted to maximum age of reproduction, and average litter size was increased or decreased by 25%. Results from the sensitivity analysis indicate that reproductive parameters and female mortality rates are the most sensitive parameters across the values tested, while male demographic values are less sensitive (Supporting Online Material SOM Fig. 2). This is logical for a polygynous species, in which females represent the breeding potential and therefore the ability of the population to grow and recover from declines.

Theoretical case studies

Importance of population size

To illustrate the importance of population size in jaguar populations, a modeling exercise was run during the workshop in which the initial population (N) was varied as well as the carrying capacity (K) when K>N and when K=N. Many different values were tested, ranging from 15 to 200. This exercise demonstrated that population size (both in terms of N and K) is a very important factor in determining the population growth, long-term persistence and genetic diversity of jaguar populations (SOM Tables 3 and 4). Small isolated populations of jaguars cannot persist in the long term. However, a high carrying capacity may decrease the impact of small population size on population growth, long-term persistence, genetic diversity and mean time to extinction, as it may allow the population to grow to a larger size, and once it is larger, it is less vulnerable. Therefore for conservation purposes, protection and maintenance of habitat quantity and quality (cover and prey base), which determines carrying capacity, are imperative for the long-term conservation of jaguars.

Impact of harvest of adult females

Killing of adult jaguars through sport hunting, traditional hunting or retaliation for economic loss all have the same result: loss of adult individuals (breeders) from the population. The sensitivity analysis showed that an increase in mortality of females negatively impacts jaguar populations. For the purpose of this exercise we modeled removal of adult female jaguars. Results show that the smaller the initial population, the higher the impact harvesting of female jaguars will be (Fig. 1). Smaller populations have higher probabilities of extinction and lower growth rates. In practical terms this means that removal of female jaguars from small isolated fragmented populations will have a much bigger impact on the population viability than removal of the same number of individuals from a larger population. Overall jaguars cannot sustain high levels of harvest given a theoretical maximum growth rate of only about 5%. Even if the initial population size is high, jaguar population growth rates will decline when harvest increases, and may ultimately drive populations to extinction.

Impact of fragmentation

Habitat loss, fragmentation and isolation of jaguar populations were repeatedly mentioned as one of the main threats to long-term persistence of jaguar populations in Brazil. Amongst its many impacts, habitat fragmentation reduces population size and smaller populations are more vulnerable to stochastic processes (including inbreeding) and have a higher risk of extinction. Corridors that link fragmented habitats are often advanced as a potential solution. During the workshop models were created to test the impact of corridors. Models suggested that corridors can either prevent or cause the extinction of jaguar populations, depending upon the situation. Metapopulation dynamics are complex and many factors come into play such as size of fragments, dispersal rate, demographic rates in the various fragments, and the survival and reproductive rates of dispersing animals (SOM Figure 4). Corridors to poor-quality or unprotected habitat ("sinks") or to areas too small to harbor a healthy breeding population can further de-stabilise the overall population. Further exploration and caution should be used when considering corridors as a conservation measure.

Translocations and re-introductions

During the workshop jaguar translocations and re-introductions were discussed. Due to logistical difficulties, potential risks and high cost, there is a lot of controversy surrounding this conservation option. As an exercise during the workshop we tested some re-introduction/translocation scenarios (SOM Table 5). The modeling showed that there are many aspects to be explored in order to guide and formulate a re-introduction program, such as age, sex, number of animals, reintroduction interval, re-introduction time period, survival and fecundity rates of reintroduced animals, and many more. The modeling exercise showed that re-introductions need to be well planned and part of a comprehensive program to be effective tools for conservation of jaguar populations.

Real case studies

During the workshop we also investigated several real case studies. The impact of hunting on a jaguar population from the Tapajós-Arapiuns Extractive Reserve, Central Amazonia was investigated using data collected by Elildo A. R. Carvalho Jr. (ICMBIO Parna Grande Sertão Veredas). Modeling was first used to evaluate the importance of some of the data gathered during the field study. For example, the model showed that data on the sex of animal hunted had a significant impact on the final outcome of the model, while knowledge of the age class of jaguars hunted (adults or sub-adults) had less impact. Modeling was then used to predict the impact of hunting and source-sink dynamics between the reserve and surrounding areas. The viability of the Minas Gerais Espinhaço jaguar population in the Cerrado was investigated, and a wide array of conservation measures to protect the population was tested using data collected

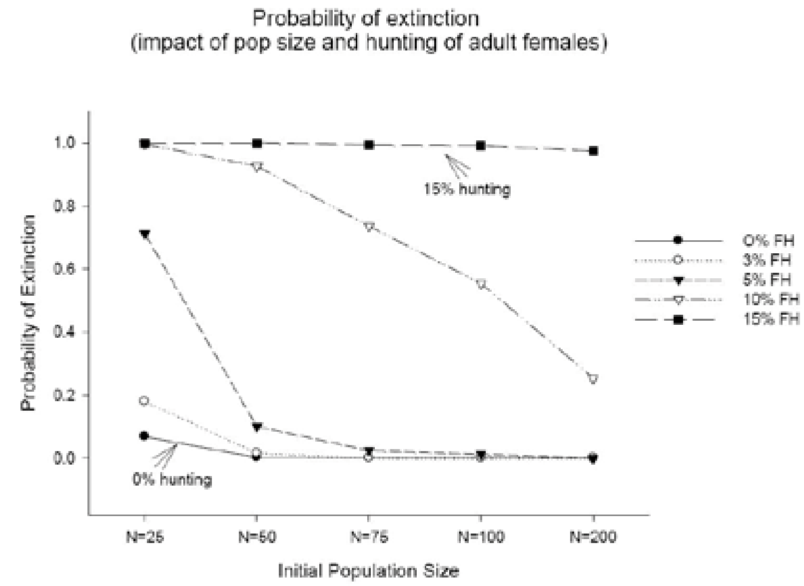

Fig. 1. Probability of extinction (within 100 years) of jaguar populations in relation to initial population size and percent harvest (H) of adult female jaguars.

by Edsel Amorim Moraes Jr and Rafael Luiz Aarão Freitas (Instituto Biotropicos). Tadeu Gomes de Oliveira (UEMA & Pro-Carnivoros) modeled the importance and impact of protecting the Nascentes Parnaíba Jaguar population in the Cerrado. The long-term viability of jaguar populations from each biome is currently being investigated and will be used to make specific conservation recommendations for each biome.

Conclusion

Using computer models such as Vortex during a workshop helps to integrate detailed data on species biology, genetics, and ecology with estimates of human-based threats to evaluate the risk of wildlife population decline or extinction under alternative future management scenarios. One of the advantages of using Vortex in a workshop is that it is a participatory exercise that helps participants understand long-term impacts, threats and probable trajectories of animal populations. It also helps experts determine the state of knowledge on the species and pinpoint areas where future research is needed. It helps to extract important data and knowledge from all participants and advance knowledge of the species. A model cannot make value decisions about what to conserve and why, nor can it guarantee that the needed actions will be implemented, but modeling does empower participants by giving them a scientifically sound method to integrate their knowledge into a comprehensive picture of population dynamics, risk analysis, and assessment of options. Thus, it can serve as an excellent tool for scientists and wildlife managers to work together in their quest to make better decisions about conservation.

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Supporting Online Material SOM is available at www.catsg.org/catnews

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