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Original contribution

MODELING THE IMPACT OF HUNTING ON THE VIABILITY OF A JAGUAR POPULATION IN AMAZONIA, BRAZIL

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Abstract
We used population viability analysis to investigate the impacts of hunting on the jaguar population of Tapajós-Arapiuns Extractive Reserve in central Amazonia. Population models were built in VORTEX, using data on jaguar biology and demography from the literature, and harvest estimates obtained in the reserve. We modeled five scenarios to explore the relative importance of carrying capacity, sex ratio and age class of harvested individuals, on the probability of extinction, genetic diversity, stochastic population growth and average number of jaguars left in the population after 100 years. The most important parameter affecting population viability was carrying capacity: the population had a high probability to persist with high genetic diversity when K=360, with a harvest of three females and nine male jaguars per year during 100 years, but went extinct when K was cut to half this value, under the same harvest rate. Sex ratio of harvested jaguars also had a considerable impact on the model outcome, with higher extinction probabilities when female mortality increased. Variations of age class of harvested animals had less impact on population dynamics. Our results suggest that due to hunting the jaguar population in the reserve can potentially act as a population sink, even in the absence of habitat loss or other threats. Long term data collection of numbers and sex of jaguars hunted as well as precise densities of jaguars are necessary to accurately model the impact of hunting on the viability of a jaguar population.
Key words: Amazonia; Jaguar; *Panthera onca*; Population Viability Analysis (PVA); VORTEX

Modelando el impacto por la cacería sobre la viabilidad de una población de jaguar en la Amazonía brasileña
Resumen
Con base en un análisis de viabilidad de poblaciones se analizó el impacto de la cacería en la población de jaguares en la Reserva Extractiva Tapajós-Arapiuns en el Amazonas brasileño. El modelo de población fue armado en VORTEX, usando registros bibliográficos e información estimada de la presión de caza en la reserva. Fueron modelados cinco escenarios para observar la importancia de: la capacidad de carga (K); la proporción sexual y la clase de edades de los individuos cazados, sobre la probabilidad de extinción, la diversidad genética; el crecimiento estocástico y la población existente después de 100 años. El parámetro más importante fue la capacidad de carga: la población tuvo elevada probabilidad de permanecer con alta diversidad genética cuando K=360, al cazar tres hembras y nueve machos por año, pero se extingue cuando K disminuyó a la mitad de su valor, siguiendo el mismo patrón de caza. La proporción sexual de los jaguares cazados también mostró un impacto en el modelo, indicando una alta probabilidad de extinción cuando incrementa la mortalidad de las hembras. La variación de las clases de edades en los animales cazados presentó menor impacto en la dinámica poblacional. Los resultados sugieren que debido a la cacería, la reserva puede contribuir en la declinación de la población del jaguar, inclusive con la ausencia de otras amenazas. Es necesario el registro de datos en una escala temporal larga sobre el número y el sexo de los individuos casados, así como también, precisar la densidad poblacional para obtener un modelo más preciso del impacto de la cacería en la viabilidad de la población.
Palabras Clave: Amazonas; Análisis de Viabilidad Poblacional (PVA), Jaguar; *Panthera onca*; VORTEX

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Introduction

Jaguars (*Panthera onca*) are considered Near Threatened by the IUCN Red List (Caso *et al.* 2008) and are declining across most of their range (Quigley & Crawshaw 1992, Zeller 2007). The main threats to jaguar are habitat loss and fragmentation, and hunting (Caso *et al.* 2008). Jaguars are hunted for reasons that include retaliation for livestock depredation, opportunistic killing, sport and commercial hunting, and fear (Zeller 2007).

The prevalence of hunting and its role as a main threat to jaguar is a well-recognized fact (Quigley & Crawshaw 1992, Altrichter *et al.* 2006, Zeller 2007, Carvalho-Jr & Pezzuti 2010), but the magnitude of poaching and its effects on population dynamics are poorly understood. Few quantitative estimates of hunting pressure on jaguars have been published (Smith 1976, Chetkiewicz & Raygorodetskt 1999, Michalski & Peres 2005, Carvalho-Jr & Pezzuti 2010), and the consequences of hunting on local population viability still needs to be addressed.

Population viability analysis (PVA) is an approach used to evaluate the probability of extinction or persistence of a population in a given period of time and under a series of assumptions regarding the biology of the species, the population being modeled, and the potential threats (Beissinger & Westphal 1998, Lindenmayer *et al.* 2003). PVA has been applied as a tool to estimate minimum viable populations, evaluate probability of species survival, as a guide to select management options, and even to model extinct populations (Brito & Figueiredo 2003, Reed *et al.* 2003, Wilkinson & O´Regan 2003, Leimgruber *et al.* 2008, Desbiez *et al.* 2009, Medici 2010).

In this study, VORTEX population viability analysis (Lacy 1993) was used to model the impacts of hunting on the jaguar population of an Amazonian extractive reserve where harvest has been quantified (Carvalho-Jr & Pezzuti 2010). This exercise was not intended to give accurate predictions, but rather to evaluate a range of alternative scenarios, and the relative importance of population parameters and harvest on model outcomes. Important parameters such as genetic diversity, population size and other threats were not considered for this exercise.

Materials and methods

Study area

Tapajós-Arapiuns is a 650,000 ha extractive reserve located at the western margin of the lower Tapajós river in central Amazonia (02°50'S, 55°25'W). The reserve is inhabited by c. 15,000 people, living in 70 villages and engaged in subsistence agriculture, fishing, hunting and extraction of forest resources (Carvalho-Jr & Pezzuti 2010). Vegetation cover is mostly undisturbed rainforest and the reserve is well-connected to other protected areas, forming a large continuous forest block. The area is home to a rich vertebrate fauna, including jaguar and many of its potential prey (Peres *et al.* 2003). Although jaguars are relatively common in the reserve, their population size is unknown. Carvalho-Jr & Pezzuti (2010) used data on population density from other area in the Amazon (c. 3.0 jaguars per 100 km^2, Silver *et al.* 2004) to estimate a population of c. 180 adult jaguars in the reserve, and data from interviews to estimate a minimum harvest of three females and nine male jaguars per year.

Methods

Baseline model

VORTEX is a Monte Carlo program that simulates the effects of deterministic forces, as well as demographic, environmental and genetic stochastic events on population dynamics (Lacy 1993, 2000, Miller & Lacy 2003). The program models population dynamics at the individual level, with discrete life-life cycle events such as breeding success, litter size and survival occurring after specified probabilities. Each run of the model gives a different result, and by running the model hundreds of times, it is possible to examine a range of probable outcomes. The program is not intended to give absolute answers, but rather to be used as a tool to explore different possibilities and the relative importance of different input parameters on the resulting population dynamics (Beissinger & Westphal 1998).

A general baseline model, built during the Jaguar National Action Plan Workshop held at Atibaia, São Paulo, Brazil in November 2009, was used as starting point to simulations (Desbiez *et al.* 2012). Input parameters for the model were defined after discussions with a group of jaguar experts, and were designed to reflect the biological potential of a non-existent, but biologically accurate, jaguar population. 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. For more details on the construction of the baseline model, including parameter definition, sensitivity analysis, and a list of participants of the input group see the workshop report (Paula *et al.* 2011).

Minor adjustments were made to the baseline model in order to simulate jaguar population dynamics specifically at Tapajós-Arapiuns Extractive Reserve (Table 1). Carrying capacity (K) was set as 360, based on the assumption that there are c. 180 adult jaguars in the reserve (Carvalho-Jr & Pezzuti 2010); adult density was multiplied by two because Vortex considers all the animals in the population, and population structure in the baseline model shows that half of the individuals in a jaguar population are adults. For the purpose of this exercise, and to be as conservative as possible, initial population size was considered to be equal to K. Breeding was considered to be density-independent, since the reserve is well connected (Nepstad *et al.* 2006). Also for the purpose of this exercise we used a stable population with good genetic diversity. Population dynamics was modeled for 100 years, running 1000 independent iterations for each alternative scenario.

Harvest scenarios

After running the baseline model, a series of alternative scenarios were run in order to explore the potential impacts of hunting. The annual harvest of three females and nine male jaguars reported by Carvalho-Jr & Pezzuti (2010) was added to the model. Then, the values of sex ratio and age class of harvested individuals were manipulated, as well as K, in order to explore the relative importance of these parameters in the model outcome. For the purpose of this exercise, no other threats were added to the model, even though disease, drought, prey losses, habitat loss and other threats could impact the population. Four alternatives to the baseline model were run (Table 2) and the relative importance of each parameter on probability of extinction (PE), genetic diversity (GD), stochastic population growth and average number of jaguars left in the population was evaluated.

Table 1. Summary of parameter input values in the baseline model for MVP analyzes of jaguar in Brazilian Amazonia.

Parameter	Baseline value
Number of populations	1
Initial population size	360
Carrying capacity	360
Inbreeding depression	6 LE
% of the effect of inbreeding due to recessive lethal alleles	50
Breeding system	Poligyny
Age of first reproduction (♀ / ♂)	3 / 4
Maximum age of reproduction	15
Annual % adult females reproducing (SD)	50% (5)
Average litter size	2
Density-dependent reproduction?	NO
Maximum litter size	4
Overall offspring sex ratio	50:50
% adult males in breeding pool	90
% mortality in age 0-1 (EV)(♀ / ♂)	42(7) / 42(7)
% mortality in age 1-2 (EV)(♀ / ♂)	17(3.5) / 17(3.5)
% mortality in age 2-3 (EV)(♀ / ♂)	20(5) / 20(5)
% mortality in age 3-4 (EV)(♀ / ♂)	6(1.5) / 25(6)
% mortality in age 4-10 (EV)(♀ / ♂)	8(1.5) / 10(2)
% mortality in age 10-15 (EV)(♀ / ♂)	Function increasing mort. by 5 % each year

Table 2. Vortex simulation results for the jaguar population in Tapajós-Arapiuns Extractive Reserve in five alternative scenarios, Brazilian Amazonia. (PE: Probability of Extinction, GD: Genetic Diversity, SPG: Stochastic Population Growth, ANJLP: Average Number of Jaguars Lefts in the Population)

Model	PE	GD (%)	SPG (SD)	ANJLP
K= 360, No threats	0	96.0	0.051 (0.077)	351
K= 360, Harvest 3 ♀ and 9 ♂	0	95.0	0.033 (0.083)	335
K= 360, Harvest 1 adult and 2 sub-adult ♀, 4 adult and 5 sub-adult ♂	0	95.1	0.035 (0.082)	339
K= 180, Harvest 3 ♀ and 9 ♂	1	0.0	-0.025 (0.145)	0
K= 360, Harvest 9 ♀ and 3 ♂	0.98	95.0	-0.043 (0.120)	4

Results and discussion

If there is no hunting and no other threats or environmental factors affecting the jaguar population in 100 years, when K=360, the population has a very high probability to persist with high genetic diversity (Figure 1a, Table 2). The relatively high stochastic growth-rate shows that the population will grow whenever it is below the carrying capacity. Although unrealistic in assuming no threats, this model serves as a best-case scenario, reflecting the biological potential of the jaguar population in the reserve, and provides a basis for comparison with the harvest models that follow.

Adding the estimated minimum annual harvest of three adult females and nine adult males for 100 years to the baseline model, the probability of extinction is not considerably increased neither genetic diversity decreases, but it does decrease stochastic population growth rates and increases its standard deviation (Figure 1b, Table 2). This means that, although the population is unlikely to become extinct because of harvesting, it would experience more difficulties in recovering from other additional threats due to this hunting pressure than it would without it. As previously noted, this is a conservative result. Further studies are needed to assess if the situation is more drastic, for example, if there is some degree of isolation or if real genetic diversity is lower (e.g., Haag *et al*. 2010).

Results were essentially the same when the annual harvest was partitioned between adults and sub-adults, when K=360 (Table 2). This was somewhat expected, because the sensitivity analysis of the general baseline model had previously showed that increases in mortality of adults or sub-adults had essentially the same impact in the population stochastic growth rate (Paula *et al*. 2011). A major consequence of this fact is that knowledge of age category of hunted animals is not a critical piece of data for the outcome: the model is robust to data deviations on age-class of harvested animals. This is convenient for the purposes of this research, because this type of data is difficult to be obtained (Carvalho-Jr & Pezzuti 2010). For the rest of the modeling, only harvest of adult jaguars will be considered, because stochastic population growth rate was slightly lower when more adults were harvested than sub-adults.

When the carrying capacity in the baseline model was cut to 180, keeping the harvest of three females and nine males in 100 years, the population becomes very susceptible to extinction (Figure 1c, Table 2). However, since the reserve is well connected, this actually means that the population of Tapajós-Arapiuns would represent a population sink for jaguars in the region. It is possible that the baseline carrying capacity estimate of 360 jaguars in the reserve may be too optimistic, since human population in the reserve is considerably high, and K may have been reduced because of habitat loss and depletion of the prey-base caused by subsistence hunting. In this case, the real population size for the reserve may be somewhere between 180 and 360.

Inverting the proportion of hunted jaguars to nine females and three males annually for 100 years in a population of 360 animals, results in a very high probability of population extinction, with the population in the reserve acting as sink (Figure 1d, Table 2). Most importantly, a higher female mortality greatly decreases the stochastic population growth, with the consequence that jaguar population will have difficulties recovering from additional threats which were not modeled in this exercise.

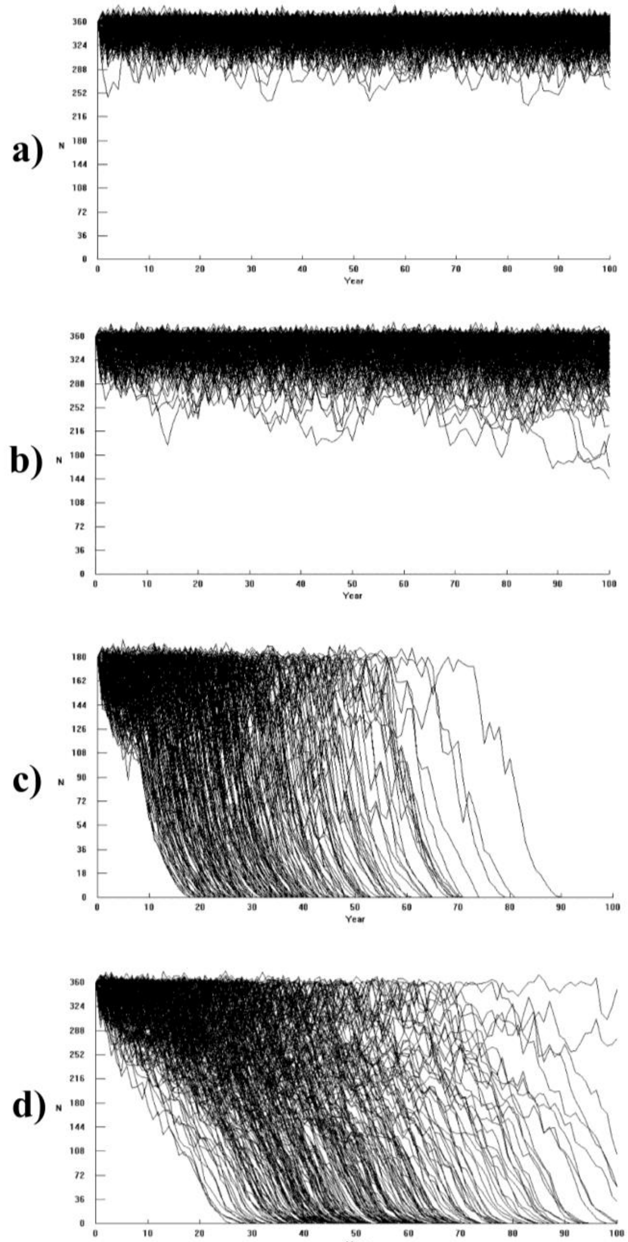

Figure 2. Vortex simulation output for the jaguar population in Tapajós-Arapiuns Extractive Reserve, showing the dynamics of 1000 simulated populations over 100 years, in four different scenarios. The x-axis represents time (in years) and the y-axis represents jaguar population size, where (a) baseline model with N=360; K=360 and no threats; (b) N=360; K=360 and harvest of 9 males and 3 females; (c) N=180; K=180 and harvest of 9 males and 3 females; (d) N=360; K=360 and harvest of 3 males and 9 females.

Since sex ratio of harvested jaguars has such a large impact in the outcome of the model, it is crucial to have reliable data on the sex of harvested jaguars. Although it may be possible that the male-biased sex ratio of hunted jaguars in the reserve (Carvalho-Jr & Pezzuti 2010) was an artifact of the short-term data collection, it should be noted that a higher male mortality is expected, since males are bolder and more prone to use human-modified landscapes such as low-intensity agriculture, cattle lands and roads (Rabinowitz 1986, Conde *et al.* 2010). Furthermore, other studies investigating jaguar hunting in Amazonia have also reported male-biased mortality (Chetkiewicz & Raygorodetsky 1999, Ramalho 2012). However, since these studies provide only a snapshot of the harvest, it would be interesting to conduct further investigations on trends in sex ratios and age structures of harvested animals, and possible effects of these trends on population dynamics. This exercise does highlight the importance of long term data collection to estimate accurate numbers and sex ratios of hunted jaguars.

Conclusions

VORTEX models the impact of stochastic variation, and cannot give absolute answers. This is particularly true for this study, since we do not have local estimations of population size and on the distribution of growth and vital rates, such as survival and fecundity, in the reserve (Coulson *et al.* 2001). However, if treated with caution, modeling can serve as a guide for conservation and management. This study points to the possibility that the jaguar population in the Tapajós-Arapiuns Extractive Reserve may act as a sink, even in the absence of habitat loss or other threats. Furthermore, even if hunting does not cause the extinction of the jaguar population in the reserve, it may decrease the population growth rate, making the population more vulnerable to other threats not considered in this model. Considering that some scenarios involve risks for the future of jaguar conservation in the reserve, it is advisable to take safeguard actions. A survey to estimate the actual jaguar population size and identify population structure in the area is recommended, as well as the adoption of measures to reduce jaguar hunting, such as the enforcement of existing laws regarding wildlife use in the reserve, education aiming to a more tolerant attitude of people towards carnivores (Conforti & Azevedo 2003), and extensive work that includes measures to decrease livestock depredation by large cats (Hoogesteijn 2004).

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