



### A vortex population viability analysis model for the Chacoan peccary (*Catagonus wagneri*)

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#### Introduction

From February 29th to March 3rd 2016, a range wide, multi-stakeholder species conservation planning workshop took place for the Chacoan peccary (*Catagonus wagneri*) in Asuncion, Paraguay. Details on the status of the Chacoan peccary, the workshop and its outcomes can be found in Altrichter et al. elsewhere in this Volume of Suiform Soundings. This paper focusses on the use of the population viability analysis software "Vortex" (Lacy and Pollak, 2015) as an integral component of the workshop.

Populations of threatened species face a multitude of threats. Often, human-caused threats cause populations to become small and fragmented. At this stage, stochastic threats, including genetic (genetic drift and inbreeding) and demographic (environmental variation, demographic variation and catastrophes) threats, automatically come into play as well. They feedback on each other and may lead the population to enter an extinction vortex, even if human-caused threats can be halted or reversed (Gilpin and Soulé, 1986). Conservation strategies thus need to evaluate how severe the chance of continued decline or extinction may be for a given set of circumstances, and which conservation measures addressing which threats, are likely to have the best chances to pull the species out of the "extinction vortex" and achieve a viable population for the future. Vortex is particularly suited to explore how these complex and interacting factors influence survival probabilities, as well as the demographic and genetic status, of small, wild and/or captive populations of threatened vertebrate species. This is because it is an agent or individual-based model that also incorporates environmental, demographic and genetic stochasticity – the effects of which become increasingly magnified in small populations (Lacy et al., 2015).

Depending on the type, amount and reliability of quantitative data available on the life history of the species and the threats it is facing, the Vortex model can be used for different purposes







(Miller, 2007), including: Simulating the effect of particular human-caused threats or particular management scenarios for a given population; testing thresholds for threat effects; prioritising data collection on threats; investigating likely relative changes in the face of different threats or management options; evaluating the likely viability in the absence of human caused threats; identifying priorities for research in basic natural history parameters; and demonstrating the general risk inherent to small populations to people without population management knowledge; among others.

Only a limited amount of data on life history parameters, population sizes, quantitative population trends and quantitative effects of threats exists for Chacoan peccaries. The aims of this Vortex simulation model were to:

- Create a baseline model for a non-threatened population of Chacoan peccaries based on the current best estimates for the various model parameters,
- Examine the scale of change in the results of the model when using minimum and maximum values around the baseline values in order to test the model's sensitivity to the uncertainty (and thus suggest priorities for research),
- Investigate minimum viable population sizes within the spread of uncertainty, and
- Run a first preliminary simulation of the potential effects of hunting on a population of this species.

#### Materials and methods

Vortex Simulation Model

We used the simulation software program Vortex (v10.1.5.0) (Lacy and Pollak, 2015) (www.vortex10.org) version 10.1.5.0 to conduct our predictive analyses. It is a Monte Carlo simulation of the effects of deterministic forces as well as demographic, environmental, and genetic stochastic events on wild or captive small populations. Vortex models population dynamics as discrete sequential events that occur according to defined probabilities. The program begins by either creating individuals to form the starting population, or importing individuals with a known pedigree from a studbook database, and then sequentially progressing through life cycle events (e.g., births, deaths, dispersal, catastrophic events), typically on an annual basis. Events such as breeding success, litter size, sex at birth, and survival are determined based upon designated probabilities that incorporate annual environmental variation, demographic stochasticity and catastrophes. Inbreeding depression is modelled as a reduction in first year survival of inbred individuals and Vortex simulates Mendelian transmission of alleles. 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 a more detailed explanation of Vortex and its use in Population Viability Analysis, see Lacy (1993, 2000), Brook et al. (2000) and Lacy et al. (2015).

#### Model input parameters

The input parameters were jointly developed during the conservation planning workshop by taking into account published literature (where available), information provided in advance of the workshop (by the authors of this paper and Ricardo Torres and Verónica Quiroga), and unpublished data and personal experiences from other workshop participants. The baseline







scenario created intends to represent a Chacoan peccary population not affected by humancaused threats, and a full overview of all the input parameters used can be found in Table 2. A detailed justification for the choice of input parameters can be found in the modeling chapter of the workshop report (Altrichter et. al, in prep) that will soon be available at www.cbsg.org, but below follows a summary for some of the important parameters.

### Inbreeding

Because no information is available on the presence or absence of inbreeding depression in Chacoan peccary populations, how it might manifest, or how many lethal equivalents are present per diploid individual, the default settings for inbreeding depression were included in the Vortex model with 6.29 Lethal Equivalents per diploid individual (based on O'Grady et al. (2006), and 50% of the genetic load due to recessive lethal alleles.

### Reproductive parameters

The Vortex mating system option that most closely describes that of the Chacoan peccary is "long-term polygyny", which implies that one male may breed with more than one female, and selected pairings will stay together for subsequent years until one partner dies. Wild Chacoan peccaries appear to live in small family groups (see section on 'maximum number of female mates' below), and both polygynandry (Brooks, 1992, 1996) and polygyny are thought to be possible breeding systems. It is also thought that pair bonds likely last for more than one year (Taber et al., 1993; Campos, pers. comm.).

We set the age of first reproduction to "1"for both males and females. Chacoan peccaries in captivity appear to be able to have their first litter between their first and second birthday (Brooks, 1992; Campos pers. comm, Meritt et al., 2014; Yahnke et al., 1997), and we considered this was equally possible in the wild. We also assumed wild Chacoan peccaries are able to breed for their entire lifespan and, adjusting data from captivity (see Meritt et al., 2014; Altrichter et al., 2015), workshop participants believed that a lifespan of 15 years for both males and females would be possible for wild peccaries. However, we also tested a minimum value of 10. All the three extant species of peccary appear to reproduce once per year in the Paraguayan and Bolivian Chaco (Taber et al., 1993; Noss, 1999; Noss et al., 2003). Combining various reports on litter sizes from the wild (Mayer and Brandt, 1982; Taber et al., 1993; Altrichter, 2005) and captivity (Yahnke et al., 1997; Brooks, 1992; Unger 1993; Meritt et al., 2014; Campos, pers. comm), we used the baseline, minimum and maximum litter size distributions reported in Table 2. Based on information from captivity, an equal sex ratio at birth was also assumed for the wild (Yahnke et al., 1997).

The percentage of adult females breeding every year was difficult to determine, as pregnancy data from wild populations usually take the form of % hunted females pregnant for Chacoan peccaries (Altrichter, 2005), collared (Pecari tajacu) (Hellgren et al., 1995; Bodmer, 1989; Gottdenker and Bodmer, 1998; Mayor et al., 2005; Noss et al., 2003; Jorgenson, 2000), and white-lipped peccaries (Tayassu pecari) (Bodmer, 1989; Gottdenker and Bodmer, 1998; Noss et al., 2003). Pregnancy rates among hunted females per year does not necessarily equate to % breeding females per year because, a) although Chacoan peccaries do reproduce year round, there is also a seasonal peak in reproduction during certain months (Taber et al., 1993; Yahnke et







al., 1997; Sowls, 1997; Altrichter, 2005) the possibility that early pregnancies may be underreported (Mayor et al., 2005) c) there must be no preferential hunting of pregnant or non-pregnant females, and d), pregnancy lasts for only about 41% of the year. In addition, we found a rate of 86% females breeding per year for white-lipped peccaries in the Peruvian amazon (Mayor et al., 2005; Mayor pers. comm.). In considering a) the drier conditions in the Chaco, and b) a lower rate of pregnancies detected among harvested females for Chacoan peccaries (20%) (Altrichter, 2005), workshop participants felt it prudent to adopt a conservative value estimate of 50% breeding females as a baseline, while also testing a minimum of 40%, and a maximum of 70%. The actual input in Vortex was then adjusted so the % of females breeding per year is halved in years when "catastrophe 1" hits (see catastrophe section below).

There is no information on the percentage of males in the breeding pool for wild Chacoan peccaries. Participants in the workshop agreed on a rate of 100 % for males that are 3 years and older, and 50% for males between 1 and 3 years, as this latter grouping of males although physically able to breed they are perhaps socially less likely to obtain access to females. Similarly, there is no data on the maximum number of female mates per male. Chacoan peccaries appear to live in smallish family groups with ranges of about 1 to 9, averaging between 2.6 and 4.5 (Altrichter, 2005; Maffei et al., 2008; Taber et al., 1993; Mayer and Brandt, 1982; Sowls, 1997). Breeding males would thus have access to a limited number of breeding females, therefore, participants of the workshop agreed to limit the "maximum number of female mates" per breeding male to 3 for the baseline scenario, while also testing a minimum number of 2 and a maximum of 5.

### Mortality parameters

There is no data on age specific mortality rates of wild Chacoan peccaries. Based on information from wild collared peccaries (Day, 1985; Hellgren et al., 1995; Gabor and Hellgren, 2000; Hellgren et al., 1995), wild white-lipped peccaries (Fuller et al., 2002) and captive Chacoan peccaries (Yahnke et al., 1997, Meritt et al., 2014, Campos pers. comm.) workshop participants suggested the following baseline, minimum, and maximum values as their best guess:

First year mortality: baseline 55%, min 40%, max 65% Adult mortality: baseline 10%, min 8%, max 13%

The actual input into Vortex was then adjusted as in Table 2 so that mortality rates increase in years when catastrophes hit (see catastrophe section below).

### Catastrophes

A catastrophe is defined as an event that happens very infrequently (e.g. only a few times per 100 years) and lasts a short time. However when it happens, it has a large negative effect on reproduction and/or survival of the species that is much larger than normal environmental variation — e.g., drought, fire, disease, civil war, etc. Possible catastrophes for Chacoan peccaries include disease (Altrichter, pers. comm.; Brooks, pers. comm.; Taber, 1991; Toone and Wallace, 2002), drought (Altrichter, pers. comm.; Giordano, pers. comm.) and fire (Altrichter, pers. comm.; Giordano, pers. comm.). Because there was no quantitative data on catastrophes, and because it is very unlikely that a given wild population will be spared from catastrophes (Reed et







al., 2003), it was agreed to incorporate two 'theoretical' catastrophes into the model – drought and disease. According to participants, a drought on average can be expected about every 13 years, and last around 2 years. According to the same participants, epidemic diseases might occur once every 100 years and last only a year. The frequency and effect on the population was entered as follows:

Tab 1. Values for frequency, duration and impact of catastrophes on Chacoan peccaries used for the Vortex model.

	Freq.	Duration	1 <sup>st</sup> Year Mortality	Adult Mortality	% Females breeding
Catastrophe 1 Drought	7.7%	2 years	20% increase	10% increase	50% decrease
Catastrophe 2 Disease	1%	1 year	50% increase	30% increase	50% decrease

Because a drought can be expected to last two years, the effect on mortality of catastrophes 1 and 2 was modelled by entering formulas in the fields for mortality, and the % females breeding in Vortex (see Table 2). For catastrophe 2. the effect on reproduction was modelled by entering 0.5 in the severity field for

catastrophe 2. Because there is a 7.7% risk every year of the onset of a 2-year drought regardless of whether or not a drought began the year before, there is a chance droughts might "piggyback" and last 3 years. There is an even smaller chance that another one might hit in year 3 thus making it a 4 year drought, etc. This is not unlike reality, where some droughts can last longer.

For the baseline scenario, the effects of the catastrophes can thus be summarized using the following functions to represent the impacts described above (Table 1):

1st Year Mortality = 55; 66; 82.5; 93.5% in the case of no Cat, Cat1, Cat2, and Cat1&2, respectively Adult Mortality = 10; 11; 13; 14% in the case of no Cat, Cat1, Cat2, and Cat1&2, respectively % Females Breeding = 50; 25; 25; or 12.5% in the case of no Cat, Cat1, Cat2, and Cat1&2, respectively

Tab. 2. Summary of Vortex model input parameters

	Minimum	Baseline	Maximum
Number of	/	500	/
iterations			
Number of years	/	100 (or ~19	/
		generations)	
Inbreeding	/	6.29 LE/50% due to	1
depression		recessive lethal alleles	
Mating system	1	Long term polygyny	/
Age first	1	1	1
breeding F&M			
Max age	10	15	1
reproduction			
Longevity	10	15	1
Sex ratio at birth	1	50	1
Max	/	1	/
#litters./year			
Litter size	(1)25%; (2)65%;	(1)18%; (2)63%;	(1)10.2%; (2)40%;
distribution	(3)10%; (4)0%	(3)16%; (4)3%	(3)43.8%; (4)3.8%
% Adult females	40-(20*(CAT(1)<2))	50-(25*(CAT(1)<2))	70-(35*(CAT(1)<2))
breeding			
% Males in	/	100-(50*(A<3))	/
breeding pool			
Max nr	2	3	5
mates/male			
1st yr Mortality	40+(8*(CAT(1)<2))	55+(11*(CAT(1)<2))	65+(13*(CAT(1)<2))
	+(20*(CAT(2)<1))	+(27,5*(CAT(2)<1))	+(32,5*(CAT(2)<1))
Adult Mortality	8+(0,8*(CAT(1)<2))	10+(1*(CAT(1)<2))	13+(1,3*(CAT(1)<2))
	+(2,4*(CAT(2)<1))	+(3*(CAT(2)<1))	+(3,9*(CAT(2)<1))







#### Results

#### Deterministic models

For deterministic projections, Vortex performs standard lifetable calculations assuming that agespecific birth and death rates are constant through time (i.e., no stochastic fluctuations); no inbreeding depression, harvest, or supplementations are included. The limitation of female mates was set to "0", and catastrophes were not incorporated. The baseline scenario for this resulted in:

Yearly growth rate (r)	0.1142
Yearly growth rate (lambda)	1.1210
Generational growth rate (R0)	1.8225
Generation time:	5.26
Proportion of individuals in age class 15:	0.003

No census based growth rates for wild Chacoan peccary populations exist that can be used for validation purposes. The only conclusion from the results of this projection is that it is not unrealistic for a species with these natural history characteristics to exhibit a deterministic growth rate of 0.1142 (or 11.4% growth per year). Because this calculation did not account for stochastic fluctuations, inbreeding depression, or the effect of catastrophes, this growth rate is an overestimation under stochastic circumstances. However, it is still useful to that the input values do not cause a deterministic decline, or a growth rate that is unrealistic for the general natural history characteristics of the species.

### Stochastic model and sensitivity testing

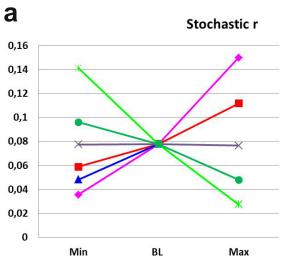
Using a theoretical population with an initial size and carrying capacity of 500 individuals, stochastic projections of the baseline scenario resulted in a zero probability of extinction, a stochastic growth rate (r) of 0.0778 (SD 0,1104), a retention of gene diversity of 96.13% (SD 0,61) and an average population size of 478.96 (SD 41.23) after 100 years

Figures 1 a-c below demonstrates the variability present among the minimum, baseline or maximum values are input into the Vortex model. The uncertainty in the % of female breeding and the 1st year mortality have the biggest influence on the population's stochastic growth rate (r), whereas uncertainty in the maximum number of female mates for breeding males has almost no effect on "r". Longevity, which in the case of the Chacoan peccary is thought to equate to the maximum breeding age, unsurprisingly has the biggest effect on the proportion of gene diversity retained; this is because it influences generation time, one of the important parameters driving the amount of genetic diversity that can be retained for a given amount of time. Uncertainty in 1st year mortality caused the second biggest difference in the proportion of gene diversity retained. First year mortality also had the largest effect on the average population size at the end of 100 years, followed by longevity, percentage of adult females breeding, and adult mortality. Since there is doubt regarding these key parameters, confidence in the model will increase as more reliable data to estimate these parameters becomes available. These parameters, i.e., the % female breeding and the 1st year mortality, should become priority research questions for the future.

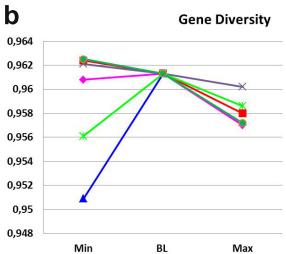












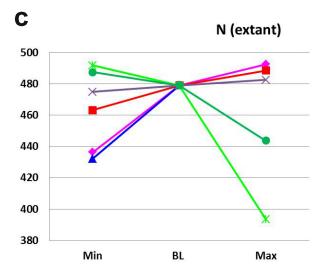


Fig.1 a-c: Sensitivity of the stochastic growth rate (r) to (a), proportion of gene diversity retained, (b) mean size of extant populations after 100 years of simulation (N(extant)), and (c), variations in % breeding females (min 40, baseline 50, max 70), litter size (min 1.85, baseline 2.04, max 2.37), longevity/max breeding age (min 10, baseline 15), maximum number of female mates for adult males (min 2, baseline 3, max 5), 1st year mortality (min 40, baseline 55, max 65), and adult mortality (min 8, baseline 10, max 13).

### Minimum Viable Population Size

The full range of uncertainty for input parameters was tested (Table 3) to obtain an initial idea of scale for a minimum viable population of the Chacoan peccaries in the absence of human caused threats. For these analyses, we defined "viable" as a population that is able to retain a minimum of 98% gene diversity after 100 years with a zero probability of extinction.

Tab. 3. Minimum population size required in the absence of human caused threats to achieve zero probability of extinction and a minimum of 98% retention of gene diversity after 100 years: under minimum, baseline, or maximum input values for % breeding females (min 40, baseline 50, max 70), litter size (min 1.85, baseline 2.04, max 2.37), longevity/max breeding age (min 10, baseline 15), maximum number of female mates for adult males (min 2, baseline 3, max 5), 1st year mortality (min 40, baseline 55, max 65) and adult mortality (min 8, baseline 10, max 13).

Scenario	Minimum population size needed IN THE ABSENCE OF HUMAN CAUSED THREATS (tested in steps of 100 individuals)			
	Minimum	Baseline	Maximum	
%Females breeding	1000	1000	1100	
Litter size	1000	1000	1100	
Longevity	1300	1000	/	
Max # mates/male	1000	1000	1100	
1 <sup>st</sup> year mortality	1200	1000	1100	
Adult mortality	1000	1000	1100	







Under the most optimistic scenarios, a population of at least 1000 Chacoan peccaries is required for a minimum viable population, in the absence of human caused threats; under the most pessimistic scenario, a minimum of 1300 is needed with no human-caused threats. For current levels of uncertainty, we would be wise to be conservative and treat these numbers as an index of scale, rather than absolute results. We should also underscore that these results assume a peccary population experiencing genetic and demographic stochasticity, including inbreeding depression and catastrophes, but no human-caused threats such as hunting, habitat loss, etc. To be clear, even protected areas frequently experience some low levels of anthropogenic threats.

### Effect of Hunting

Altrichter (2005) studied the hunting of all three peccary species in a 1.2 million hectares area of the semi-arid Argentine Chaco called Impenetrable, located in western Chaco Province of Argentina. She estimated that 870 Chacoan peccaries were hunted per year. During the workshop, we estimated this area to contain about 1 million ha of habitat for the Chacoan peccary. Ages of harvested individuals were fairly evenly distributed with one exception: fewer old animals were being harvested, not unexpected given that fewer animals were present in that age class. For the model, we applied the same rate of mortality to both 1st year individuals, and adults of both sexes. The density of peccaries in non-hunted sites was found to be 0.44 individuals/ km² (Altrichter, 2005). In applying this to a potential area of occurrence of 1 million ha, it suggests a starting population size of 4400 individuals; 870 peccaries is 20% of 4000 individuals.

Hunting was incorporated into the baseline model, and the increased mortality due to hunting was entered in the mortality fields rather than the harvest section because 0-1 year old individuals were also harvested. We used the following formulae:

Juveniles: =(55+(11\*(CAT(1)<2))+(27,5\*(CAT(2)<1)))+9Adults: =(10+(1\*(CAT(1)<2))+(3\*(CAT(2)<1)))+18

If we assume that without hunting, 1st year mortality is approximately 55%, then hunters kill 20% x 45% = 9% of those that otherwise would have lived, resulting in a total first year mortality of 64%. The above formula also accounts for higher natural mortality in catastrophe years; using the similar reasoning, we did the same for adults. We modeled harvest rates of 10% and 5% respectively by adjusting the formulas accordingly.

In addition, because of the current level of uncertainty with regard to both lifehistory parameters for the Chacoan peccary, and quantitative measures of hunting pressure,

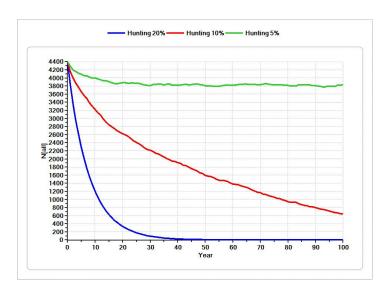


Fig. 2. Average size of all populations (N(all) – including those that went extinct) over time for the baselines scenario with 20% (blue), 10% (red) or 5% hunting (green).







different hunting rates were tested with the minimum and maximum values for those parameters that caused the biggest fluctuations in model results: % breeding females; longevity; first year mortality; and adult mortality. Baseline parameters, 20% and 10% of hunting (as it was entered into the model), were not considered sustainable, whereas 5% was (Fig. 2).

When we tested the effect of uncertainty of input values for % breeding females, 1st year mortality, longevity (maximum breeding age) and adult mortality, we determined that 20% hunting was unsustainable for all input values (Fig. 3), 10% hunting became sustainable only with the maximum entry for % breeding females (70%) and the minimum entry for 1st year mortality (Fig. 4), and 5% hunting was sustainable only under baseline conditions, the maximum entry for % breeding females (70%), the minimum entry for 1st year mortality and the minimum entry for adult mortality (Fig. 5).

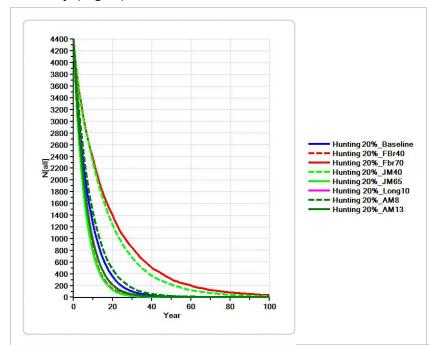


Fig. 3. Average size of all populations (N(all) – including those that went extinct) over time for 20% hunting, with the baselines scenario, and under minimum or maximum input values for % breeding females (min 40, max 70), 1st year mortality (min 40, max 65), longevity/Max breeding age (min 10), and adult mortality (min 8, max 13).

Fig. 4. Average size of all populations (N(all) – including those that went extinct) over time for 10% hunting, with the baselines scenario, and under minimum or maximum input values for % breeding females (min 40, max 70), 1st Year mortality (min 40, max 65), longevity/max breeding age (min 10), and adult mortality (min 8, max 13).

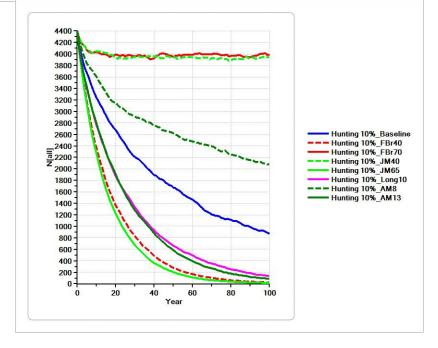
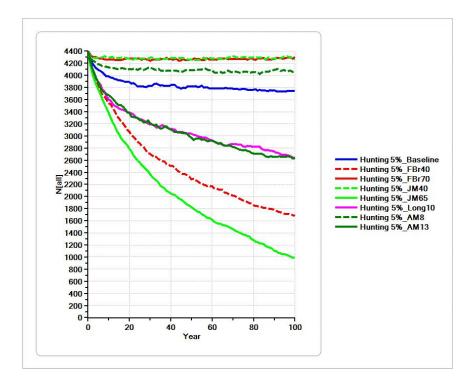








Fig. 5. Average size of all populations (N(all) – including those that went extinct) over time for 5% hunting, with the baselines scenario, and under minimum or maximum input values for % breeding females (min 40, max 70), 1st year mortality (min 40, max 65), longevity/max breeding age (min 10), and adult mortality (min 8, max 13).



#### **Discussion and Conclusions**

The uncertainty in life history parameters, and particularly the % of breeding females, 1st year mortality, longevity/maximum age of breeding and adult mortality, can all cause considerable variation in model outcomes. Learning more about these parameters through field research should be considered one of the biggest research priorities for the Chacoan peccary.

Given current levels of uncertainty, it is not possible to make confident predictions regarding the viability, sensitivity to threats, or effects of hypothetical management scenarions, for a specific Chacoan peccary population. However, by testing the full range of possible input parameters, we obtained our first estimate of the parameters impacting population viability of Chacoan peccaries. As further information on these most important life history parameters become available, these estiamtes should be refined in consecutive Population Viabiliaty Analyses.

Having tested a full spectrum of uncertainty using reasonable parameters, the most pessimistic of these scenarios suggests that in the absence of human-caused threats, a population of at least 1300 Chacoan peccaries would be required to maintain 98% of gene diversity after 100 years to achieve a zero probability of extinction. Under the current levels of uncertainty, and keeping in mind that these results assume a peccary population that experiences no human caused threats, the precautionary principle should apply here, and these numbers should merely indicate scale and magnitude, and not be treated as absolutes. The new vision statement for the Chacoan peccary as defined during the workshop calls for the maintenance of viable populations in contiguous habitat across the distribution of the species. The scale suggested by the Vortex model of minimum viable population size (upwards of 1300 – perhaps 1500-2000) can be of assistance in determining priority areas for conservation. Given a declining current population (Altrichter et al., 2015) in rapidly disappearing habitat, perhaps it may be possible to retain or establish 2- 3 viable and connected populations. However it appears that almost all populations, even in the most remote areas, are subject to some level of human threat, especially







deforestation and fragmentation (Ferraz et al. this issue). Aditionally, as the interaction between fragmentation, climate change/ drought, and disease intensifies, it might be necessary to consider more frequent "catastrophes" in future analyses incorporating more complex models.

Finally, uncertainty regarding life history parameters, population densities, and quantitative measures of hunting pressure on the Chacoan peccary prevent us from making confident predictions on the current impact hunting is having on populations, or the hunting intensity that a population of a given size is able to withstand. If we assume hunting was indeed 20% in the population we studied, and if the way it is currently modelled accurately reflects what has been occurring in real life, it appears that this is unsustainable, regardless of the uncertainty in life history parameters. Altrichter (2005), in using the Unified Harvest Model and the estimated density data to evaluate the sustainability of the harvest of Chaocan peccaries in the Argentine Chaco, concluded that Chacoan peccaries were overharvested, but deemed sustainable when density and reproduction data from the literature were used in the harvest model. Altrichter (2005) reported hunting rates from the year 2000. If these rates had continued to the present day, our Vortex model would suggest a population crash to very low numbers, however current data on population estimates do not reflect this crash. In fact, hunting has significantly decreased since 2000 in the Argentine Chaco in part due to government programmes promoting alternative sources of food for local people, as well as to changes in the main livelihoods of local people (Camino et al., 2015). There are no recent data regarding hunting levels, but participants at the workshop felt hunting pressure may well have halved since then. As hunting activity and the need for wild protein among local people varies following larger economic changes (Altrichter, 2006), one cannot expect hunting pressure to remain low. Strict enforcement of regulations, as well as participatory research involving local people, are needed to eliminate hunting completely, or at least maintain it at minimum levels.

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