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Management implications of capybara (*Hydrochoerus hydrochaeris*) social behavior

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ABSTRACT

Capybaras (*Hydrochoerus hydrochaeris*) are the world's largest rodent. Free-living populations are commercially harvested for their meat and leather in Colombia, Venezuela and Argentina; however, there is concern that legal and illegal harvesting is not sustainable. Since capybaras are considered an economic resource, there have been several attempts to explore the effect of different hunting strategies on its population dynamics. Two previous population models have been developed with this goal; however neither included capybara social behavior that may affect population dynamics. We developed an age-structured, density-dependent model of capybara herd dynamics to explore the demographic consequences of different hunting strategies. We then added infanticide and female reproductive suppression to explore the demographic consequences of such behavior. We conducted five different simulations and used ANOVA to estimate the effect of hunting females, hunting males, hunting both males and females, and the independent effects of reproductive suppression and infanticide on population size after 50 years. Our model suggests that suppression has the largest effect on population size, followed by hunting females and males hunting, female hunting, male hunting and infanticide. Thus, to develop more realistic harvesting models, managers should determine the degree of reproductive suppression and the frequency of infanticide by males.

1. Introduction

Capybaras (*Hydrochoerus hydrochaeris*) are the world's largest rodent, ranging from Panama through the eastern savannas of Colombia, Venezuela, Brazil, Ecuador, Peru, Paraguay and Uruguay to northern Argentina (Ojasti, 1973; Azcarate, 1980; Mones and Ojasti, 1986). Free-living populations are commercially harvested for their meat and leather in Colombia, Venezuela and Argentina (Ojasti, 1991). Even though capybaras are rodents and have high reproductive rates, there is concern that legal and illegal harvesting is not sustainable (Ojasti, 1991). There have been several studies of capybara population dynamics (Ojasti, 1973; Macdonald, 1981; Jorgenson, 1986), and two demographic models have been developed and used to evaluate the impact of hunting on population dynamics (Federico and Canziani, 2005; Mesa, 2005). However, capybaras are highly social and these previous models have not integrated possible demographic consequences of sociality. Social behavior may be affected by management decisions and behavior may influence demography and population dynamics via a number of mechanisms (Greene et al., 1998; Macdonald et al., 2007). Such mechanisms are related to the intense reproductive competition acting within both males and females that character-

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izes highly social species (Blumstein and Armitage, 1998; Anthony and Blumstein, 2000).

We suggest two mechanisms by which capybara sociality may influence demography. One mechanism is infanticide by males where males may kill un-related young when they take over a group (Anthony and Blumstein, 2000; Ebensperger and Blumstein, 2007). Infanticide by males (i.e., sexually-selected infanticide) is an ancestral trait in muroid and sciurid rodents and it is hypothesized to have evolved as a foraging function and later exapted into other functions (Blumstein, 2000). Infanticide also has been considered an adaptive behavior (Hausfater, 1984) that is expected to induce premature estrous in females, thereby reducing the inter-birth period of the affected females (Swenson, 2003). Infanticide mainly affects the population size by decreasing the survival rate of infants and reducing juvenile recruitment (Anthony and Blumstein, 2000). Sexually-selected infanticide has been documented in a variety of carnivores (e.g., bears (*Ursus arctos*) and lions (*Panthera leo*)–Swenson, 2003), non-human primates (e.g., languars (*Presbytis entellus*)–Sommer, 1987 and chimpanzees (*Pan troglodytes*)–Sakamaki et al., 2001), and many rodents (Ebensperger and Blumstein, 2007), including a recent report in capybara (E. Congdon, pers. comm.).

The second mechanism we explore is female density-dependent reproductive suppression whereby potentially fertile females do not breed (Solomon and French, 1997). Reproductive suppression is widely reported in social animals, including rodents (Solomon and French, 1997) and is often associated with cooperative breeding, where reproduction is not equally distributed among group members (Hacklander et al., 2003). If females living closely with others compete reproductively, then not all females breed or litter sizes are reduced. Additionally, more social rodents seem to invest more in fewer young (Blumstein and Armitage, 1998). In either case, the number of young produced in a year may vary as a function of the number of other adult females present. We know that capybaras are plural breeders (i.e., more than a single female reproduces in each social group (Macdonald et al., 2007)), and not all the females are reproductively active in a certain period of time (Ojasti, 1973; Jorgenson, 1986). This suggests that there is a mechanism of suppression, although there is no definitive evidence for suppression.

Harvest models developed for other species have demonstrated that harvest levels for species that engage in sexually-selected infanticide must be reduced because males, which are typically not considered important in most demographic models, protect young and therefore play an important role in infant survival (Greene et al., 1998; Swenson, 2003). The loss of these males by hunting has three main consequences: the male social organization is disrupted as the turnover of resident males increases, the population growth rate decreases, and adult male survival is reduced.

Despite some knowledge of capybara social behavior (Macdonald, 1981; Jorgenson, 1986; Herrera and Macdonald, 1989), behavior has not been formally integrated into population management. Given that capybaras are intensively hunted, it is reasonable to explore the potential demographic consequences of infanticide by males and reproductive suppression by females. If they indeed exist and there are substantial effects, then it would be prudent to determine its prevalence to help establish sustainable harvest levels.

We develop a harvesting model to evaluate the potential effects of infanticide by males, and female reproductive suppression on capybara herd dynamics under variable harvesting regimes. We first developed an age-structured model of capybara herd dynamics to explore the demographic consequences of different hunting strategies. We then introduced infanticide behavior as a function of the harvesting of dominant males, and female reproductive suppression as a function of female density. Our goal was to evaluate the potential effects of these behaviors on the herd size after 50 simulated years of hunting.

2. Materials and methods

2.1. *Developing the population model*

We used STELLA^{TM} Research 8.0 modeling software (High Performance Systems Inc.,, 2004), to construct a deterministic, age-structured, density-dependent population model (Appendix 1). We focused on the herd as the modeling level since it is the basic unit of capybara social organization. The model assumed: (1) herds behave similarly; (2) there is no dispersal; (3) the death of an alpha male creates a situation whereby infanticide by males occurs; (4) infanticide affects only infant survival; and (5) female reproductive suppression is present and is related with social structure (as seen in Damaraland mole-rats (*Cryptomjs damarensis*)- Cooney and Bennett, 2000, and Mongolian gerbils (*Meriones unguiculatus*)-Saltzman et al., 2006). The modeled herd characteristics were: (1) age structure was estimated from wild capybara population data; (2) individuals reached sexual maturity at different ages; and (3) there were a maximum of 25 individuals (Macdonald et al., 2007) that we called the herd's carrying capacity. Because herds were assumed to be independent, the herd was treated as a "closed system" that was sustained solely by birth, not immigration. We modeled time by setting time steps to months. We followed the number of infants, juveniles, and adults and used the number of individuals in the herd (herd size) as the system's response variable because of previous suggestions that in social species the colony size is influenced by hunting pressure (Verdade, 1996). Demographic parameters (e.g., mortality rates, fecundity, and gestation time) used to build the model were taken from the literature and are described in Table 1.

We used a simplified age structure to describe capybaras' life cycle because it is not easy for a hunter to differentiate among individuals older than two years in the field. The three age classes modeled were: infants (from birth to 6 months), juveniles (6–12 months in females, and 6–18 months in males), and adults (individuals that have reached sexual maturity). Each of these demographic classes has different physical characteristics and reproductive contributions to the population; however, we assumed that there were no differences in demographic parameters within the adult class.

The number of individuals within each age class at time *t*, correspond to the number of capybaras present in the cate-

Table 1 – Descriptions of parameters variables used in the capybara harvesting model along with their initial settings

	Value	Description
Parameter		
T	600	Length of the simulation (months)
MxHd	25	Maximum herd size of a herd observed in the field (i.e., herd carrying capacity)
B		Numbers of individuals born and added to the herd in each period of time
G	6	Time an infant spends in this category (months)
MtAF	12	Time a juvenile female spends growing up to adult stage (months)
MtAM	18	Time a juvenile male spends growing up to adult stage (months)
S	0.55	Male–female ratio
MoI	0.029	Monthly rate of natural infant mortality
MoJ	0.0125	Monthly rate of natural juvenile mortality
MoA	0.025	Monthly rate of natural adult female and male mortality
hAF	0	Hunting Rate of adult females. Default setting
hAM	0	Hunting Rate of adult males. Default setting
AcF	5	Number of adult females that are reproductively active in a time period (*t*). Default setting
Ge	4	Time of gestation of an adult female (months)
R		Number of pups that reproductively active adult females give birth to in a time period (*t*)
Dalfa	8.31×10^{-3}	Estimated theoretical probability of infanticide caused by the dominant male death probability
Variables		
I^*	2	Number of infants in a herd at a time *t* (*N* individuals). Initial value was estimated from field data
J^*	3	Number of juveniles in a herd at a time *t* (*N* individuals). Initial value was estimated from field data
AF^*	7	Number of female adults in a herd at a time *t* (*N* individuals). Initial value was estimated from field data
AM^*	4	Number of male adults in a herd at a time *t* (*N* individuals)
Hd		Size of the herd at a period of time *t* (*N* individuals)
HAf		Number of adult females or males that are hunted in a time of period *t* (*N* individuals)
DAF (DAM; DJ; DI)		Number of individuals of the respective age class that die in a period of time *t* (*N* individuals)

* Initial values were estimated from field data.

gory each month, plus the number of individuals that moved from the previous category in response to a specific biological process, minus the number of individuals that died because of natural mortality or hunting. The number of individuals within each class was calculated according to the equations presented in Appendix 2.

Adult class was divided by sex because individuals of each sex reached sexual maturity at different ages, while juveniles and infants were modeled without sex differences. Adult population size was affected by hunting pressure, while infant population size was affected by infanticide.

Fecundity was density-dependent. Thus, if the herd size exceeded its maximum size, none of the females breed. Each herd had 54% of males and 46% of females (OIKOS, 2003) and an age structure of 73:18:9 of adults:juveniles:infants (ALCOM, CORPORINOQUIA, CAPIBARA, ALCALDIA DE TAME, 2007). Capybara females give birth an average 1.55 times in a year producing an average of 4 pups per litter (Ojasti, 1973). Total reproduction, however, depends on the number of reproductively active females in a male's harem.

Infanticide by males was assumed to occur when the dominant male died. This mortality could happen naturally, or it could be induced by hunting. The probability of natural death was enhanced by the effect of hunting. We assumed a natural probability of the dominant male dying (i.e., monthly mortality rate) of 8.31×10^{-3}, because male dominance hierarchies are stable over a period of three years (Herrera and Macdonald, 1989). If a dominant male died, we removed all the infants from the time period when the death occurred.

Based on the monthly percentage of reproductive females reported by Ojasti (1973), we constructed a graphical reproductive suppression function (Fig. 1). We assumed that reproductive suppression followed a negative logistic relationship

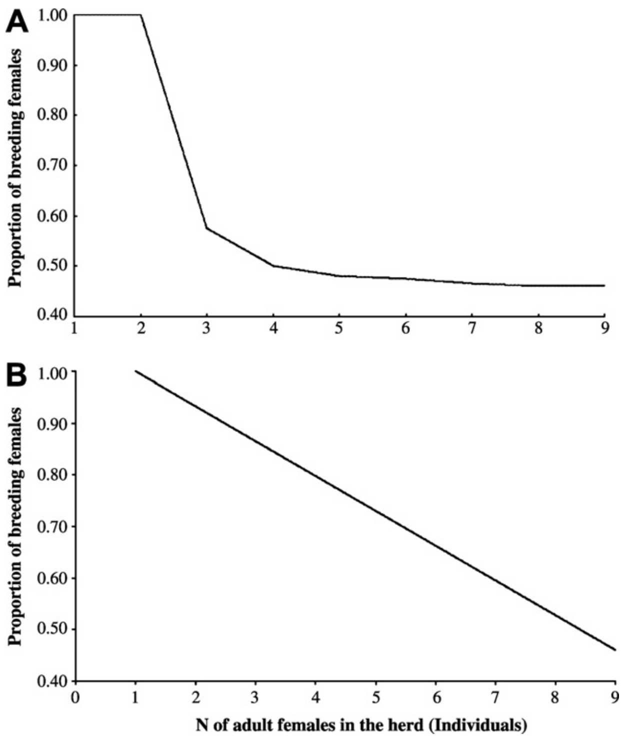

Fig. 1 – The reproductive suppression function used in the sensitivity analyses illustrating the proportion of breeding females as a function of the number of adult females in the herd [(A) negative logistic and (B) negative linear].

Table 2 – Descriptions of the scenarios implemented in the model

Scenario	Characteristic
Hunting-only	Varied hunting intensities when none of the social traits were expressed
Infanticide	Varied hunting intensity when infanticide by males occurred
Suppression	Varied hunting intensity when reproductive suppression occurred
Infanticide + suppression	Varied hunting intensity when both infanticide and suppression occurred

with a maximum of 46.8% of the herd's females reproducing when the suppression function is active; in either case, all adult females were reproductively active. Thus, as the number of adult females in the group increased, the probability that a given female reproduced decreased. The suppression function affects the infant stage by modifying the numbers of individuals added in each period of time.

Since capybaras are subjected to commercial harvesting (Ojasti, 1991; Herrera, 1999), we modeled several hunting levels that ranged from 0% annually hunted (i.e., no hunting) to 50% of the herd hunted annually. We also explored the effects of different age-class selective harvesting strategies that consisted of hunting (1) adult females, (2) adult males, and (3) adult females and adult males. The number of hunted adults corresponded to the proportion of individuals within the adult class (female and male) killed each month. Default settings are presented in Table 1.

For every model setting, 100 simulations were run for 50 years. A total of 6400 runs quantified the effects of hunting at 0, 10, 20, 30, 40, and 50% harvesting of males, females, and males and females in the presence of infanticide, reproductive suppression, neither, or both.

2.2. *Simulation analyses*

We conducted a sensitivity analysis for both infanticide, and reproductive suppression (Fig. 1). We used a baseline scenario with no hunting or reproductive suppression to examine the effect of different probabilities of alpha male death (8.33×10^{-3}, 8.33×10^{-4}, 8.33×10^{-5}) and different graphical functions for reproductive suppression (negative logistic and negative linear). Further, we compared the baseline scenario with four scenarios were we introduced infanticide and female reproductive suppression traits (Table 2). We used ANOVA to test differences in the population size after 50 years. We calculated the partial eta-square value and use these as a metric of effect size. By tradition, small effects are inferred when partial eta-square values are about 0.2, medium effects when partial eta-square values are about 0.5, and large effects when partial eta-square values are about 0.8 (Cohen, 1988).

3. Results

The sensitivity analyses were revealing. When we ran the model with different probabilities of alpha male death, we obtained a similar pattern to that obtained in the basic model. However the time to reach carrying capacity increased with the probability of male death. Varying the suppression function had a more profound effect. A negative stepped function approximated the results of our negative logistic suppression function, but a negative linear suppression function led to the herd increasing to almost its carrying capacity. From this we conclude that the exact nature of the suppression function has a strong effect on herd dynamics.

The results of the simulations and the statistical analysis shows that reproductive suppression had the largest effect on population size after 50 years, followed in order by hunting females and males, hunting only females, hunting only males, and infanticide (Table 3). In general, with limited hunting (i.e., 10% and 20%), the population was able to grow to and maintain its population size at its carrying capacity. However, some situations led to a reduced population size (i.e., 30%), and others led to population extinction (i.e., 40% and 50%). In the sex biased harvesting strategy, when 40% or 50% of females were hunted, the herd went extinct, suggesting that this is an unsustainable level of harvesting. By contrast, harvesting as many as 50% of the males resulted in a sustainable herd.

Carrying capacity was reached in all the scenarios when less than 30% of hunting was present. However, the inflexion point at which it was reached differs between scenarios and showed the capacity of the herd to recover from hunting pressure. With no-hunting, the baseline and infanticide scenarios, reached its carrying capacity at month 48 of the simulation (Fig. 2A). However, in some simulations infanticide exhibited a time delay and reached its carrying capacity at month 60. With reproductive suppression and infanticide-suppression scenarios, the herd was prevented from reaching its carrying capacity and herd size grew up to 12 individuals (48% of the baseline carrying capacity).

Infanticide by males had a limited effect on population dynamics (Table 3). In this scenario, herd size had the same response pattern than the one obtained in the hunting-only scenario (Fig. 2B). Whenever an infanticide event occurred, the population size immediately decreased but the time length to recovery was not consistent.

The tendency of the herd size in the reproductive suppression scenario was similar to the previous scenarios; however as mentioned before, the maximum herd size obtained was 12 individuals (Fig. 2C). The small herds resulting from this scenario, thus, show the importance of this potential social trait on herd dynamics.

The combined effects of infanticide and suppression had an enhanced effect on population dynamics. As expected, hunting females had a larger effect on herd size than hunting males; in fact, our model suggests that harvesting 30% of females or females and males, would not be sustainable. Hunting only males was affected by whether or not there was female reproductive suppression (Fig. 2D).

Table 3 – ANOVA results studying the effects of suppression, infanticide and hunting on capybara population size after 50 years of simulated dynamics

Source	Type III sum of squares	df	Mean square	*F*-value	*p*-value	Partial eta-squared
Corrected model	481600.000	6	802170.020	4152.089	<0.001	0.796
Intercept	660278.840	1	660278.840	34153.929	<0.001	0.842
Suppression	201582.142	1	201582.142	10427.143	<0.001	0.620
Female–male hunting	183425.955	1	183425.955	9487.987	<0.001	0.597
Female hunting	166478.205	1	166478.205	8611.339	<0.001	0.574
Male hunting	13382.943	1	13382.943	692.253	<0.001	0.098
Infanticide	4036.633	1	4036.633	208.801	<0.001	0.032
Suppression × infanticide	27.082	1	27.082	1.401	0.237	0.000
Error	123592.301	6393	19.332			
Total	1578000.000	6400				

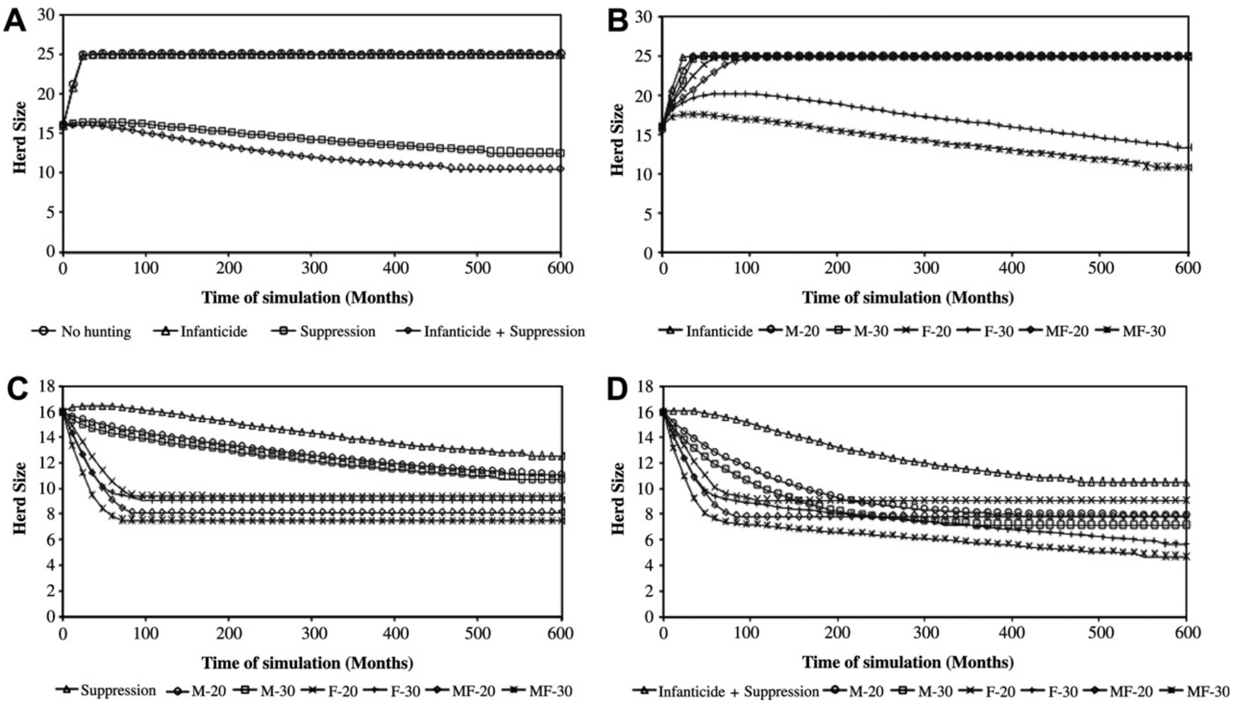

Fig. 2 – Capybara herd size after 600 months of simulation. For all simulations, the carrying capacity was set to 25 individuals. (A) Basic model without hunting. (B) The effect of hunting intensity combined with infanticide. (C) The effect of hunting intensity with reproductive suppression. (D) The effect of hunting intensity with infanticide and suppression.

4. Discussion

The importance of this paper is that our model explored the population consequences of two potential capybara social traits that had formally not been either recognized or integrated into formal models. By doing so, it helps focus future research. Thus, the scenario we applied for capybara is a tool that may be of general use to wildlife managers armed with limited knowledge of social behavior of a focal species. As expected in a polygynous species, selectively hunting females had a large effect on herd dynamics, while hunting only males had a much smaller effect. This result was constant in all the scenarios we explored, and is consistent with the results obtained by Federico and Canziani (2005) and Mesa (2005). Even though, Federico and Canziani (2005) divided adults into five stages, their results showed that adult females from 18 to 36 months had the highest reproductive values, indicating the highest contribution of this class to population dynamics. In the same way, Mesa's (2005) three age class model concluded that hunting only females has a large effect on population dynamics and showed that hunting only males had a much smaller effect. Furthermore, our simulations emphasize the important role that reproductive suppression may have on population dynamics (see Table 3).

Simulations suggest that capybara populations could sustain a relative high male harvesting level (see Fig. 2B–D);

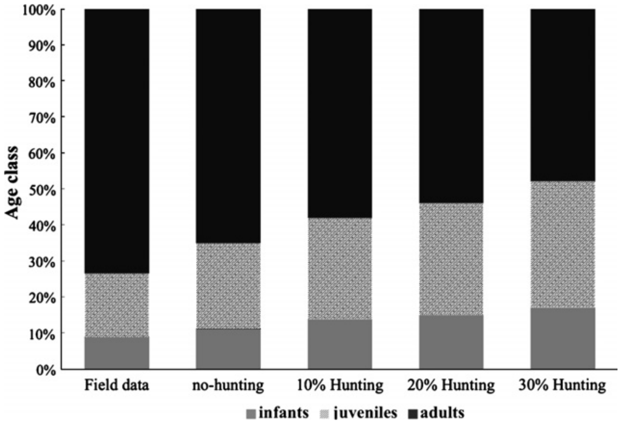

Fig. 3 – The effect of hunting males and females on herd age-structure in the basic model without infanticide or suppression.

however, selective male hunting may bias the population sex ratio toward females, reduce the average male age (Milner et al., 2007) and induce sexually-selected infanticide. Also it could have potentially deleterious genetic implications that we have not considered. Indeed, the main difficulty for a sex-biased hunting strategy is that capybaras are not extremely sexually dimorphic (Perea and Ruiz, 1977; González-Jiménez, 1995; Ferraz et al., 2005), and thus hunting is expected to be relatively non-selective.

While subsistence capybara hunters are non-selective and kill all age and sex classes (Ojasti, 1991), commercial hunters select large body-sized animals (Ojasti, 1991; Mesa, 2005)–a common pattern in commercially harvested species (Milner et al., 2007). Thus, under either scenario, we expect mostly adults to be killed. Even though our model suggests that an age-class harvesting strategy could be proposed, it is known that such strategy will modify the population age-structure (Ginsberg and Milner-Gulland, 1994) as well as other aspects of group composition such as the ratio of adult males to females, and the degree of relatedness among group members. Changes in capybara group age-structure can be seen in Fig. 3, where a higher hunting pressure leads to an increased number of infants and juveniles and a consequently reduced number of adults. This variation in group composition may be deleterious for such plural breeding species, because it may influence individual reproductive performance of females and might also lead to the loss of important social skills or social cognition (Silk, 2007). Indeed, prairie vole pups that are reared in groups with helpers spend less time alone in the nest, develop faster, and weight more at weaning than pups reared by a breeding pair alone (Solomon, 1991). Differences between the non-hunting scenario and the age-structure observed in the field (see Fig. 3) could be explained by habitat quality influencing female fecundity; a situation that we do not consider in our model. The field age structure corresponded to a wild population in the savannas of Arauca (Colombia), where habitat quality was improved by building structures to keep water available throughout the dry season.

In capybaras, body size is correlated with age (Soini, 1993), and there is a relationship between female size and fecundity (Ojasti, 1973). Thus, if large body-sized females are hunted more intensively, either, animals could fail to breed, or there might be a decrease in female fecundity (Ojasti, 1991). Body size is also correlated with a male's dominance rank (González-Jiménez, 1995) and thus killing a dominant male may lead to infanticide. Because capybaras are territorial (Herrera and Macdonald, 1989; González-Jiménez, 1995), this infanticide is expected to disrupt social structure (e.g., Greene et al., 1998).

Our model suggests that such non-sex selective hunting may be viable when less than 20% of the adults are killed annually. This harvesting rate is sustainable for neotropical social mammals according to the levels reported for capybaras (Federico and Canziani, 2005; Mesa, 2005) and guanacos (*Lama guanicoe*- Franklin and Fritz, 1997). Simulations also show that herds could sustain a harvesting level of 30%. A 30% quota has been used in Venezuela with good results (Ojasti, 1997), but harvesting at this level reduces the population to below its carrying capacity (Mesa, 2005). Thus, field experiments to quantify reproductive rates when adults are harvested are warranted.

Since reproductive suppression has a larger impact on herd size than infanticide it is necessary to explore its biological mechanism in capybara population. Reproductive suppression may affect population dynamics by reducing the number of individuals breeding in the population and by increasing the reproductive skew (Anthony and Blumstein, 2000). Suppression may be related to social status where non-breeders are reproductively suppressed by dominant females (Fitzpatrick et al., 2006). Even if infanticide had a relatively small effect on herd size and our model was not able to identify its population consequences, it is clear in other species that sexually-selected infanticide is a significant cause of mortality (Hrdy, 1979; Ebensperger and Blumstein, 2007) and it may have important demographic consequences. Infanticide may disrupt the male social structure and may reduce female inter-birth intervals by modifying female reproductive physiology and sexual receptivity. These effects were not formally studied in this model, but what is clear from our model is that infanticide enhanced the effect of female hunting by reducing the number of juveniles recruited over time. The fact that infanticide did not substantially affect the herd size, suggests that infanticide effects were compensated by female reproductive behavior.

Exploring the effect of hunting pressure in social behavior requires sufficient data about human hunting pressure as well as a deep understanding of the natural social behavior (Verdade, 1996). Although capybara are diurnal and have been studied by several research groups, we still lack a detailed understanding of key behaviors that may influence demography (e.g., the intensity of infanticide or the mechanism of reproductive suppression). In this way, our model is the first step in determining the demographic impact of human hunting. While we used herd size as our response variable, previous capybara models focused on density. Future density-based models should explore the effects of habitat structure and quality on capybara density because of its influence on density estimations and population dynamics (i.e., limited dispersal opportunities may select for natal philopatry and greater family group stability–Krebs and Davies, 1993). Finally, human hunting pressure could have other behavioral effects on the exploited population. For instance, hunting could alter animal movement and daily activity patterns (Verdade, 1996), which ultimately could affect population dynamics.

In conclusion, our simulations, while simple, suggest that incorporating social behavior in a harvesting model has identified potentially unviable harvesting strategies. By design our model excluded a number of potentially important factors such as inter-herd dynamics, delayed reproduction following hunting, and delayed social reorganization following hunting, as well as alternative reproductive strategies. In this sense, future efforts should focus on understanding the effects of these potentially important traits. Given that infanticide by males has just been documented in capybara (E. Congdon, pers. comm.), it behooves managers to better understand it and properly model its effects. Presently, however, given the option of studying infanticide or female reproductive suppression, reproductive suppression has a much larger effect on population dynamics than infanticide by males.

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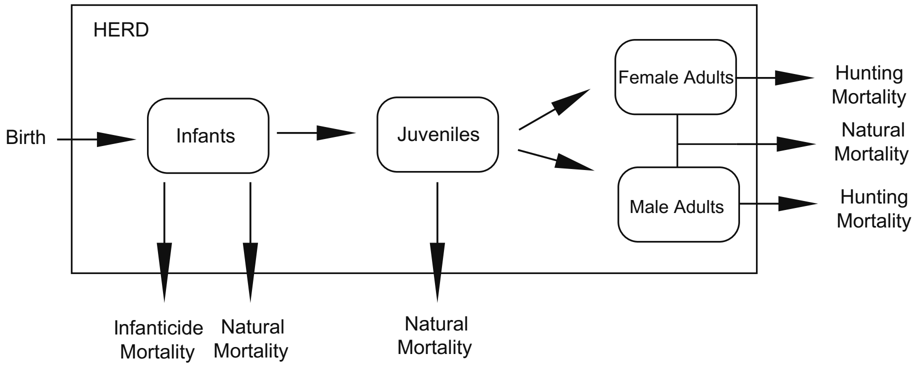
Appendix 1

Schematic illustrating capybara harvesting-model implemented in Stella. Paths outside the box represent factors impacting the herd. Inner boxes represent the state variables. The lines connecting boxes illustrate links between state variables



Appendix 2

Basic equations in Stella language, used in herd dynamic of the capybara harvesting-model.

$\mathrm{AF}(t) = \mathrm{AF}(t - \mathrm{dt}) + (\mathrm{MtAF} - \mathrm{DAF} - \mathrm{HAF}) * \mathrm{dt}$
$\mathrm{AM}(t) = \mathrm{AM}(t - \mathrm{dt}) + (\mathrm{MtAM} - \mathrm{DAM} - \mathrm{HAM}) * \mathrm{dt}$
$\mathrm{MtAF} = J * (1 - S)/\mathrm{tMtAF}$; $\mathrm{MtAM} = J * S/\mathrm{tMtAM}$
$\mathrm{DAF} = \mathrm{AF} * \mathrm{MoA}$; $\mathrm{DAM} = \mathrm{AM} * \mathrm{MoA}$
$\mathrm{HAF} = \mathrm{AF} * \mathrm{hAF}$; $\mathrm{HAM} = \mathrm{AM} * \mathrm{hAM}$

$I(t) = I(t - \mathrm{dt}) + (B - G - \mathrm{MoI} - \mathrm{In}) * \mathrm{dt}$
$B = R/\mathrm{tGe}$
$G = I/\mathrm{t\_G}$
$\mathrm{DI} = I * \mathrm{MoI}$
$\mathrm{In} = \text{ if Dalfa} <((00.1/12) + \mathrm{tHAM}) \text{ then } I \text{ else } 0$

$J(t) = J(t - \mathrm{dt}) + (G - \mathrm{MtAF} - \mathrm{MtAM} - \mathrm{MoJ}) * \mathrm{dt}$
$G = I/\mathrm{t\_G}$
$\mathrm{DJ} = J * \mathrm{MoJ}$

$\mathrm{Hd} = I + J + \mathrm{AF} + \mathrm{AM}$

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