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ORIGINAL ARTICLE

How many lowland tapirs (*Tapirus terrestris*) are needed in Atlantic Forest fragments to ensure long-term persistence?

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Tapirus terrestris populations are declining due to habitat loss and hunting. Our objective is to estimate the minimum viable population size for tapirs in the Atlantic Forest. A Population Viability Analysis was conducted using VORTEX. Demographic parameters were based on data published in the scientific literature. Demographically and genetically viable populations should have more than 30 and 200 individuals, respectively. Sensitivity analysis suggests that mortality rate, sex ratio and inbreeding depression are important for population persistence. Preserving tapir populations is important to avoid local extinction, preserve intra-specific diversity, maintain evolutionary potential and ensure tapirs play their ecological roles within ecosystems.

Keywords: Brazil; extinction; Population Viability Analysis (PVA); VORTEX

Introduction

Conservationists attach importance to the knowledge of population size because small populations are more likely to go extinct than large ones (Pimm & Readfearn 1988; Caughley & Gunn 1996). Therefore, estimating minimum viable population size (MVP) is a fundamental cornerstone of conservation biology (Shaffer 1981; Belovsky 1987). The MVP approach seeks to determine the minimum number of individuals a population needs to persist for a certain time period (Shaffer 1981; Gilpin & Soulé 1986; Soulé 1987). Franklin (1980) proposed that the effective population size (N_e) should not be less than 50 individuals in order to ensure short-term survival, and a N_e of 500 individuals would be needed to ensure long-term persistence. Taken together, MVPs for both short- and long-term survival have resulted in the so-called 50/500 rule, which has been widely implemented as a management goal for a large number of threatened species (Lande & Barrowclough 1987). However, recent research suggests that these population sizes are likely too large a simplification for several reasons, and MVP sizes may be considerably different than the 50/500 rule (Lynch & Lande 1998; Reed & Bryant 2000). A MVP can be thought of as a set of products of a systematic process for estimating species, location and time-specific criteria for persistence. The process itself is referred to as Population Viability Analysis (PVA) (Soulé 1987). Despite recent criticism (Coulson et al. 2001; Ellner et al. 2002), PVA has already proved its usefulness as a valid and useful tool (Reed et al. 1998; Brook et al. 2000, 2002), particularly in identifying research gaps and providing guidelines for choosing among management options (Boyce 1992; Lindenmayer et al. 1993; Possingham et al. 1993, 2001). PVA also furthers a preventive management philosophy: it is best to protect species before they become threatened. Efforts to conserve small populations can be expensive, difficult to carry out and less likely to succeed (Conway 1995).

The Atlantic Forest is one of the most biodiverse and threatened biomes of the world (Myers et al. 2000; Mittermeier et al. 2005), being listed as one of the world's 34 Biodiversity Hotspots (Mittermeier et al. 2005). The remaining forest cover is estimated to be about 7% of its original area, and most of the forest remnants are privately owned, their fate highly dependent on the attitudes of farmers and local communities (Viana et al. 1997). The majority of the Brazilian population and large urban areas are also found within the Atlantic Forest limits, representing a serious threat to its biodiversity.

The lowland tapir *Tapirus terrestris* occurs through a wide geographic range in South America, from southern Brazil to Venezuela (Padilla & Dowler 1994). In the Amazon there currently is abundant forest, but deforestation is increasing and it is suspected that in

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time the region will experience the same population fragmentation and reduction already experienced by tapir habitats in other regions (Naveda et al. 2008). This is especially true in the Atlantic Forest and Cerrado ecosystems, where its populations are declining at an alarming rate mainly due to habitat loss, degradation and fragmentation, and hunting (Cullen et al. 2000; Naveda et al. 2008). *Tapirus terrestris* is listed as Vulnerable in the 2009 IUCN Red List of Threatened Species (Naveda et al. 2008). Surprisingly it is not listed in Brazil's national red list of threatened animals (Machado et al. 2005), but it is recognized as regionally threatened in several state red lists in Brazil: Critically Endangered in the states of Minas Gerais (Machado et al. 1998) and Rio Grande do Sul (Fontana et al. 2003); Endangered in the states of Paraná (Mikich & Bérnils 2004), São Paulo (Secretaria do Meio Ambiente 1998), Rio de Janeiro (Bergallo et al. 2000) and Espírito Santo (Mendes et al. 2006). *Tapirus terrestris* is also listed in the appendix II of CITES (UNEP-WCMC 2007).

The objective of the present study is to estimate demographic and genetic MVPs for *T. terrestris* that could be used as quasi-extinction thresholds for future population modeling of the species in the Atlantic Forest and guide management of populations in such a fragmented landscape.

Materials and methods

Life history of the lowland tapir

Adult *T. terrestris* weigh up to 250 kg (Padilla & Dowler 1994). *Tapirus terrestris* inhabits lowland South American forests. Habitat association varies extensively, although the most important habitats tend to be moist, wet or seasonally inundated areas (Bodmer & Brooks 1997). Tapirs move between forests and thickets in the day, but at night feed in grassy or scrubland areas, marshes, lakes and streams (Padilla & Dowler 1994). These daily migrations result in well-worn paths, sometimes used by hunters (Padilla & Dowler 1994). Their major predators are jaguars (*Panthera onca*) and crocodilians (Padilla & Dowler 1994). *Tapirus terrestris* is also a host for a variety of endo- and ectoparasites (Padilla & Dowler 1994). It is a generalist browser and grazer, with the bulk of the diet usually being green shoots of common browse plants (Padilla & Dowler 1994). Its diet also includes fruits, leaves, stems, fresh sprouts, small branches, grasses, aquatic plants, the bark of trees and aquatic organisms, possibly including fish (Padilla & Dowler 1994). Lowland tapirs also play key roles in tropical communities, being important seed dispersers and predators (Bodmer 1990, 1991; Rodrigues et al. 1993; Fragoso 1997; Olmos 1997; Affonso 1998).

Tapirs are solitary, being found in groups only during the mating season. In the wild they are active at all times except the hottest periods of the day, but are most active at dawn and dusk. First reproduction occurs at approximately four years, and the oldest individual known to give birth was 22 years old (Medici et al. 2007). At each pregnancy, females give birth to only one young (Padilla & Dowler 1994; Medici et al. 2007). Sex ratio at birth is assumed to be 50%. There is no *a priori* evidence to suggest a skewed sex ratio at birth in the wild (Medici et al. 2007).

PVA model

VORTEX is a long-standing PVA software package that models the impact of deterministic forces and stochastic events on wildlife population dynamics (Miller & Lacy 1999). This package is one of the most often used for PVA in workshops and other exercises that include conservation practitioners and land management agencies (Lindenmayer & Lacy 1995). A detailed description of the package and its features is given in Lacy (1993, 2000) and Miller & Lacy (1999).

Demographic parameters were based on previously published data on *T. terrestris* (Eisenberg 1989; Nowak 1991; Padilla & Dowler 1994; Emmons & Feer 1997; Gatti 2005; Medici et al. 2007), and on other PHVA analyses for the species (Medici et al. 2007). A summary of input data used to model *T. terrestris* in VORTEX is given in Table 1 and detailed information on PVA data for *T. terrestris* may be found in Medici et al. (2007).

Scenarios and sensitivity analysis

The dynamics of single isolated populations of 10, 20, 30, 40, 50, 100, 200, 300, 400 and 500 *T. terrestris* was simulated. Five hundred iterations were run for each scenario and a time frame of 100 years was used (Medici et al. 2007). The initial population size for all scenarios was half of their carrying capacity. Data derived from the computer simulation analysis using VORTEX were: (1) deterministic growth rate (λ); (2) population growth rate ($\pm$ 1 SD); (3) probability of population extinction ($\pm$ 1 SE); (4) mean time to extinction ($\pm$ 1 SD); (5) mean population size ($\pm$ 1 SD); and (6) decline in genetic variability, expressed as the expected heterozygosity or gene diversity. A population was considered demographically viable when it had a $\leq$5% probability of extinction during a 100-year period (Soulé 1987), and genetically viable when populations had a $\leq$10% decrease

Table 1. Life history parameters of *Tapirus terrestris* used as input to the computer package VORTEX for population viability analysis (input data based on Medici et al. 2007).

Parameter	Baseline value
Number of populations	1
Initial population size	100
Carrying capacity	100
Inbreeding depression	3.14 LE
% of the effect of inbreeding due to recessive lethal alleles	50
Breeding system	Monogamy
Age of first reproduction (♀ / ♂)	4 years
Maximum age of reproduction	22 years
Annual % adult females reproducing (SD)	60 (6)
Density dependent reproduction?	No
Maximum litter size	1
Overall offspring sex ratio	50:50
% adult males in breeding pool	90
% mortality from age 0 to 1 (SD)	10 (2.5)
% mortality from age 1 to 2 (SD)	15 (3.75)
% mortality from age 2 to 3 (SD)	15 (3.75)
% mortality from age 3 to 4 (SD)	15 (3.75)
% mortality from age above 4 (SD)	8 (2)
Catastrophe	None
Harvest	None
Supplementation	None

LE, Lethal Equivalents.

in expected heterozygosity during a 100-year period (Foose et al. 1986; Foose 1993).

Sensitivity analysis measures the extent of change in the modeled population output values due to a known change in assumptions. It identifies those assumptions that are important to accurately estimate, those to which the model is particularly sensitive, and those which are less influential (McCarthy et al. 1995; Reed et al. 1998; Possingham et al. 2001). The model was examined for sensitivity to variation in mortality rate, sex ratio, percentage of reproductive females and inbreeding depression. Sensitivity to variation in mortality rate, sex ratio, percentage of reproductive females and age of sexual maturity were examined by changing ± 5% the value in the baseline scenario. The effect of inbreeding was examined by introducing inbreeding depression to the scenarios. As the actual impact of inbreeding on *T. terrestris* populations is unknown, the impact of inbreeding was modeled as 3.14 lethal equivalents, the median value estimated from analysis of studbook data for 40 captive mammal populations (Ralls et al. 1988). As VORTEX only models inbreeding impact on juvenile survival, the simulated effect of inbreeding is probably conservative (Lacy 1993). Sensitivity analysis was conducted for the two population sizes identified as quasi-extinction thresholds for demographic and genetic modeling of *T. terrestris* populations. The significance of the difference in output between the baseline scenario and changed models is tested using a Student's two-tailed *t*-test (Zar 1996).

Results

MVP sizes and quasi-extinction thresholds

There was a reduced likelihood of extinction among larger populations of *T. terrestris*, and more genetic diversity was conserved in such populations than in smaller ones (Table 2). At smaller population sizes, increased demographic fluctuations, reflected by the values for SE (r) (Figure 1), depressed population growth and led to substantial probabilities of extinction (Table 2). Extinctions occurred among small isolated populations of *T. terrestris* even when no inbreeding depression was incorporated in the analyses (Table 2). Demographic stochasticity alone jeopardized population stability in these scenarios and populations of 30 or more may be necessary to reach more than 95% probability of demographic persistence over 100 years. However, there was a significant (>10%) loss of genetic variability from populations of this size, and only populations with about 200 animals might be genetically stable during a 100-year period (Table 2). Therefore, a population size of 30 individuals should be set as a quasi-extinction threshold for demographic analysis, whereas the quasi-extinction threshold taking into account genetic modeling should be set at 200 animals.

Table 2. Simulation results of modeling different population sizes of the lowland tapir for a time period of 100 years, using the computer program VORTEX.

Carrying capacity (*K*)	Population growth rate (*r*) [mean (SE)]	Probability of extinction (SE)	Years to extinction [mean (SE)]	Size of all populations [mean (SE)]	Expected heterozygosity [mean (SE)]
10	0.0141 (0.0012)	0.8520 (0.0159)	28.66(1.19)	1.22(0.13)	0.2894 (0.0253)
20	0.0136 (0.0010)	0.8220 (0.0171)	41.96(1.22)	1.55(0.14)	0.2938 (0.0233)
30	0.0344 (0.0004)	0.0380 (0.0086)	53.79(5.54)	26.52(0.30)	0.6615 (0.0054)
40	0.0397 (0.0003)	0.0040 (0.0028)	22.00(2.00)	38.02(0.19)	0.7461 (0.0038)
50	0.0408 (0.0003)	0.0040 (0.0028)	55.00(22.00)	48.01(0.21)	0.7918 (0.0033)
100	0.0459 (0.0002)	0.0000 (0.0000)	0.0000(0.0000)	98.65(0.17)	0.8936 (0.0010)
200	0.0481 (0.0002)	0.0000 (0.0000)	0.0000(0.0000)	198.52(0.21)	0.9451 (0.0004)
300	0.0490 (0.0002)	0.0000 (0.0000)	0.0000(0.0000)	298.69(0.25)	0.9633 (0.0002)
400	0.0495 (0.0002)	0.0000 (0.0000)	0.0000(0.0000)	398.71(0.26)	0.9724 (0.0002)
500	0.0492 (0.0002)	0.0000 (0.0000)	0.0000(0.0000)	499.44(0.28)	0.9779 (0.0001)

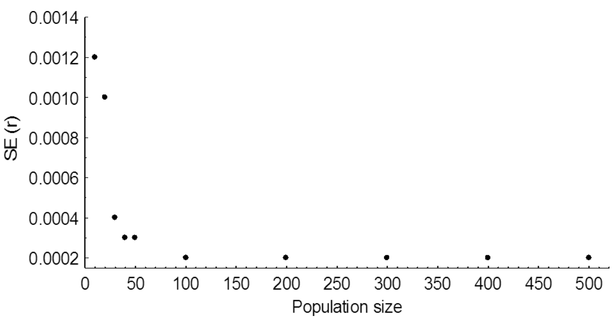

Figure 1. Relationship between population size and demographic stochasticity, expressed as SE (*r*), from *Tapirus terrestris* populations of different sizes, within a time frame of 100 years.

Sensitivity analysis

In the population threshold size of 30 individuals, population growth rate was significantly different in each sensitivity scenario (Figure 2). There was an increased probability of extinction for sensitivity scenarios modeling inbreeding depression, high mortality rate, high sex ratio and lower reproduction (Figure 2), and a decreased probability of extinction when a lower mortality rate was modeled (Figure 2). Lower mortality resulted in a larger population size (Figure 2). However, inbreeding depression, high mortality, higher sex ratio and lower reproduction all resulted in smaller population sizes (Figure 2). There was no difference in genetic diversity in any of the sensitivity scenarios analysed (Figure 2).

For the critical population size of 200 individuals, probability of extinction was zero for all scenarios. Evaluating population growth rate, we observed that inbreeding depression, higher mortality rate, changes in sex ratio (both male or female-biased) and lower reproductive rates resulted in a decrease in population growth (Figure 3), whereas a lower mortality rate and higher reproduction accelerated population growth (Figure 3). Population size was equal in almost all scenarios, with the exception of the lower mortality scenario, which increased final tapir population sizes (Figure 3). Lower mortality and inbreeding depression resulted in higher genetic diversity (Figure 3). Sensitivity analysis suggests that demographic parameters are sensitive and therefore important to be measured as accurately as possible in modeling *T. terrestris* populations, regardless of population size (Figures 2, 3). This also suggests that management strategies should target improvement of demographic parameters for tapir populations.

Discussion

Tapirus terrestris has a wide geographic distribution (Padilla & Dowler 1994; Naveda et al. 2008), but it is locally extinct or threatened in several regions due to habitat loss, fragmentation, and hunting (Bodmer 1995; Bodmer & Brooks 1997; Affonso 1998; Flesher 1999; Medici 2004; Naveda et al. 2008). In the northern Brazilian Amazon, the lowland tapir is one of the species most exploited by indigenous communities (Souza-Mazurek et al. 2000). Due to its low reproductive rate, the observed levels of poaching might not be sustainable in the long term (Bodmer & Brooks 1997). Flesher (2005) reports that the lowland tapir was locally extinct from Atlantic Forest remnants in southeastern Brazil circa 1850–1880, even though suitable habitat still exists. *Tapirus terrestris* populations were extirpated when the landscape was almost completely forested and human population densities were relatively low, indicating that even subsistence hunting may be capable of extirpating tapirs, and that tapirs are particularly threatened by hunting pressure in the Atlantic Forest (Flesher 2005). Palm overexploitation in the Atlantic Forest, the Cerrado and the Amazon could also have serious impacts upon lowland tapir

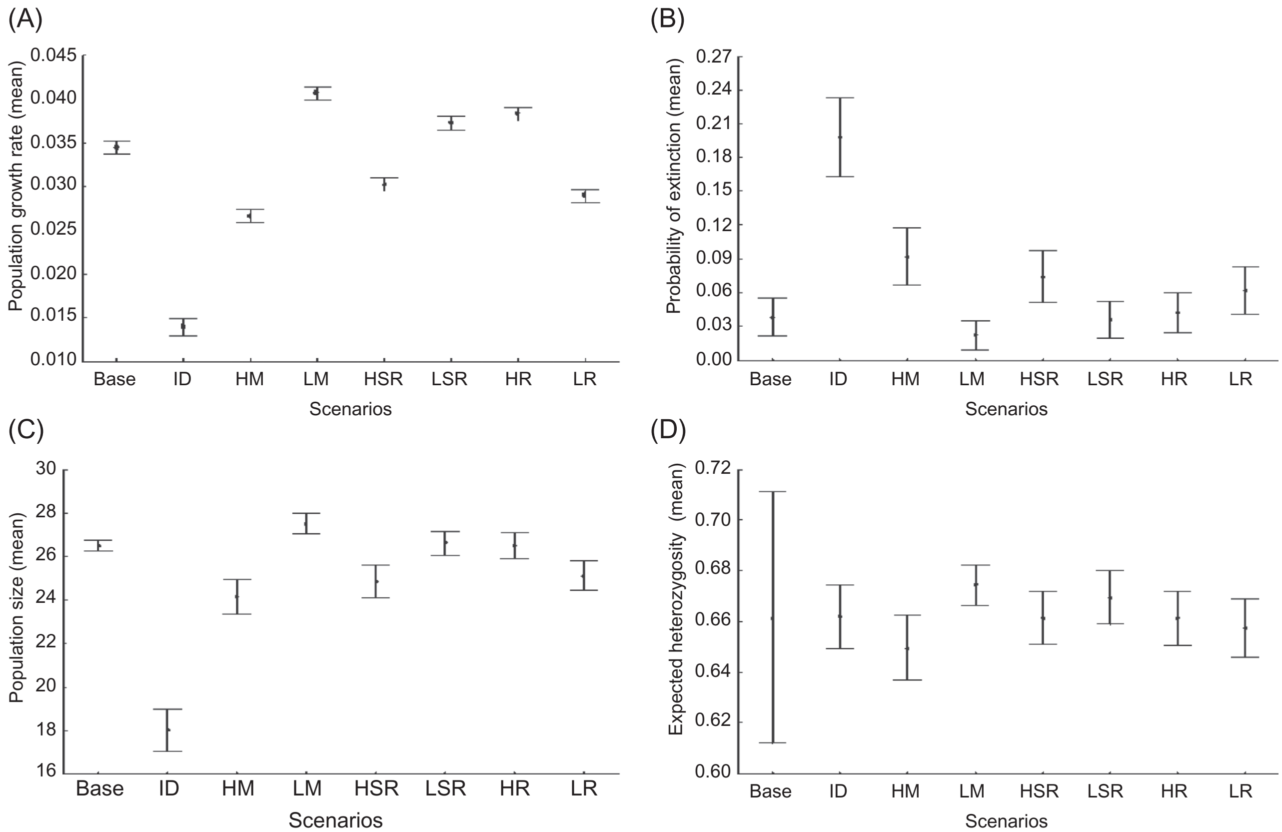

Figure 2. Sensitivity analysis: changes in assumptions and the resulting effects on the model outcome for the population size estimated as demographic quasi-extinction thresholds ($n = 30$). Bars indicate the confidence interval for (A) population growth rate (r); (B) probability of extinction; (C) population size; (D) expected heterozygosity. Base, scenario base; ID, inbreeding depression; HM, high mortality; LM, low mortality; HSR, high sex ratio; LSR, low sex ratio; HR, high reproduction; LR, low reproduction.

populations (Bodmer 1990; Bodmer & Brooks 1997; Affonso 2002; Medici 2002; Quiroga 2003).

Assuming a mean population density of 0.4 individuals/km^2 in the Atlantic Forest (Cullen et al. 2000), and MVPs of 30 and 200 individuals (see Results), it may be suggested that demographically and genetically viable populations of *T. terrestris* in this biome would require habitat areas with at least 75 and 500 km^2, respectively. Redford & Robinson (1991) estimated that a minimum area of 1620.5 km^2 would be needed to maintain a viable lowland tapir population with 500 individuals. In the Atlantic Forest, populations of *T. terrestris* were observed in small protected areas that have been isolated for a few decades (Córrego Grande Biological Reserve with 1.504 ha and Córrego do Veado Biological Reserve with 2.400 ha) (Chiarello 1999, 2000). However, a modeling study suggests that these small reserves do not hold viable tapir populations in the long term (Gatti 2005). From the point of view of many species, many landscapes are in the process of crossing, or have recently crossed the boundary between the states in which they are and in which they are no longer able to support viable populations. Nonetheless, especially if the environmental change has been fast, it takes time following habitat loss before the species reaches the new equilibrium corresponding to the current structure of the landscape (Hanski & Ovaskainen 2002). Tilman et al. (1994) have coined the term extinction debt to refer to situations in which, following habitat loss, the threshold condition for survival is no longer met for some species, but these species have not yet gone extinct because of the time delay in their response to environmental change. This may explain the small tapir populations observed in the small protected areas in Espírito Santo state.

Lowland tapirs have important roles in the maintenance of ecological processes within Neotropical forest ecosystems, like herbivory, seed dispersal and seed predation (Padilla & Dowler 1994; Bodmer & Brooks 1997; Medici 2002; Medici & Foerster 2002; Fragoso et al. 2003). *Tapirus terrestris* is an efficient seed disperser, particularly for some palm species (Olmos 1997). Such ecological roles of the lowland tapir support the implementation of actions to ensure

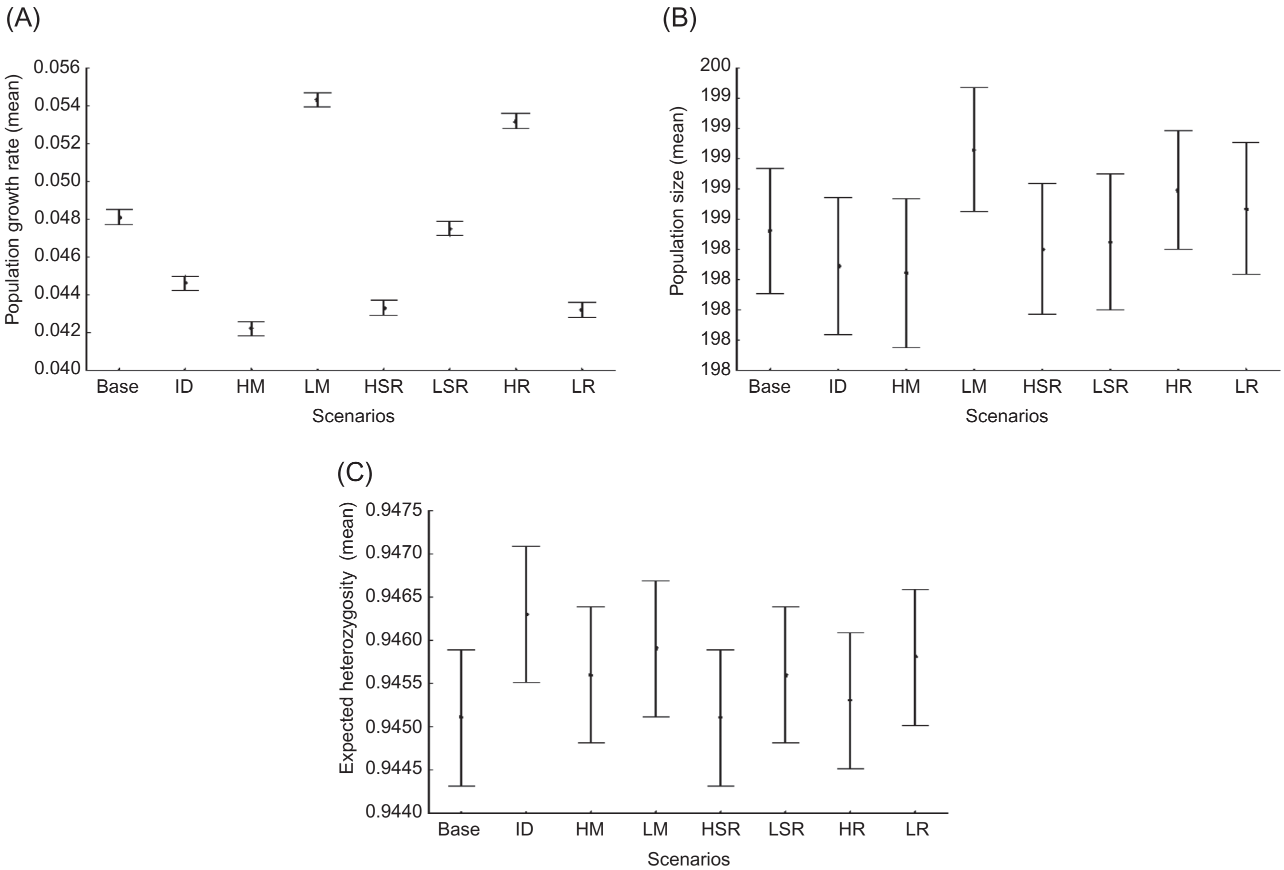

Figure 3. Sensitivity analysis: changes in assumptions and the resulting effects on the model outcome for the population size estimated as demographic quasi-extinction thresholds ($n = 200$). (A) Population growth rate (r); (B) population size; (C) expected heterozygosity. Base, scenario base; ID, inbreeding depression; HM, high mortality; LM, low mortality; HSR, high sex ratio; LSR, low sex ratio; HR, high reproduction; LR, low reproduction.

population persistence, since local extinctions could have impacts upon the structure and composition of plant communities (Bodmer et al. 1993; Affonso 1998; Medici 2002). If local tapir population densities decline to very low numbers they may no longer be able to play these ecological roles within ecosystems, a process known as ecological extinction (Redford 1992; Brito & Fernandez 2000).

In order to minimize human impacts on lowland tapir populations in the Atlantic Forest and avoid local extinctions, the creation and implementation of conservation programs are of high importance. Besides scientific projects to address conservation issues, the development of environmental education programs to reinforce the role and importance of large herbivores for the forest ecosystems for the general audience are of paramount importance to help protect this species (Bodmer & Brooks 1997; Medici & Foerster 2002). Besides that, the creation of new protected areas and the expansion of existing ones in the Atlantic Forest, coupled with actions to increase landscape connectivity, could improve the effectiveness of protected area networks in maintaining viable populations (Gatti 2005), since isolation of existing tapir populations seems to be a serious threat in this biome (e.g. Chiarello 1999, 2000; Moraes et al. 2003; Gatti 2005). Another important issue in lowland tapir conservation would be to control illegal hunting (Bodmer & Brooks 1997; Flesher 2005; Naveda et al. 2008).

Such actions should help preserve and restore *T. terrestris* populations and their habitats, as well as movement and dispersal routes. Another factor of importance to lowland tapir conservation in the Atlantic Forest are roads. Several forest remnants and protected areas in the Atlantic Forest are close to, or crossed by, roads. Roads can represent barriers to dispersal, increase mortality due to roadkills and facilitate the access of hunters to lowland tapir habitat (Forman & Alexander 1998). Wildlife passageways are a rarity within the road system in Brazil but could assist local tapir populations by reducing road mortality and improving connectivity between existing habitat patches.

Besides model outcomes, one of the most important results in wildlife modeling is to identify gaps in species knowledge. Applying our VORTEX model helped us to identify such knowledge gaps on *T. terrestris* natural history and ecology, thus assisting future research on this species. Population dynamics studies, estimating survival rates and reproductive success in the wild are urgently needed, as well as studies evaluating the potential impacts of infectious diseases on tapir demographic parameters. Management strategies such as translocation and reintroduction could be adopted, since the lowland tapir seems to have high plasticity, inhabiting even highly altered forest remnants in São Paulo state (EP Medici, personal communication). But the implementation of such actions needs previous knowledge on species demography, ecology, behavior and genetics, which are essential to refine and improve population modeling and consequently provide better guidance for population and habitat management targeting *T. terrestris* conservation.

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