Family Planning: Does Variation in Reproductive Strategies Affect Vulnerability to Extinction in the Greater Spear-Nosed Bat *Phyllostomus Hastatus*?

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Family planning: does variation in reproductive strategies affect vulnerability to extinction in the greater spear-nosed bat *Phyllostomus hastatus*?

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Different reproductive strategies among populations might affect population growth rates, and a population's vulnerability to threats. Population viability analysis may help guide population management and the identification of populations more prone to decline, allowing a preventive approach to avoid population declines and extinctions. The objective of the present study was to evaluate if differences in reproductive strategy translate into differential intrinsic vulnerability among different populations of *Phyllostomus hastatus*. We used the software VORTEX to model the dynamics and viability of *P. hastatus* populations under different reproductive scenarios. We modeled a total of 12 scenarios evaluating variations in reproductive characteristics of the species (monoestry vs polyestry, harem size, and infant mortality rate). *Phyllostomus hastatus* populations were viable under most scenarios, except with scenarios incorporating monoestry and high pup mortality. Our results demonstrate that both reproductive strategies (monoestry and polyestry) found in *P. hastatus* result in viable and stable populations under natural conditions. However, polyestrous populations have higher growth rates, making them more resilient to natural and/or anthropogenic disturbances. A significant portion of the more resilient populations in South America overlap the Amazon Forest, a continuous and preserved habitat under low human pressure, which bodes well for the long-term persistence of these populations. On the other hand, the populations of the species that evolved the monoestrous reproductive strategy are located in Mesoamerica, a Biodiversity Hotspot that is under severe human impacts, particularly from habitat loss. Conservation biologists and managers must take into account intra-specific demographic differences of species when planning for their long-term persistence.

Key words: monoestry, polygyny, population viability analysis, VORTEX

INTRODUCTION

There is evidence that certain biological characteristics such as lower fertility, higher body mass, lower dispersal capacity, and longer generation times, may increase the susceptibility to extinction in mammals (Polischuck, 2002; Cardillo *et al.*, 2005; Collen *et al.*, 2006). For bats, in addition to the previous characteristics, geographic range size, wing morphology, sensitivity to habitat fragmentation, and edge effects are also correlated with extinction risk (Jones *et al.*, 2003; Safi and Kerth, 2004; Duchamp and Swihart, 2008; Meyer *et al.*, 2008). Therefore, different reproductive strategies among populations, such as the number of broods or litter size, might affect population growth rates, and a population's vulnerability to threats.

Phyllostomus hastatus is widespread in Central and South America (Gardner, 2008). It is omnivorous and roosts preferably in caves (Santos *et al.*, 2003). The species is socially structured into two kinds of groups: (1) bachelor groups composed exclusively of non-reproductive males, and (2) harems, where one male might have from seven up to 100 females (McCracken and Wilkinson, 2000; Santos *et al.*, 2003). Each harem persists for about three years, and during this period the male strongly controls female reproduction, which guarantees up to 90% paternity success in the litters produced (McCracken and Bradbury, 1981; McCracken and Wilkinson, 2000). Individuals become sexually mature at two years of age (McCracken and Bradbury, 1981) and reproduction is synchronous among harems (Porter and Wilkinson, 2001). Juveniles disperse in order to form new social groups (McCracken and Bradbury, 1981). Colonies are composed of individuals born in different social groups, as indicated by genetic and paternity analyses (McCracken and Bradbury, 1981; McCracken and Wilkinson, 2000). Social groups may be stable for years (McCracken and Bradbury, 1981). Females from the same harem show extra-parental behavior, but infanticide towards pups from other harems is not uncommon (Bohn *et al*., 2009). Individuals may live up to 20 years in the wild (Santos *et al*., 2003). Pup mortality varies greatly among different social groups and may range from zero to 85% (Stern and Kunz, 1998; Boughman, 2006). Reproductive strategy varies geographically, with populations from Central America showing a monoestrous reproductive pattern, whereas South American populations are polyestrous (Wilson, 1979).

Population viability analysis (PVA) is a modeling tool that allows the comparison of how different scenarios affect population persistence (Beissinger and McCullough, 2002; Brito, 2009). Therefore, PVA may help guide population management and the identification of populations more prone to decline, allowing a preventive approach to avoid population declines and extinctions (Reed *et al*., 2002). The objective of the present study is to evaluate whether differences in reproductive strategy (monoestry vs polyestry; large harems vs small harems; high infant mortality versus low infant mortality) among different populations of *P. hastatus* might represent greater intrinsic vulnerability of monoestrous populations to decline.

Materials and Methods

We used the software VORTEX (Lacy *et al*., 2009) to model the dynamics and viability of *P. hastatus* populations under different reproductive scenarios. VORTEX is widely used in PVA (Brook *et al*., 1999), and provides useful guidance in wildlife management and the identification of threats and populations vulnerable to decline (Brook *et al*., 2000). Demographic, reproductive, and social data on *P. hastatus*, which were used as input for the PVA, were obtained from the published scientific literature (McCracken and Bradbury, 1981; Stern and Kunz, 1998; McCracken and Wilkinson, 2000; Porter and Wilkinson, 2001; Santos *et al*., 2003; Boughman, 2006; Bohn *et al*., 2009 — Table 1).

We modeled a total of 12 scenarios, based on variations in reproductive characteristics found within the species: (1) bimodal polyestry and monoestry (Wilson, 1979); (2) pup mortality (10%, 40% or 85%) (Stern and Kunz, 1998; Boughman, 2006); and (3) harem structure (small harems with seven females to each male and large harems with 100 females for each male) (McCracken and Wilkinson, 2000; Santos *et al*., 2003). We ran 1,000 iterations for each scenario modeled. We considered populations that had at least 95% probability of persistence (Soulé, 1987) and that maintained at least 90% of the original genetic diversity for a period of 100 years to be viable (Foose, 1986, 1993).

Results

The majority of reproductive scenarios resulted in viable populations of *P. hastatus*. Populations were not viable only when we modeled scenarios which combined monoestry and high pup mortality (probability of extinction equal to 99%). Polyestrous populations have higher growth rates (under low and medium mortality rates) and therefore are likely to be more resilient towards threats and disturbances (Fig. 1). High mortality rates depress growth rates both for monoestrous and polyestrous populations, but the latter show fewer fluctuations in growth rates and are more stable. High mortality depressed population growth rate regardless of harem size or reproductive strategy (monoestry or polyestry). There were no significant differences observed in population growth rate due to differences in harem size (Fig. 1). Monoestrous populations facing high mortality showed marked declines in genetic diversity. A monoestrous strategy also resulted in higher genetic diversity if the population was structured in large harems (Fig. 2). Our results show that high pup mortality is the most sensitive reproductive parameter for the persistence of *P. hastatus* populations, and that reproductive strategy (monoestrous or polyestrous) and harem size play secondary roles in determining a population's vulnerability to decline.

Table 1. Life history parameters of *P. hastatus* used as input to the VORTEX program

Parameter	Value	Reference
Breeding system	Polygynous	Santos *et al*. (2003)
Age of first reproduction	2	McCracken and Bradbury (1981)
Maximum breeding age	18	Santos *et al*. (2003)
Sex ratio at birth	1:1	
% adult males in the breeding pool	6 and 85	
% adult females breeding	100	
Litter size	1 and 2	Santos *et al*. (2003)
% mortality rate (males/females)	10, 40 and 85	Stern and Kunz (1998), Boughman (2006)
Initial population size	500	
Initial carrying size	1,000	

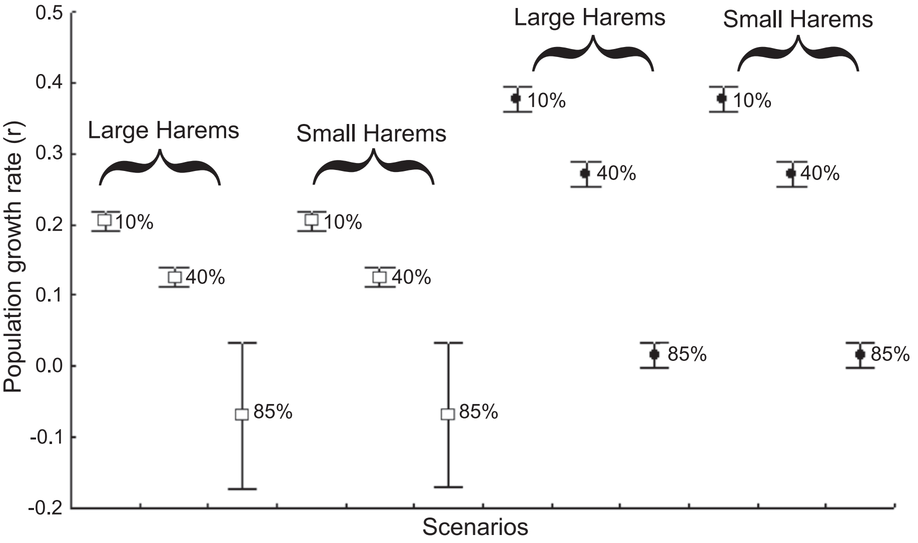

FIG. 1. Variation in population growth rate (r) for *P. hastatus* populations under different reproductive strategies (☐ – monoestry and ● – polyestry), harem structure (small or large) and infant mortality rate (10%, 40% or 85%). Percentage values represent mortalities of infants

DISCUSSION

Our results clearly demonstrate that both reproductive strategies found in *P. hastatus* (monoestry and polyestry) result in viable and stable populations under natural conditions. However, polyestrous populations have higher growth rates, making them more resilient to natural and/or anthropogenic disturbances. It is important to note that a significant portion of the distributional range of the more resilient South American populations (with polyestrous reproduction) overlap the Amazon Forest, a continuous and relatively well-preserved habitat for the species, under comparatively low, although increasing, human pressure (Mittermeier *et al.*, 2003), what should guarantee the long-term persistence of these populations. On the other hand, the populations of the species that evolved the

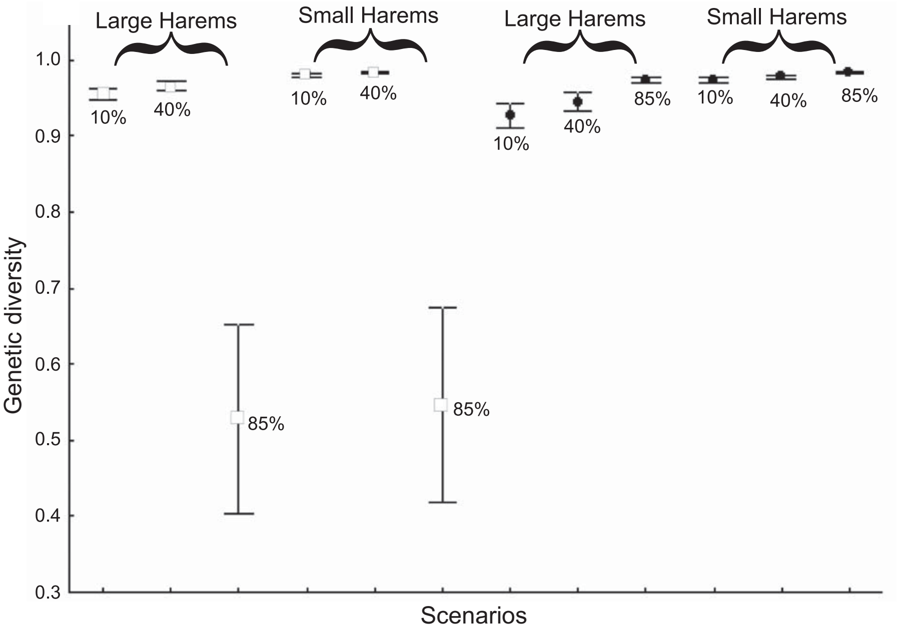

FIG. 2. Variation in genetic diversity (measured as expected heterozygosity) for *P. hastatus* populations under different reproductive strategies (☐ – monoestry and ● – polyestry), harem structure (small or large) and infant mortality rate (10%, 40% or 85%). Percentage values represent mortalities of infants

monoestrous reproductive strategy are located in Mesoamerica (Santos *et al*., 2003), a biodiversity hotspot that is undergoing severe disturbances due to human impacts, particularly from habitat loss (Myers *et al*., 2000).

Local population extirpation is a prelude to species extinction (Ceballos and Ehrlich, 2002). The loss of populations affect ecosystem functioning (Redford, 1992), ecosystem services (Luck *et al*., 2003), and result in biodiversity loss at infra-specific levels (e.g., genetic diversity) (McCauley, 1991; Hughes *et al*., 1997). Conservation biologists and managers must take into account intra-specific demographic differences of species when planning for their long-term persistence. Currently, taxonomists recognize two valid subspecies for *P. hastatus*: *P. h. hastatus* south of the Andes (with monoestrous reproduction) and *P. h. panamensis* in Mesoamerica and north of the Andes (with polyestrous reproduction — Santos *et al*., 2003; Wilson and Reeder, 2005). Therefore, when conservation strategies for the species are developed, such infraspecific biodiversity must be taken into account. Our results show that *P. h. panamensis* is more vulnerable to disturbances due to its natural reproductive pattern. *Phyllostomus h. hastatus* is common in forest habitats, but in savanna ecosystems it is uncommon and depends on forest formations (Medellín and Redford, 1992). This highlights the populations in the Cerrado and in the Caatinga, ecoregions that are undergoing major economic and infrastructure development actions, as targets for population monitoring programs, since they are naturally small within such ecoregions.

PVA models might be a useful tool to guide bat conservation strategies due to the long lifespan of most species. Predictive models (e.g., PVA) allow conservation actions to be proactive, identifying threats and vulnerable populations even before actual declines take place. Unfortunately, the use of such models to comprehend ecological processes, to understand the impacts of threats, and to guide conservation actions in bats is still scarce (e.g., Pryde *et al*., 2005; Aguiar *et al*., 2010). Besides that, the lack of even the most basic demographic data for most bat species is a setback for the widespread use of PVA models. In our particular case, the parameters used as input in the model, originated from very few populations. We suggest that population monitoring programs should be implemented in order to have such estimates for more populations and properly capture population-level variation in such characters, and improve the use of PVA models as tools for bat conservation.

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