Original Article

The Impacts of Population Subdivision on the Viability of *Brachyteles hypoxanthus*

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Abstract

Habitat loss and fragmentation turn continuous large populations into metapopulations of smaller populations, more prone to the negative effects of stochastic processes. We modeled scenarios simulating the subdivision of *Brachyteles hypoxanthus* populations under different dispersal rates. Results show the existence of a population subdivision threshold, below which subdivision causes the metapopulation structure to collapse. Management should target first the increase in local populations through habitat restoration/protection, and only after populations are sufficiently large, connectivity strategies should take place.

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Introduction

Habitat fragmentation is one of the main threats to the world's biodiversity [Vié et al., 2009]. One of the consequences of habitat fragmentation is population subdivision, where one (or a few) large populations inhabiting a continuous habitat is converted into several small populations (or subpopulations) inhabiting the remnants of native habitat [Fahrig, 1997, 2001]. It is already known that small populations are more prone to suffer from stochastic events and processes [Lacy, 2000], and because of that may decline towards extinction [Hanski et al., 1996].

The Atlantic Forest is one of the world's ecosystems most impacted by habitat fragmentation [Myers et al., 2000; Mittermeier et al., 2005]. Estimates show that only between 11 and 16% of the original native vegetation cover is left [Ribeiro et al.,

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2009]. Brazil's major cities and economic centers, and most of the country's human population (approx. 70% or 169 million), are found within the Atlantic Forest [Jacobsen, 2003]. As a result, what is left of the Atlantic Forest is scattered as small and isolated forest remnants [Ribeiro et al., 2009].

Large forest remnants within a fragmented landscape are important for preserving mammal community structure [Chiarello, 1999, 2000], but the role of small habitat remnants in maintaining native populations must also be taken into account when planning for species persistence [Turner and Corlett, 1996]. However, the effects of landscape alterations on population viability mediated by changes on population structure are highly complex and are still not fully understood.

The northern muriqui *(Brachyteles hypoxanthus)* is endemic to the Atlantic Forest [Mendes et al., 2005]. Northern muriqui populations were extirpated throughout the species range, mainly due to habitat loss, habitat fragmentation and hunting [Mendes et al., 2005]. Because of the severity of these impacts, nowadays only 13 highly fragmented and small populations persist [Mendes et al., 2005], and it is no surprise that the species is classified as 'Critically Endangered' in the IUCN's Red List of Threatened Species [IUCN, 2011]. Our objective is to model the impact of population subdivision, due to habitat fragmentation, on the viability of *B. hypoxanthus*.

Methods

Target Species

B. hypoxanthus is endemic to the Atlantic Forest [Aguirre, 1971]. It is highly folivorous but its diet also includes fruits, flowers and, to a lesser degree, other plant items such as bark [Strier, 1991a; Carvalho et al., 2004]. Muriquis are diurnal and arboreal, but they may descend to the ground to cross forest gaps, drink water and sometimes to play [Dib et al., 1997; Mourthé et al., 2007; Tabacow et al., 2009]. They are social and troops may have up to 100 individuals [Strier et al., 2006], with males being philopatric and females dispersing when they reach sexual maturity (6 years old) [Strier and Ziegler, 2000]. The mean age at first reproduction is estimated as 7 years for males and 9 years for females [Strier and Ziegler, 2000; Strier, 2005]. Females give birth to one baby and there is a 3-year interbirth interval [Strier, 1991b; Strier et al., 2001]. Longevity is estimated to be 35 years [Strier, 2000].

Population Viability Analysis Model and Scenarios

We used the software Vortex (version 9.92) [Lacy et al., 2008] to model our scenarios. Vortex is a Monte Carlo simulation of the effects of deterministic forces as well as demographic, environmental and genetic stochasticity and catastrophes on the dynamics of wildlife populations [Lacy, 1993; 2000; Lacy et al., 2008]. Our model incorporates stochasticity in mortality rates and reproductive rates (e.g. percentage of individuals reproducing in each year; for details on which parameters of the model are deterministic and which are stochastic, see Appendix). The use of population viability analysis models (PVA) to guide the management of the northern muriqui has been identified as one of the priority conservation actions for the species [Mendes et al., 2005].

Critical threshold population sizes for the persistence of *B. hypoxanthus* have already been identified [Brito and Grelle, 2006]. Population sizes of 40 and 700 individuals should ensure safety from the effects of demographic and genetic stochasticity, respectively [Brito and Grelle, 2006]. Given these data, the dynamics of populations of *B. hypoxanthus* with 40 and 700 individuals were explored. Dynamics of metapopulations (a group of connected populations of the same species found within a given region) where the original population size (40 and 700) was subdivided into 2, 4 and 8 populations, were modeled. The dispersal rates among populations were set as 0, 0.05, 0.10 or 0.20. In Vortex, dispersal rates specify the probability that a given

Table 1. Results of the PVA for a *B. hypoxanthus* metapopulation size of 40 individuals for a time period of 50 generations, subdivided into 1, 2, 4 or 8 subpopulations and connected by dispersal rates of 0, 5, 10 or 20% per year

Scenarios	Dispersal rate, %	Population growth rate ± SD	Probability of extinction	Population size ± SD, n	Heterozygosity ± SD	Time to extinction, generations
1 × 40	–	0.061 ± 0.067	0.000	39.33 ± 2.01	0.178 ± 0.209	–
2 × 20	0	0.059 ± 0.065	0.042	31.74 ± 10.95	0.377 ± 0.227	36.24
	5	0.051 ± 0.064	0.008	34.39 ± 8.02	0.192 ± 0.213	35.18
	10	0.045 ± 0.064	0.006	35.47 ± 6.78	0.219 ± 0.217	37.16
	20	0.031 ± 0.065	0.032	35.14 ± 7.65	0.254 ± 0.219	39.38
4 × 10	0	0.046 ± 0.088	0.980	0.20 ± 1.36	0.000 ± 0.000	19.71
	5	0.019 ± 0.083	0.954	0.59 ± 2.94	0.050 ± 0.136	24.11
	10	0.003 ± 0.085	1.000	0.00 ± 0.00	0.000 ± 0.000	12.10
	20	−0.018 ± 0.093	1.000	0.00 ± 0.00	0.000 ± 0.000	4.50
8 × 5	0	0.017 ± 0.096	1.000	0.00 ± 0.00	0.000 ± 0.000	10.40
	5	−0.015 ± 0.100	1.000	0.00 ± 0.00	0.000 ± 0.000	5.36
	10	−0.026 ± 0.101	1.000	0.00 ± 0.00	0.000 ± 0.000	3.02
	20	−0.025 ± 0.098	1.000	0.00 ± 0.00	0.000 ± 0.000	2.15

Scenarios indicate number of populations × population size.

individual will disperse from one population to another in a specific year [Lacy et al., 2008]. We completed 500 simulations for each scenario. A time frame of 50 generations was selected according to the biology of the target species [Armbruster et al., 1999]. Demographic parameters used as input to the model were based on previously published demographic data and PVA studies on *B. hypoxanthus* [Strier, 1991b, 1993/1994; Rylands et al., 1998; Strier, 2000, 2005; Brito and Grelle, 2006; Strier et al., 2006; Coutinho, 2007; Brito et al., 2008]. Here, a population is considered demographically viable if it presents <10% extinction probability in 50 generations and genetically viable if it retains >90% of its original genetic diversity in 50 generations [Foose et al., 1986; Soulé, 1987].

Results

No extinctions were observed when we modeled single continuous populations of 40 or 700 individuals (tables 1, 2). However, scenarios that included population subdivision resulted in a decrease in population growth rate and final metapopulation size, and an increase in population fluctuation and probability of extinction (tables 1, 2). The results show that dispersal rates do not counter the negative effects of population subdivision in small populations (table 1). In particular, when subdivision was more severe, an increase in dispersal was not capable of negating deleterious effects from fragmentation (table 1).

Our results show that small populations (40 individuals) do not support subdivision (table 1). Even the smallest level of subdivision resulted in a decrease in time to extinction (table 1). The scenarios evaluating the subdivision of a large population

Table 2. Results of the PVA for a *B. hypoxanthus* metapopulation size of 700 individuals for a time period of 50 generations, subdivided into 1, 2, 4 or 8 subpopulations and connected by dispersal rates of 0, 5, 10 or 20% per year

Scenarios	Dispersal rate, %	Population growth rate ± SD	Probability of extinction	Population size ± SD, n	Heterozygosity ± SD	Time to extinction, generations
1 × 700	–	0.062 ± 0.050	0.000	698.63 ± 7.99	0.910 ± 0.019	–
2 × 350	0	0.063 ± 0.041	0.000	696.39 ± 9.52	0.914 ± 0.018	–
	5	0.056 ± 0.041	0.000	696.88 ± 9.27	0.916 ± 0.018	–
	10	0.049 ± 0.041	0.000	696.27 ± 9.84	0.921 ± 0.018	–
	20	0.034 ± 0.039	0.000	691.04 ± 13.41	0.929 ± 0.014	–
4 × 175	0	0.063 ± 0.035	0.000	696.45 ± 9.22	0.922 ± 0.013	–
	5	0.042 ± 0.034	0.000	690.43 ± 11.52	0.927 ± 0.014	–
	10	0.020 ± 0.032	0.000	679.21 ± 17.87	0.932 ± 0.014	–
	20	−0.023 ± 0.063	1.000	0.00 ± 0.00	0.000 ± 0.000	11.07
8 × 87	0	0.063 ± 0.032	0.000	694.36 ± 9.21	0.934 ± 0.008	–
	5	0.013 ± 0.029	0.000	652.09 ± 24.07	0.932 ± 0.014	–
	10	−0.034 ± 0.063	1.000	0.00 ± 0.00	0.000 ± 0.000	7.36
	20	−0.050 ± 0.067	1.000	0.00 ± 0.00	0.000 ± 0.000	4.14

Scenarios indicate number of populations × population size.

(700 individuals) shows that subdividing the original population into two subpopulations does not affect long-term persistence, regardless of the dispersal rates among them (table 2). Scenarios of highly subdivided populations with no dispersal or low dispersal rates do not have negative effects for the populations (table 2).

Discussion

Theoretical studies indicate that population subdivision negatively affects demographic and genetic parameters of wildlife populations [Shaffer, 1981]. PVA models based on empirical data also showed the same trend for some mammals [Lacy and Lindenmayer, 1995; Lindenmayer and Lacy, 1995a; Brito and Fonseca, 2007; Brito, 2009a]. In a metapopulation structure, the size of the constituent populations seems to be an important factor for long-term persistence [Fahrig, 1997, 1998, 2001; Hanski and Gaggiotti, 2004]. Our results clearly show that dispersal does not seem to play an important role in the persistence of subdivided muriqui populations.

The subdivision of small populations (40 individuals) was detrimental to their long-term persistence, depressing growth rate and increasing demographic stochasticity [Shaffer, 1981; Soulé, 1987; Brito, 2009b]. Enhancing connectivity through dispersal had the result of further increasing population instability through metapopulation stochasticity [Lindenmayer and Lacy, 1995a, b; Brito and Fonseca, 2007; Brito, 2009a]. Dispersal among populations may also generate synchronous population dynamics, where temporal fluctuations in population size coincide (e.g. all popula-

tions decline or increase in size at the same time), and increased susceptibility to extinction [Heino et al., 1997; Bjørnstad et al., 1999]. Unfortunately we were not able to measure population synchrony in our model, but if it takes place our results underestimate the extinction risk due to dispersal-driven synchrony among populations.

From a demographic point of view, it is generally accepted that dispersal of individuals among populations has a positive effect on persistence [Brown and Kodrick-Brown, 1977; Simberloff et al., 1992; Frankham, 1995, 1999; Lande, 1998; Waite et al., 2005], even though the onset of other biological processes, such as disease transmission, might turn dispersal into a detrimental effect to population persistence. However, our results suggest that, even considering only demographic processes, there is evidence that a threshold exists below which stochastic events through metapopulation instability have a more powerful grip on population dynamics and dispersal might be detrimental to persistence [Lindenmayer and Lacy, 1995a, b; Lacy and Lindenmayer, 1995; Brito and Fonseca, 2007; Brito, 2009b]. In another PVA model, dispersal was not detrimental to the persistence of a small *Alouatta palliata mexicana* population (approx. 75 individuals) in a fragmented landscape with fragments ranging from 15 to 60 ha [Mandujano and Escobedo-Morales, 2008]. However, we observed detrimental effects for *B. hypoxanthus*, suggesting this process may also affect medium and large mammals.

Our results corroborate previous theoretical and empirical evidence that high dispersal rates may be detrimental to small populations in highly fragmented landscapes due to stochastic events [Lindenmayer and Lacy, 1995b]. In these cases, the loss of even a few individuals due to unsuccessful dispersal attempts may counteract the possible benefits of a metapopulation structure, increasing the likelihood of extinction [Lindenmayer and Lacy, 1995b]. In metapopulations comprising small populations, the mortality of dispersing individuals due to stochastic events taking place during dispersal represents a proportionally greater negative impact on population dynamics [Lindenmayer and Lacy, 1995b]. In such scenarios, each individual represents a greater proportion of the population, and as populations become smaller, the loss of individuals during dispersal (resulting in unsuccessful dispersal) will be more detrimental than possible rescue effects from successful dispersal attempts [Lindenmayer and Lacy, 1995b]. However, even though our theoretical modeling approach suggests the possible existence of such a metapopulation/connectivity threshold for northern muriquis, we must take into account that the dispersal rates used to model the populations are theoretical. We still understand very little about how muriquis move among fragments, and about how different matrix types translate into landscape permeability for the species, as well as having few estimates of dispersal rates and little information on dispersal behavior. Fieldwork focusing on muriqui dispersal capability (or lack of) is of paramount importance, not only for advancing knowledge about the biology of the species, but also for refining models on how the landscape structure might affect the species persistence, and if, as our model suggests, it might be susceptible to connectivity thresholds. Besides that, our results may be conservative, since we did not take into account several human activities such as hunting and fires that act synergistically with habitat fragmentation and are likely to affect northern muriqui populations in fragmented landscapes [Rylands et al., 1998].

These analyses warn that caution must be taken when devising conservation actions in highly fragmented landscapes, as to date commonplace strategies to counter

fragmentation are based on improving connectivity through dispersal corridors. In the case of the northern muriqui, empirical data on dispersal are urgently needed. Before management strategies are put into place, it would be wise to evaluate the landscape context each remnant population inhabits in order to estimate if it is below or above the subdivision threshold. Then, we could identify the most adequate habitat management plan for each situation, focusing on habitat restoration [Pontual and Boubli, 2005] or habitat connectivity, according to the landscape configuration where the population occurs.

Appendix

B. hypoxanthus demographic data used as input values to Vortex.
Extinction is defined as no animals of one or both sexes.

No inbreeding depression
First age of reproduction for females: 9, for males: 7
Maximum breeding age (senescence): 35
Sex ratio at birth (percent males): 35.600000
Polygynous mating
100.00% of adult males in the breeding pool
26.50% of adult females produce litters
EV in % adult females breeding = 12.40 SD
Of those females producing litters, …
100.00% of females produce litters of size 1
2.00% mortality of females between ages 0 and 1
EV in % mortality = 1.000000 SD
5.70% mortality of females between ages 1 and 2
EV in % mortality = 2.800000 SD
1.00% mortality of females between ages 2 and 3
EV in % mortality = 1.000000 SD
3.60% mortality of females between ages 3 and 4
EV in % mortality = 1.800000 SD
1.00% mortality of females between ages 4 and 5
EV in % mortality = 1.000000 SD
1.00% mortality of females between ages 5 and 6
EV in % mortality = 1.000000 SD
1.00% mortality of females between ages 6 and 7
EV in % mortality = 1.000000 SD
1.00% mortality of females between ages 7 and 8
EV in % mortality = 1.000000 SD
1.00% mortality of females between ages 8 and 9
EV in % mortality = 1.000000 SD
1.00% mortality of adult females (9 · age · 35)
EV in % mortality = 1.000000 SD
4.80% mortality of males between ages 0 and 1
EV in % mortality = 2.400000 SD
5.60% mortality of males between ages 1 and 2
EV in % mortality = 2.800000 SD
11.80% mortality of males between ages 2 and 3
EV in % mortality = 5.900000 SD

1.00% mortality of males between ages 3 and 4
EV in % mortality = 1.000000 SD
1.00% mortality of males between ages 4 and 5
EV in % mortality = 1.000000 SD
1.00% mortality of males between ages 5 and 6
EV in % mortality = 1.000000 SD
1.00% mortality of males between ages 6 and 7
EV in % mortality = 1.000000 SD
1.52% mortality of adult males (7 · age · 35)
EV in % mortality = 1.500000 SD
EVs may be adjusted to closest values possible for binomial distribution
EV in reproduction and mortality will be concordant
EV in carrying capacity = 0.00 SD
Deterministic population growth rate (based on females, with assumptions of no limitation of mates, no density dependence, and no inbreeding depression):
r = 0.063, λ = 1.065, R0 = 3.402
Generation time for females = 19.57, for males = 17.87

EV = Environmental variation; SD = standard deviation.

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