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Viability Analyses of an Isolated Population of Muriqui Monkeys *(Brachyteles arachnoides)*: Implications for Primate Conservation and Demography

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Introduction

The utility of population viability analyses (PVAs) for assessing extinction risks for endangered primates has recently been challenged on both practical and scientific grounds (Harcourt 1995). In addition to the practical difficulties of obtaining accurate demographic data for long-lived primates, PVA programs make assumptions about demographic processes that may not apply uniformly to all species (Walters 1991; Reed and Dobson 1993). Little is known, for example, about the actual effects of inbreeding depression in the wild (Caughley 1994), or about the degree to which rules of thumb that emphasize reproductive variables such as female age at first reproduction or reproductive rates can be generalized across primates with different life histories (Dobson and Lyles 1989; Soulé 1987). Demographic models also need to more fully integrate the effects of ecological variables on primate populations (Shaffer 1987; Lande 1988; Boyce 1992). As Harcourt (1995) notes, in most cases this involves incorporating the effects of habitat disturbance or loss into primate viability models. In some instances, however, modeling improvements in habitat availability and size may be more appropriately justified.

Despite these caveats, PVAs can still be productive first steps in the process of understanding how endangered primate populations may respond to specified demographic events. By comparing observed and hypothetical demographic parameters for particular populations that have been monitored closely over time, PVAs can also help to identify species-specific rules of thumb for evaluating data from censuses or short-term field studies.

This paper examines the viability of one population of muriqui monkeys *(Brachyteles arachnoides)* inhabiting the 800 ha forest at the Estação Biologica de Caratinga (EBC), located at Fazenda Montes Claros in Minas Gerais, Brazil (Strier 1991, 1992). The demographic and life history data, compiled over a 12-year period, are also used to evaluate some fundamental assumptions that may affect the reliability of PVAs for muriquis, and possibly other primates, and to identify key demographic variables that can be readily obtained from census data at other sites.

Muriquis meet established criteria for critically endangered species (IUCN 1994), largely because deforestation throughout their Atlantic forest habitat in southeastern Brazil has led to a highly fragmented distribution with small population sizes. In 1987, muriquis were known to occur at only 11 locations (Mittermeier *et al.* 1987). Although recent reports of additional localities in the states of Espírito Santo (Mendes and Chiarelli 1993) and São Paulo (Martuscelli *et al.* 1994) have nearly tripled the number of forests now known to support muriquis, estimates of the size of most of these populations are alarmingly low. The absence of long-term demographic and life history data for all but the EBC muriquis imposes severe limitations on the wider application of these viability analyses for the species (Soulé 1987; Soulé and Kohn 1987). Nonetheless, data derived from this population provide a basis for assessing both the future of the EBC muriquis and the critical variables that may affect the viability of muriquis at other sites.

Muriquis are also ideally suited for evaluating the presumed importance of inbreeding depression, female age at first reproduction, and reproductive rates to demographic models of population viability. For example, although demographic models and captive data indicate that inbreeding has deleterious effects on reproduction and survival, particularly among infants and juveniles (Ralls *et al.* 1986), there have been few supporting data from wild populations until recently (Pettersson 1985; Charlesworth and Charlesworth 1987; O'Brien *et al.* 1987; Shaffer 1987; Wildt *et al.* 1987; Boyce 1992; Caro and Laurenson 1994; Caughley 1994; Jiménez *et al.* 1994; Keller *et al.* 1994; Merola 1994; Vrijenhoek 1994; Fitzsimmons *et al.* 1995; Harcourt 1995).

The failure to consider the evolutionary history of species such as muriquis can also obfuscate extrapolations from theory to reality. Like other endemic Atlantic forest fauna, muriquis have a long evolutionary history of population fragmentation due to the expansion and contraction of the Atlantic forest during the Pleistocene glaciations (Kinzey 1982). The isolation of populations within Pleistocene refugia suggests that muriquis may have survived multiple genetic bottlenecks and repeated bouts of inbreeding and loss of genetic heterogeneity in their evolutionary past. It is unclear, however, how such a history of genetic isolation has affected their fitness, or whether such episodes in the past differ markedly from the fragmentation of their habitat due to human activities over the last quarter century (Strier 1992). If current conditions of fragmentation resemble those induced by climatic changes during the muriqui's evolutionary history, then the deleterious effects of inbreeding on their viability may not be as evident as demographic models might predict (Soulé and Kohn 1987; Lande 1988; Boyce 1992; Caughley 1994). Comparing extinction probabilities and projected population sizes under simulated inbreeding conditions may provide indirect evidence into the relative importance of considering a species' evolutionary history when evaluating its future viability (Strier in press a).

The demographic patterns of the EBC muriquis show no evidence that inbreeding has had deleterious effects on their survival or fecundity, despite the geographic and genetic isolation of these muriquis for at least the last 40 years. The main study group at this site has increased at a steady rate from 22 to 51 individuals between June 1982 and August 1993 due to extremely low mortality rates and correspondingly high birth rates (Strier 1991, 1993, in press b). With one exception, all females have transferred from their natal group at adolescence (5-7 years of age), and emigrations by natal females have been offset by female immigrations from one of the other two muriqui groups in the forest (Strier *et al.* 1993). Births have been strongly female-biased throughout the study period, and the interbirth interval, estimated at 36.37 ± 4.3 mos (median = 36.00 mos) from 19 successive births involving 11 females has remained stable (Strier in press b). Age at first reproduction, based on the only female known to have reproduced in her natal group, is estimated at 7.5 years, well within the three interbirth intervals identified by Dobson and Lyles (1989) in their comparative data on expanding primate populations (Strier 1991).

The rapid and steady increase in the size of this group has also resulted in a shift in the group's composition. The proportion of adult females (>7 years, see below) to immature females declined from 67% in 1982 to 54% in 1993, and there is some indication that the group may be approaching a stable age distribution in which the proportion of individuals in each age class remains constant (Emlen 1984). Both the skewed age distribution, which included a total absence of juvenile females, and the small group sizes suggest that the population had experienced a bottleneck prior to 1982 due to an unknown catastrophe from which it has been recovering ever since. Evaluating simulated effects of catastrophes on reproduction and survival, as well as differences in female age at first reproduction and infant sex ratios, can provide insights into the ways that these demographic variables affect population viability.

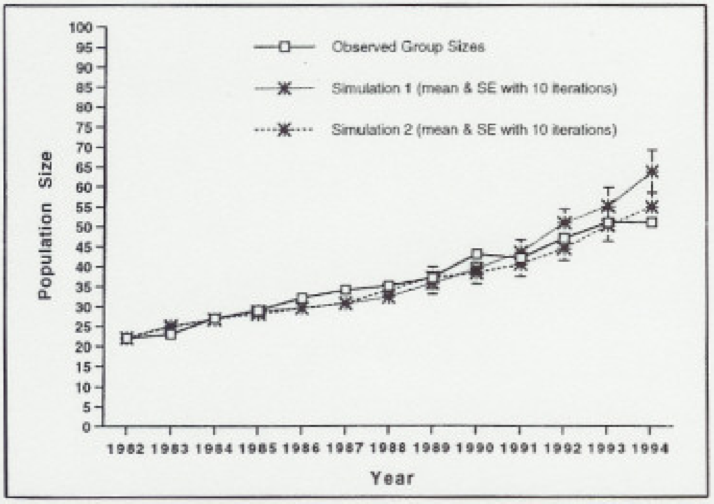

Fig. 1. Comparison of VORTEX trial simulations and observed group sizes. No difference between observed and expected (simulations) was detected. See text for explanation.

Unlike many other endangered primates, muriquis at the EBC have been well-protected. Prohibitions against hunting were in effect prior to the onset of the study, and large feline predators such as jaguars, which are known to prey on muriquis at other locations (e.g., Olmos 1994), are not present at this site, or, in the case of ocelots, have only recently begun to return (Strier pers. obs.). Selective logging has persisted in the forest, but comparative data from other study sites indicate that secondary and regenerating habitats created by such extraction actually support higher muriqui densities than the more floristically pristine forests (Fonseca 1985; Stalling and Robinson 1991; Strier 1992; Pinto *et al.* 1993; Stuart *et al.* 1993). The perimeter of the forest at the EBC has also expanded over the past decade as pasture and cultivated land have been allowed to regenerate. Consequently, both the effective forest size and muriqui carrying capacity at this site have been increasing. The effects of habitat improvement and variance in carrying capacity may thus be especially relevant ecological variables for assessing the future viability of muriquis at this and other privately-owned forests where disturbances due to human activities occur.

Methods

The demographic and life history data compiled for the EBC muriquis were adapted to meet the parameters required by VORTEX v.6 (Lacy 1993; Lacy *et al.* 1993). VORTEX was selected because of its widespread use in species' action plans for other endangered primates, but like all such programs, it makes specific assumptions that may not necessarily apply to all primates. To evaluate the appropriateness of VORTEX for muriquis, two trial

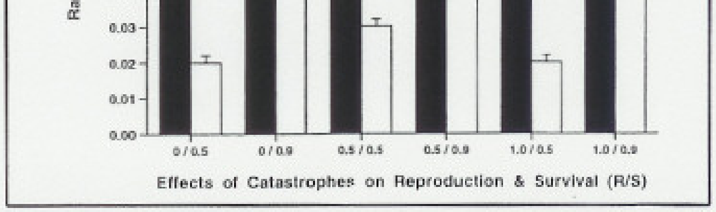

Fig 2. Effects of catastrophes on rates of population increase (mean and SE). A stable K and no inbreeding depression were modeled here. Effects of catastrophes on reproduction were modeled as 0 (total reproductive failure in years of catastrophes), 0.5 (50% loss in reproduction), and 1.0 (100% reproduction). Effects of catastrophes on survival were modeled as 0.5 and 0.9 (50% and 90% survival in catastrophic years). Paired comparisons between female first reproduction at 7 versus 11 years were significant (t = 11.00, df=5, p < 0.001).

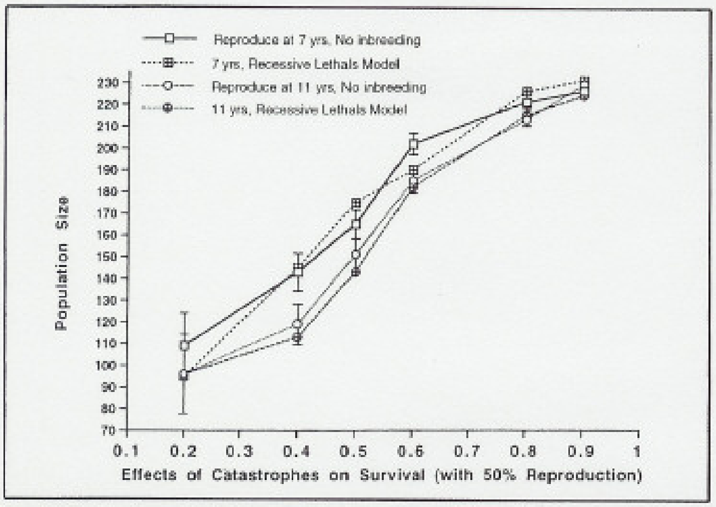

Fig. 3. Effects of survival in catastrophic years on population sizes at 100 years (mean and SE). A stable K was modeled here. Effects on catastrophes on survival were varied to range from 0.2-0.9 (only 20-90% of the population survived catastrophic years).

simulations with 10 iterations were run for the same 12-year period for which actual data are available. These trials used the 1982 age distribution and the life history and ecological parameters compiled during this period from one of the three muriqui groups now inhabiting this forest.

Both trial simulations yielded annual group sizes nearly identical to the actual group sizes observed during the same 12-year period ($r = 0.997$, $p < 0.001$, Fig. 1). Standard errors for each set of 10 iterations were minimal until the final years of the trial. These results suggest that VORTEX can provide credible estimates of group size with the demographic parameters observed during the study period.

The same demographic parameters calculated from the main study group were adopted in the extended simulations. Some of the variables in the VORTEX program were quantitatively derived from the actual 1982-1993 data base; others could only be estimated or anticipated. In both cases, multiple simulations were run with different values to assess the relative effects of each parameter. Variable values and their rationales are provided in the Appendix.

Extended simulations were run for 100 years with 100 iterations each. Means and standard errors based on the 100 iterations are presented. Rates of increase (*r*), extinction probabilities, and population sizes at 10 year intervals and at 100 years were compared under different simulated conditions.

Results

Effects of Catastrophes

The rate of population growth proved to be insensitive to the effects of catastrophes (estimated to occur at a rate of 1 per 15 years; see Appendix) on reproduction, even when total reproductive failure occurred in catastrophic years ($R = 0$; Fig. 2). Rates of population growth were, however, highly sensitive to the effects of survival during catastrophic years: higher survivorship (0.90, or 90%, in catastrophic years) also resulted in larger population sizes at 100 years than did lower survivorship (50%), whereas differing effects of catastrophes on reproduction were not detectable.

Both *r* and population size at 100 years (Fig. 3) increased with survivorship during catastrophic years. Extinction probabilities were inversely related to survivorship, and were less than 10% when at least 50% of the population survived catastrophes. Extinction probabilities did, however, increase dramatically when survivorship dropped below 50%.

Effects of Age at First Reproduction

Rates of population increase were consistently and significantly lower when females began reproducing at 11 years of age than when they began reproducing at 7 years (Fig. 2). Across the different effects of catastrophes modeled, age at first reproduction did not correspond to significant differences in population sizes at 100 years when deleterious inbreeding was absent and K was held constant, or when K increased without inbreeding depression or with the recessive lethals model of inbreeding. Population sizes at 100 years were significantly smaller when females delayed reproduction until 11 years only when both a constant carrying capacity and the recessive lethal model of inbreeding depression were specified (Figure 3). Extinction probabilities did not differ for early or late age at first reproduction across any of the varying inbreeding or K conditions.

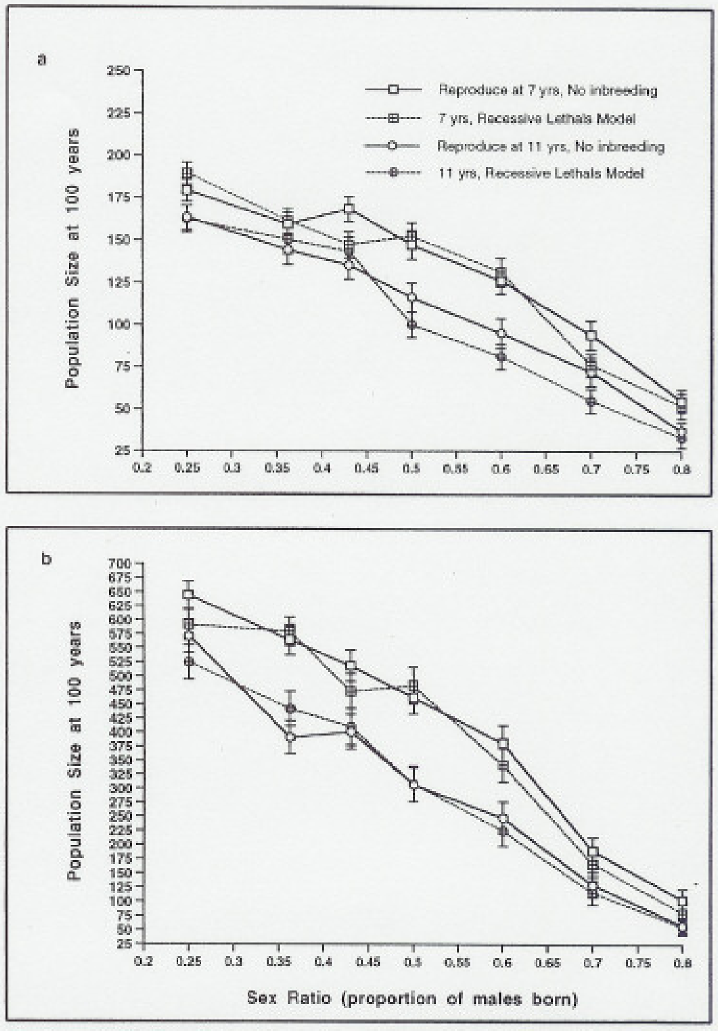

Fig. 4a and b. Effects of sex ratios and constant carrying capacity on population sizes at 100 years (mean and SE). No reproduction and 50% survival in catastrophic years were specified. a) K is modeled at a constant 240 individuals; b) K is modeled to increase 5% for 50 years.

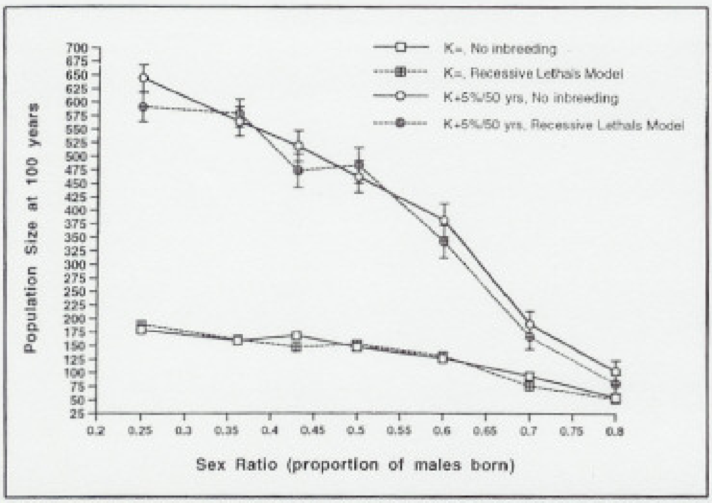

Fig. 5. Effects of varying sex ratios and carrying capacities on population sizes at 100 years (mean and SE). K is modeled at a constant 240 individuals (K=) or permitted to increase 5% for 50 years (K+5%/50 yrs). Female first reproduction at 7 years and no reproduction and 50% survival in catastrophic years were specified. No inbreeding depression and the recessive lethals model of inbreeding depression are compared.

Infant Sex Ratios

Varying the sex ratio of infants had similar effects on population sizes at 100 years independent of whether K was constant (Fig. 4a) or increased (Fig. 4b). Female-biased sex ratios resulted in consistently larger population sizes at 100 years than did male-biased sex ratios. Extremely male-biased sex ratios (0.80) led populations under expanding K conditions to converge on the smaller population sizes when K was held constant (Fig. 5). By 20-30 years into the simulation, populations with infant sex ratios of 0.50 or higher plateaued or began to decline (Fig. 6). The probability of extinction increased as sex ratios increased when K was held constant and when K expanded.

Inbreeding Models

There were no significant differences between any pairwise comparisons of inbreeding conditions when mean *r*, extinction probabilities, and population size at 100 years were compared for the six sets of catastrophic effects when K was held constant and permitted to increase 5% over 50 years. Population sizes were larger with no inbreeding depression, intermediate with the recessive lethals model, which assumes that each offspring inheriting homozygote lethals is immediately eliminated, and smaller for six of the 10-year intervals with the heterosis model of inbreeding using the default, median value of lethal equivalents supplied by VORTEX (Lacy 1993). Nonetheless, final population sizes at 100 years converged for each condition (Fig. 7).

Effects of Carrying Capacity (K)

The effects of catastrophes on reproduction and survival were consistent and proportionate across varying models of carrying capacity. The reproductive consequences of catastrophes were undistinguishable, while higher survival in catastrophic years resulted in larger population sizes. Greater increases in K always resulted in larger population sizes at 100 years.

Population sizes at 100 years were more than 50% larger when K was permitted to increase under severe catastrophic effects (no individuals reproduced and 50% survived) than when K was held constant under the most benign catastrophic conditions. Furthermore, under severe catastrophic conditions, population sizes were much more sensitive to the effects of increasing K than to inbreeding depression. For both early and delayed age at first reproduction, even populations modeled to experience inbreeding depression began to diverge between 20-30 years, or roughly 2-3 muriqui generations, when K was permitted to expand (Fig. 8a and b).

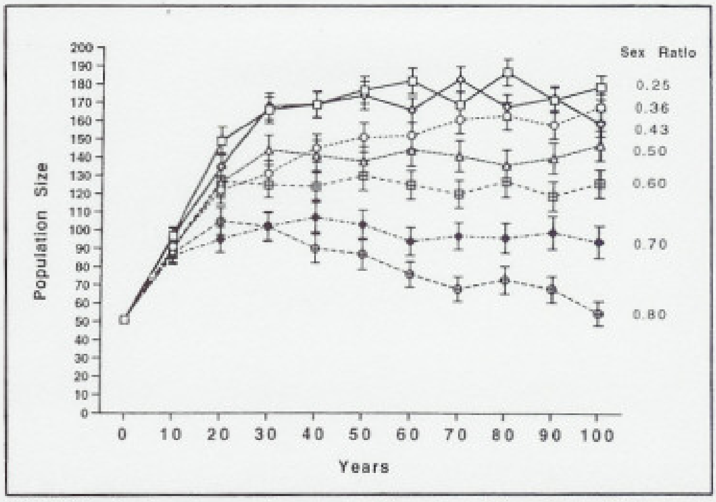

Fig. 6. Effects of varying sex ratios on population sizes at 10 year intervals (mean and SE). Female first reproduction at 7 years, constant K of 240 individuals, no inbreeding depression, and no reproduction and 50% survival in catastrophic years were specified.

Effects of Environmental Variance

Differences in environmental variance resulted in significantly different population sizes at 100 years across the various catastrophic conditions. Population sizes were generally larger when the variance in K was low (SD = 10%, or 24 individuals) than when it was high (SD = 50%). Under severe catastrophic conditions, population sizes deviated significantly at 10 year intervals before ultimately converging (Fig. 9). Consistent with the effects of increased K, the greatest differences from environmental variance occurred 20-30 years into the simulation. The mean probability of extinction was twice as high when environmental variance was 50% (0.08 ± 0.03) than when it was 10% (0.04 ± 0.02), but first population extinction occurred at 43 years in both cases. Indeed, although the number of extinctions caused solely by environmental variance is small compared to other causes in these simulations, the population is nonetheless vulnerable to environmental effects.

Discussion

Variables Affecting the Viability of the EBC Muriquis

The simulations presented here indicate that the EBC muriquis have a low probability of extinction during the next 100 years. This optimistic assessment is based on the unrealistic assumption that the extraordinarily low mortality, high fecundity, and female-biased sex ratios documented over the last 12 years will persist in the future (see Ginzburg *et al.* 1990). While there is no evidence to date that reproduction is density dependent, it is likely that this situation will change as population size increases unless the carry-

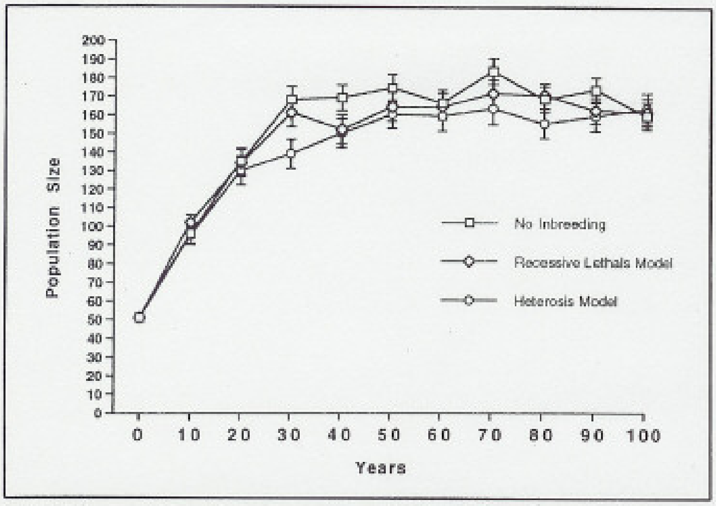

Fig. 7. Effects of inbreeding depression on population size at 10 year intervals (mean and SE). A constant K, female first reproduction at 7 years, and no reproduction and 50% survival in catastrophic years were modeled here. Both models of inbreeding depression in the VORTEX v.6 program are used.

ing capacity of this forest can be increased beyond the monkeys' capacity to populate it (Boyce 1992). Similarly, the strongly female-biased sex ratio is likely to be a stochastic phenomenon (Gabriel *et al.* 1991; Caughley 1994). Increasingly male-biased sex ratios, in addition to higher mortality rates, would have profound effects on the population's viability, as demonstrated by the higher extinction probabilities when sex ratios were simulated at ≥0.50 and survivorship in catastrophic years dropped below 50%. The importance of continued monitoring of these variables in the EBC muriquis is strongly indicated.

The fact that rates of population increase, extinction probabilities, and population sizes at 100 years were not affected by reproductive failure during catastrophic years may be a consequence of the muriquis' long interbirth intervals. Because only about a third of mature females reproduce in any year, the consequences of a bad year for reproduction are proportionately lower than they would be for a species that reproduced at shorter intervals (Belovsky 1987). More frequent catastrophes that led to total reproductive failure could, nonetheless, inhibit population recovery (Gabriel *et al.* 1991), making continued monitoring of female reproductive success imperative. Similarly, although female age at first reproduction did not alter extinction probabilities, delayed reproduction did result in slower rates of growth. In contrast to Dobson and Lyles' (1989) rule of thumb, however, population growth was still positive when female age at first reproduction was 11 years, and therefore greater than 3 interbirth intervals under the existing female-biased infant sex ratio.

Among the most striking findings to emerge from these simulations is that inbreeding depression, at least as it is modeled in VORTEX v. 6, does not appear to be a serious concern for the EBC muriquis in the next 100 years. This may reflect the fact that muriqui numbers at this site are presently above some critical size, that 100 years is insufficient time for inbreeding depression to affect population size with the muriquis long generation lengths, or that their high birth rate and low mortality rate permit population size to increase above this level fast enough to compensate for losses due to inbreeding (Caughley 1994). Behavioral patterns in which female muriquis do not mate with their sexually active sons, and daughters emigrate from their natal groups during adolescence may also limit the opportunities for inbreeding between close relatives (Strier in press c). The effects of inbreeding depression might become more evident if the number of muriquis at this site dropped due to severe mortality in response to catastrophes or strongly male-biased sex ratios that lower overall fecundity or restrict the availability of unrelated mates (Soulé and Kohn 1989; Boyce 1992).

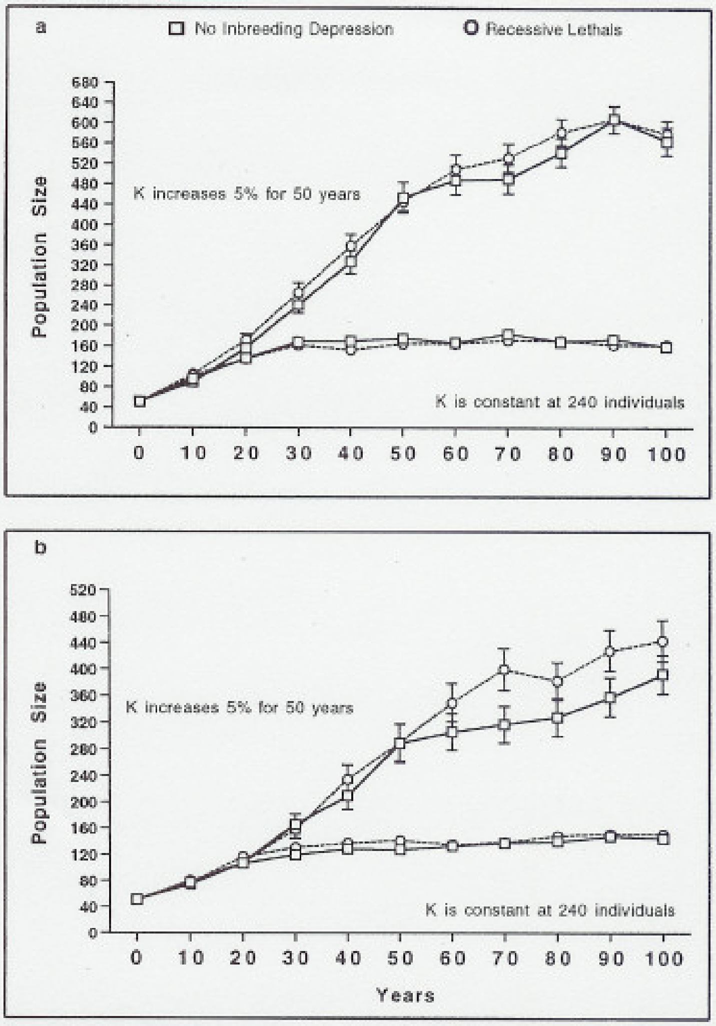

Fig. 8a and b. Effects of changes in carrying capacity on population size at 10 year intervals when a) female first reproduction is 7 years, and b) when female first reproduction is 11 years. No inbreeding depression and the recessive lethals model of inbreeding depression are compared with K is constant or increases 5% for 50 years. No reproduction and 50% survival in catastrophic years were modeled here.

While it is not possible to control mortality rates or infant sex ratios, the simulations indicate that even a modest increase in the carrying capacity at this site could help buffer this population from catastrophic or stochastic demographic events (Harcourt 1995). Expanding the available habitat now, while mortality rates and sex ratios are still low and birth rates are still high, would permit the population to increase to the point that its long-term viability would not be jeopardized by temporary declines in survival or reproduction.

Increasing carrying capacity and reducing environmental variance in K should lead to larger populations within 20-30 years under the current demographic conditions specified in the simula-

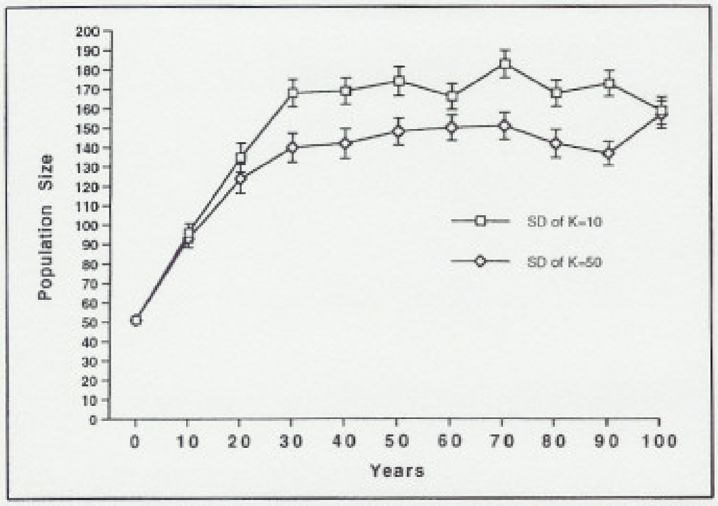

Fig. 9. Effects of environmental variance (SD[K]) on population size at 10 year intervals. A stable K, female age at first reproduction of 7 years, and no inbreeding depression were modeled here. See appendix for explanation of environmental variance. No reproduction and 50% survival in catastrophic years were modeled here. Paired comparisons across the 10 year intervals between SD(K) =1 0% and SD(K) =5 0% were significantly different ($t= 5.50$, $df = 9$, $p < 0.001$).

tions. The fact that 20-30 years into the simulations is also the point at which the effects of higher infant sex ratios on population size become apparent further emphasizes that action to ensure habitat expansion during the next 2-3 muriqui generations will be critical to their long-term viability at this site.

The minimum impact that inbreeding depression appears to have on extinction probabilities and population size at 100 years also supports the argument that translocations to increase genetic diversity are not yet warranted for these muriquis (Strier 1991, 1992). The relatively long generation length for muriquis permits time to develop an informed response to increases in mortality or sex ratios that may ultimately lead to population decline, but immediate attention to habitat recovery and expansion will help to insulate this population from such demographic shifts (Goodman 1987).

Implications for Muriquis at Other Sites

The protected status, habitat expansion, and increase in muriqui numbers at the EBC make extrapolations from the present PVA to muriquis at other sites extremely tenuous (Reed and Dobson 1993). It is questionable whether the life history parameters calculated from the long-term data at the EBC are applicable to other populations of muriquis, particularly when the morphological and genetic evidence supporting the distinction of muriquis into northern *(Brachyteles arachnoides hypoxanthus)* and southern *(B.a. arachnoides)* subspecies are considered (Vieira 1944; Lemos de Sá and Glander 1993). Despite the successful interbreeding of individuals from these regions in captivity (Coimbra-Filho *et al.* 1993, 1994), it is not known whether the earlier ages at first reproduction for both females and males and the shorter interbirth intervals from captivity reflect subspecific or populational variability, or their release from social and/or ecological stresses that may affect wild animals (Strier in press b).

The demographic parameters calculated from the EBC muriquis are even less likely to apply to muriquis inhabiting ecologically different forests. Forest size and composition, degree of human disturbance, sympatric food competitors, and predator pressures are known to vary widely (Fonseca 1985; Stalling and Robinson 1991; Strier 1992; Pinto *et al.* 1993; Stuart *et al.* 1993). It will only be possible to assess the degree to which these factors affect forest carrying capacity and muriqui demography and viability when comparative data become available. Indeed, even in the present analyses where the relevant demographic variables are well-documented, the constant K of 240 individuals estimated is subject to doubt (see also rationale in Appendix). The density of 0.3 individuals/ha may be an overestimate of the actual carrying capacity at EBC because sympatric brown howler monkeys *(Alouatta fusca)* and capuchin monkeys (*Cebus apella*) may deplete or compete with muriquis for shared food sources (Mendes 1989; Rímoli in prep.). Conversely, it may underestimate EBC carrying capacity because the extreme heterogeneity of the forest, which includes primary as well as secondary and regenerating forest (Hatton *et al.* 1983), may provide essential microhabitats that can support more muriquis than forests where no primary forest vegetation occurs.

Larger, less disturbed forests support uniformly lower muriqui densities than the smaller disturbed forests like EBC (e.g., Pinto *et al.* 1993), but the suggestion that these differences are due to the absence of abundant secondary and regenerating food resources in the pristine areas remains a hypothesis (Strier 1992). The impact of predation on muriqui mortality rates, which is likely to be greater at large, less disturbed forests where predators are more abundant, also requires further comparative data to evaluate.

Despite these limitations, the EBC data provide potential insights into assessing the viability of muriquis at other localities. First, small populations, with fewer than 50 individuals, are predictably more vulnerable to extinction than larger populations (see Franklin 1980). Enhancing the size of these remnant populations by introducing muriquis would only be warranted, however, in well-protected areas where carrying capacity can be reasonably estimated and the impact of muriquis on other sympatric species can be monitored. Based on the consistent patterns of female dispersal and male philopatry among the EBC muriquis, such introductions should involve only females, but even then, the risks of exposing individuals with parasitic infections to naive hosts must be weighed (Boyce 1992; Strier 1993; Stuart *et al.* 1993).

Populations with more than 50 individuals may prove to be viable and capable of recovering without costly or risky intervention programs provided that they and their habitats are well-protected and that mortality rates are low and birth rates are high. While it is difficult to estimate mortality and birth rates from census data, it is possible to calculate sex ratios from counts of unhabituated animals. Visual determination of sex is relatively easy in muriquis because both males and females have pendulous genitalia that are distinguishable within a few months of birth. Inferring from the present study, populations with infant sex ratios lower than 0.5 are expected to have a higher probability of recovery than those with male-biased sex ratios (Caughley 1994).

The results of the present analyses imply that even small muriqui populations surviving in disturbed habitats merit conservation efforts. The evidence that small-scale disturbances that increase the heterogeneity of these forests may actually increase forest carrying capacity also suggests that controlled, sustainable extraction programs in collaboration with the private owners of these forests may be beneficial to muriquis as well.

Implications for Interpreting PVAs on Other Primates

The indistinguishable effects of inbreeding depression on muriqui extinction probabilities and population sizes suggest that the deleterious effects of inbreeding may be overrated in demographic models or that the inbreeding depression modeled in VORTEX is inappropriate for a variety of reasons. Indeed, VORTEX assumes that inbreeding impacts only juvenile survival, and that all animals are initially unrelated. The fact that at least some of the EBC muriquis are known relatives (parent-offspring or siblings), as is likely to be the case in other closed primate populations, suggests that inbreeding projections simulated in VORTEX may not always apply. In addition, because the recessive lethals model of inbreeding assumes that homozygotes are eliminated from the population, there are few ways in which lethals can accumulate in populations such as that of the EBC muriquis, where females migrate between groups within a single, related population (Charlesworth and Charlesworth 1987). Finally, it is possible that although inbreeding had minimal effects on final population sizes at 100 years in the present simulations, populations with different starting sizes may have higher extinction probabilities (Bowman and Falconer 1960).

It is also possible that other aspects of muriqui life histories or demography compensate or override the effects of inbreeding, including their behavioral avoidance of matings between close relatives (Strier in press c). Alternatively it is possible that inbreeding may affect different species to different degrees depending on their evolutionary history (Walters 1991; O'Brien 1994). Mutation rates and genetic heterogeneity are known to vary widely across primates (Caughley 1994), and these differences may be important to consider when applying inbreeding models to viability analyses (Allendorf 1986; Soulé and Kohn 1989; Boyce 1992).

The effects of infant sex ratios on muriqui viability also suggest significant implications for other primates. The finding that EBC muriquis continue to exhibit population growth even when female age at first reproduction exceeds 3 interbirth intervals may be a consequence of their strongly female-biased sex ratio. Evaluating the effects of skewed sex ratios on other primates may lead to refinements in the demographic models used to assess population viability (Gabriel *et al.* 1991; Boyce 1992; Caughley 1994).

Population sizes were consistent in diverging from one another between 20-30 years into simulations comparing different sex ratios, carrying capacities, and environmental variance. If these projections, which correspond to 2-3 muriqui generations, also apply to other primates, they present a paradox for conservation strategies. Species with long generation lengths are generally considered to be more vulnerable to extinction because of their slower reproductive rates (Belovsky 1987). Yet, the same 20-30 years that appear to be critical for ensuring the viability of muriquis may be too long for species with shorter generations. Greater insights into the interactions between generation length and extinction risks are clearly needed.

While it is unadvisable to extend the results from viability analyses of a single population to other populations of the same species or to other species (Gilpin and Soulé 1986), the popular adoption of PVAs by policy makers make evaluating the reliability of PVAs an urgent concern. The limited contributions of female age at first reproduction, reproductive consequences of catastrophes, and inbreeding depression to muriqui viability in the present analyses support suggestions that models emphasizing these variables may not be widely applicable to wild populations (Thomas 1990). At the same time, the apparent importance of infant sex ratio, catastrophic survival, and carrying capacity to the viability of the EBC muriquis provide examples of alternative variables that may merit closer scrutiny.

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Literature Cited

Allendorf, F.W. and R.F. Leary. 1986. Heterozygosity and fitness in natural populations of animals. In: *Conservation Biology: The Science of Scarcity and Diversity*, M.E. Soulé (ed.), pp. 57-76. Sinauer Associates, Sunderland, Massachusetts.

Belovsky, G.E. 1987. Extinction models and mammalian persistence. In: *Viable Populations for Conservation*, M.E. Soulé (ed.), pp. 35-57. Cambridge University Press, Cambridge.

Bowman, J.C. and D.S. Falconer. 1960. Inbreeding depression and heterosis of litter size in mice. *Genetic Research Cambridge* 1:262-274.

Boyce, M.S. 1992. Population viability analysis. *Ann. Rev. Ecol. Syst.* 23:481-506.

Caro, T. and M.K. Laurenson. 1994. Ecological and genetic factors in conservation: a cautionary tale. *Science* 263:485-486.

Caughley, G. 1994. Directions in conservation biology. *J. Anim. Ecol.* 63:215-244.

Charlesworth, D. and B. Charlesworth. 1987. Inbreeding depression and its evolutionary consequences. *Ann. Rev. Ecol. Syst.* 18:237-268.

Coimbra-Filho, A.F., A. Pissinatti and A.B. Rylands. 1993. Breeding muriquis *Brachyteles arachnoides* in captivity: the experience of the Rio de Janeiro Primate Centre (CPRJ-FEEMA). *Dodo, J. Wildl. Preserv. Trusts* 29:66-77.

Coimbra-Filho, A.F., A. Pissinatti and A.B. Rylands. 1994. Muriquis at the Rio de Janeiro Primate Centre. *Neotropical Primates* 2(1):5-7.

Dobson, A.P. and A.M. Lyles. 1989. The population dynamics and conservation of primate populations. *Conservation Biology* 3:362-380.

Emlen, J.M. 1984. *Population Biology: The Coevolution of Population Dynamics and Behavior*. MacMillan Publishers, New York.

Fitzsimmons, N.N., S.W. Buskirk and M.H. Smith. 1995. Population history, genetic variability, and horn growth in bighorn sheep. *Conservation Biology* 9:314-323.

Fonseca, G.A.B. 1985. The vanishing Brazilian Atlantic forest. *Biol. Conserv.* 34:17-34.

Franklin, I.R. 1980. Evolutionary change in small populations. In: *Conservation Biology, an Evolutionary-Ecological Perspective*, M.E. Soulé and B.A. Wilcox (eds.), pp.135-149. Sinauer Associates, Sunderland, Massachusetts.

Gabriel, W., R. Bürger and M. Lynch. 1991. Population extinction by mutational load and demographic stochasticity. In: *Species Conservation: A Population-Biological Approach*, A. Seitz and V. Loeschke (eds.), pp. 49-59. Birkhäuser Verlag, Basel.

Gilpin, M.E. and M.E. Soulé. 1986. Minimum viable populations: processes of species extinction. In: *Conservation Biology: The Science of Scarcity and Diversity*, M.E. Soulé (ed.), pp. 19-34. Sinauer Associates, Sunderland, Massachusetts.

Ginzburg, L.R., S. Ferson and H.R. Akçakaya. 1990. Reconstructibility of density dependence and the conservative assessment of extinction risks. *Conservation Biology* 4:63-70.

Goodman, D. 1987. The demography of chance extinction. In: *Viable Populations for Conservation*, M.E. Soulé (ed.), pp.11-35. Cambridge University Press, Cambridge.

Harcourt, A.H. 1995. Population viability estimates: theory and practice for a wild gorilla population. *Conservation Biology* 9:134-142.

Hatton, J.C., N.O.E. Smart and K. Thomas. 1983. An ecological study of the Fazenda Montes Claros forest, Minas Gerais, Brazil. Interim Report, University College, London.

IUCN. 1994. *IUCN Red List Categories*. IUCN Species Survival Commission, Gland, Switzerland.

Jiménez, J.A., K.A. Hughes, G. Alaks, L. Graham and R.C. Lacy. 1994. An experimental study of inbreeding depression in a natural habitat. *Science* 266:271-273.

Keller, L.F., P. Arcese, J.N.M. Smith, W.M. Hochachka and S.C. Stearns. 1994. Selection against inbred song sparrows during a natural population bottleneck. *Nature* 372:356-357.

Kinzey, W.G. 1982. Distribution of primates and forest refuges. In: *Biological Diversification in the Tropics*, G.T. Prance (ed.), pp.55-482. Columbia University Press, New York.

Lacy, R.C. 1993. VORTEX: a computer simulation model for population viability analysis. *Wildl. Res.* 20:45-65.

Lacy, R.C., K.A. Hughes and T.J. Kreeger. 1993. *VORTEX Users Manual, Second Edition: A Stochastic Simulation of the Extinction Process*. IUCN SSC Captive Breeding Specialist Group, Apple Valley, Minnesota.

Lande, R. 1988. Demographic models of the northern spotted owl (*Strix occidentalis caurina*). *Oecologia* 75:601-607.

Lemos de Sá, R.M. and K.E. Glander. 1993. Capture techniques and morphometrics for the woolly spider monkey, or muriqui (*Brachyteles arachnoides*, E. Geoffroy 1806). *Am. J. Primatol.* 29:145-153.

Martuscelli, P., L.M. Petroni and F. Olmos. 1994. Fourteen new localities for the muriqui, *Brachyteles arachnoides*. *Neotropical Primates* 2(2):12-15.

Mendes, S.L. 1989. Estudo ecologico de *Alouatta fusca* (Primates: Cebidae) na Estação Biologica de Caratinga, M.G. *Rev. Nordestina Biol.* 6:71-104.

Merola, M. 1994. A reassessment of homozygosity and the case for inbreeding depression in the cheetah, *Acinonyx jubatus*: implications for conservation. *Conservation Biology* 8:961-971.

Mittermeier, R.A., C. Valle, K.B. Strier, A.L. Young, S.G. Paccagnella and R.M. Lemos de Sa. 1987. Current distribution of the muriqui in the Atlantic forest region of eastern Brazil. *Primate Conservation* (8):143-149.

O'Brien, S.J. 1994. The cheetah's conservation controversy. *Conservation Biology* 8:1153-1155.

Olmos, F. 1994. Jaguar predation on muriqui, *Brachyteles arachnoides*. *Neotropical Primates* 2(2):16.

Pettersson, B. 1985. Extinction of an isolated population of the middle spotted woodpecker *Dendrocopos medius* (L.) in Sweden and its relation to general theories on extinction. *Biol. Conserv.* 32:335-353.

Pinto, L.P.S., C.M.R. Costa, K.B. Strier and G.A.B. Fonseca. 1993. Habitats, density, and group size of primates in the Reserva Biologica Augusto Ruschi (Nova Lombardia), Santa Teresa, Brazil. *Folia Primatol.* 61:135-143.

Ralls, K., P.H. Harvey and A.M. Lyles. 1986. Inbreeding in natural populations of birds and mammals. In: *Conservation Biology: the Science of Scarcity and Diversity,* M.E. Soulé (ed.), pp.35-56. Sinauer Associates, Sunderland, Massachusetts.

Reed, J.M. and A.P. Dobson. 1993. Behavioral constraints and conservation biology: conspecific attraction and recruitment. *Trends in Ecology and Evolution* 8:253-256.

Shaffer, M.L. 1987. Minimum viable populations: coping with uncertainty. In: *Viable Populations for Conservation*, M.E. Soulé, (ed.), pp.69-86. Cambridge University Press, Cambridge.

Soulé, M.E. 1987. Introduction. In: *Viable Populations for Conservation*, M.E. Soulé, (ed.), pp.1-10. Cambridge University Press, Cambridge.

Soulé, M.E. and K.A. Kohn (eds.). 1989. *Research Priorities for Conservation Biology*. Island Press, Washington, DC.

Stallings, J.R. and J.G. Robinson. 1991. Disturbance, forest heterogeneity and primate communities in a Brazilian Atlantic forest park. In: *A Primatologia no Brasil-3,* A.B. Rylands and A.T. Bernardes (eds.), pp. 357-368. Sociedade Brasileira de Primatologia, Fundação Biodiversitas, Belo Horizonte.

Strier, K.B. 1986. The Behavior and Ecology of the Woolly Spider Monkey, or Muriqui (*Brachyteles arachnoides*, E. Geoffroy 1806). Unpubl. Ph.D. dissertation, Harvard University, Cambridge, MA.

Strier, K.B. 1987. Reprodução de *Brachyteles arachnoides*. In: *A Primatologia no Brasil-2*, M. T. de Mello (ed.), pp.163-175. Sociedade Brasileira de Primatologia, Brasília.

Strier, K.B. 1991. Demography and conservation in an endangered primate, *Brachyteles arachnoides. Conservation Biology* 5:214-218.

Strier, K.B. 1992. *Faces in the Forest: the Endangered Muriqui Monkeys of Brazil*. Oxford University Press, New York.

Strier, K.B. 1993. Conservation of the muriqui in the state of Espírito Santo, SE Brazil. *Neotropical Primates* 1(3):1-2.

Strier, K.B., F.D.C. Mendes, J. Rímoli and A.O. Rímoli. 1993. Demography and social structure in one group of muriquis (*Brachyteles arachnoides*). *Int. J. Primatol.* 14:513-526.

Strier, K.B. In press a. Behavioral ecology and conservation biology of primates and other animals. *Advances in the Study of Behavior*.

Strier, K.B. In press b. Reproductive ecology of female muriquis. In: *Adaptive Radiations of Neotropical Primates*, M. Norconk, A. Rosenberger and P. Garber (eds.). Plenum Press, New York.

Strier, K.B. In press c. Mate preferences of wild muriqui monkeys (*Brachyteles arachnoides*): reproductive and social correlates. *Folia Primatol.*

Stuart, M.D., K.B. Strier and S.M. Pierberg. 1993. A coprological survey of parasites of wild woolly spider monkeys, *Brachyteles arachnoides*, and brown howling monkeys, *Alouatta fusca. J. Helminth. Soc.* 60:111-115.

Thomas, C.D. 1990. What do real population dynamics tell us about minimally viable population sizes? *Conservation Biology* 4:324-327.

Vieira, C.C. 1944. Os símios do estado de São Paulo. *Pap. Avulsos de Zool. (São Paulo)* 8:341-474.

Vrijenhoek, R.C. 1994. Genetic diversity and fitness in small populations. In: *Conservation Genetics*, V. Loeschcke, J. Tomiuk, and S.K. Jain (eds.), pp.37-53. Birkhäuser Verlag, Basel.

Walters, J.R. 1991. Application of ecological principles to the management of endangered species: the case of the red-cockaded woodpecker. *Ann. Rev. Ecol. Syst.* 22:505-523.

Wildt, D.E., M. Bush, K.L. Goodrowe, C. Packer, A.E. Pusey, J.L. Brown, P. Joslin and S.J. O'Brien. 1987. Reproductive and genetic consequences of founding isolated lion populations. *Nature, Lond.* 329:328-331.

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Appendix

VORTEX variables and rationales for values entered

Number of iterations: 100 (10 for trial simulations)
Number of years: 100 (12 for trial simulations)
Extinction reports: 10 years (annually for trial simulations)
Number of populations: 1

Rationale: All demographic data were derived from one of the three muriqui groups now inhabiting the EBC forest. It is assumed that these data represent this entire population. The group was modeled as a single population owing to the lack of validity of generalizing the demographic parameters from this site to others.

Inbreeding depression: Varied (No for trial simulations)

Rationale: The lack of evidence of deleterious effects of inbreeding on the EBC muriquis over the past 12 years justified specifying no inbreeding in the trial simulations. However, simulations comparing population viability without inbreeding depression and with both the recessive lethals model and the heterosis model were run holding K constant with female age at first reproduction of 7 years. All other simulations were run without inbreeding depression and with the recessive lethals model of inbreeding depression. The recessive lethals model was used because it assumes that all lethal alleles are removed by natural selection when homozygous and that each founder member of the population carries a single recessive lethal and non-lethal allele. The fact that the population appeared to be recovering from a bottleneck that eliminated nearly the entire juvenile class at the onset of the study provided justification for the assumption that lethal equivalents were low at the onset of the simulations. Survivors are expected to be highly homogeneous. See Charlesworth and Charlesworth (1987) and Lacy (1993) for further details.

Number of types of catastrophes: 1 (0 for trial simulations)

Rationale: Any of several possible catastrophes (e.g., drought, fire, epidemic) could occur, but each is assumed to affect reproduction and survivorship similarly.

Probability of catastrophe: 6.67%

Rationale: The estimated probability of catastrophes of 1 per 15 years (0.0667) is based on the assumption that a catastrophe had occurred prior to the onset of the study in 1982 when the original group size was small and group composition highly skewed toward adults. A fire that burned roughly 30 ha of forest in 1990 occurred beyond the muriquis' home range, but by 1994 the muriquis had begun to exploit this regenerating area.

Breeding system: Polygynous

Rationale: Determined from data (Strier 1986, 1987, 1992).

Age females begin breeding: Varied (7 years for trial simulations)

Rationale: Female age at first reproduction was determined from data to be 7.5 years (Strier 1991). This estimate was based on a single female who reproduced in her natal group. She was an infant in June 1982 and gave birth to her first offspring in September 1989. This may be younger than the age that most females who emigrate from their natal groups reproduce. Indeed, the average age of migration is 72 mos (± 5.5 mos; Strier in press b), and the estimated age that immigrant females begin reproducing is 9 years (± 2 years; Strier in press b). Thus, extended simulations using 7 and 11 years for female first reproduction were compared.

Age males begin breeding: 7

Rationale: Determined from data (Strier in press b). Much younger males have achieved successful fertilizations in captivity (Coimbra-Filho *et al.* 1993), suggesting that social and/or ecological factors may delay the onset of reproductive maturity in the wild.

Age of senescence: 35

Rationale: There are no data on senescence in muriquis, but dental examination of wild muriquis at another site led to an estimated age of >29 years for one female (Lemos de Sá and Glander 1993).

Proportion of males at birth: Varied (0.366 for trial simulations)

Rationale: Of a total 35 infants born in the study group from 1983-1993 and the 6 infants that were present in the group in 1982, 26 were females and 15 were males. The sex of one of a set of twins was not determined prior to its death and is not included among the 41 infants on which this ratio is based. The only other infant mortality documented, a male, is included in this ratio. The female-biased sex ratio may be atypical for these muriquis, or may reflect female age or reproductive experience (Strier in press b). To examine the effects of variation in sex ratios, simulations were also run using ratios from 0.25 (strongly female-biased) to 0.80 (strongly male-biased).

Maximum Litter Size: 2

Rationale: One set of twins was born during the study period (Strier 1991).

Is reproduction density dependent: No

Rationale: There is currently no evidence that reproduction in this group has been affected by group size or density.

Percent of females producing litter sizes (SD) of

0: 69.5 (19.8)

1: 29.7 (20.5)

2: 0.8 (2.9)

Rationale: Calculations are based on all infants born between 1983-1993. Interbirth intervals average roughly 3 years (see text; Strier in press b), so in most years, females are associated with a single infant. Of the 35 births between 1983-1993, 97.14% involved single infants. An average SD of 20 was calculated based on the average 3-year interbirth interval, with 31% of the females reproducing annually from 1982-1993.

Age-specific mortality (mean and [SD]):

Age	Females	Males
0-1	0 (0)	0 (0)
1-2	0 (0)	0 (0)
2-3	0 (0)	0 (0)
3-4	6.3 (17.7)	10 (22.4)
4-5	0 (0)	0 (0)
5-6	0 (0)	0 (0)
6-7	0 (0)	0 (0)
>7	0 (0)	3.4 (8.1)

Rationale: Determined from data. Mean mortality rates and SD for each age-class were calculated by obtaining the proportion of individuals that died for each year interval, summing these proportions, and dividing them by the number of years in which there were entries for those age classes. For example, there were 5 years in which males fell or should have fallen into the 3-4 year age class. Four of these years had 0% mortality, in one year, 1 of 2 males, or 50% of the 3-4 year old males disappeared and is presumed dead. The total mortality, 50%, was divided by the 5 years in which this age class was represented to yield an average of 10% mortality and an SD of 22.4%. Two of the 11 years in which males were classified in the >7 year age class suffered 25% and 12.5% mortalities (2/8 and 2/7, respectively); the other 9 years included 0% mortalities among adult males. Female disappearances from 5 years of age are treated as emigrations with 0% mortality based on confirmation of their successful integration into new groups. Note that with such low mortality rates, it may be inappropriate to distinguish age and sex specific mortality values.

Do all adult males breed: Yes

Rationale: Determined from data (Strier 1994, in press c).

Stable age distribution: No

Age	Females (1993)	Males (1993)	Females (1982)	Males (1982)
1	2	2	4	2
2	6	2	0	0
3	1	1	0	0
4	2	0	0	0
5	1	2	0	0
6	3	1	0	2*
7	0	1	0	0
8	1	2	8*	6*
9	0	0		
10	5	0		
11	0	0		
12	2	2		
13	0	0		
14	0	0		
15	1	0		
16	1	0		
17	0	1		
18	0	0		
19	8*	4*		
≥20	0*	0*		

Rationale: Age distributions were determined from actual situation at the onset of the study in 1982 for the trial simulations and as of August 1993 for the extended simulations. All adults at the onset of the study were assigned a minimum age of 8 years. Asterisks indicate that these are estimated values that may underestimate true age.

Carrying capacity: 240 (100 in trial simulations)

Rationale: Carrying capacity was estimated based on the highest reported density for muriquis, where 12 individuals occupied a 40 ha forest (Lemos de Sá and Glander, 1993). A density of 0.3 individuals per ha at EBC yields a K of 240 muriquis in this 800 ha forest. See text for further qualifications.

SD in K due to EV: Varied (10% in trial simulations)

Rationale: Environmental variance was estimated to be 10%, equal to 24 individuals in the extended simulations and 10 individuals in the trial simulations. Extended simulations were also run with an EV or 50%, equal to 120 individuals. The EV of 10% reflects the highest mortality observed for any age class, but otherwise there is no empirical basis for this or the higher estimated value.

Trend in K? Varied (Yes in trial simulations)

Rationale: Habitat regeneration along the perimeter of the forest during the 12-year study period has resulted in an increase in K. The muriquis have extended their home range to include these regenerating areas where greater heterogeneity in vegetation increases food supplies (Strier *et al.* 1993). Extended simulations were run holding K constant at 240 individuals and increasing K to various degrees.

Years K changes: Varied (12 in trial simulation)

Rationale: K was permitted to increase over 25 and 50 years in some extended simulations. See below.

Percent increase in K: Varied (5% in trial simulations)

Rationale: Extended simulations in which K showed a trend compared the effects of increasing K 2% over 50 years, 5% over 25 years, and 5% over 50 years. The 5% increase in K over 50 years is likely to be an underestimate of the actual transformation of regenerating forest into exploitable food sources, particularly because some pasture areas that previously isolated the EBC forest from neighboring forests are regenerating into corridors that make neighboring forests accessible to muriquis.

No harvesting or other manipulation of population during this period were modeled.