BIOTROPICA 32(4b): 903–913 2000

Population Viabilities and Conservation Implications for Muriquis (*Brachyteles arachnoides*) in Brazil's Atlantic Forest[1]

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ABSTRACT

Muriquis (*Brachyteles arachnoides*) are endemic to the Atlantic Forest of southeastern Brazil, where an estimated 1200 individuals are distributed unevenly among only 19 populations. Despite the fact that over two-thirds of all muriquis live at low densities in large and protected, undisturbed forests, virtually nothing is known about the demography of these populations. Consideration of the mechanisms underlying the low extinction probabilities simulated for muriquis inhabiting the small, disturbed forest at the Estação Biologica de Caratinga (EBC), Minas Gerais, where long-term demographic and behavioral studies have been conducted, provides disturbing predictions about the viability of other populations living at lower densities. Local resource competition may be responsible for the female-biased infant sex ratio documented at the EBC under the female-biased dispersal regime exhibited by muriquis. At lower population densities, however, release from competition may lead to male-biased infant sex ratios, and correspondingly slower population growth rates. High densities at the EBC also result in frequent intergroup encounters, permitting muriquis there to avoid close inbreeding through extra-group copulations; but at low densities, opportunities to avoid inbreeding may be more limited. Finally, habitat heterogeneity at the EBC, particularly the greater dietary diversity supported by secondary and regenerating vegetation in disturbed forests, not only may support higher muriqui densities but also provide greater dietary buffers against catastrophic fruit scarcities compared to undisturbed forests. Comparative demographic data on muriqui populations inhabiting undisturbed forests are critically needed to evaluate these predictions and to develop informed management plans for this endangered primate.

RESUMO

Muriquis (*Brachyteles arachnoides*) são primatas endêmicos da floresta atlântica do sudeste do Brasil, onde um número estimado de 1200 indivíduos está distribuído de forma desigual entre apenas 19 populações. Apesar de mais de dois terços de todos os muriquis viverem em baixas densidades em grandes áres protegidas de florestas não perturbadas, virtualmente nada é conhecido a respeito da demografia dessas populações. Estudos demográficos e comportamentais a longo prazo têm sido conduzidos em pequenos fragmentos de floresta perturbada na Estação Biológica de Caratinga (EBC), Minas Gerais, onde muriquis ocorrem em altas densidades. Os estudos conduzem a algumas considerações sobre os mecanismos subjacentes às baixas probabilidades de extinção simuladas para muriquis habitando estes habitats e oferecem predições perturbadoras sobre a viabilidade das populações de muriquis que vivem em baixas densidades. A competição por recursos locais pode ser responsável por uma razão sexual dos infantes desviada para o sexo feminino documentada para a EBC, onde a população adulta de muriquis exibe uma razão sexual também desviada para as fêmeas. Entretando, em baixas densidades, a liberação da competição pode levar a uma razão sexual dos infantes desviada para o sexo masculino e, conseqüentemente, uma taxa de crescimento populacional lenta. A alta densidade populacional na EBC também resulta em uma maior freqüência de encontros entre-grupos, permitindo que os muriquis evitem endogamia através de cópulas extra-grupo; por outro lado, em baixas densidades as oportunidades de evitar a endogamia podem ser mais limitadas. Finalmente, a heterogeneidade ambiental na EBC, particularmente a grande diversidade de dieta suportada pela vegetação secundária e em regeneração das florestas perturbadas, pode não só sustentar densidades mais altas de muriquis como servir como tampões alimentares contra a escassez catastrófica de frutos, se comparada com florestas não perturbadas. Dados demográficos comparativos entre populações de muriquis vivendo em florestas não perturbadas são necessários com urgência para avaliar estas predições e para o desenvolvimento de planos de manejo adequados para este primata ameaçado.

Key words: *Atlantic forest;* Brachyteles; *habitat heterogeneity; inbreeding; muriqui; population density; population viability; sex ratio.*

THE MURIQUI (*BRACHYTELES ARACHNOIDES* E. GEOFFROY 1806) IS AN ENDANGERED PRIMATE endemic to what remains of the Atlantic Forest in southeastern Brazil. Habitat destruction has fragmented muriqui populations, reducing their numbers to < 1200 individuals. These are distributed unevenly among only 19 known populations that inhabit forest tracts differing from one another in size, degree of disturbance, and protected status (Strier & Fonseca 1996/1997).

[1] Received 13 August 1998; revision accepted 20 April 1999.

Morphological and genetic differences between southern populations from São Paulo state and northern populations from the states of Minas Gerais and Espírito Santo, have led to proposed taxonomic revisions that recognize separate subspecies (*B. a. arachnoides* and *B. a. hypoxanthus*) or even species (*B. arachnoides* and *B. hypoxanthus*) for the southern and northern varieties, respectively (Vierra 1944, 1955; Lemos de Sá *et al.* 1990, 1993; Rylands *et al.* 1995, 1996; Pope 1998). Interpretations of some of the interpopulation variation remain controversial (Leigh & Jungers 1994), but differences in the habitats that support southern and northern muriquis leave little disagreement about the need for regional approaches to their conservation.

The majority of southern muriquis (87.5%) inhabit the large, undisturbed forests protected by the São Paulo State Park system, which also accounts for most of the available muriqui habitat remaining in this region. In contrast, 56 percent of all northern muriquis are found in small, privately owned forests that represent $<$ 2 percent of available muriqui habitats in this region (Strier & Fonseca 1996/1997). The largest known population, estimated at 500 individuals, survives in the $>$ 37,000-ha forest at the Parque Estadual de Carlos Botelho (PECB) in São Paulo. The third largest population, consisting of *ca* 100 muriquis (nearly 10% of the genus), persists in an 860-ha tract of privately owned forest at the Estação Biologica de Caratinga (EBC), situated on Fazenda Montes Claros in Minas Gerais.

The risks of stochastic demographic and environmental processes, together with the expected effects of genetic drift and inbreeding, should make small populations such as the EBC muriquis more vulnerable to extinction than larger populations inhabiting undisturbed forests. Yet, over the past 16 years, the EBC muriqui population has been expanding steadily due to low mortality rates among all age and sex classes and a strongly female-biased infant sex ratio (Strier 1991a, 1996). Recent population viability analyses (PVAs) using VORTEX (Lacy 1993, Lacy *et al.* 1993) simulated surprisingly low extinction probabilities for this population over the next 100 years, with no evidence of deleterious inbreeding effects (Strier 1993/1994, Rylands *et al.* 1998). Indeed, under current demographic conditions, the size of the EBC population was projected to increase with the area of suitable habitat available.

With such paradoxically encouraging suggestions on the viability of the EBC muriquis, it is tempting to be even more optimistic about the viabilities of larger extant populations inhabiting undisturbed forests. It is risky, however, to extrapolate low extinction probabilities from the EBC muriquis to other populations, particularly if the demographic and ecological conditions that affect extinction probabilities differ among them. For example, at $>$ 0.1 individuals/ha, the EBC forest supports one of the highest known densities of muriquis. In contrast, censuses in three large, undisturbed forests have indicated muriqui densities that are ten-fold lower (Paccagnella 1991; Stallings & Robinson 1991; Pinto *et al.* 1993; reviewed in Strier & Fonseca 1996/1997).

Despite the fact that over two-thirds of all muriquis live at low densities in undisturbed forests, virtually nothing is known about the demography of their populations or how they respond to annual fluctuations in the availability of key food resources. Factors responsible for maintaining low muriqui densities in these undisturbed forests and the potential effects of low density on demographic variables, such as sex ratios, and risks of inbreeding, could affect population viabilities drastically; yet information about these factors does not exist. Understanding the mechanisms underlying the apparent viability of the EBC muriquis can provide a basis for generating predictions about some of the constraints that may affect the viability of other muriqui populations living at lower densities in undisturbed forests.

This paper explores the broader implications of three of the most striking results that emerged from the PVA and ongoing behavioral observations on the EBC muriquis. First, the female-biased infant sex ratio among the EBC muriquis is considered from the perspective of evolutionary strategies that influence infant sex ratios under different competitive and dispersal regimes. Second, the risks of inbreeding are examined in terms of opportunities that facilitate the behavioral avoidance of inbreeding through mate choice. Finally, habitat heterogeneity resulting from human disturbances is considered in terms of its effects on both muriqui carrying capacities and the ability of muriquis to respond to natural catastrophes that affect food availability.

BACKGROUND

Demographic variables.—Systematic monitoring of one muriqui group at the EBC was initiated in June 1982, and continues through the present (Strier 1992a, 1999). Muriquis are easily distin-

guishable by their natural markings, making it possible for trained observers to recognize individuals for both demographic and behavioral sampling. Since the onset of the study, the size of the main study group has increased from 22 to its present (July 1998) 62 individuals. Local people state that muriquis have not been hunted for many years prior to the onset of the study, and the reasons for the initially small population size cannot be determined. The subsequent expansion has been attributed to low mortality among all age and sex classes accompanied by a steady birth rate. As of August 1993, when the initial PVA data were compiled, there were 51 members, including 18 sexually mature females, in the study group (Strier 1993/1994).

Emigrations by natal females from the study group ($N = 20$) have recently outnumbered immigrations by females from another muriqui group at this site ($N = 12$; Strier 1999). Males are philopatric, evidently remaining in their natal groups for life.

Female age at first reproduction was estimated to be minimally 7.5 years, based on the age of one atypical female when she gave birth in her natal group (Strier 1991a). All other natal females have left the study group, most between 5 and 7 years of age. Assuming similar dispersal ages for immigrant females that subsequently gave birth in the study group, however, first reproduction more typically occurs at *ca* 11 years (Strier 1996).

Reproductive variables.—Interbirth intervals, based on 19 known parturition dates involving 11 different females, averaged 36.4 ± 4.3 mo during the period encompassed by the PVA (Strier 1996). Interbirth intervals have not increased with group size (Rylands *et al.* 1998, Strier 1999), and do not differ with maternal parity or offspring sex (Strier 1996, 1999).

The mating system of the EBC muriquis is highly promiscuous. Philopatric males become sexually active between 5.5 and 9.5 years of age (Strier 1996). The number of sexually active males in the group has increased from 6 to 13 since the study began, as natal males have matured (Strier 2000).

Unlike most primates, muriqui males mate in full view of one another without any evidence of aggressive or interference competition (Milton 1985a, b; Strier 1992b). In addition, since the late 1980s, a cohort of six males from another muriqui group in the EBC forest has been observed associating and occasionally mating with study group females (Strier *et al.* 1993, Strier 1994). These extra-group copulations, like those between study group males and females, were concentrated during the rainy season months, when most conceptions occurred (Strier 1996, 1997a), but the proportion of extra-group copulations did not correlate with changes in group size, number of sexually active males or females, or the ratio of sexually active females to males (Fig. 1).

In years when rainfall exceeded the annual average of 1119 ± 189 mm, copulations with both group and extra-group males have continued into the dry months (June–August; Strier 1996). Analyses of muriqui fecal steroids indicate that the resumption of postpartum ovulation typically coincides with the onset of the rainy season, but may occur during the dry season if an infant dies (Strier & Ziegler 1994, 1997). Male fecal testosterone levels do not appear to exhibit seasonal patterns in years of typical rainfall, but may be elevated through the dry season if sexually active females are present (Strier *et al.* 1999).

Ecological variables.—The vegetation at the EBC is characterized as tropical semi-deciduous mesophytic broadleaf forest (Fonseca 1985). Altitudes range from 400 to 640 m elevation, resulting in a mosaic of successional stages that includes primary forest species in the valleys and secondary growth on many slopes (Hatton *et al.* 1983). In addition, human disturbances from selective logging and agricultural activities around the perimeter of the forest contribute to the heterogeneous composition of this forest.

During 1983 and 1984, the 23–26 members of the study group utilized an area of 168 ha and spent more time in secondary forest habitat than expected from the representation of this habitat type in their home range (Strier 1987). By 1990, when the size of the study group had increased to 43 members, the group had expanded its range to nearly double its original area by incorporating parts of the forest it had not occupied previously (Strier *et al.* 1993). More recently, the group has expanded its home range even farther to encompass regenerating pastures and fields along the forest's edges (Strier 1993/1994).

INFANT SEX RATIOS

Rationale.—Population sex ratios are a product of the interacting effects of stochastic demographic processes and reproductive strategies that affect the sex and survivorship of offspring. Age- and sex-specific mortality and maturation rates, and dis-

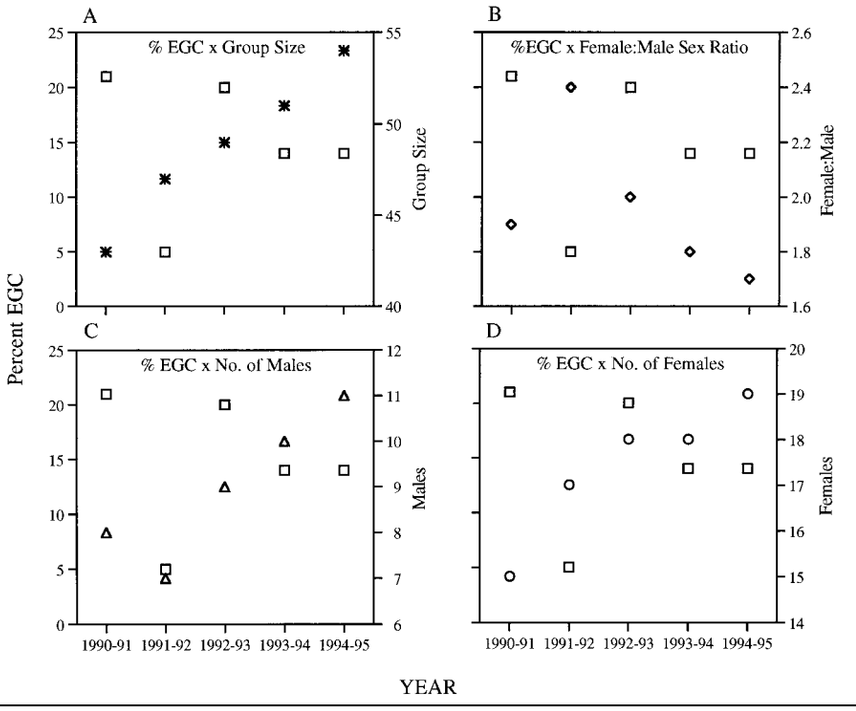

FIGURE 1. (a) Annual proportions of extra-group copulations (squares) relative to group size; (b) ratio of sexually-active females to males; (c) number of sexually-active males; and (d) females.

persal patterns operate on infant sex ratios, which are affected by maternal reproductive strategies that vary at different times in their life histories under different social and ecological conditions (Trivers & Willard 1973, Gomendio *et al.* 1990, Boyce 1992, Caughley 1994, Gomendio 1995). Although the mechanisms underlying determination of primary infant sex ratios are still poorly understood, data from a variety of primates and other mammals are consistent with evolutionary theories about sex ratio allocations (Clutton-Brock & Iason 1986, Johnson 1988, Frank 1990, Hiraiwa-Hasegawa 1993).

Under the local resource competition hypothesis, mothers should bias the sex of their infants in favor of the dispersing sex to avoid competition for themselves and their future offspring (Clark 1978). The advantages of biasing infant sex ratios in favor of the dispersing sex should be greatest for mothers living in populations that are at or close to carrying capacity (*e.g.*, Holekamp & Smale 1995), as well as among low-ranking mothers that suffer more than dominant mothers from resource competition within any particular population (Silk 1983, Hiraiwa-Hasegawa 1993).

Local resource competition should be relaxed when population densities are below carrying capacity (Holekamp & Smale 1995), or for dominant mothers that can obtain priority of access to limited resources (Silk 1983; van Schaik & Hrdy 1991; see also Komdeur 1996 for birds). Release from local resource competition should alleviate the advantages of biasing infant sex ratios in favor of the dispersing sex. Indeed, local resource enhancement may favor mothers that produce more offspring of the philopatric sex if these individuals provide assistance (Gowaty & Lennartz 1985, Emlen *et al.* 1986).

The absence of dominance relationships among muriquis, which distinguish their societies from those of most other primates (Milton 1985a, b; Strier 1992b), together with their female-biased pattern of dispersal, make them ideal primates in which to examine the effects of population density on infant sex ratios. Specifically, at high population densities, such as at the EBC, local resource competition should favor the production of dispersing daughters over philopatric sons. In contrast, at the low population densities that prevail in the larger undisturbed forests, relaxation of local resource

competition should reduce the benefits of producing daughters and may even favor a disproportionate production of philopatric sons. Because female-biased sex ratios facilitate population expansion while male-biased sex ratios increase the probability of extinction (Gabriel *et al.* 1991), the effects of population density on muriqui infant sex ratios, and ultimately population viabilities, should be pronounced.

EVIDENCE.—Daughters have accounted for 64 percent of the 59 documented infants born in the EBC muriqui study group since the onset of the study. The female-biased infant sex ratio has been evident since the start of the study when group size and population density were lower (Strier 1991a, 1993/1994). Even more striking, however, is the fact that the female-biased infant sex ratio appears to be maintained exclusively by multiparous mothers. Whereas nearly equal numbers of daughters ($N = 7$) and sons ($N = 6$) were produced among the 12 known first-time mothers, infant sex ratios among multiparous mothers appear to become increasingly female-biased with each successive birth; most mothers that have given birth to three or more infants have produced more daughters than sons (Strier 1999).

Reducing local resource competition among maturing offspring may be particularly important to muriqui mothers because their offspring take so long to mature. Conversely, primiparous mothers, particularly if they reproduce soon after joining the group, might benefit as much by producing a son, and future ally, as by producing a daughter that will disperse and thus reduce competition with future offspring.

IMPLICATIONS.—Varying infant sex ratios for the EBC population resulted in declining population growth rates as the proportion of sons born increased after *ca* 15 to 20 years into the simulation (Strier 1993/1994). The low extinction probabilities generated for the EBC muriquis under existing conditions therefore seem to be dependent, at least in part, on the persistence of female-biased infant sex ratios. A reduction in the density of muriquis at the EBC, which could occur from any of a number of possible catastrophic events, could relax local resource competition and lead to shifts toward male-biased infant sex ratios and ultimately, a higher probability of extinction.

Interactions between low population densities and the relaxation of local resource competition might affect muriquis living in large, protected forests. Released from the selective advantages of producing more dispersing daughters, infant sex ratios in these populations could become skewed in favor of philopatric males. Low population densities therefore could result in correspondingly slower population growth rates, making it more difficult for these muriqui populations to recover in size than for muriquis already living at higher densities.

RISKS OF INBREEDING

RATIONALE.—Inbreeding is a serious concern for small, isolated populations with limited or nonexistent opportunities for gene flow or outbreeding. Inbreeding among close relatives contributes to the loss of genetic diversity within a population, and increases the probability that lethal or deleterious recessive alleles will be expressed in the homozygote condition. Risks of inbreeding are increased further in long-lived animals, such as muriquis, in which overlapping generations mean that parents and offspring are sexually active at the same time.

Most primates appear to avoid the risks of close inbreeding, either as an indirect consequence of dispersal mechanisms that effectively minimize reproductive opportunities between parents and offspring and among siblings, or as a result of individuals actively selecting nonrelatives, or rejecting close kin, as mates (Moore & Ali 1984). As with maternal sex ratio allocations, little is known about the mechanisms of kin recognition in primates. Furthermore, without genetic paternity data, most evidence of inbreeding avoidance necessarily has been restricted to maternal geneaologies accumulated during long-term observational studies. Among the EBC muriquis, for example, the potential for close inbreeding can be assessed only among the six mother–son dyads and the one maternal brother–sister dyad known in the study group.

Female muriquis presumably leave their fathers and brothers when they disperse from their natal groups, and appear to remain in the group in which they initiate their long (>15 yr) reproductive careers. Thus, mothers are still reproductively active, and potential mates, when their philopatric sons become sexually mature.

EVIDENCE.—The low birth rates and high infant mortality rates symptomatic of highly inbred populations (Ralls *et al.* 1986) might have been expected to characterize the EBC muriquis because of their isolation from other populations. Yet, birth rates have remained constant and infant mortality rates have been remarkably low during the 16 years

since the onset of the study. Indeed, no effects of deleterious inbreeding were detected in the PVA, which encompassed multiple muriqui generations within the 100-year simulation period (Strier 1993/1994).

What the PVA could not take into account is that, despite their promiscuity, the EBC muriquis appear to modify their mate choices in ways that are consistent with the avoidance of close inbreeding. Only one known mother–son copulation has been observed, and copulations between recent female immigrants and males from their natal groups were rare during intergroup encounters. In contrast, mothers of sexually active sons accounted for a disproportionate number of all extra-group copulations, even when compared to other long-term female residents in the study group (Strier 1997a).

Females seeking mates other than their sons have ample opportunities to find them at the EBC because the high density of muriquis results in frequent intergroup encounters. The rate of intergroup encounters has increased over the years as both the size of the study group and the density of muriquis at this site have increased (Strier *et al.* 1993). Thus, opportunities for the EBC muriquis to avoid close inbreeding through their mate choices may be enhanced by their high population density in this forest.

Implications.—Muriquis living at low population densities may have fewer opportunities to avoid close inbreeding because encounters with other groups are rare. One muriqui study group with up to 31 members at the PECB utilized a home range of at least 800 ha, and was never observed to encounter or vocalize in response to the proximity of another muriqui group (de Carvalho 1996; Moraes *et al.* 1998). In contrast, 46 percent of the original 168-ha home range of the 23 to 26 member EBC study group also was utilized by another muriqui group (Strier 1987), and the proportion of overlap with the current study group's expanded home range now approximates 100 percent (Strier *et al.* 1993).

Intergroup encounters provide opportunities for adolescent females to disperse from their natal groups (Strier 1996, Printes *et al.* 1997) and provide a wider variety of mate choices among both males and females. If the rate of intergroup encounters is a consequence of population density, then even large populations of muriquis, such as those at the PECB, may experience a higher incidence of incestuous liaisons and correspondingly higher risks of deleterious inbreeding. Because inbreeding depression can affect reproductive rates as well as survivorship, the viability of muriqui populations living at low densities may be reduced. Furthermore, if multiparous females in these populations produce sons at higher rates than those in the EBC population (see above), then the probability of incestuous fertilizations between mothers and their mature sons may be even higher than predicted by the rate of intergroup encounters.

HABITAT HETEROGENEITY

Rationale.—Several possible factors could account for the low densities of muriquis (and other sympatric primates) in undisturbed tracts of the Atlantic Forest. Large, undisturbed forests may support larger populations of natural predators that could reduce population numbers and lower densities over time (Pinto *et al.* 1993, Strier & Fonseca 1996/1997). Habitat fragmentation also might lead to artificially high densities by compressing populations into smaller, disturbed forests (Robinson & Ramirez 1981), but it is unlikely that these densities would be sustained or increase as has occurred at the EBC, unless sufficient quantities of edible foods were available. Indeed, the fact that secondary forests, with their more heterogeneous vegetation, may support higher densities of edible foods than undisturbed, primary tropical forests (Foster 1980, Ganzhorn 1995, Peres 1996) is consistent not only with the apparently higher carrying capacity of forests such as the EBC, but also with the increase in muriqui population size and the expansion of the EBC study group's home range into areas with regenerating early successional growth.

Muriquis possess anatomical specializations that permit them to rely heavily on leaves when their more preferred fruit and flower foods are seasonally scarce (Zingeser 1973, Rosenberger & Strier 1989). Independent of rainfall and seasonality, the annual diets of muriquis in disturbed forests include higher proportions of leaves compared to those of muriquis in undisturbed forests such as the PECB (Table 1). Muriqui feeding party sizes are also significantly smaller at the PECB despite the larger size and higher density of their fruit patches in this forest compared to the EBC (Moraes *et al.* 1998).

These population differences in muriqui diet and grouping patterns, which appear to co-vary with one another and with differences in ranging patterns (see above), may be a consequence of the effects of habitat heterogeneity on population den-

TABLE 1. *Comparative data on diet and grouping in* Brachyteles.

Location	Folivory (%)	Grouping	Habitat	Study period
Fazenda Esmeralda, Minas Gerais[a]	51	Cohesive	Disturbed, 44 ha	July 1986–Jan. 1987
EBC, Minas Gerais[b]	51	Cohesive	Mixed, 800 ha	June 1983–July 1984
Fazenda Barreiro Rico, São Paulo[c]	>50	Fluid	Mixed, 422 ha	Aug. 1982–June 1983
Parque Estadual de Carlos Botelho, São Paulo[d]	33	Fluid	Primary, 37,797 ha	Feb. 1990–Nov. 1993

[a] Lemos de Sá 1991.
[b] Strier 1991b.
[c] Milton 1984.
[d] de Carvalho 1996.

sities. At the same time, access to greater dietary diversity, including a wide variety of digestible leaf species, in disturbed forests may provide a buffer against starvation during catastrophic failures in the productivity of key fruit species. Consequently, muriquis inhabiting undisturbed forests with more homogeneous vegetation and a correspondingly greater dietary reliance on fruit may be more vulnerable to starvation at times of exceptional fruit scarcity.

Evidence.—Expanding the area of suitable habitat available to the EBC muriquis emerged as one of the most significant determinants of their population size over the next century in the PVA (Strier 1993/1994, Rylands *et al.* 1998). Ongoing habitat expansion has occurred through the natural regeneration of cultivated fields and pastures abutting the forest since 1982, and both these areas and regenerating areas within the forest are routinely exploited by muriquis for food. Even during the early years of the study, when group size was smaller and muriqui density was lower, the muriquis exploited secondary forest habitat significantly more often than expected from its representation in their home range (Strier 1987).

Increases in the size of the study group and the density of muriquis at the EBC have been accompanied by an increase in the proportion of home range overlap between the two original groups (Strier *et al.* 1993). A corresponding increase has been documented in the population of sympatric brown howler monkeys (*Alouatta fusca*; Hirsch 1995), the diet of which overlaps considerably with muriquis and includes an even higher proportion of leaves (71%; Mendes 1989). Hunting of primates does not appear to have been an issue at the EBC, at least based on reports from local people and the ease with which the primates habituated to researchers. The resulting increase in biomass density is consistent with greater overall resource use (Peres 1996), and is reflected in both the behavioral adjustments made by muriquis at this site (Strier *et al.* 1993) and the variation in muriqui feeding, grouping, and ranging patterns detected between populations (Moraes *et al.* 1998).

Implications.—Dietary and behavioral flexibility appear to be critical to the viability of the EBC muriquis. Access to a wide diversity of edible foods, including young leaves produced by early successional species, in these heterogeneous habitats not only may support higher population densities, but also may provide essential buffers against catastrophic failures in the production of important fruit crops. The fact that muriquis in disturbed forests exhibit seasonal dietary shifts in response to the availability of preferred fruit sources (*e.g.*, EBC: Strier 1991b; Fazenda Esmeralda, Minas Gerais: Lemos de Sá 1991; Fazenda Barreiro Rico, São Paulo: Milton 1984) emphasizes the importance of alternative food resources to their survival in these areas.

At the EBC, preferred fruit and flower resources are more abundant during the rainy season than during the dry season, and muriquis shift their monthly diets in response to the availability of these preferred food resources (Strier 1991b). Average day ranges were significantly longer during the rainy season (1427 ± 597 m), when muriquis traveled between widely dispersed fruit patches, than during the dry season (960 ± 631 m), when they relied more heavily on abundant leaf resources (Strier 1987).

The higher proportion of fruits in the diets of muriquis living in undisturbed forests may reflect

lower intra- and interspecific feeding competition resulting from lower population densities (Moraes *et al.* 1998). Alternatively, greater frugivory could reflect a more general scarcity of alternative dietary supplements such as leaves. Phenological data on muriqui food resources at the undisturbed PECB forest indicate year-round stability in the availability of fruit sources, which also may contribute to the more frugivorous diet that these muriquis maintain (de Carvalho 1996).

It is not yet known how muriquis inhabiting undisturbed forests such as the PECB would respond if key fruit species in their diets were to fail. It is possible that they could increase their day ranges to exploit remaining fruit patches, or shift their diets to include higher proportions of leaves; however, if the low muriqui densities in undisturbed forests reflect lower carrying capacities at these sites due to an absolute scarcity of edible leaf sources, then these populations could be more vulnerable to potentially devastating consequences of catastrophic fruit crop failures than populations inhabiting disturbed forests in which more diverse dietary options are available.

DISCUSSION AND IMPLICATIONS FOR CONSERVATION

The female-biased infant sex ratios and inbreeding avoidance exhibited by muriquis at the EBC appear to be facilitated by their high population density. Diverse dietary options resulting from habitat disturbances in and around the perimeter of this forest may be responsible for sustaining high densities of muriquis (and at least one other primate) at the EBC. In contrast, lower muriqui densities in undisturbed forests may result in male-biased infant sex ratios and correspondingly slower rates of population growth, and infrequent intergroup encounters, which limit opportunities for dispersal as well as mate choices that reduce the risks of close inbreeding. Habitat homogeneity also may restrict dietary options, making these muriquis more vulnerable to annual fluctuations in the availability of key fruit resources.

The female-biased infant sex ratio and correspondingly high rate of population growth predicted for muriquis living at high densities in the EBC were associated directly with the effects of local resource competition under their female-biased dispersal regime. In primates with male-biased dispersal, local resource competition would lead to male-biased infant sex ratios, as has been observed in an expanding population of white-fronted capuchin monkeys (*Cebus capucinus*) in Costa Rica (Fedigan *et al.* 1996). Thus, the effects of density on population growth rates appear to be different under divergent systems of dispersal.

Dispersal regimes also may affect the relationships among population density, the frequency of intergroup encounters, and the opportunities for inbreeding avoidance hypothesized for muriquis. In primates such as red howler monkeys (*Alouatta seniculus*), for example, in which both sexes disperse from their natal troops, population growth leads to an increase in the number and density of troops, rather than to larger troop sizes (Crockett 1996). Mechanisms for inbreeding avoidance under these circumstances would be more likely to involve secondary dispersal or monopolized mating opportunities than extra-group copulations.

The effects of dietary breadth on population vulnerability are even more difficult to generalize. It is unclear whether muriquis inhabiting undisturbed forests rely more heavily on fruit because of its greater abundance, relative to population density and more temporal stability in its availability, or because insufficient alternative foods are present. Comparative feeding studies on sympatric brown howler monkeys, which at the EBC are more folivorous than muriquis, would be potentially informative in distinguishing between these alternatives, particularly if the energetic constraints associated with their quadrupedal locomotion affect their ability to exploit the patchy fruit resources that muriquis, with their rapid, suspensory mode of locomotion, evidently can.

Evaluating the grim predictions about the viability of muriqui populations living at low densities compared to the EBC population is difficult without comparative demographic, behavioral, and ecological data (Strier 1997b). Indeed, without comparative data from other populations, even the explanations proposed to account for the apparent viability of the EBC muriquis must be regarded as highly speculative. For example, the low mortality and high birth rates that have been documented in the EBC population may reflect the small number of muriqui generations that the more than 16-year study has spanned. Recent analyses of 32 allozyme loci from an even smaller muriqui population than the EBC indicate high levels of polymorphism and mean heterozygosity per locus that have been attributed to the recent genetic isolation of that population relative to muriqui generation length (Pope 1998). An increase in mortality or decrease in birth rates among the EBC muriquis resulting from loss of genetic variation as more generations elapse

could lower population densities, with deleterious consequences on infant sex ratios, opportunities to avoid inbreeding, and ultimately, population viability. Continued monitoring of the EBC muriquis, together with increased efforts to obtain comparative demographic data from undisturbed forests, will be necessary to determine which, if any, muriqui populations warrant informed intervention to reduce extinction risks.

ACKNOWLEDGMENTS

Permission to conduct research in Brazil was provided by CNPq and IBAMA, with sponsorship by Drs. C. Valle, C. Ades, and G. A. B. Fonseca. Logistical facilities at the EBC were provided by Fundação Biodiversitas. The field research was supported by NSF grants BNS 8305322, BNS 8619442, BNS 8959298, and SBR 9414129, the Fulbright Foundation, grant no. 213 from the Joseph Henry Fund of NAS, Sigma Xi, the L.S. B. Leakey Foundation, the World Wildlife Fund, the Seacon Fund of the Chicago Zoological Society, the Liz Claiborne and Art Ortenberg Foundation, the Scott Neotropic Fund of the Lincoln Park Zoo, and the Graduate School of the University of Wisconsin–Madison. N. Bejar, A. Carvalho, D. Carvalho, C. G. Costa, P. Coutinho, L. T. Dib, J. Gomes, M. A. Maciel, F. D. C. Mendes, F. Neri, S. Neto, C. P. Nogueira, A. Odalia Rímoli, A. Oliva, L. Oliveira, R. Printes, J. Rímoli, W. Teixeira, and E. M. Veado contributed to the long-term demographic data. I am grateful to Dr. P. C. Morellato for inviting me to contribute to this volume, S. L. Mendes, P. L. R. Moraes, C. P. Nogeiro, and A. B. Rylands for discussions and suggestions, and two anonymous reviewers and the editor for their constructive comments.

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