

Chapter 6

The Northern Muriqui (*Brachyteles hypoxanthus*): Lessons on Behavioral Plasticity and Population Dynamics from a Critically Endangered Species

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Abstract Since its onset in the early 1980s, our ongoing field study of the northern muriqui in southeastern Brazil has yielded original data on the behavioral ecology, reproductive biology, and life histories of one of the most critically endangered primates in the world. At the same time, a sixfold expansion in the size of our study population has provided insights into the plasticity of behavior and life history patterns that have important implications for muriqui conservation as well as for comparative models of primate socioecology. In this review of the history, growth, and diversification of our long-term study, we describe the transformation of our field site into a federally protected private reserve, the progression of the research questions as our knowledge has increased, and our predictions about the effects of increased population density on key demographic and life history variables. We also reiterate the need for more comparative studies of other muriqui populations, and reflect on the essential role that long-term, international collaborations have played in advancing the scientific and conservation agendas we have pursued from the start.

6.1 Introduction

Like most other members of the Atelinae, the northern muriqui (*Brachyteles hypoxanthus*) is a large-bodied New World monkey characterized by slow, ape-like life histories and a social system that includes male philopatry and female-biased dispersal (Strier 1992a, 1999a; Nishimura 2003; Di Fiore et al. 2011;

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Fig. 6.1 Male northern muriquis (*Brachyteles hypoxanthus*) at the RPPN-Feliciano Miguel Abdala, Minas Gerais, Brazil. Photo © Carla B. Possamai

Fig. 6.1). Unlike the other three genera of Atelinae (*Ateles*, *Lagothrix*, and *Oreonax*), muriquis are endemic to the Atlantic Forest of southeastern Brazil, with the southern muriqui (*Brachyteles arachnoides*) found in the states of Rio de Janeiro and São Paulo and in forest fragments in Paraná (Aguirre 1971; Koehler et al. 2002), and the northern muriqui, restricted to only a dozen of the remaining forest fragments in the states of Minas Gerais and Espírito Santo (Mendes et al. 2005a). With a known population of less than 1,000 individuals, the northern muriqui is one of the most critically endangered primates in the world (Mittermeier et al. 2006).

Concern for the muriqui's conservation status dates back more than 40 years, when it was still considered to be a monotypic genus and virtually nothing about its behavior and ecology was known (Aguirre 1971; Coimbra-Filho 1972). Subsequent analyses of the morphological and genetic differences between northern and southern populations led to their reclassification as separate species (Rylands et al. 1995; Groves 2001; Rylands and Mittermeier 2009). The two muriqui species face different kinds of primary threats from habitat loss and hunting, respectively (Strier and Fonseca 1996/1997).

The elevation of the northern muriqui to separate species status is only one of the many changes we have witnessed since 1982, when unbeknownst to us and by independent paths, we had separately visited the same small patch of privately owned Atlantic Forest, located on Fazenda Montes Claros in the municipality of Caratinga, Minas Gerais, and had each caught our first glimpses of a wild muriqui. One of us (K.B. Strier) had gone there with the explicit goal of assessing the feasibility of studying muriquis; the other (S.L. Mendes) went to evaluate the prospects for a study of the sympatric brown howler monkey (*Alouatta guariba*; previously, *Alouatta fusca*), another species endemic to the Atlantic Forest and just

as poorly known as the muriqui. We both opted to return to the forest to pursue our respective studies in 1983, which thus marks the beginning of what has developed into the longest-running field study on the northern muriqui, as well as our mutual enduring interest in the future of this forest and the endangered primates it supports.

We begin this chapter by reviewing the history of our long-term study site and the administrative and ecological changes it has undergone as a result of international and Brazilian conservation efforts mediated through some key nongovernmental organizations (NGOs) and the conservation initiatives taken by members of the family that owns the forest. We then summarize some of the main findings that have emerged from the nearly 30 years that this muriqui population has been systematically monitored. As is true for most long-term field studies, the focus of our research has shifted from initial quantitative depictions of basic behavior and ecology to analyses of reproductive patterns and life history strategies, which are only possible to investigate with data and perspectives obtained over the course of multiple generations in the muriquis' lives (Strier 2003a, 2009; Strier and Mendes 2009). Our key findings thus include the insights into the behavioral consequences of demographic changes that could not have been made during a shorter study period. We also discuss some of our predictions about the effects of demography on fundamental variables such as female dispersal and male maturation. We conclude by reflecting on the synergy between the two driving forces – conservation and research – that have fueled the long-term study from its inception.

6.2 History and Ecology of the Study Site

In 1944, Sr. Feliciano Miguel Abdala purchased a plot of land about 60 km south of Caratinga, Minas Gerais, a town that sits at the crossroads between the transnational highways that connect São Paulo in the south with Bahia in the north, and Belo Horizonte in the west with Vitória in the east. The land, known as Fazenda Montes Claros, was a productive coffee plantation and cattle ranch, but also included what has remained one of the largest privately owned tracts of Atlantic Forest in the region. According to local history, Sr. Feliciano promised the fazenda's previous owner that he would preserve the forest and protect its inhabitants (Abdala Passos 2003). The area is known today as the Reserva Particular do Patrimônio Natural (RPPN)-Feliciano Miguel Abdala; its persistence as a federally recognized "Private Natural Heritage Reserve" is a testimony to Sr. Feliciano's honored promise (Castro 2001).

The presence of muriquis at this site was first reported to the scientific community by zoologist Álvaro Aguirre in 1971. By the late 1970s, zoologists from the Universidade Federal de Minas Gerais (UFMG), led by the indefatigable Professor Célio Valle, had initiated a campaign for the protection and scientific study of this area. Japanese primatologist Akisato Nishimura (1979) visited the site and provided some of the first observations of muriqui behavior. Other primatologists and

conservationists, stimulated by Russell A. Mittermeier, Ademar F. Coimbra Filho, and Ibsen G. Câmara, joined Célio Valle's group from UFMG in an international collaborative effort to study and preserve the local biodiversity (Mittermeier et al. 1982). Besides the presence of brown howler monkeys and muriquis, the discoveries of another endangered primate, the buffy-headed marmoset (*Callithrix flaviceps*), and of a large population of tufted capuchin monkeys (*Cebus nigritus*) signaled the forest's unusual potential to become a major site for field research on wild primates in the Atlantic Forest of Brazil. To help realize this potential, Sr. Feliciano donated a small house at the edge of the forest, and in collaboration with the UFMG, the World Wildlife Fund (WWF), and the Brazilian Foundation for the Conservation of Nature (FBCN), the Estação Biológica de Caratinga (EBC) was inaugurated in May 1983.

The EBC provided essential infrastructure for researchers and was thus critical for establishing our long-term study (Strier and Mendes 2003). Although the accommodations are simple, the house has undergone many improvements over the years, including the acquisition of electricity from nearby power lines, the expansion of living space for researchers and visitors, and the construction of a laboratory for storing and processing materials such as plants (Boubli et al. in press) and feces used for the noninvasive analyses of muriqui gastrointestinal parasites (Stuart et al. 1993; Santos et al. 2004), steroid hormones (e.g., Strier and Ziegler 1997, 2000), and genetics (Fagundes et al. 2008). The EBC has also undergone transitions in its administration, which passed from the FBCN to Fundação Biodiversitas, then to Conservation International-Brasil, and, in 2001, to the Sociedade para a Preservação do Muriqui, or SPM, established by the Abdala family to administer the activities in their Reserve.

Consistent with Sr. Feliciano's conservation vision for his forest, the Reserve's most important function continues to be the sanctuary it offers to its endangered flora and fauna. The natural regeneration of nearly 100 ha of pasture and agricultural land within and surrounding the Reserve has provided additional habitat that all four species of primates increasingly exploit (Strier and Boubli 2006). In addition, plans to create corridors to link the Reserve with some of the smaller forest fragments that remain on other privately owned properties surrounding it are underway; once established, the corridors will increase the available habitat for muriquis and thus should permit the population's continued expansion (Strier et al. 2005; Tabacow et al. 2009b).

The local predator community has increased in diversity along with the increased habitat protection and expansion over the past three decades. Suspected muriqui predators include tayra and large hawks (Printes et al. 1996), and possibly semi-feral dogs (Mourthé et al. 2007). The first ocelot since the onset of the study was sighted in 1990 (Strier 1999b), and scat analyses have since confirmed that muriquis in our study population are among their prey (Bianchi and Mendes 2007).

Over the past three decades, many of the plants and animals, and all four species of primates, have been the targets of systematic field studies. The integration of research with conservation efforts, like our own work with the muriquis, has characterized many of these other projects and benefitted from the strong

international collaborations that were initiated decades ago when the value of the forest for conservation and for science was first recognized. These collaborations, along with our mutual commitment to capacity building, have been critically important to the continuity of our long-term study. Since 1983, some 45 Brazilian students have participated in the muriqui project alone, and many of these students have gone on to pursue scientific and conservation-oriented careers (Strier and Mendes 2003, 2009; Strier and Boubli 2006).

6.3 Demography, Group Dynamics, and Life Histories

Systematic studies were initiated on one of the two original muriqui groups (Matão group) present in the forest in 1982, yielding detailed individual life history data since July 1983. Systematic studies on the other groups in this population were initiated in 2002, yielding demographic and life history data on the entire population from 2003 through the present. One of these groups (Jaó) was present in 1982; the other two groups were established when the Jaó group fissioned in 1988 (M2 group) and 2002 (Nadir group) (Strier et al. 1993, 2006). Thus, as of June 2010, our accumulated demographic and life history data span a 28-year period on the Matão group and the last 7 years on the entire population.

All individuals in this isolated population can be identified by their natural markings and are monitored by teams of trained Brazilian students who are in the forest on a near-daily basis. This has made it possible to follow known individuals from their birth through maturity, and to track females after they disperse from their natal groups (Strier and Mendes 2009).

6.3.1 Population Expansion

The Matão group has increased steadily from 22 to 107 individuals between July 1982 and June 2010 (Fig. 6.2). Some of its original members are still alive, including five adult females estimated to be >35 years old. The increase in this group's size and in the number of muriqui groups (from 2 to 4) can be attributed to the increase in the population's size and density during its recovery from past disturbances that included the forest's initial fragmentation, selective logging, and fire (Strier 1999b; Strier and Boubli 2006). In the late 1960s, the muriqui population was estimated at 20–25 individuals (Aguirre 1971) and by the early 1980s, it was estimated at 40–50 individuals (Valle et al. 1984); as of June, 2010, the population included 288 individuals. This sixfold size increase in less than 30 years has offered us an unanticipated opportunity to document the muriquis' behavioral responses to demographic changes (e.g., Dias and Strier 2003; Strier et al. 2006; Tabacow et al. 2009a; Strier 2011).

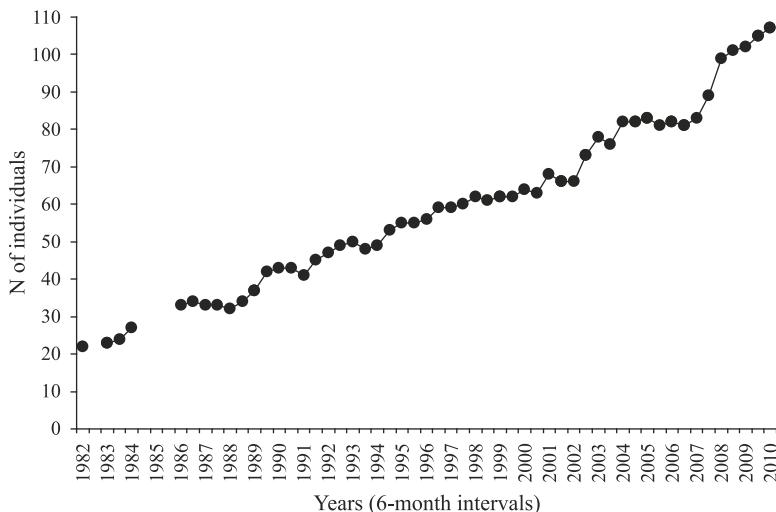


Fig. 6.2 Changes in the size of the Matão group. Group counts are shown at 6-month intervals, beginning in July 1982; gaps indicate missed counts. Updated from Strier (2005)

6.3.2 Behavioral Stability and Plasticity

Despite the group and population expansion, there have been no changes in the unusually peaceful, egalitarian relationships that distinguish the societies of northern muriquis from those of other primates (Strier 1990, 1994; also reviewed in Di Fiore et al. 2011). There is no overt evidence of dominance relationships among or between males and females, and both the rates and intensity of intragroup aggression have remained relatively low (Strier 1992b; Strier et al. 2000). Philopatric males maintain particularly close spatial associations and do not interfere with one another's access to fertile females, who routinely mate with multiple partners at times in their cycles when they are most likely to conceive (Strier 1997a; Strier and Ziegler 1997; Strier et al. 2002; Possamai et al. 2007). Despite more than 28 years of near-continuous field observations in our main study group, there has never been any indication of the kind of lethal aggression that has been observed in spider monkeys, which also show male philopatry (Campbell 2006), and in one population of southern muriquis living under different ecological conditions than those at our study site (Talebi et al. 2009).

Nonetheless, other behavioral changes can be directly attributed to the dramatic demographic changes the population has undergone. For example, within 15 years after the systematic monitoring had begun, the size of both the Matão group and its home range had roughly doubled. Although there was no corresponding increase in their daily travel distances, the group's previously cohesive pattern of association shifted to more fluid associations involving variably sized parties (Dias and Strier 2003) like those seen in other primates in which fission–fusion sociality is

associated with the avoidance of direct feeding competition (Aureli et al. 2008). Indeed, shifts from cohesive to fluid grouping patterns appear to be a consistent response to increasing group sizes that distinguishes primates living in patrilocal societies from those living in matrilocal societies (Strier 2009).

The fluid grouping patterns that now characterize the Matão group may be responsible, at least in part, for the persistence of this group despite its continued (and ongoing) growth. In contrast to the Jaó group, which has undergone two prior fissioning events since the onset of the population monitoring in 1982 (Strier et al. 2006), the Matão group has maintained its integrity as a group, as evidenced by the routine reuniting of subgroups as well as by its fidelity to a common home range. Previous predictions about the Matão group's fate have focused on the effects of group size, age and sex composition, and intra- and intergroup male relationships (Strier et al. 1993; Strier 2011). For example, increasingly male-biased adult sex ratios might lead to higher rates of male–male aggression or even favor male dispersal if the sex ratios in other groups are more favorable than those in their natal groups (Strier et al. 2006). Evaluating these predictions is an empirical question that only ongoing observations over the long term will be able to resolve.

With roughly 0.30 muriquis per hectare, our study population's density is now one of the highest known for this species (Mendes et al. 2005a). Extensive home range overlap among the four groups that now occupy the forest (Boubli et al. 2005) and a decline in the density of sympatric brown howler monkeys, whose diets overlap with those of muriquis (Almeida-Silva et al. 2005), provide indirect indications that our study population might be approaching the carrying capacity of this forest. In addition, the documented increase in the use of terrestrial substrates by members of the Matão group may reflect an expansion in their vertical niches (Mourthé et al. 2007; Tabacow et al. 2009a). Moreover, recent sightings of nulliparous females from our study population moving between the Reserve and some neighboring forest fragments located adjacent to the Reserve suggest that they may be seeking new habitat to colonize as the population density of muriquis inside the Reserve has increased (Tabacow et al. 2009b).

Although much of our ongoing research is now focused explicitly on understanding the effects of habitat saturation on the muriquis' behavior and ecology, there are also some intriguing illustrations of the synergistic interactions between behavior and population dynamics that we are simultaneously pursuing. For example, the increase in terrestrial behavior in our main study group appears to have occurred along two dimensions: The first involved the expansion from essential activities, such as feeding and drinking, to include nonessential activities, such as resting and socializing; the second involved the spread of the behavior along male social networks and subsequently to females including recent female immigrants to the group (Tabacow et al. 2009a). The terrestrial behavior of the Matão group can be considered a new local tradition according to the criteria applied to other types of traditions in other organisms (see Perry et al. 2011): it was socially transmitted and adopted by the all or most group members, and it has endured over time (Tabacow et al. 2009a). Consequently, we are now investigating whether females who have acquired this terrestrial tradition in their natal Matão group import it into the groups

into which they disperse, and thereby effectively diffuse the custom of engaging in nonessential terrestrial activities throughout the population.

6.3.3 *Habitat Saturation and Female Dispersal*

We can expect flexibility in life history components in response to density dependent effects associated with habitat saturation. For example, the effects of high levels of intragroup competition in large groups might include delays in the maturation of philopatric individuals and earlier dispersal ages in the dispersing sex, whereas high levels of intergroup competition in saturated habitats can result in delays in dispersal age and in extreme cases may lead to the permanent retention of both sexes in their natal groups (e.g., Alberts and Altmann 1995; Ferrari and Digby 1996; Altmann and Alberts 2003; Charpentier et al. 2008).

Plasticity in dispersal provides a mechanism for adjusting the size and sex ratio of breeding groups relative to those of other groups in the population (Moore 1992; Strier 2003b). Dispersal costs previously documented for female muriquis include reduced survivorship, with 28.4% mortality estimated for 38 females of dispersal age (5–7 years) from 2002 to 2007 compared to 4.55% mortality for philopatric males in the same age class. There was also significantly later ages at first reproduction compared to females that remained and reproduced in their natal group. Specifically, natal Matão females have dispersed at 5.25–7.85 years of age (mean = 6.15 ± 0.60 years, $N = 34$; updated from Strier et al. 2006), prior to the onset of sexual activity or hormonal evidence of puberty (Strier and Ziegler 2000). Age at first reproduction was significantly earlier in the Matão females that reproduced in their natal group (7.77 ± 0.72 years, $N = 3$) compared to females that dispersed from the Matão group and whose first reproductions in their new groups have been documented (9.58 ± 0.87 years, $N = 9$; $z = 2.40$, $p < 0.02$); this difference can be attributed to the earlier onset of puberty in the non-dispersing females instead of shorter cycling-to-first conception delays (Martins and Strier 2004).

Delayed reproduction associated with dispersal has been documented in red howler monkeys (*Alouatta seniculus*), where it may be associated with eviction from their natal groups (Crockett and Pope 1993), but not in mountain gorillas (*Gorilla beringei*), where the voluntary dispersal of nulliparous females from their natal groups (Robbins et al. 2009) more closely resembles that of muriquis to date (Printes and Strier 1999). Nonetheless, fluctuations in group and population conditions in our study population could alter both the contexts under which females disperse and the consequences of dispersal for reproduction. For example, if females are sensitive to levels of intragroup competition, then we might expect the age at dispersal of female muriquis to decline as the size of their natal group increases. However, there is no evidence that this has occurred over the decades during which the Matão group has been monitored (Fig. 6.3).

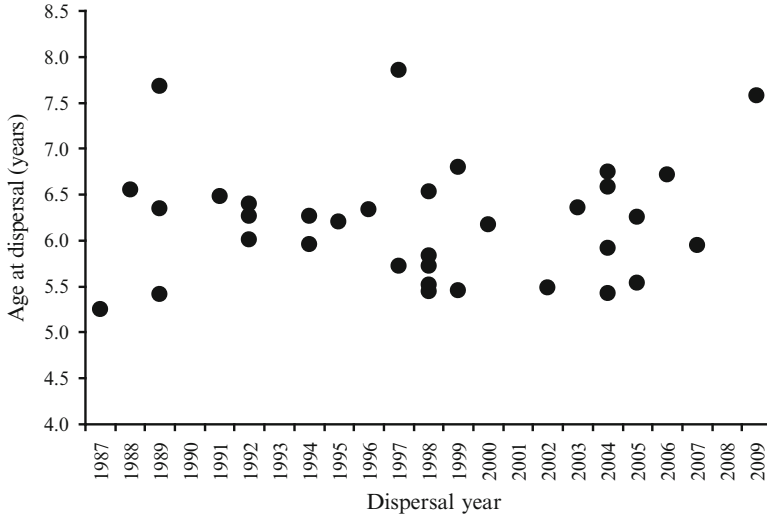


Fig. 6.3 Female dispersal age over time. Natal Matão group females ($N = 34$) have dispersed between 5.25 and 7.85 years of age, and there is no evidence for changes in female dispersal age despite increases in group size, population size, and population density over time

Alternatively, if females are sensitive to intergroup competition associated with population density, then they might postpone dispersal from their natal groups, and experience higher levels of aggression from females in the groups they try to join and higher mortality costs during dispersal as population density increases. Although high population density should facilitate encounter rates with other groups (Strier 2000a), increased competition and aggression should make joining these groups more difficult now than it has been in the past. However, although we found early on that the rate at which females received displacements from other female was higher for new immigrants than for long-term residents (Printes and Strier 1999), this difference has not increased, nor have we seen increases in the rate of aggression directed at immigrants.

6.3.4 Male Maturation and Philopatry

Changes in female dispersal and maturation can have significant implications for breeding sex ratios as population density has increased, and thus affect levels of male competition within and between groups, particularly in species in which males remain in their natal groups (Strier 2000b, 2011). To date, males in the Matão group become sexually active between 4.10 and 8.27 years of age (mean = 6.18 ± 1.04 , $N = 26$) and when they have reached sexual maturity, defined behaviorally by their first observed copulation that culminates with ejaculation, between 5.21 and 8.36 years of age (mean = 6.81 ± 0.86 , $N = 25$). Males in the Matão group have

thus entered the potential breeding population about 0.3 years (4 months) younger, on average, than the age at which the females that have (atypically) remained in their natal groups have conceived (7.10 years; calculated from subtracting the hormonally determined mean gestation length of 216 days, or 0.59 years; Strier and Ziegler 1997), and more than 2.2 years earlier than the average age at which dispersing females have conceived.

Despite more than a 3-year range of variation in age of male sexual maturity, there has been no pattern of change in the variation over time (Fig. 6.4). This consistency in the age of sexual maturation in male muriquis might reflect a balance between demographic pressures that should delay maturation on the one hand, and the effects of increased competition on survivorship that should favor faster maturation on the other hand (Janson and van Schaik 1993). Alternatively, it could reflect a lag between the effects of group size and density effects, such that social pressures have not yet begun to exert the expected delaying effect on male life histories (Joffe 1997). As operational sex ratio in the Matão group becomes increasingly male-biased (Strier et al. 2006) and scramble competition for access to females correspondingly increases (Strier et al. 2002; Strier 2003b), we expect increasing delays in the onset of male sexual maturity and possibly dispersal to groups with more favorable breeding sex ratios. Extraordinary demographic conditions may underlie other examples of deviations from male philopatry, such as in an isolated chimpanzee community at Bossou, New Guinea (Sugiyama 2004), in the case of male bonobos thought to have transferred into a community with more favorable sex ratios (Hohmann 2001), and in one group of woolly monkeys in a population that might have been affected by past hunting (Di Fiore and Fleischer

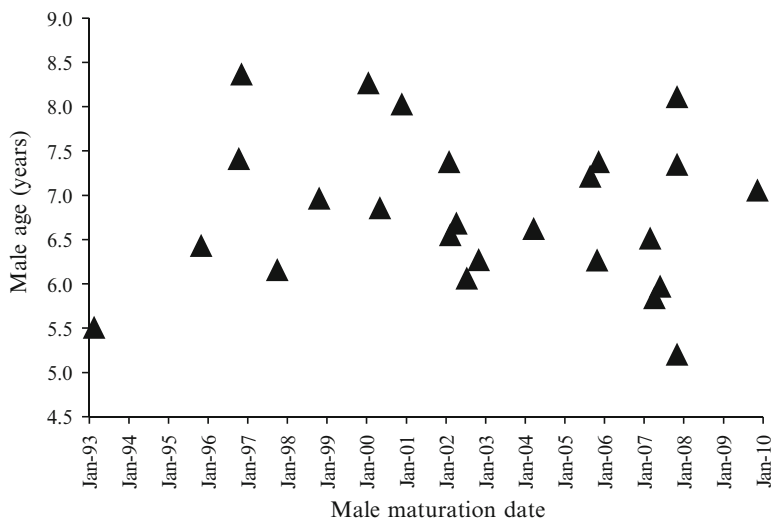


Fig. 6.4 Male age at sexual maturity over time. Matão males ranged from 5.21 to 8.36 years ($N = 25$) and there was no obvious change over time despite increases in group size, population size, and population density

2005; Di Fiore et al. 2009). Indeed, the social flexibility seen in both woolly monkeys and northern muriquis may extend to their dispersal patterns (Di Fiore and Strier 2004), and thus provide a mechanism to offset the predicted effects of increased social and ecological competition on male maturational stages.

6.4 Past Perspectives and Prospectives

After nearly 30 years of field research on the northern muriqui, we have gained some clear insights into features of the behavioral ecology, reproductive biology, and life histories of our study population. Although our understanding of other muriqui populations is still limited, both the changes and the equally important lack of changes we have documented in our study population provide a crucial comparative context for research on these populations. Neither the extent of the population expansion nor the corresponding behavioral changes that our study has tracked were anticipated aims of the project from the onset. Yet, in many respects it has been this first-hand glimpse into the dynamics of the muriquis' lives that has captured – and continues to hold – our attention.

Reflecting on the history of our long-term field study, five particular points come to mind, and all are connected in one way or another to the northern muriquis' critically endangered status. Perhaps the most obvious of these has been the methodological choices we have made to minimize the impact of our research on the animals. Thus, we have restricted ourselves and our students to observational studies instead of field experiments, even though the careful deployment of feeding platforms or of controlled playback techniques might have permitted us to discriminate between correlated and causal responses. We have also opted to restrict investigations of muriqui parasites, hormones, and genetics to what could be gleaned from analyses of their dung. This has sometimes meant greater costs and longer delays than we might have incurred, for example, if we had captured the muriquis to obtain samples of their blood for genetic analyses before the techniques for extracting and amplifying DNA from dung were developed. Yet, even with these self-imposed constraints, we are cautious about the possible impacts of our long-term research presence (Strier 2010).

A second major consideration pertains to the demographic fluctuations and behavioral plasticity we have documented. The increases in the size of our main study group and the entire study population have clearly shown that primate groups and populations are not static entities with fixed properties, but instead, that they have group and population histories of their own (Strier 1997b). This realization raises all kinds of questions about how much we can conclude about the behavioral adaptations of northern muriquis – or any other primates – that are currently living under what are likely to be highly altered ecological and demographic conditions (Strier 2003b, 2009). Indeed, after all of these years, we cannot determine what group size or population density would be typical for this species or the extent to which these vary among populations. Nonetheless, we think that questions about

how much of the behavior we observe in our study subjects today reflect adaptations as a result of past selection pressures versus mismatches between past and current conditions that could negatively impact their survival are important and interesting, not only for northern muriquis, but for all other primates whose futures are threatened (Strier and Mendes 2009).

Demographic changes in our main study group were responsible for a third significant shift in our perspective, for as the number of natal female emigrants began to exceed the number of female immigrants, our focus expanded from studying a single group to studying the dynamics of the entire population (Strier 2005; Strier et al. 2006). This catapulted the importance of this particular population – and of this particular forest, which supports nearly 30% of the entire species – into a broader perspective, stimulating our interest in facilitating new research initiatives on the vegetation and ecology of the forest (Strier and Boubli 2006; Boubli et al. in press) and our ongoing collaboration with the NGO that now administers the protected reserve.

The expansion and diversification of research contributed to a fourth major advance, which involved the launching of comparative field studies of other populations of northern muriquis. This includes one at the municipality of Santa Maria de Jetibá (SMJ), Espírito Santo State (Mendes et al. 2005b) that is particularly valuable because the demography of that population differs greatly from that at the RPPN-FMA. Whereas our study population includes multiple large social groups in a single isolated forest of nearly 1,000 ha, the SMJ population is represented by at least 13 single small groups of 2–20 individuals occupying forest fragments of 60–350 ha, where opportunities for dispersal are limited (updated from Mendes et al. 2005b). Although the behavioral and ecological comparisons between these populations hold great theoretical potential, our greatest concern at the moment is how to apply what we have learned about northern muriquis so far to insure the survival of both of these – and other – remaining populations.

A final reflection that we are in a privileged position to make involves our ongoing appreciation for the synergy that can come from a true international collaboration (Strier and Mendes 2009). The continuity in our long-term study of the northern muriqui would not have been possible without it.

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