Primates (2021) 62:861–868
https://doi.org/10.1007/s10329-021-00953-3

EDITORIAL

The limits of resilience

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Received: 20 September 2021 / Accepted: 22 September 2021 / Published online: 12 October 2021

Resilience is a concept that describes the ability of a system to absorb or rebound from external disturbances or perturbations. Synonyms for resilience include flexibility, pliability, plasticity, and elasticity, each of which has nuanced connotations depending on the field of application (Hodgson et al. 2015). Within ecology, for example, divergent definitions and emphases range from what resilience means about the ability of a system to shift between alternative states (Holling 1973; Gunderson 2000), to how resilience affects the long-term variability of a system subject to repeated disturbances (Carpenter and Ives 2007). Frameworks for ecological resilience have typically been applied to evaluating ecosystem functions and services among communities of species (Holling 1973; Carpenter et al. 2001; Chambers et al. 2019), while those for demographic resilience have focused on the comparative capacity of species to persist or recover from episodic disturbances (Capdevila et al. 2020). However, evaluating demographic resilience requires extensive knowledge of population structure and the factors regulating population growth, which can take decades to acquire and, even then, can be difficult to interpret (Ziebarth et al. 2010; Capdevila et al. 2020).

The resilience of primates has typically been considered in two contexts, each of which has direct implications for their conservation (Estrada et al. 2017). The first pertains to the vital ecosystem services primates provide in their roles as pollinators and especially seed dispersers, and the disruptions to the ecological communities caused by the loss of these services due to primate extirpations. The second context pertains to the limitations of primate persistence in the face of ongoing anthropogenic disturbances such as forest fragmentation and degradation. These kinds of sustained, long-duration "press" disturbances obviously differ from discrete "pulse" disturbances, such as those caused by events such as fires, hurricanes, or disease (Capdevila et al. 2020). Both types of disturbances can interact to affect resilience at different spatial, temporal, and demographic scales. Thus, although behavioral flexibility and other social, cognitive, and life history traits may buffer primates from some environmental perturbations (Morris et al. 2011; Campos et al. 2017), their ability to recover from sudden, extreme pulse-like disturbances may still be constrained by conditions imposed by extended press disturbances.

A clear example of these dynamics has been presented by Bicca-Marques and colleagues (2020), whose recent analyses of howler monkeys (*Alouatta* spp.) across a range of habitats reveal high individual tolerance but low population persistence in degraded, fragmented forests. Howler monkeys exhibit high levels of behavioral and dietary flexibility that permit them to persist in degraded habitat. Yet, this flexibility does not necessarily buffer them and may even "mask" the limits of their populations to recover from discrete disturbances, such as the recent yellow fever outbreaks

Fig. 1 Northern muriquis (*Brachyteles hypoxanthus*) at the Reserva Particular do Patrimônio Natural-Feliciano Miguel Abdala, Caratinga, Minas Gerais, Brazil. Photo by Carla B. Possamai/Projeto Muriqui de Caratinga. All rights reserved©

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that caused significant mortality and many local extinctions across regional scales (Bicca-Marques et al. 2020).

Northern muriquis (*Brachyteles hypoxanthus*) provide a complementary example of both the adaptive potential and limitations of population persistence under different disturbance regimes (Fig. 1). During the past 39 years, my colleagues and I have documented behavioral and demographic changes in one isolated population inhabiting a small forest fragment in southeastern Brazil (Strier et al. 2006; Strier and Mendes 2012). There are no other neighboring muriqui populations for recruitment through immigrations to occur, so all of the demographic changes have occurred in what is essentially a closed system. During the first 32 years, the population increased by sevenfold, growing from about 50 individuals living in two multi-male, multi-female groups, to 356 individuals divided among five mixed-sex groups. before declining by one-third of its maximum size in just 5½ years (Fig. 2). With 234 individuals present in August 2021, the population was still almost five times larger than it was when the study began nearly four decades ago. Nonetheless, the alarming rapidity by which the numerical gains made during decades of population growth have been lost raises compelling questions about the limits of these muriquis' resilience and what these may mean for the future of this Critically Endangered species.

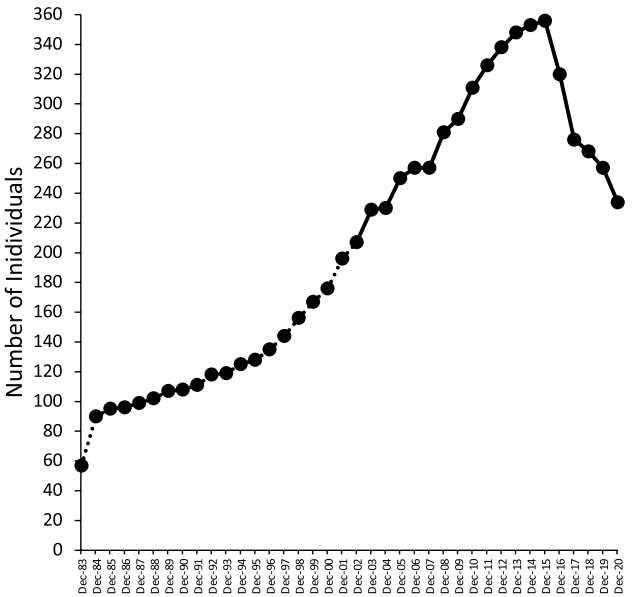

Fig. 2 Changes in the population size of northern muriquis at the Reserva Particular do Patrimônio Natural-Feliciano Miguel Abdala, Caratinga, Minas Gerais, Brazil. Annual population size data from 1985–2000 (dotted line) are based on calculations using updated biography data as described in Strier et al. (2010). From 2001–2020 (solid line), data are based on all individuals, which can be identified by their natural markings. Totals are the numbers of individuals that were confirmed to have survived as of the month and year shown

A brief history

Muriquis are the largest nonhuman primates of the Americas, and endemic to the Atlantic Forest of southeastern Brazil. The northern muriqui was previously classified with the southern muriqui in a monotypic genus, *Brachyteles arachnoides*, but taxonomic revisions based on morphological and molecular analyses have led to its reclassification as a distinct species, *B. hypoxanthus*, with the divergence from the southern muriqui estimated to have occurred about 2 million years ago (reviewed by Chaves et al. 2019). Similar to the plights of many other threatened primates in the Brazilian Atlantic Forest and throughout the tropics, past and ongoing habitat destruction and hunting pressures have fragmented their populations and reduced their total numbers. Only about 1000 northern muriquis are now estimated to occur, distributed unevenly in isolated populations across a dozen or so of the remaining forest tracts (Melo et al. 2021).

My first sighting of muriquis was in 1982, while visiting a small, privately owned forest located on Fazenda Montes Claros, in Caratinga, Minas Gerais (19.7333 S, 41.8167 W). This 957 ha of largely regenerating Atlantic Forest is surrounded by coffee and pastureland, but both the forest and the muriquis had been protected by its owner from the time he purchased the property in the mid-1940s (Fig. 3). In 2001, the owner's family honored his memory by converting the forest into a protected natural heritage area, known as the Reserva Particular Patrimônio Natural (RPPN)-Feliciano Miguel Abdala.

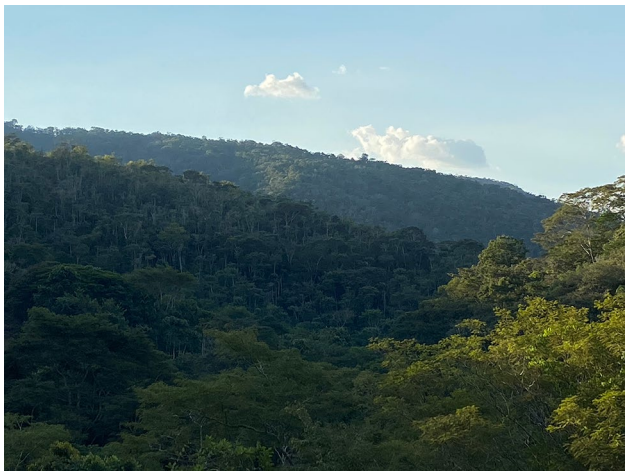

Fig. 3 Forest at the Reserva Particular do Patrimônio Natural-Feliciano Miguel Abdala, Caratinga, Minas Gerais, Brazil. Natural regeneration combined with the forest's protected status has increased the habitat available to muriquis since the Muriqui Project of Caratinga began in 1983. Photo by Karen B. Strier/Projeto Muriqui de Caratinga. All rights reserved©

The late Japanese primatologist Akisato Nishimura was the first foreigner to study the muriquis there during a week-long visit in August 1977 (Nishimura 1979). Despite the brevity of his visit and acute language barriers, Nishimura-san made a very favorable impression on everyone, including Senhor Feliciano and the local farmers, who referred to him frequently and with great fondness for many years (Fig. 4). Their positive recollections of Nishimura-san paved the way for me, another foreigner, and I was warmly welcomed when Russ Mittermeier introduced me to the forest and its muriquis in 1982, and then again when I returned to conduct the first extended, systematic study on them for my 14-month doctoral dissertation research in 1983.

During the subsequent years of this ongoing field study, the number of people and projects concerned with muriqui conservation has grown. The Muriqui Project of Caratinga, as the project is now known, has provided training and financial support for some 80 Brazilian students, most of whom have remained actively involved with primatology, science, and conservation. Some of these former students have continued to work with me and other colleagues on the Caratinga muriquis and other sympatric primates in this forest, while others have used their experience on the project to launch important new comparative studies and conservation and management initiatives involving other populations of muriquis (Strier et al. 2017). The contributions of these teams of sequential students to the Muriqui Project of Caratinga have made it possible to monitor individual muriquis for the duration of their lives, and to document how the muriquis' behavior and their population have changed over time (Strier 2019).

Fig. 4 Senhor Feliciano Miguel Abdala and Akisato Nishimura, circa 1977, at Fazenda Montes Claros, Caratinga, Minas Gerais, Brazil. The forest was later converted by Senhor Feliciano's family into a private natural heritage reserve, known as the RPPN Feliciano Miguel Abdala. The late Nishimura-san visited the site in 1977 to observe the muriquis, and I believe he gave me this photo as a gift when he learned about my research there

Behavioral flexibility and demographic fluctuations

Early observations of these elusive muriquis revealed a uniquely peaceful, egalitarian society in which philopatric males spent most of their time in close proximity and tolerated one another's mating activities, and females dispersed from their natal groups prior to the onset of sexual maturity (Strier et al. 2002, Strier et al. 2015). These distinguishing characteristics of northern muriqui social organization appear to be highly conservative, having persisted despite ecological and demographic variation over time in this population and also occurring across space in other populations living under different conditions (Fig. 5). Other behavior patterns, by contrast, have been more flexible. We have documented two major behavioral shifts in the muriquis' grouping patterns and use of vertical space, each of which emerged during sequential phases in the population's demographic history. These shifts were consistent with predictable

Fig. 5 Northern muriqui males engaging in a friendly "huddle" at the Reserva Particular do Patrimônio Natural-Feliciano Miguel Abdala, Caratinga, Minas Gerais, Brazil. The affiliative relationships among philopatric males and the overall peacefulness of muriqui society seem to be highly conservative traits. Photo by Fernanda P. Tabacow/Projeto Muriqui de Caratinga. All rights reserved©

kinds of facultative responses to the demographic pressures accompanying population expansion. However, the extent to which they reflect the muriquis' adaptive potential or obscure the real limits to their resilience is still unclear.

The first behavioral transition was documented in the main study group (Matão), which shifted from its original pattern of traveling and associating as a cohesive unit (Fig. 6) to one in which group members increasingly split up into temporary subgroups that varied in size and composition (Dias and Strier 2003). The shift from cohesive to fission–fusion dynamics (sensu Aureli et al. 2008) was a process that did not become established until well into the first 15 or so years of the project, by which time the group had nearly tripled in size (from 23 to 63 individuals between July 1983 and July 1989) as a product of low mortality across all age-sex classes, steady production of births (with exceptionally high infant survivorship) at 3-year intervals, and a strongly female-biased birth sex ratio. Not surprisingly, the larger group also utilized a larger home range, presumably driven by the need for a larger food supply area. Yet, there was no corresponding increase in their daily distances traveled. It seemed that by fissioning into smaller temporary parties, the muriquis not only avoided potential increases in intergroup feeding competition, but also maintained per capita travel costs that were similar to those when the group was much smaller.

The second behavioral transition involved the muriquis' increasingly frequent use of the ground, initially for feeding but then for nonessential activities as well (Mourthé et al. 2007; Tabacow et al. 2009) The shift to increased feeding on terrestrial substrates became notable during the early 2000s, some 20–25 years into the project (Fig. 7), by which time we were monitoring the entire muriqui population in addition to my original study group. The other original group had also grown and had already fissioned twice (Strier et al. 2006; Tokuda et al. 2014). By 2010–2011, more than 300 muriquis distributed among the four groups in the population were using nearly 900 of the 1000 ha forest fragment, most within the boundaries of the reserve, with the remainder being continuous regenerating forest surrounding it (Lima et al. 2019). The population appeared to be approaching or to have reached a point of habitat saturation, and with nowhere else to go, it made sense that the muriquis would have intensified their use of available habitat by expanding their vertical niche (Fig. 8).

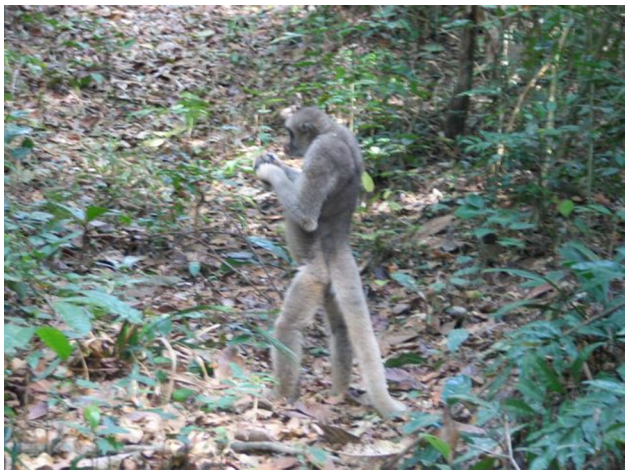

Fig. 7 An adult male northern muriqui feeding while upright on the ground at the Reserva Particular do Patrimônio Natural-Feliciano Miguel Abdala, Caratinga, Minas Gerais, Brazil. Photo by Fernanda P. Tabacow/Projeto Muriqui de Caratinga. All rights reserved©

Fig. 6 A large subgroup of northern muriquis feeding at the Reserva Particular do Patrimônio Natural-Feliciano Miguel Abdala, Caratinga, Minas Gerais, Brazil. Photo by Carla B. Possamai/Projeto Muriqui de Caratinga. All rights reserved©

Fig. 8 A huddle of adult male northern muriquis relaxing on the ground at the Reserva Particular do Patrimônio Natural-Feliciano Miguel Abdala, Caratinga, Minas Gerais, Brazil. Photo by Marlon Lima/Projeto Muriqui de Caratinga. All rights reserved©

By 2010, the demographic processes responsible for the population's continuing growth had also changed significantly (Strier and Ives 2012). Birth sex ratios had shifted from being female- to male-biased, and mortality had increased across all age-sex classes, including among prime-aged adult males, the age-sex class that most frequently spent time on the ground. However, instead of a corresponding decline in fertility, as expected by density-dependent effects, birth intervals following surviving offspring were shorter than they had previously been, offsetting the dampening effects of the other demographic processes and sustaining the population's growth (Fig. 9). Feedback between the muriquis' behavioral responses to demographic pressures may have also affected the demographic processes. For example, habitat saturation and limited resources may have stimulated the muriquis' initial increased use of the ground, where they were more vulnerable to predators and pathogens and thus experienced higher mortality, but where they also gained access to terrestrial food resources that could enhance feeding efficiency and nutrition and thus contribute to increased fertility.

We anticipated in 2010 that sustained population growth under saturated conditions was unlikely to persist. But evaluating this prediction has been confounded by environmental and demographic disruptions caused by drought and disease.

Disturbances and demographic resilience

In 2014 and 2015, an extreme drought affected much of Brazil. Cumulative rainfall in the reserve during these years was more than two standard deviations below the annual average. Births still offset the increased mortality in the population in these years, such that by the end of 2015, the population had returned to its maximum size. However, despite their initial resilience to presumed stress during the prolonged drought, within a few months of its peak recovery the population began an extended period of decline (Fig. 10).

The decline preceded a severe yellow fever outbreak, which coincided with the accelerated loss of nearly 10% of the population during a 6-month period from October 2016 through April 2017 (Strier et al. 2019), and it extended until a brief period of recovery during the 2018 birth season. Since then, however, we have seen annual cyclical fluctuations in the population, similar to those during the 2014 and 2015 drought years, except that the recent temporary annual upturns in population size due to births have been offset by even greater losses to mortality, resulting in a net population decline that has extended through June 2021.

What will happen to this population in coming years is still anyone's guess. This year could resemble the past three years, when the promising gains made during the birth seasons were undermined by even greater mortality losses, and the population could continue on a trajectory of decline. Alternatively, the 2021 birth season could be a pivotal point that marks the return of the population's earlier explosive

Fig. 9 A northern muriqui mother with her infant and juvenile son at the Reserva Particular do Patrimônio Natural-Feliciano Miguel Abdala, Caratinga, Minas Gerais, Brazil. Photo by Carla B. Possamai/Projeto Muriqui de Caratinga. All rights reserved©

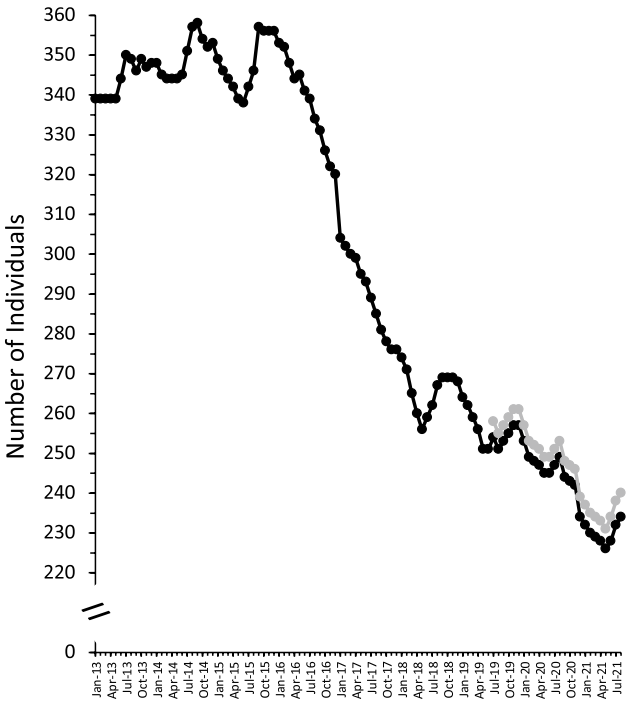

Fig. 10 Monthly population of northern muriquis at the Reserva Particular do Patrimônio Natural-Feliciano Miguel Abdala, Caratinga, Minas Gerais, Brazil. Data expand on the annual data after December 2012, as summarized in Fig. 2. Note that the *Y*-axis here is truncated to show small numerical changes. Gray line shows the population including individuals that have not been sighted since June 2019 ($n=4$), Nov 2020 ($n=1$), or May 2021 ($n=1$) but are suspected of still being alive

growth or the beginning of a new phase of population stability. In ecology, stability is also considered to be a form of resilience (Pimm 1984), because a population that is resistant to repeated disturbances may look stable over the long term when disturbances are viewed as part of the natural variation of things.

Despite these uncertainties, it is clear that the muriquis' behavioral flexibility contributed to the population's long-term resilience. Between their shift to fission–fusion dynamics and an expansion of their vertical niche, the muriquis at least temporarily escaped or reduced the detrimental effects of high population density on resource competition, per capita travel costs, and female fertility. These behavioral adjustments permitted the population to grow beyond the size predicted by density-dependent processes, providing a critical demographic buffer during the dramatic population declines that have occurred recent years. In this sense, the muriquis provide a textbook example of why a population's long-term persistence is at least partially dependent on the population's size (Shaffer 1981).

Ultimately, however, there may be limits to how much the muriquis' behavioral flexibility can buffer them from extended press disturbances such as those caused by ongoing habitat degradation and climate change (Lima et al. 2020; Stewart et al. 2020).

Reinforcements for resilience

During the nearly 40 years I have been involved in muriqui research and conservation efforts, my colleagues and I have witnessed the extinction of one much smaller muriqui population and the near extinction of another (Melo et al. 2005; Nogueira et al. 2010). However, some small, isolated populations have also benefited from successful management efforts involving the translocation of solitary females, most of which were suspected of having dispersed from their natal groups across a fragmented landscape without finding other muriquis to join (Tabacow et al. 2021).

These and other coordinated management and conservation efforts for the northern muriqui have been greatly facilitated by the Brazilian National Action Plan for the Conservation of Muriquis (Jerusalinsky et al. 2011; Strier et al. 2021). In this plan, the muriqui population of Caratinga was recognized as a priority for conservation, in part because of the value of the long-term research and in part because it continues to be one of the largest of the remaining populations of the species. The forest at RPPN Feliciano Miguel Abdala is the anchor for the state forest institute's "Sossego-Caratinga Corridor" (Brazil 2014), which will connect it with another private natural heritage reserve, the RPPN Mata do Sossego, where a single isolated group of some 25 muriquis is found (Tabacow et al. 2021). Plans to expand this corridor to include two other large muriqui populations are now underway (reviewed by Baêta 2021), with promising prospects for the future.

Many of these ongoing and new initiatives are being led by a new generation of muriqui researchers and conservationists, some of whom participated in the Muriqui Project of Caratinga or have worked with long-term colleagues on other muriqui projects elsewhere. Indeed, perhaps the greatest hope for the persistence of northern muriquis and other threatened primates is through the new generations of primatologists that we train.

Acknowledgements I thank Editor-in-Chief Masayuki Nakamichi-san for inviting me to contribute this Editorial, and for his kind patience during its preparation. I also thank Tony Ives and Jon Marks for providing helpful comments on the text. I am grateful to everyone who has helped me to conduct research in Brazil, from the Brazilian government CNPq and Preserve Muriqui for permissions to my long-term collaborators on the Muriqui Project of Caratinga, including especially Sérgio L. Mendes, Carla B. Possamai, Fernanda P. Tabacow, and Fabiano R. de Melo. The names of funding sources and all participants on the Muriqui Project of Caratinga can be found at: https://strierlab.anthropology.wisc.edu/muriqui-project-of-caratinga-acknowledgements/

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