Demographic Effects of the Translocation of a Female Northern Muriqui (*Brachyteles hypoxanthus*) in an Atlantic Forest Fragment in Minas Gerais, Brazil

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Abstract: Habitat fragmentation due to human activities is one of the principal threats to all primates and is particularly so for arboreal platyrrhines. Its impact has been extreme in the Brazilian Atlantic forest, where most primate populations have been severely reduced in numbers and their distributions restricted, resulting in low probabilities of long-term persistence. One of the most severely affected species is the northern muriqui (*Brachyteles hypoxanthus*), which today has fewer than 1,000 individuals distributed over only a dozen populations and is considered to be Critically Endangered. Most of these populations are isolated and smaller than 50 individuals, including the population inhabiting the Sossego Forest in Simonésia, Minas Gerais. With fewer than 30 individuals associating in one social group, the Sossego muriqui population is doomed to extinction unless emergency management measures are implemented to protect it. We monitored the demography of the Sossego muriquis to evaluate the impacts of the introduction of a reproductive-aged female that was translocated into this population in December 2006. Data were collected on all individuals, identifiable from their natural markings, during 3 to 12 monthly surveys conducted each year from July 2012 to June 2020. They revealed that the population grew from 32 individuals in July 2012 to a peak of 38 in September 2015, but then declined to a low of 22 individuals in September 2017, coinciding with a yellow fever outbreak in the region. As of June 2020, there were 24 individuals present. Four of the surviving individuals were the translocated female and three of her five offspring. One of her daughters was confirmed to have emigrated to another forest fragment and a second daughter has not been seen since March 2019 and is suspected to have emigrated. During the eight years of monitoring, we recorded 17 births (11 females and six males) and 25 disappearances involving 17 females, including the female confirmed to have dispersed, and eight males. Our results emphasize the risks of demographic stochasticity in small, isolated populations. The confirmed emigration of one dispersal-aged female that failed to locate a group to join, and the absence of any immigrants, call attention to the demographic implications of translocation as a potential conservation tool for small, isolated populations of species such as the northern muriqui in which female dispersal and male philopatry are typical.

Key words: *In situ* management, Conservation, Critically Endangered species, Female dispersal, Sex ratio

Introduction

Primates are among the most endangered mammals in the world, with more than half of all taxa at risk of extinction (Estrada *et al*. 2017). Brazil is one of the four countries with the largest numbers of threatened primate species (Estrada *et al*. 2018). Habitat loss and fragmentation are among the most serious threats in the Brazilian Atlantic forest

(Mittermeier *et al*. 2005; Strier 2007; Kierulff *et al*. 2007; Ribeiro *et al*. 2009), where roughly 70% of the endemic primates are threatened (Brazil, ICMBio, MMA 2018). The risks of fragmentation are especially high for primates with restricted geographic distributions. The golden lion tamarin (*Leonthopitecus rosalia*), for example, is restricted to fragments in a small area in the state of Rio de Janeiro (Kierulff 1993; Kierulff *et al*. 2002; Rylands *et al*. 2002), the

northern brown howler monkey (*Alouatta guariba guariba*) is restricted to fragments in southern Bahia (Neves *et al.* 2015), and the northern muriqui (*Brachyteles hypoxanthus*) is found only in forest fragments in the states of Espírito Santo, Minas Gerais, and the north of Rio de Janeiro (Strier 1993/94; Mendes *et al.* 2005a; Strier *et al.* 2017; Chaves *et al.* 2019). The risks of inbreeding are especially high in small, isolated populations with a single social group because there are no opportunities for gene flow (Fahrig and Merriam 1985; Lacy 2000; Brito 2009). Consequently, these populations have low chances of long-term persistence without management programs that include translocations (Mendes *et al.* 2005a; Kierulff *et al.* 2007; Lanna 2015).

The northern muriqui has been reduced to fewer than 1,000 individuals distributed across 12 populations (Strier *et al.* 2017). Five of these populations have fewer than 50 individuals, and do not, therefore, meet the criteria for minimum viable size (Rylands *et al.* 1988; Brito and Grelle 2006). This situation is extremely worrisome considering the risks of demographic and enviromental stochastic processes and low genetic variation (Strier 2000; Strier *et al.* 2019). These risks are magnified because of the slow life histories of muriquis, in which females give birth to their first offspring at an average age of nine years and typically produce single offspring at three-year intervals (Strier *et al.* 2001; Strier *et al.* 2006; Strier and Ziegler 2000; Strier and Mendes 2012). Moreover, males remain in their natal groups, while females disperse before the onset of puberty (Printes and Strier 1999; Strier and Ziegler 2000). Thus, isolated populations either suffer from close inbreeding because daughters have nowhere to disperse, or else they lose females as a result of female dispersal to locate other populations, especially because male philopatry constrains the formation of new groups and therefore the colonization of new fragments (Strier *et al.* 2015).

Here, we present demographic data on one small population of northern muriquis inhabiting an isolated forest fragment of 800 ha, known as the "Mata do Sossego" or the Sossego forest, in Minas Gerais, Brazil. In 2006, the population consisted of a single group of 42 individuals including 10 adult females of reproductive age (Mendes 2007). In an effort to increase the population size and its potential viability, an emergency management intervention involving a female translocation was conducted (Barros *et al.* 2011). Previous translocations involving northern muriquis have been mostly successful (Table 1). We examine the

Table 1. History of translocations of the northern muriqui (*Brachyteles hypoxanthus*).

No.	Date	Individual (name)	Location captured*	Location released	Fate	Management type
1	July 2005	Subadult female (Renata)	Mata Bélem, Santa Maria Jetibá, ES	Córrego do Ouro[1], Santa Maria Jetibá, ES	Reproduced in new group[1,2,3]; alive as of Dec 2018[4]	Wild
2	December 2006	Subadult female (Eduarda)	Santa Margarida, MG	Mata do Sossego, Simonesia, MG	**This study**	Wild
3	August 2008	Adult male (Zidane)	Fazenda Esmeralda, Rio Casca, MG	Fundação Zoo-Botânica, Belo Horizonte, MG	Died in June 2016[3,5,6]	Captive
4	October 2016	Subadult female (Mica)	Mata Bélem, Santa Maria Jetibá, ES	Reserva Augusto Ruschi, Santa Teresa, ES	Not seen after release in October 2016[4,7]	Wild
5	January 2017	Adult female (Esmeralda)	Fragment in Esmeralda de Ferros, MG	Mata do Luna, Ibitipoca, Lima Duarte, MG	Not seen after September 2017[8]	Wild
6	March 2019	Adult female (Ecológica)	Fragment near Mata do Sossego, MG	Comuna do Ibitipoca, Lima Duarte, MG	Reproduced in new group; alive as of January 2020[9,10]	Captive
7	May 2019	Adult male (Bertolino)	Mata do Luna, Ibitipoca, Lima Duarte, MG	Comuna do Ibitipoca, Lima Duarte, MG	Copulated in new group; alive as of January 2020[9,10]	Captive
8	August 2019	Adult male (Luna)	Mata do Luna, Ibitipoca, Lima Duarte, MG	Comuna do Ibitipoca, Lima Duarte, MG	Attempted copulation in new group; alive as of January 2020[9,10]	Captive
9	October 2019	Adult female (Socorro)	Fragment near Mata do Sossego, MG	Comuna do Ibitipoca, Lima Duarte, MG	Copulated in new group; alive as of January 2020[9,10]	Captive
10	November 2020	Subadult female (Nena)	Fragment near Parque Nacional do Caparaó, ES	Comuna do Ibitipoca, Lima Duarte, MG	Alive as of January 2020[10]	Captive

*State abbreviations: ES = Espírito Santo; MG = Minas Gerais.

References: [1]Mendes *et al.* (2005); [2]Lanna (2015); [3]Jerusalinsky *et al.* (2011); [4]S. L. Mendes, pers. comm.; [5]Nogueira *et al.* (2010); [6]F. R. Melo, pers. comm.; [7]Teixeira *et al.* (2018); [8]Milagres *et al.* (2019); [9]Tabacow *et al.* (2019); [10]F. P. Tabacow, pers. comm.

consequences of this translocated female and her offspring on the demographic structure and dynamics of the population from July 2012 through June 2020. We know that population growth in another population of northern muriquis has been influenced by the number of reproductive females and female reproductive rates (Strier 2014). We, therefore, expected that offspring produced by the translocated female, together with the original eight adult females, would help to increase the size and genetic variation of the Sossego population. We also expected that the extent of her contribution to this population would depend on the sex of her offspring given that male muriquis are philopatric and females typically disperse from their natal groups, and opportunities for forming new groups are limited (Strier et al. 2006). If her daughters disperse prior to reproducing, then they would have no impact on this population. By contrast, if her daughters remain and reproduce in their natal group, they could contribute to the population size and genetic diversity, as long as they exhibit the same avoidance toward inbreeding with their fathers or brothers that has been documented in another muriqui population (Strier et al. 2011). However, if the translocated female produces sons that remain in their natal group, then she would contribute to both population size and to genetic variation with the offspring sired by her sons with other females. All of her offspring that remain in their natal group as subadult and adults would increase the ratio of mature:immature individuals and the sex ratio of reproductive-aged individuals according to their sex.

Methods

Study area

The 800-ha Sossego forest is located in the municipality of Simonésia, Minas Gerais (20º06'5"S, 41°59'30"W; Fig. 1), with altitudes ranging from 1200–1647 m above sea level (Fundação Biodiversitas 2014). The forest is characterized as seasonal, semi-deciduous montane (Veloso et al. 1991; Silva Júnior et al. 2010) with approximately 563 ha of well-preserved forest in advanced stages of succession protected under law as a private reserve (Silva Júnior et al. 2009). Compared to other Atlantic Forest sites, the Sossego forest has the highest Shannon diversity index (H' = 4.343) and evenness (J = 0.873), indicative of a later secondary succession stage than the other forest fragments evaluated (Silva Júnior et al. 2010). Its water comes from a network of springs within the forest, and the surrounding area is characterized by eucalyptus (Eucalyptus sp.) and coffee (Coffea arabica) plantations that are the primary commercial cultivation in the region (Santos 2013). The local climate is highly seasonal with a strong summer rainy season and winter dry
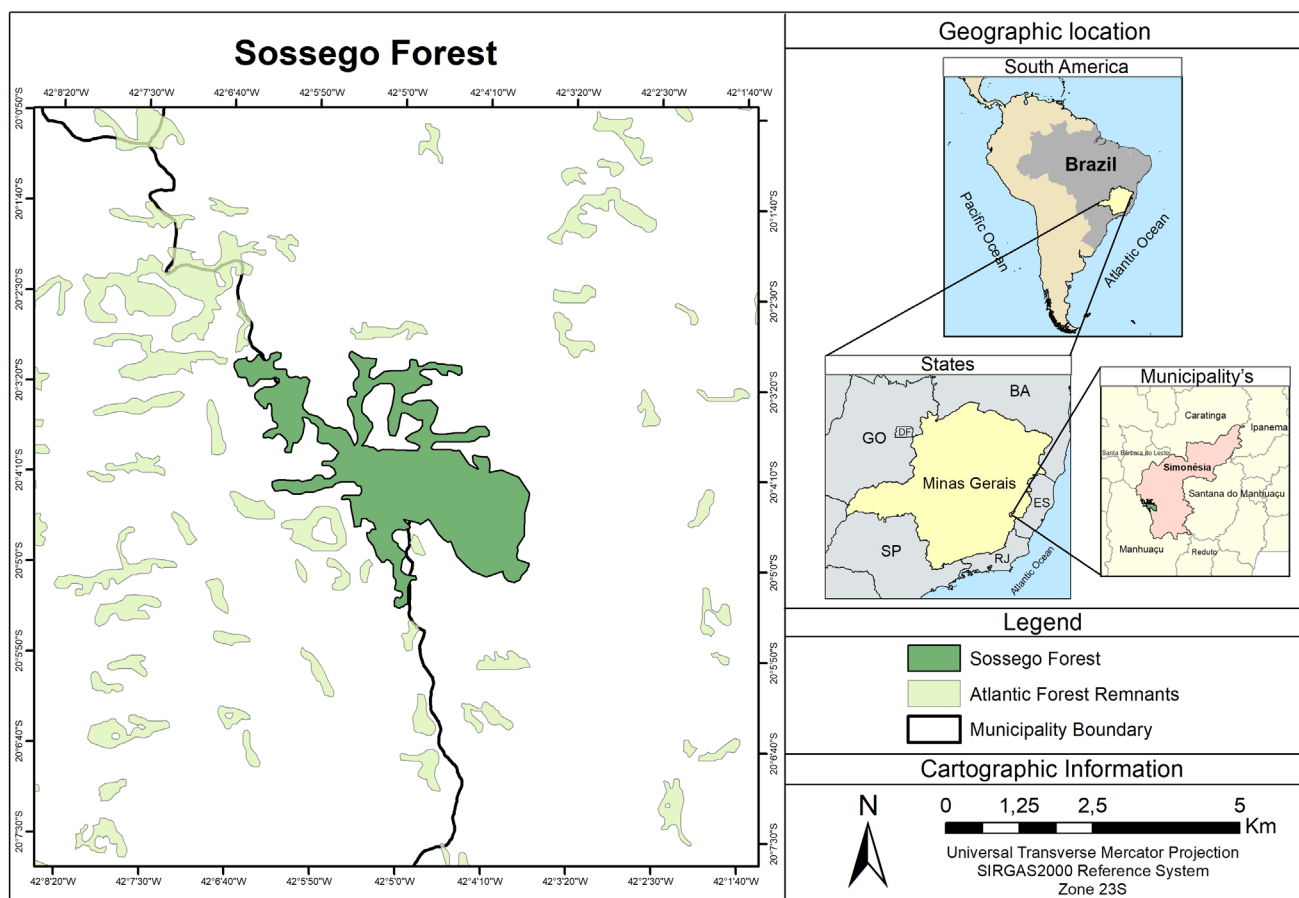

Figure 1. Map of the study area in Símonesia, Minas Gerais, Brazil.

season. During the period from September 2011 to August 2012, the highest average monthly maximum temperature was 27.14°C in February, and the minimum was 11.35°C in July. Total rainfall during that year was 1,088 mm.

History of the study group

The Sossego study group is the only muriqui group present in this forest, and is, thus, synonymous with the study population (Mittermeier *et al*. 1987; Petroni and Steinmetz 2000; Dias *et al*. 2005; Mendes 2007). When it was first described in 1984, there was a minimum of about 20 individuals (Mittermeier *et al*. 1987; Petroni and Steinmetz 2000). In 2004, some 40 individuals were counted (Dias *et al*. 2005), but we cannot be sure whether this reflected population growth or an incomplete count in 1984.

In December 2006, a female muriqui estimated to be 8–9 years old was introduced with the goal of reinforcing the Sossego population (Mendes *et al*. 2007; Barros *et al*. 2011). The female had been found alone in a small, isolated forest fragment near the Parque Estadual Serra do Brigadeiro, in the municipality of Santa Margarida, Minas Gerais, about 60 km in a straight line from the Sossego forest. She was suspected of having dispersed from the Brigadeiro population in an unsuccessful search for another group. The female, identified as EDA-T in our demographic records, was released with a radio collar (Mendes *et al*. 2007), which she continues to wear. During the first year of her release, EDA-T was monitored by radio collar as part of the first behavioral and ecological study of this group (Mendes 2007; Mendes *et al*. 2007). In February 2008, she was observed with her first offspring, a male that is now 12 years old and has been observed mating with other females in his natal group. EDA-T gave birth to four more offspring from 2010 to 2018, all of them females (Fig. 2).

Data collection

Between May 2011 and July 2012, all members of the Sossego muriqui group were habituated to the presence of human observers and identified individually using their natural markings, following the protocols employed in the long-term demographic and life history study of northern muriquis at the Reserva Particular do Patrimônio Natural Feliciano Miguel Abdala, in the municipality of Caratinga, Minas Gerais (Strier *et al*. 2006, 2017). From July 2012 to the present (June 2020), all muriquis in the Sossego study group have been monitored individually during systematic surveys conducted by trained observers at variable intervals with from 3 to 12 monthly surveys per year (Table 2). During each survey, an effort was made to locate all individuals in the study group.

Each time an individual was sighted, its identification code and the date were recorded. Births were the only source of new individuals in the population. Birthdates were estimated based on the midpoint between the last date a female was observed without the infant and the first she was seen carrying the infant, following Strier *et al*. (2001,

Figure 2. The translocated female, EDA-T, in 2018, soon after the birth of her most recent daughter, EST-S, in the muriqui population at Mata do Sossego, Minas Gerais, Brazil. Note that EDA-T's collar is not visible in this photo. Photo: Theo Anderson Ferreira / Projeto Muriquis do Sossego.

2010). In our database, the interval between when a female was observed with and without a new infant ranged from 15 days to 82 days (median = 30 days; n = 17). The last date each individual was sighted was updated following each survey.

Data analyses

All demographic records were analyzed on a monthly basis between July 2012 and June 2020 (see Table 2 for the survey schedule and number of records). Individual life history data are maintained following the protocols described in the Primate Life History Database (Strier *et al*. 2010). An individual was included as present if it was sighted on any day that month, and we retroactively included an individual in that monthly count if it was sighted in subsequent months.

Using the records of the last observed sightings, we could reconstruct the earliest possible date on which an animal disappeared. All dependent animals were considered to have died if their mothers were observed without them during two consecutive surveys. Independent immature males and adult males and females were considered to have disappeared if they were not observed for at least 12 months. Immature females that disappeared may have dispersed from their group and in one case (the oldest daughter of EDA-T), the emigration was confirmed.

We used published criteria to estimate the ages or age-sex class categories of all individuals. Following Strier *et al.* (2017), we classified individuals known or estimated to be 0–3 years of age as Infants, those 3–6 years as Juveniles, those 6–8 years as Subadults, and those >8 years old as Adults.

We calculated the sex ratio of the entire group, and of only reproductive-aged individuals in the group in December of each year, corresponding to the peak mating season month recorded in Caratinga (Strier *et al.* 2001). We used long-term data from the Caratinga muriquis to classify individuals as reproductive-aged. In Caratinga, males began copulating as early as five years of age, but the age at first copulation with ejaculate for males was 6.8 years (Possamai *et al.* 2005) and the youngest male known to have sired an offspring was just over 8 years (Strier *et al.* 2011). The youngest age at which a female reproduced in her natal group in Caratinga was 7.7 years, even though the average

age at first reproduction for most females that disperse from their natal groups has been nine years (Strier *et al.* 2006; Strier and Mendes 2012). For the Sossego group, we considered subadults and adults of both sexes to be potentially reproductively active. We also calculated the ratio of mature (adult and subadult) to immature individuals to assess changes in population structure.

Estimated birth intervals were calculated for each female from the difference between the birthdates of each successive offspring. Because we could not monitor all females all of the time, it is possible that we missed a birth followed by a death, which would result in our over-estimation of average birth intervals in this population (Strier *et al.* 2001).

We evaluated the influence of the translocated female and her reproductive-aged offspring on population size, population structure (the ratio of mature:immature individuals), breeding-aged sex ratios, and compared her birth intervals to those of native females. We compared the actual

Table 2. Number of days per survey (D) and number of records (R) of at least one muriqui sighting that day in the Sossego muriqui population from July 2012 to June 2020.

Month	2012		2013		2014		2015		2016		2017		2018		2019		2020		Total	
	D	R	D	R	D	R	D	R	D	R	D	R	D	R	D	R	D	R	D	R
Jan					11	7			10	4	9	0	23	1	18	2	7	1	78	15
Feb					8	5	6	0	4	3	7	0	19	2					44	10
Mar			10	5	10	0	5	2	5	2	8	5	16	3	16	1	12	0	82	18
Apr			7	3	14	5					14	7	16	3			21	0	72	18
May			12	7					5	0	10	4					19	0	46	11
June			7	3	8	4	10	4	6	2	10	3	15	3	16	2	6	4	78	25
July	10	7	12	4	15	7	12	6	5	2	14	7	14	9					82	42
Aug	11	7	5	0	5	3	17	8	2	1	17	7	15	2					72	28
Sep	11	0	10	6	15	7	10	5	4	0	12	6	17	3					79	27
Oct	12	4	7	0	18	8	8	0	6	2	10	6	18	4					79	24
Nov	10	5	8	5					12	7	12	4	14	4					56	25
Dec			10	7	3	0					8	3							21	10
Total	54	23	88	40	107	46	68	25	59	23	131	52	167	34	50	5	65	5	789	253
Mean	10.80	4.60	8.80	4.00	10.70	4.60	9.71	3.57	5.90	2.30	10.92	4.33	16.70	3.40	16.67	1.67	13.00	1.00	65.75	21.08
± SD	0.84	2.88	2.35	2.54	4.81	2.88	4.03	3.05	2.96	2.06	2.97	2.50	2.75	2.17	1.15	0.58	6.82	1.73	19.58	9.36
Total months	5		10		10		7		10		12		10		3		5		72	

population (including EDA-T and her offspring) with the same information if the female had not been introduced (excluding EDA-T and her offspring). We used nonparametric statistics because the small number of complete years in our sample (N = 8) would not meet the criteria for normality (Torman *et al*. 2012). For the comparisons of mature-immature ratios and reproductive-aged sex ratios with and without EDA-T and her offspring, we used the Wilcoxon test (Siegel and Castellan Jr 2006) and considered our results to be significant if p<0.05.

Results

Population size and composition

At the onset of this study in July 2012, the population consisted of 32 individuals including EDA-T and two of her offspring (Fig. 3). The population grew to 38 individuals in September 2015 and remained at this size until April 2016. By December 2016, the population had declined to 26 individuals, and dropped even further, to 22 individuals by September 2017. It did not grow again until June 2018, and as of June 2020, the population consisted of 24 individuals, including EDA-T and three of her offspring. Without EDA-T and her offspring, the population would be 16.67% smaller (n = 20) than its actual size (Fig. 3).

The ratio of mature-to-immature individuals was biased in favor of mature individuals throughout the study period, with inter-annual fluctuations corresponding to differential patterns of disappearances (including presumed deaths and emigrations) and births (Table 3). The proportion of mature individuals relative to immatures would have been significantly higher without EDA-T and her offspring (Wilcoxon Z = -2.38, N = 8, p<0.05) than it was (Fig. 4a).

The overall sex ratio (all females divided by all males) declined from female-biased to male-biased over the study period. The change from a female- to male-biased sex ratio was not a result of birth sex ratios, which were female-biased in all but two years (Table 3). The decline in sex ratio was most noticeable among reproductive-aged animals. From December 2012 to December 2019, the sex ratio of adults and subadults was reduced by half (Table 3). Moreover, of the six reproductive-aged females in December 2019, two were present as young infants in the group when habituation was initiated in 2011. By January 2020, both of these females had matured and reproduced in their natal group. When we compared the sex ratio of reproductive-aged animals with and without EDA-T and her only offspring, a son (EDU-S), to reach reproductive age in the group to date, we found a significant difference (Wilcoxon Z = -2.52, N = 8, p<0.05). However, this result is deceptive because although EDA-T contributed to a female-biased breeding
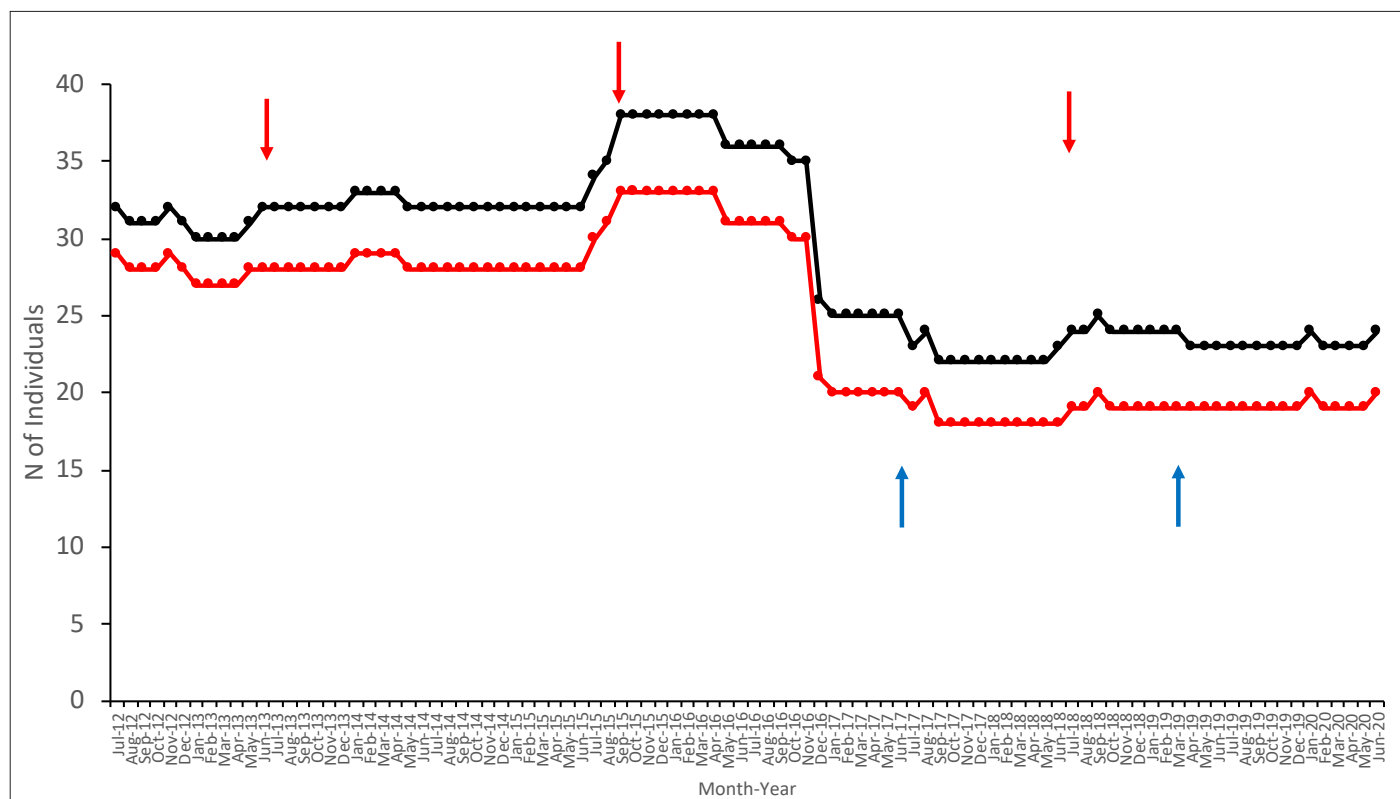

Figure 3. Changes in population size of the Sossego muriquis by month from July 2012-June 2020. Black line shows the actual population size with EDA-T and her offspring; the red line shows the hypothetical population without EDA-T and her offspring. EDA-T and two offspring were present in the group in July 2012. The red arrows show the three offspring born to EDA-T during the present study period; the blue arrows show her two female offspring that emigrated (ECO-S) and disappeared (ESP-S) during the study.

sex ratio during the first years of this study, the reproductive maturation of her son in 2014 counteracted the influence of her presence. Her daughter also contributed to the female-biased sex ratio when she reached subadult age in 2016, but this declined with her emigration from the population (Fig. 4b).

Emigrations, disappearances, and deaths

Seventeen of the 25 individuals that disappeared from the study group were females (Table 4). Six of these females disappeared when they were subadults of dispersal age. One of these, ECO-S, was the oldest daughter of EDA-T. ECO-S is currently the only subadult female whose emigration has been confirmed. She was last seen in the study group on 4 June 2017 when she was estimated to be 8 years old and re-encountered on 29 August 2017 in a small forest fragment some 11 km from the center of the home range of the forest used by the group. She was monitored until 28 March 2019, when she was captured and translocated to Ibitipoca, Minas Gerais, where she is now part of a captive breeding program (Tabacow *et al.* 2019). Before her translocation, ECO-S was observed to move between forest fragments and at the time of her capture, she was in a fragment only 4 km from her natal forest.

EDA-T's second daughter, ESP-S, was last seen in her natal group on 4 March 2019, when she was 6 years of age, which is the median age of female dispersal in the Caratinga muriquis (Strier *et al.* 2015). However, ESP-S has not yet been re-sighted and therefore we do not know whether she is alive in another forest fragment or has died. The fates of the other four females that disappeared as subadults of dispersal age are similarly unknown.

Births and birth intervals

A total of 17 births involving 10 different females were recorded during the study period, with 11 (64.70%) females and 6 (35.30 %) males born. Births were recorded in all but two years (Table 5), but the long intervals between surveys may have resulted in our missing infants that died before their births could be recorded.

We calculated eight birth intervals from five females in which both the first and second births in the intervals occurred during the present study period. These birth intervals averaged 2.88 $\pm$0.47 years (median = 2.81; min-max = 2.28–3.60 years; n = 8). EDA-T's birth intervals were within the range of those of other females (Fig. 5). When we included an additional six infants produced by five females prior to the onset of the study period and whose

Table 3. Age-sex class composition of the Sossego muriqui population from July 2012 to June 2020.

| Sex/Age	No. of individuals in December of year shown									
	July 2012	2012	2013	2014	2015	2016	2017	2018	2019	June 2020
Adult female	9	9	10	10	10	6	4	4	6	6
Adult male	7	6	6	6	10	7	7	7	8	8
Subadult female	1	1	0	0	1	1	2	2	0	1
Subadult male	1	1	4	6	2	0	1	1	0	1
Juvenile female	2	2	3	4	4	5	3	3	2	1
Juvenile male	6	6	2	1	1	1	1	3	3	3
Infant female	5	5	6	4	6	3	1	3	3	3
Infant male	1	1	1	1	4	3	3	1	1	1
Total	32	31	32	32	38	26	22	24	23	24
Proportion mature (adult and subadult): immature	1.29	1.21	1.67	2.20	1.53	1.17	1.75	1.40	1.56	2.00
Proportion reproductive-aged (adult and subadult) females:males	1.25	1.43	1.00	0.83	0.92	1.00	0.75	0.75	0.75	0.78
Proportion Infants females:males	5.00	5.00	6.00	4.00	1.50	1.00	0.33	3.00	3.00	3.00

4A.
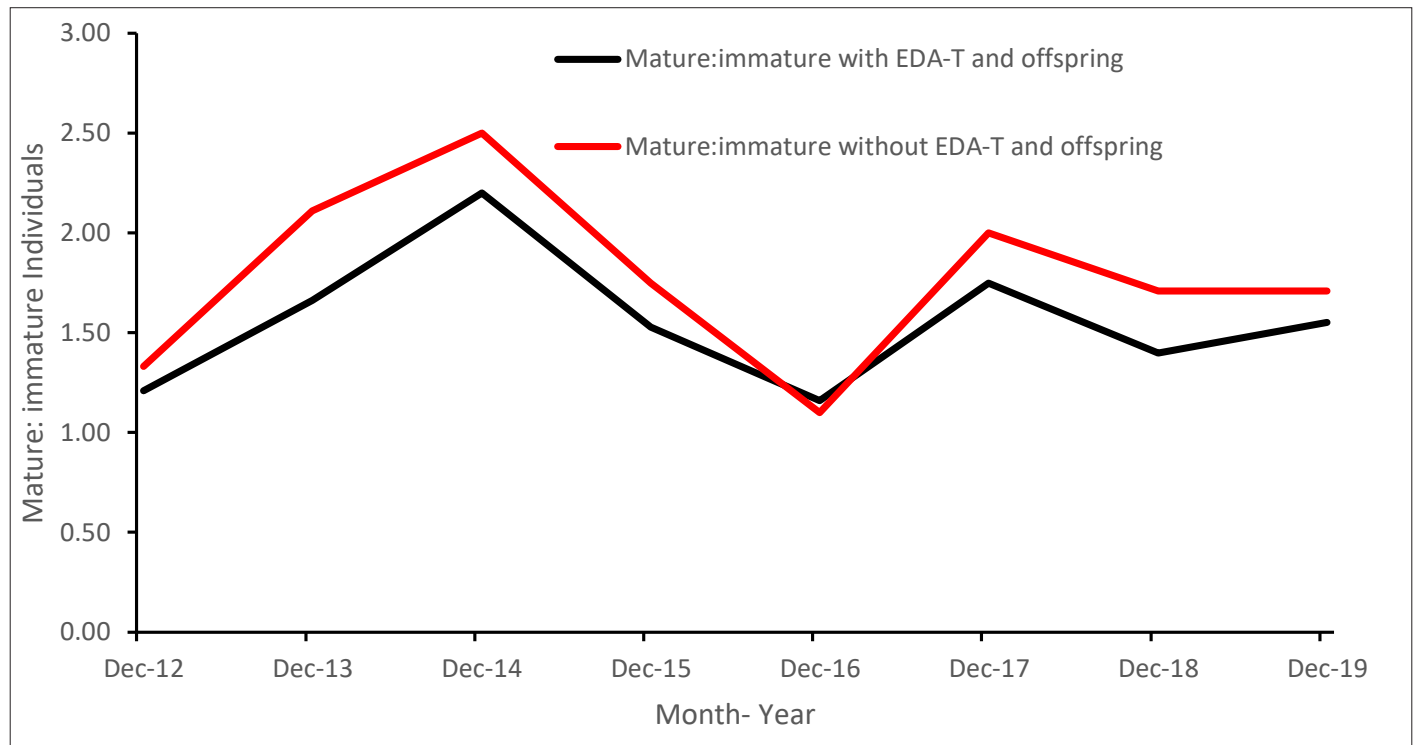
4B.
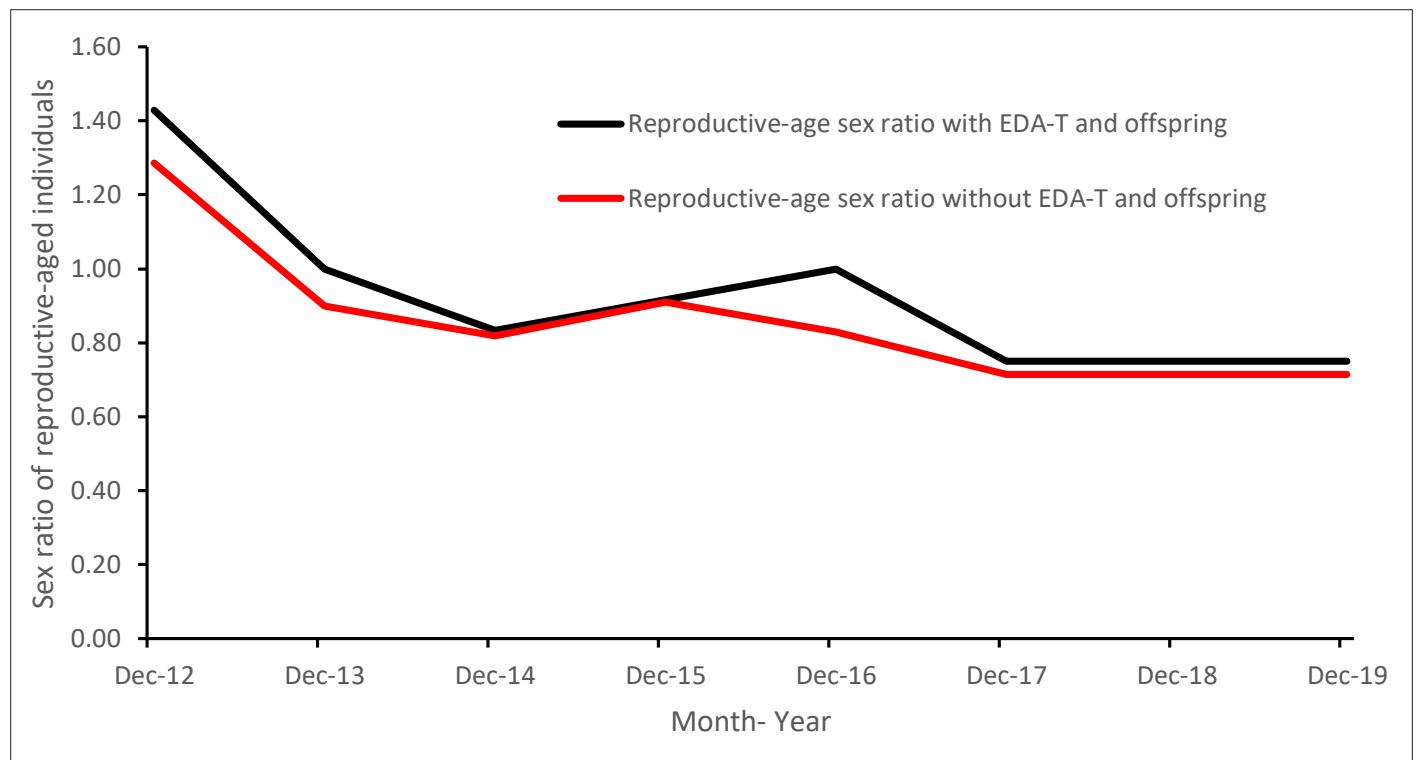
Figure 4. Changes in population structure of the Sossego muriquis by month from July 2012-June 2020. **A**. Ratio of mature to immature individuals. **B**. Sex ratio of reproductive-aged individuals. In both panels, the black line shows the actual population structure with EDA-T and her offspring; the red line shows the hypothetical population structure without EDA-T and her offspring. In both panels, EDA-T is present as an adult throughout the study, her son (EDU-S) is classified as a subadult and reproductive-aged beginning in 2014, and her oldest daughter (ECO-S) is classified as a subadult and reproductive-aged in 2016 until her emigration in 2017.

ages were more roughly estimated, the birth intervals were only slightly longer (Mean $\pm$ sd = 3.02 $\pm$ 0.59 years; median = 2.95; min-max = 2.00–3.90 years; n = 14).

Discussion

During the eight years spanned by our demographic data, the muriqui population in the Sossego forest grew from 32 to 38 individuals, but ultimately fell to 24 individuals, representing a decline of 25%. During the peak months of a severe yellow fever outbreak in the region, the population dropped from 34 individuals in October 2016 to 25 in April 2017 (Strier *et al*. 2019), and by the end of December 2017, the population had dropped further to 22 individuals. From January 2018–June 2020, the five births outnumbered the three disappearances, all of which were young females that may have died or emigrated from the forest in seach of a new group.

It is important to note that EDA-T and all four of her offspring born prior to the yellow fever outbreak survived it (Strier *et al*. 2019). Although we have no direct evidence about resistence to yellow fever, loss of genetic variability has been implicated in lower resistance to pathogens in species such as Grauer's gorillas (*Gorilla beringei graueri*; Van der Valk *et al*. 2019) and ring-tailed lemurs (*Lemur catta*; Charpentier *et al*. 2008). Thus, we cannot discount the possibility that EDA-T's offspring, which were the products of outbreeding, should have greater genetic variability compared to other members of the inbred Sossego population, and therefore greater disease resistance. Indeed, EDA-T was originally captured near the Parque Estadual Serra do Brigadeiro (Barros *et al*. 2011) where preliminary genetic analyses have revealed the muriquis to possess seven haplotypes including five unique ones (Chaves *et al*. 2011). Thus, it is likely that both she and the offspring she produced after being introduced into the Sossego population were less inbred than the original Sossego muriquis, where only one haplotype was found (Chaves *et al.* 2011).

As we predicted in this particular case, the translocated female and her offspring contributed to the population's structure. Although it was biased in favor of mature (adult and subadult) individuals throughout the study, the bias would have been even greater without EDA-T and her offspring, only three of which are still present in the group. However, for a species with such a slow life history (Strier and Mendes 2012), it may take longer than the eight years of the present study to fully understand the impact of her translocation on the age distribution of this population.

Also in accord with our predictions, the translocated female influenced the breeding-age sex ratio. In addition to herself and consistent with the male philopatry and female dispersal documented in this species (Strier *et al.* 2006), EDA-T's son, EDU-S, matured to reproductive age in his natal group, where he has remained and has been observed to copulate with other females. By contrast, one daughter of reproductive age is known to have left her natal group but was not able to find another group and lived as a solitary female until she was captured more than a year later. A second female is suspected of having dispersed but has not yet been located and may have died. As of June 2020, EDA-T and her three remaining offspring account for 16.67% of the current population. Prior to EDU-S's maturation, EDA-T's presence contributed to the female bias among reproductive-aged individuals. However, once

Table 4. Disappearances of muriquis in the Sossego muriqui population by age-sex class.

Age-class	Females	Males
Adult	6	7
Subadult	6	
Juvenile	1	
Infant	4	1
Total	17	8
Total without confirmed (n = 1) or possible emigrations (n = 5) of subadults	11	8

Table 5. Annual births recorded in the Sossego muriqui population during the present study period.

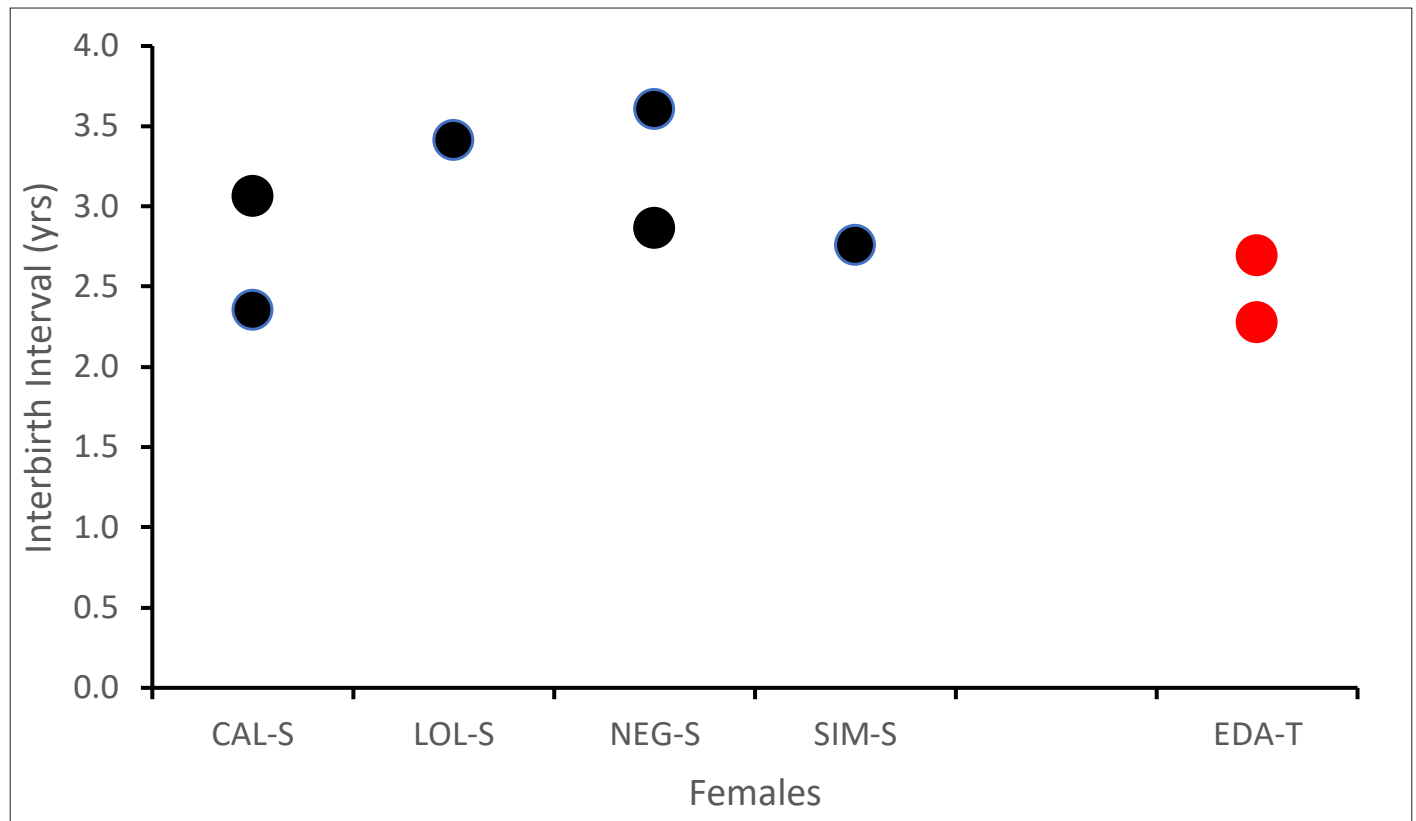|	No. of births recorded annually									
Sex	July-Dec 2012	2013	2014	2015	2016	2017	2018	2019	Jan-June 2020	Total
Female	1	2	1	3	0	0	3	0	1	11
Male	0	0	1	3	0	1	0	0	1	6
Total	1	2	2	6	0	1	3	0	2	17

Figure 5. Birth intervals (n = 8) of natal females versus translocated female (EDA-T) in the Sossego muriqui population. Black points show birth intervals for four females from Sossego; red points show birth intervals for the translocated female. All birth intervals shown involve births that occurred after the onset of the study period in July 2012.

EDU-S matured, his presence offset her's. Similarly, as a subadult, her oldest daughter, ECO-S, increased the female-bias breeding-aged sex ratio, but when she emigrated the breeding-aged sex ratio declined.

The geographic isolation of the Sossego muriquis from other populations due to past habitat fragmentation pre-cludes the immigration of new group members. This was the rationale for the translocation of EDA-T, and apart from her, as expected, any increase in the number of reproduc-tive-aged females could only be a result of females that were born and remained in the group. During the present study, two natal females that were estimated to be 1-year old in July 2012 were observed carrying infants in July 2018 and in January 2020 estimated to be 1-mo and 3-mos of age, respectively. If these were their first offspring, they would have been approximately 7 and 7 ½ years old at first reproduction, respectively. This is younger than the average age at first reproduction for females that disperse from their natal groups in the Caratinga population (Strier 2014), but similar to the age of three females that reproduced in their natal group there (Martins and Strier 2004; Strier 2008).

The Sossego females that remained and reproduced in their natal group contributed to the sex ratio of reproduc-tive-aged individuals and to the population's growth. They might also contribute to increased levels of inbreeding if they reproduce with close male relatives. However, if they reproduced selectively with the son of the translocated female, they could contribute to the genetic diversity as well. In larger populations, such as Caratinga, females avoid mating with their close male relatives (Strier 1997; Possa-mai *et al*. 2007), and genetic data confirm that no males have sired offspring with closely related maternal kin (Strier *et al*. 2011). By contrast, in small populations, there are few opportunities to choose unrelated reproductive partners and the only way to reduce close inbreeding is by introducing females from other locations, as was done with the transloc-ation of EDA-T in the present study and with the transloca-tion of another female in the small population of northern muriquis in Santa Maria de Jetibá, Espirito Santo, Brazil (Mendes *et al*. 2005b; Lanna 2015).

The emigration of subadult females from the Sossego population, including at least one of EDA-T's daughters, decreased the group's reproductive-aged sex ratio. In the Caratinga population, where females have the option to dis-perse into non-natal groups living in the same forest fragment, mortality among dispersing females has been estimated at about 28% (Strier 2014; Strier *et al*. 2015). In the Sossego population, it is impossible to calculate the mortality rate for dispersing females unless they are re-encountered after they leave the forest, as was the case with ECO-S. With only one muriqui group present, the cost of female dispersal in terms of lost reproductive potential for the population is 100%.

Our sample size was small but the interbirth intervals of EDA-T fell within the range of those of the other Sossego muriquis and of the Caratinga muriquis (Strier *et al*. 2001). A similar effect of translocated primates exhibiting similar reproductive patterns as conspecifics in their new habitat has also been observed in a 7-year study of a male-female pair of translocated black-and-golden howler monkeys (*Alouatta caraya*; Rossi and Santos 2018).

Although not all translocation efforts will be equally successful (for example, Table 1, individuals 4 and 5), our study contributes to a growing appreciation that the translocation of reproductive-aged females to increase population size and gene flow can be an effective tool in the conservation management of small, isolated populations of northern muriquis (Mendes *et al*. 2005b) and other Neotropical primates (for example, black lion tamarins, *Leontopithecus chrysopygus* [see Rezende 2016]; golden lion tamarins, *Leontopithecus rosalia* [Kierulff *et al*. 2012; Moraes *et al*. 2017, 2018], and howler monkeys, *Alouatta* spp. [Rodríguez-Luna and Córtes-Ortíz, 1994; Ostro *et al*. 1999; de Thoisy *et al*. 2001; Printes and Malta 2005]) where females typically disperse from their natal groups. However, as our data from Sossego show, the degree of positive impact is dependent on the sex of the offspring produced and the trade-offs between the loss of females when daughters disperse versus their persistence in their natal group, where their reproductive options may be exclusively or mostly limited to related males. At the same time, translocations may also be beneficial to the well-being of the individual, especially in social species such as these, because of the stress of isolation and risks associated with living alone instead of in a group during unsuccessful dispersal attempts (Beck 2019). We believe this was the case for the females described here (EDA-T and ECO-S).

Because of the isolation of this population, dispersing females cannot encounter another established group to join. Moreover, male philopatry in this species makes it unlikely that dispersing females can form a new reproductive group. The fissioning of mixed-sex groups has been observed in Caratinga, but those groups were much larger than that of the Sossego population (Strier *et al*. 2006). The destinies of females born into the Sossego population are, therefore, limited to remaining and reproducing in their natal group or dispersing and leading either solitary lives or, conceivably, joining one another in a new fragment without access to males, as has been observed elsewhere (Tabacow *et al*. 2009).

Although additional translocations involving other solitary females may be a short-term solution, this type of management would not be sufficient to ensure the population's long-term persistence without at least a second group to sustain some gene flow. Indeed, the exchange of females between the two original groups within the Caratinga population is believed to have contributed to its early growth (Strier 2005). Efforts to identify a potential candidate group comprised of adults of both sexes with low viability in another isolated forest are underway, following the protocols developed in the *National Action Plan for the Conservation of Muriquis* (Jerusalinsky *et al.* 2011).

Ultimately, however, the establishment of connectivity, in the form of corridors that link the Sossego muriquis with its neighboring Caratinga population 50 km away will be the only long-term solution to their conservation management. In the state of Rio de Janeiro, the establishment of 25 forest corridors totaling 338 ha of restored forest has been instrumental in enabling population growth and gene flow among the endangered golden lion tamarins (Ruiz-Miranda *et al*. 2019). In the state of Minas Gerais, the importance of the "Sossego-Caratinga Corridor" for the conservation of muriquis has been recognized by the state forest institute (Brazil, IEF 2014). Transforming this recognition into reality, however, will require greater knowledge of the landscape ecology relative to the dispersal patterns of muriquis and other endangered fanuna in addition to economic incentives for local landholders (Moraes *et al*. 2018).

Acknowledgments

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