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ORIGINAL ARTICLE

Demography and life-history parameters of mantled howler monkeys at La Flor de Catemaco: 20 years post-translocation

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Abstract

Translocations usually aim at maintaining and enhancing wild populations. Thus, the long-term monitoring of translocated individuals is critical for assessing translocation success. In this study, we report the demographic and life-history parameters of mantled howler monkeys that were translocated to La Flor de Catemaco (Los Tuxtlas, Mexico) to determine the success of the translocation process. Nine individuals belonging to two social groups living in areas that were going to be destroyed were released into La Flor de Catemaco between 2002 and 2004. Before 2022 there were no resident monkeys at the site. From January 2012 to December 2021, we recorded births, deaths, migrations, and group formation (1535 sampling days). The population grew until reaching 35 mantled howler monkeys. Two new groups including both individuals born at the site and migrants were founded. Mean ± SD group size was 8.1 ± 1.1 individuals. We recorded 42 births and 14 deaths, mostly of young infants (< 6 months of age). We recorded emigrations and immigrations of adult and immature individuals as well as several instances of individuals that remained and reproduced in their natal groups. Mean female age at first birth was 57.8 ± 18.5 months, interbirth intervals were 23.3 ± 11.3 months, and birth rates were 0.5 ± 0.2 births per female per year. The growth and persistence of the groups at the site, as well as similarity in demographic and life-history parameters between this and unmanaged populations, suggest that mantled howler monkeys living at La Flor de Catemaco represent a stable population and thus that this was a successful translocation.

Keywords Birth rates · Dispersal · Fertility · Fecundity · Mortality · Population growth

Introduction

With more than 60% of taxa currently threatened by extinction (IUCN 2022), primates require urgent conservation and management actions for their protection. Although ex situ conservation plays an important role in terms of research, education, and preservation of genetic variability (Ferrie 2017), primate conservation has mostly relied on in situ actions (Blair et al. 2013; Marsh 2003). Translocation is an in situ conservation strategy whereby organisms are moved from one site to another, either between habitats or from captivity into nature, for the purpose of conservation or management (IUCN/SSC 2013). Primate translocations have been carried out with several species and for different reasons (Beck 2016). However, given that ultimately translocations should aim at maintaining and enhancing wild populations, the long-term monitoring of translocated individuals is critical in assessing their success (Baker 2002).

The post-release monitoring of translocated wildlife involves several challenges. The most common difficulties reported by wildlife managers are the inability to follow translocated individuals (e.g., lack of personnel, failure to locate animals) and lack of funding for field activities (Berger-Tal et al. 2020). Still, several primate translocations have succeeded in monitoring populations in the long term. The translocation of chimpanzees (*Pan troglodytes*) to the River Gambia National Park is an example of a successful long-term post-release monitoring program. Twenty-five years after the release of the first individuals, two generations of offspring had been born at the release

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site and reproductive parameters (e.g., female age at first reproduction, interbirth intervals) were comparable to other wild chimpanzee populations (Marsden et al. 2006). In 1983, captive-born and wild golden lion tamarins (*Leontopithecus rosalia*) were translocated into protected habitat. Thirty years later, the population of golden lion tamarins had increased notably and 42% of all tamarins were descendants of translocated individuals (Ruiz-Miranda et al. 2019). These examples illustrate the importance of post-release monitoring to assess the success of translocations in terms of the survival and reproduction of individuals, which are critical to the persistence of populations (Batson et al. 2015).

Howler monkeys (*Alouatta* spp.) are platyrrhines that are distributed from Mexico to Argentina. Although they are more resilient to habitat disturbance than other primates and mammals (e.g., Rangel-Negrín et al. 2014; Terborgh et al. 2001), of the 21 taxa currently included in the Red List of Threatened Species, 14 are in threatened categories (IUCN 2022). Howler monkeys have been the target of several translocation programs which, as in other primates, have been conducted with different aims (e.g., rescue: Aguilar-Cucurachi et al. 2010, Rangel-Negrín et al. 2011; reintroduction: Horwich et al. 1993). Several translocation projects either do not report (e.g., Konstant and Mittermeier 1982) or included only short-term post-release monitoring (e.g., 4 months: de Vries 1991). Post-release monitoring encompassing several years has been documented for at least three species, black howler monkeys (*A. pigra*: Ostro et al. 2001), black-and-gold howler monkeys (*A. caraya*: Rossi and Dos Santos 2018), and mantled howler monkeys (*A. palliata*: Carrera-Sanchéz et al. 2003). The three projects report that translocation resulted in the establishment of viable populations based on the observation of population growth, reproduction, and/or female reproductive parameters (e.g., interbirth intervals). Thus, translocation seems to be a feasible in situ conservation strategy for howler monkeys.

Here we present the results of a post-release monitoring of mantled howler monkeys that were translocated 20 years ago. Specifically, we focused on demographic (group formation, group size and composition, births and deaths, migrations) and life-history (female age at first reproduction, interbirth intervals) parameters to examine the success of the translocation process.

Methods

Study site

La Flor de Catemaco is a private ranch located on the shores of Lake Catemaco, in southern Veracruz State (Mexico; Fig. 1). La Flor de Catemaco encompasses 165 ha, of which

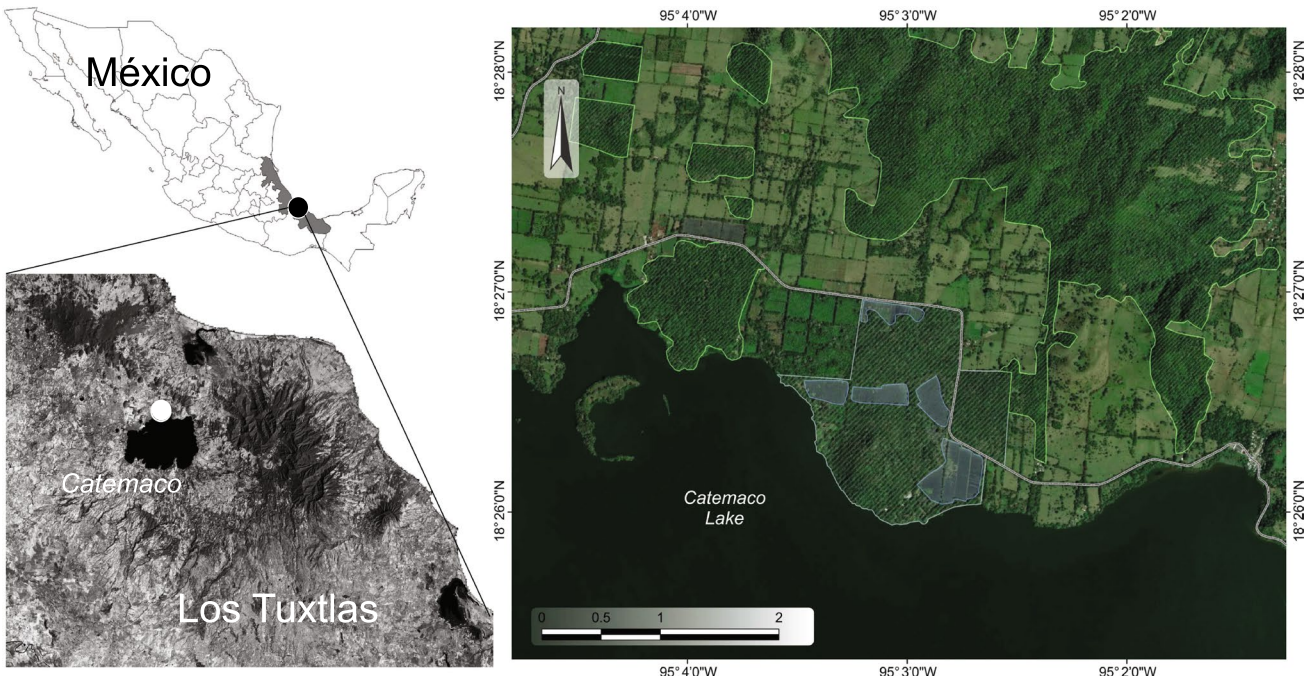

Fig. 1 Location of Los Tuxtlas in the Veracruz state (*top left*) and of La Flor de Catemaco within Los Tuxtlas (*bottom left*). On the right, La Flor de Catemaco appears in the center with the *cyan polygon*, with the areas where plants are gown in the shade illustrated in *light gray polygons*. Other forest fragments in the surrounding area are indicated with *green dashed polygons*. Roads are depicted as *gray lines*

100 ha corresponds to high evergreen rain forest. Since 1989, the owners have preserved the original vegetation of the property and allowed for the regeneration of forest in some areas (e.g., right-of-way of abandoned power lines). From 1990 to 1994, the main economic activity of the ranch was intensive livestock farming, but by 1995, feedlots were converted to shades for the growth of ornamental plants. The understory and floor of the forest were also cleared in some parts for ornamental plant growing. Since that moment, the main activity of the ranch has been the production of palms and ferns.

Translocation process

During the early 1980s, it became evident that Mexican primates were being extirpated from several areas due to human disturbance (Estrada and Coates 1984). It was by then that the Instituto de Neuro-etología of the Universidad Veracruzana (Mexico) began a translocation program with the aim of rescuing groups of howler (*A. palliata* and *A. pigra*) and spider (*Ateles geoffoyi*) monkeys that were at risk (Rodríguez-Luna et al. 1993). As part of this program, in 2002 we were informed that the habitat of a mantled howler monkey group living in the vicinity of the Cascajal del Río village (Veracruz, 17° 59′ 01.08″ N, 95° 09′ 50.34″ W) would be slashed and burned. The group (Group 1) was captured following well-established protocols (Canales-Espinosa et al. 2011) and taken to facilities of the Instituto de Neuro-etología (UMA Hilda Ávila de O´Farril) where individuals went through a process of health screening (e.g., complete blood count and blood chemistry analyses; body weight) until release in December of that year. In 2004, another mantled howler monkey group (Group 2) had to be rescued from the same area and went through a similar translocation process, being released in September of that year (Aguilar-Cucurachi et al. 2010; Shedden-González and Rodríguez-Luna 2010).

As part of the translocation process, we surveyed the Los Tuxtlas region for suitable habitat for the release of mantled howler monkeys using satellite imagery. We specifically searched for preserved forests with a size > 8 ha (a threshold for mantled howler monkey occupation in the area: Mandujano and Estrada 2005) which were then visited to determine if they were occupied by howler monkeys. As a result of surveys, we located La Flor de Catemaco where, by 2002, no mantled howler monkeys lived. Following an agreement with the owners of the property for the release and protection of primates, we assessed the vegetation to determine if the area could support mantled howler monkey groups. In 100 25 × 25-m quadrats randomly distributed in a 23-ha area, 184 tree species were identified (A. López-Galindo y P. Quintana-Morales unpubl. data), including 12 species of *Ficus*, which is a keystone resource in the diets of mantled howler monkeys (Serio-Silva et al. 2002). The commitment of the owners to protect both the forest and primates, the large size of the forest fragment, the vegetation composition, and the absence of resident primates, led us to decide that La Flor de Catemaco was a suitable site for the translocation of mantled howler monkeys.

Demographic sampling

Variation in physical traits (e.g., body size, patches of blond hair in the fingers and tail) allows for the recognition of individual mantled howler monkeys. Thus, both translocated (identified during capture) and non-translocated (i.e., individuals born at La Flor de Catemaco and migrants from other forest fragments, identified through detailed observations using binoculars) subjects could be individually identified and their presence at La Flor de Catemaco assessed through time. Except for three periods when observations encompassed several months (September to December 2004 and March to June 2005: Shedden-González and Rodríguez-Luna 2010; December 2010 to January 2011: Velez del Burgo 2011), the two groups of mantled howler monkeys residing at La Flor de Catemaco were visited sporadically from December 2002 to December 2011. From January 2012 on, the two translocated groups were sampled for a week every 10–15 days except in the months of December, in which each group was usually sampled for a single week. In June 2015 and April 2020, we began sampling newly established groups (Group 3 and Group 4, respectively), usually for 2 to 3 days per month. In the period between January 2012 and December 2021 we sampled groups for a mean (± SD) of 151.7 ± 22.1 days per year.

During each sampling day, we recorded the identity of all individuals in the groups. Individual ages were determined based on (i) the observation of births, (ii) assessments of dental occlusal wear during capture (for founding individuals), or (iii) inferred through the observation of behavioral and morphological traits as defined by Balcells and Veà (2009). In this study, we assessed demographic parameters following Cristóbal-Azkarate et al. (2017). Accordingly, we defined: births as the presence of a newborn; deaths when we found the body of an individual, when a dependent (< 14 months of age) infant disappeared but its mother was still present, or when an injured or ill individual was not located; emigrations when a weaned individual that was not injured or ill when last observed was not located in its group; immigrations as the presence of a new individual in a group; transference when an individual emigrated from a known group and immigrated to another known group without spending time living solitarily.

Data organization and analysis

We report the abundance of mantled howler monkeys at La Flor de Catemaco between December 2002 and December 2021 (i.e., 20 years). However, for the period encompassing December 2002 to December 2011 we only use data from December 2002 and December 2004, as these were dates associated with the release of the translocated groups at the site and systematic demographic surveys began until January 2012. We calculated the finite growth ratio (λ) by dividing the number of individuals living at La Flor de Catemaco in December of a given year by the number of resident individuals in December of the previous year for which data was available. $\lambda > 1$ indicates population increase, $\lambda < 1$ indicates population decrease, and $\lambda = 1$ indicates stability.

We used descriptive statistics to report demographic and life-history parameters for the January 2012-December 2021 period. We used a Spearman correlation test to assess the association between the number of infant births and deaths per month. We report life-history parameters in number of months except for interbirth intervals (IBI), which we calculated as the number of days between the birth of two consecutive infants of a given female.

Results

Population history

In December 2002, the first mantled howler monkey group was released in La Flor de Catemaco. The group (Group 1) comprised one adult female (ca. 12 years old), two adult males (17 and 7 years old), one subadult female (3.5 years old), and one subadult male (3 years old; Supplementary information Table S1). In September 2004, a second group (Group 2) including two adult females (10 and 7 years old) and two adult males (11 and 8 years old) was released. By then, ten individuals lived at La Flor de Catemaco, as an infant was present in Group 1. Since that moment, no further individuals were released in the area and demographic changes resulted from births, deaths, and migrations.

Group 3 was founded in 2012, when an infant female joined a maternal sibling (a subadult male at the time), which had emigrated from his natal group (Group 1) 1 month before. This dyad left the La Flor de Catemaco property briefly (2 months) in 2015 and came back with an additional adult female. In November 2019 a solitary male was observed for the first time at La Flor de Catemaco. This male remained alone in the area for the next five months when an adult female that immigrated from outside La Flor de Catemaco joined him. This dyad (Group 4) has remained together since that moment.

During the last 20 years, the abundance of mantled howler monkeys at La Flor de Catemaco varied between 5 (2002) and 35 (2021) individuals, with a mean (± SD) of 22.8 ± 9 individuals per year (Table 1). Although there were declines in population size in some years (2014 and 2018), it tended to increase (i.e., $\lambda > 1$).

Group size and composition

Between 2012 and 2021, mean ± SD group size varied from 6.7 ± 4.5 (2012 and 2014) to 9.7 ± 5.5 (2019) individuals, with a mean across all years of 8.1 ± 1.1 individuals per group (Table 2). Group 2 was usually larger than the other groups, followed in size by Group 1, Group 3, and Group 4 (Table 3). Groups comprised a mean ± SD of 2.3 ± 0.3 adult

Table 1 The abundance and population growth rate (λ) of mantled howler monkeys at La Flor de Catemaco over a 20-year period (2002–2021)

Year	Abundance	λ				
		Population	Group 1	Group 2	Group 3[a]	Group 4[b]
2002	5					
2004	9	1.8	0.8			
2012	20	2.5	1.8	2.8		
2013	22	1.1	1.1	1.1	1.0	
2014	20	0.9	0.6	1.1	1.0	
2015	21	1.1	1.2	1.0	1.0	
2016	27	1.3	1.2	1.1	3.0	
2017	27	1.0	1.3	1.0	0.7	
2018	25	0.9	0.9	0.9	1.0	
2019	29	1.2	1.3	1.2	1.0	
2020	34	1.2	1.2	1.1	1.0	
2021	35	1.0	1.0	1.1	1.0	1.0

[a]Group formed in 2012

[b]Group formed in 2020

Table 2 Mean (±SD) group size and composition of mantled howler monkeys at La Flor de Catemaco during a 10-year period (2012–2021)

Year	Group size	Adult males	Adult females	Subadults	Juveniles	Infants
2012	6.7 ± 4.5	2.0 ± 1.7	2.0 ± 2.0	1.0 ± 0.0	0.0 ± 0.0	1.7 ± 1.2
2013	7.3 ± 5.0	2.3 ± 1.2	2.3 ± 2.5	0.0 ± 0.0	1.0 ± 1.0	1.7 ± 1.5
2014	6.7 ± 5.7	2.0 ± 1.0	2.0 ± 2.0	1.0 ± 1.0	0.7 ± 0.7	1.0 ± 1.7
2015	7.0 ± 5.6	2.0 ± 1.0	3.0 ± 1.0	1.0 ± 1.0	1.0 ± 1.0	1.0 ± 0.0
2016	9.0 ± 4.4	2.0 ± 1.0	3.3 ± 0.6	1.0 ± 1.0	0.7 ± 0.7	2.0 ± 2.0
2017	9.0 ± 5.0	2.3 ± 1.2	3.0 ± 1.0	0.0 ± 0.0	2.3 ± 2.3	1.3 ± 0.6
2018	8.3 ± 4.5	2.7 ± 1.5	3.3 ± 1.2	1.0 ± 1.7	0.7 ± 0.7	0.7 ± 0.6
2019	9.7 ± 5.5	2.7 ± 1.5	3.3 ± 1.5	0.7 ± 0.6	1.3 ± 1.3	1.7 ± 1.5
2020	8.5 ± 6.6	2.5 ± 1.7	3.0 ± 1.6	0.8 ± 1.0	1.5 ± 1.5	0.8 ± 1.0
2021	8.8 ± 7.0	2.5 ± 1.7	3.5 ± 2.1	0.5 ± 1.0	1.8 ± 1.8	0.5 ± 0.6
Total (mean ± SD)	8.1 ± 1.1	2.3 ± 0.3	2.9 ± 0.6	0.7 ± 0.4	1.1 ± 0.7	1.2 ± 0.5

males, 2.9 ± 0.6 adult females, 0.7 ± 0.4 subadults, 1.1 ± 0.6 juveniles, and 1.2 ± 0.5 infants.

Births and deaths

We recorded 42 births (mean ± SD = 3.5 ± 10.4 births per female). Variation in female age and residence time at La Flor de Catemaco seems to associate with the number of births per female but not with female fecundity (i.e., number of immatures that survive > 20 months; Table 4). Mean infant survival was 60 ± 36% across all females. We could determine the sex of 22 individuals born at the site, nine males and 13 females (sex ratio at birth = 0.75).

The months with more births were January and August (seven births) whereas November (0), February (1), and May (2) had the lowest frequencies of births (Fig. 2). Overall, the number of births per month did not correspond well with immature survival ($r_s = 0.34$, $n = 10$, $P = 0.334$), given that more infants survived in months with low birth frequency (September, October, December) compared with months with several births (July and August). The month with more immature deaths was September (3), whereas no deaths were recorded in several months. All immatures presumed to have died ($n = 12$) were less than 6 months old, with the majority being ≤ 1 month (4) and 2 months old (4), followed by infants with 3 (2), 4 (1), and 5 (1) months. Two adult individuals were presumed to die, as they were injured before disappearing, one of the founder females (at ca. 22 years of age) and a male (at 4.75 years).

Migrations

Of the 30 individuals born at La Flor de Catemaco that survived > 1 year of age, ten remained in their natal groups into adulthood, followed by individuals that emigrated and left the site ($n = 9$), individuals that were not adults (i.e., < 36 months) by the end of the study and were still in their natal groups ($n = 8$), and individuals that transferred between groups ($n = 3$). Mean age at emigration was 35.9 ± 12.1 months (range, 25–55 months) whereas age at transference was 35.0 ± 22.3 months (range, 10–53 months). A total of five individuals immigrated to La Flor de Catemaco from other areas: one female to Group 3 that then transferred to Group 1; one female to Group 3; one female to Group 1; one male that lived solitarily for 5 months and was then joined by a new immigrant female.

Life history

The mean age of females when they gave birth to their first infant was 57.8 ± 18.5 months (range, 43–88 months, $n = 5$ females; Table S1). The mean interbirth interval (IBI) was 23.3 ± 11.3 months (range, 8–51, $n = 28$ IBI), being this interval shorter when the infant at the beginning of the interval died (18.6 ± 15.7, range, 8–51, $n = 8$ IBI) than when it lived (25.0 ± 9.0, range, 13–50, $n = 20$ IBI). Incomplete IBI (i.e., considering time elapsed between the date of the last birth and the end of the study, December 2021) ranged between 5 and 71 months, with a mean of 31.6 ± 21.8 months ($n = 9$ IBI). The 71 months IBI corresponds to a founder female (Negra) that has not given birth to an infant since February 2016.

Discussion

In this study, we report demographic and life-history parameters of a mantled howler monkey population 20 years following the release of the first of two groups that were translocated to La Flor de Catemaco (Los Tuxtlas, Mexico). The population grew gradually through time due to births and the arrival of individuals from neighboring forest fragments. Long-term observations allowed us to document the age of females when they gave birth to their first offspring,

Table 3 Group sizes and compositions of four mantled howler monkeys at La Flor de Catemaco during a 10-year period (2012–2021)

Group	Year	Adult males	Adult females	Subadults	Juveniles	Infants	Total	Migrants[l]
Group 1	2012	3	2	1[a]	0	1[a]	7	0
	2013	3[b]	2	0	0	3	8	0
	2014	2	2	0	1	0	5	0
	2015	2	2	1	0	1	6	0
	2016	2	3[c]	1	1	0	7	1
	2017	3	3	0	2[d]	1	9	1
	2018	3	4[e]	0	0	1	8	2
	2019	3	3	0	2	2	10	2
	2020	4	3	1	3	1	12	2
	2021	4	4	0	3	1	12	2
Group 2	2012	3	4	1	0	3	11	0
	2013	3[f]	5[g]	0	2	2	12	0
	2014	3	4	2	1	3	13	0
	2015	3	4	2	3	1	13	0
	2016	3	4	2	1	4	14	0
	2017	3	4	0	5	2	14	0
	2018	4[i]	4	3	1[h]	1	13	0
	2019	4	5	1	2	3	15	0
	2020	4	5	2	3	2	16	0
	2021	4[j]	6	2	4	1	17	0
Group 3	2012	0	0	1	0	1	2	0
	2013	1	0	0	1	0	2	0
	2014	1	0	1	0	0	2	0
	2015	1	3	0	0	1	5	2
	2016	1	3[k]	0	0	2	6	1
	2017	1	2	0	0	1	4	1
	2018	1	2	0	1	0	4	1
	2019	1	2	1	0	0	4	1
	2020	1	3	0	0	0	4	1
	2021	1	3	0	0	0	4	1
Group 4	2020	1	1	0	0	0	2	2
	2021	1	1	0	0	0	2	2

[a]These individuals left the group and formed Group 3; [b]One adult male transferred to Group 2 where he stayed for 4 months; [c]One adult female transferred from Group 3; [d]One juvenile male emigrated; [e]One adult female immigrated from another fragment; [f]One adult male transferred to Group 2 where he stayed for four months before disappearing; [g]One female transferred to Group 1 at 41 months of age; [h]One juvenile male emigrated; [i]One natal male that emigrated in 2015 returned to the group following a peripheral period but died after 3 months; [j]One adult male disappeared in September; [k]One adult transferred to Group 1; [l] number of group members that immigrated from outside La Flor de Catemaco

interbirth intervals, and the fate of infants born at La Flor de Catemaco. The growth and persistence of the groups at the site as well as life-history parameters suggest that mantled howler monkeys living at La Flor de Catemaco represent a stable population, and thus, that this was a successful translocation.

The abundance of mantled howler monkeys at La Flor de Catemaco has increased over the 20-year period encompassed by this study. Compared to other groups and populations of this species, growth at La Flor de Catemaco is lower (Fedigan et al. 1998), similar (Arroyo-Rodríguez et al. 2008; Cristóbal-Azkarate et al. 2017), or higher (Glander 1980; Clarke et al. 1986; Milton et al. 2019; Bolt et al. 2022). These differences may result from variation in several factors, including the temporal and spatial scale of studies [e.g., yearly (Cristóbal-Azkarate et al. 2017) vs. beginning/end surveys (Clarke et al. 1986)] and the methods used to estimate howler monkey abundance [quadrat sampling (Clarke et al. 1986) vs. trail walking (Milton et al. 2019)]. Population growth at La Flor de Catemaco is comparable to that of the translocated mantled howler monkey population of the Agaltepec Island (Carrera-Sanchéz et al.

Table 4 Age/time of residence and birth data for a 10-year period (2012–2021) for 12 adult females at La Flor de Catemaco

Female	Age/residence time	No. of births[e]	Birth rate[f]	Survived > 1 year	% survived > 1 year
Hembra 1	31[a]	7	0.70	6	86
Negra	27 [a]	5	0.50	5	100
Con Cría	24[a]	5	0.50	4	80
Hembra 2	15.5[a,d]	2	0.67	0	0
Anillada	13[b]	4	0.40	4	100
Pata Manchada	13[b]	6	0.60	4	67
Barbona	12 [b]	3 (2)	0.33	1	50
Frida	6.6[c]	2	0.30	1	50
Julieta	6.25[c]	3	0.48	1	33
Pata de Guante	5.8[b]	2	0.67	1	50
Dedos	5.75[b]	2 (1)	0.67	1	100
Sorda	3.2[c]	1	0.31	0	0

[a]Founding female whose age was inferred via dental inspection (i.e., morphology and wear of the occlusal surface) during capture

[b]Female born during the study

[c]Residence time at La Flor de Catemaco of an adult female that immigrated from another area

[d]Founder female that died in January 2014

[e]Numbers in parenthesis indicate the number of infants that were ≥ 1 year old by the end of the study and were used in the calculation of the percentage of infants that survived > 1 year

[f]Calculated as the number of recorded births divided by the number of years in which females were sampled. For females born during the study, we considered the number of years after they reached sexual maturity (i.e., 36 months of age: Glander 1980)

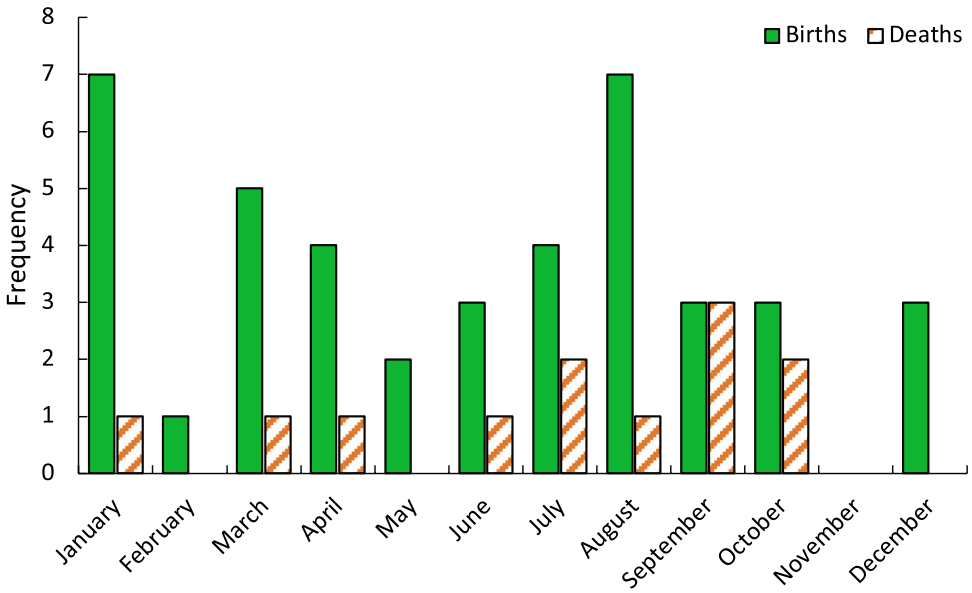

Fig. 2 The number of births (*solid bars*) and deaths (*bars with stripes*) at La Flor de Catemaco between January 2002 and December 2021

2003). This similarity is striking given that many factors constraining howler monkey population growth at La Flor de Catemaco and elsewhere are absent from Agaltepec Island, including predation (Oklander et al. 2021) and parasitism by bot flies (Milton 1996; Carrera-Sanchéz et al. 2003, Arroyo-Rodríguez et al. 2008). It is possible, however, that habitat saturation limits growth at the Agaltepec Island (Rodríguez-Luna et al. 2003) and other sites where howler monkey populations have reached the carrying capacity of the habitat (Zucker and Clarke 2003). Population density at Agaltepec, for instance, is more than 30 times larger than at La Flor de Catemaco (0.35 vs. 11.5 ind/ha) and population growth in this and other howler monkey species has been linked to forest regeneration (e.g., Fedigan et al. 1998;

Rudran and Fernandez-Duque 2003; Alcocer-Rodríguez et al. 2021). The long-term demographic follow-up of mantled howler monkeys at La Flor de Catemaco will allow determining whether population growth at this site will parallel that observed elsewhere.

The size of the two translocated groups remained relatively stable during the 10 years of continuous systematic observations and is within the range reported for the species (reviewed in Di Fiore and Campbell 2007). Stability in group size was mainly a result of low variation in the adult composition of groups (4–8 individuals in Group 1 and 7–10 in Group 2), given that the number of immatures (i.e., subadults, juveniles, and infants) per year varied between one and seven. Changes in adult composition were primarily linked to the maturation of natal individuals in their groups (four females), on occasions after spending some time living as solitaries (two males). Less frequent were transferences between groups (one female), and immigration of individuals arriving from outside La Flor de Catemaco (three females and one male). The formation of Group 3 is noteworthy. Parallel dispersion by maternal siblings has been reported in howler monkeys (Pope 1990; Van Belle et al. 2014), but we believe this to be the first observation of group formation by a brother-sister dyad in this species. Overall, this evidence indicates that group dynamics at La Flor de Catemaco is based on the same mechanisms reported for other mantled howler monkey populations (e.g., Nififfer and Cortés-Ortiz 2015; Cristóbal-Azkarate et al. 2017).

It is likely that we did not record all births that occurred at La Flor de Catemaco from 2012 to 2021, as several infants died shortly after birth, and we did not sample groups daily. Thus, birth rates and life-history parameters reported here should be treated with caution. Still, age at first reproduction, interbirth intervals, and birth rates are comparable to those reported elsewhere (Glander 1980; Fedigan et al. 1998; Arroyo-Rodríguez et al. 2008; Cristóbal-Azkarate et al. 2017), suggesting that the reproductive performance of females living at La Flor de Catemaco is similar to that of females from unmanaged populations. There is, however, some variation between this and previous studies in other life-history parameters. For instance, compared to Hacienda La Pacifica (Costa Rica: Glander 1980), at La Flor de Catemaco primiparous females lose a lower proportion of their first offspring and most infants die within the first 4 months of life. Additionally, no seasonal variation in births and deaths was apparent in our data, contrasting with trends recorded elsewhere (Fedigan et al. 1998; Cristóbal-Azkarate et al. 2017). As the reproductive performance of female mantled howler monkeys is energetically constrained (Rangel-Negrín et al. 2018, 2021), variation among sites in factors such as food availability (Cano-Huertes et al. 2017) or stochastic factors (Ameca et al. 2015) could account for differences in fecundity and fertility and, as a consequence, in the timing of reproduction. Still, functional interpretations of this variation are precluded by the small sample of births that have been recorded in all studies conducted to date ($n=31$ in Glander 1980, $n=54$ in Fedigan et al. 1998, $n=75$ in Cristóbal-Azkarate et al. 2017, $n=42$ in this study).

Overall, the demographic and life-history parameters described here, and the behavior of individuals reported elsewhere (e.g., Reynoso-Cruz et al. 2016; Ceccarelli et al. 2019; de la Torre et al. 2021), are within the ranges reported for other populations of this species. These similarities suggest that mantled howler monkeys may persist at this site in the long term, indicating that this was a successful translocation. This success is probably linked to the fact that this translocation faced less challenges than other translocation processes (Berger-Tal et al. 2020). For instance: (i) due to the experience and expertise of our research group in the management of primates (e.g., Rodríguez-Luna et al. 1993; Canales-Espinosa et al. 2011) no animals were injured or died during capture; (ii) the institutional support provided by the Universidad Veracruzana facilitated several aspects of the process, including funding, infrastructure, and a permanent inflow of students and personnel that were involved in the follow-up of the released individuals; (iii) the collaborative actions of stakeholders (owners of the property and researchers) have safeguarded primates and their habitat (e.g., lack of hunting and logging) for the past 20 years.

On a broader scale, the dispersal of individuals from and toward La Flor de Catemaco may have implications for the viability of mantled howler monkeys living at Los Tuxtlas. The genetic diversity of mantled howler monkeys at Los Tuxtlas is low compared to other regions, a probable consequence of limited gene flow associated with small population size and fragmentation (Melo-Carrillo et al. 2020; Solórzano-García et al. 2021). As observed in other primate species (Moraes et al. 2017), admixture between local and translocated individuals could improve genetic diversity in the area and thus decrease the vulnerability of the population to the detrimental effects of genetic drift and inbreeding (Radespiel and Bruford 2014). A crucial step for the conservation of this species at Los Tuxtlas, including La Flor de Catemaco, will thus be genetic monitoring.

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