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Long-term assessment of the translocation of an endangered primate into an agroforestry system

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ABSTRACT: Translocation is increasingly being used as a conservation tool in wildlife management, but long-term assessments of the animals' establishment in the new habitat are rarely done. In addition, finding protected areas for translocations can often be a limitation, but habitat patches managed for productive purposes could potentially be used for translocations. Here, we present a translocation case study of the Endangered Mexican howler monkey *Alouatta palliata mexicana* into a forest fragment managed as an agroforest in the Los Tuxtlas Biosphere Reserve (Mexico). We compared the behavior of the translocated focal group 6 yr after translocation with that observed 1 yr after translocation (Year 1 vs. Year 6), and with reference parameters for conserved forest. We also examined the 14 yr trajectory of the translocated population through published data. We found that in Year 6, monkeys spent less time on locomotion and more time consuming fruit than in Year 1. The focal group in Year 6 had doubled its activity area compared to Year 1. All behavioral parameters during Year 6 were similar to those reported for the species in conserved forest. During the first 14 yr, the translocated population increased at a rate of 1.29 ind. yr^{-1}. We conclude that this translocation succeeded in establishing a thriving population and that certain agroforestry systems may be adequate habitat for primate translocations. We also discuss how the translocation of howler monkeys into defaunated habitats might help restore ecological functions associated with these primates, such as the dispersal of large-seeded plants. Long-term information on successful primate translocations has high practical value for designing adequate conservation strategies in anthropogenic landscapes.

KEY WORDS: *Alouatta palliata mexicana* · Primate conservation · Animal conservation · Defaunation · Reintroduction · Wildlife management · Ornamental palm oil · Community managed forest · Agroecosystem

1. INTRODUCTION

Anthropogenic pressures are rapidly transforming natural ecosystems into modified landscapes (Steffen et al. 2015, Curtis et al. 2018). This transformation causes widespread loss and degradation of wildlife habitats, which in turn are major causes of defaunation (Dirzo et al. 2014). Faced with the threat of losing animal populations and the ecosystem functions and services they provide, wildlife managers and stake-

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holders are increasingly implementing refaunation programs through conservation translocations (Galetti et al. 2017). While wild animals may be translocated for many purposes, the main aims of conservation translocations are to improve the conservation status of a focal species and/or to restore ecological processes carried out by the translocated species (Seddon et al. 2014, Genes & Dirzo 2022).

Historically, most conservation translocations have focused on the first objective (Day et al. 2009, Leroux et al. 2019). When the success of these translocations is assessed, demographic parameters are measured but other potentially important ecological indicators of success (e.g. behavior) are less often considered (Beck 2019). On the other hand, while translocation for restoring ecological processes has been less common, there is a fast-growing awareness of the need for and benefits of applying this practice in defaunated ecosystems (Beschta & Ripple 2016, Correia et al. 2017, Genes & Dirzo 2022). However, evaluating the success of restoring ecological processes can be more challenging, and for this reason, it is rarely carried out (Genes et al. 2019). Despite existing guidelines (Guidelines for Reintroduction and other Conservation Translocations; Translocation Tactics Classification System; IUCN/SSC 2013), translocation outcomes are variable, and their success is hard to evaluate (Batson et al. 2015, Beck 2019). Even when the main purpose of a translocation is one of the two mentioned (species conservation or restoration of ecological processes), often both can be achieved simultaneously. This is certainly the case when the translocated species is both threatened and functionally important, as is the case with most primates (Arroyo-Rodríguez et al. 2015).

In tropical forests, primates are crucial seed dispersers, and their declines are associated with strong negative effects on forest regeneration (Andresen et al. 2018, Gardner et al. 2019). At the same time, tropical forest primates are one of the most endangered animal groups, suffering population declines due to a variety of anthropic threats (Estrada et al. 2017). Yet certain primate species can be relatively resilient to disturbances (Barelli et al. 2015). This seems to be the case for howler monkeys *Alouatta* spp. in the Neotropics, which are able to survive in disturbed habitats (e.g. forest fragments, rustic shade plantations; Zárate et al. 2014, Klass et al. 2020). Nonetheless, howler populations living in very small and/or highly degraded habitat patches are likely to suffer negative effects in the long run (Milton et al. 2019), such that active conservation measures, including translocations, may be necessary. Furthermore, howler monkeys disperse the seeds of many Neotropical tree and liana species (Arroyo-Rodríguez et al. 2015), and the loss of these primates from forest patches has been related to changes in plant regeneration (Anzures-Dadda et al. 2011). Thus, the translocation of howler monkeys into defaunated habitat could aid both the conservation of the species and the restoration of ecological processes such as seed dispersal (Genes et al. 2019).

Translocation success depends strongly on having an adequate destination for the translocated individuals (Seddon et al. 2014, Beck 2019). However, finding suitable sites for wildlife translocations can be challenging, particularly in tropical regions where the expansion of anthropogenic land cover is occurring very rapidly (Haddad et al. 2015). Nonetheless, certain types of tropical shaded agroecosystems (e.g. agroforestry systems such as shade-grown crops) can be used as alternative habitat by many animal species, including primates (Estrada et al. 2012, Butynski & de Jong 2014). Worldwide, around 60 primate taxa use ~40 types of agroecosystems, which provide alternative habitat, food resources, shelter, and/or dispersal routes (Estrada et al. 2012). Primates in agroecosystems can provide valuable ecosystem services, such as favoring primary productivity (Estrada et al. 2012), promoting plant regeneration through seed dispersal (Andresen et al. 2018), controlling insect populations (Raboy et al. 2004), and fertilizing the soil (Feeley 2005). Although primates in some Paleotropical agroecosystems can cause human–primate conflicts when they feed on crops (Gameda 2019), this problem is less common in the Neotropics, where primates are well tolerated by farmers (Loría et al. 2021). Hence, shaded agroforestry systems could potentially be used as sites for wildlife translocation programs.

Here, we present a translocation case study of the Mexican howler monkey *Alouatta palliata mexicana* into a forest fragment managed as an agroforest for the production of an ornamental palm. In Mexico, deforestation and other disturbances (e.g. illegal pet trade) have negatively affected the 2 species of howler monkeys found in the country (*A. palliata mexicana* and *A. pigra*), and both are classified as Endangered (IUCN 2021). In 2004, 4 individuals living in a small forest fragment (~5 ha), where long-term population viability was unlikely, were moved to a large forest fragment (~100 ha) managed as an agroforestry system for palm production in the understory, where primates were no longer present. Our main goal was to determine if this translocation has been successful so far, by (1) evaluating the population trajectory to assess whether a self-sustaining population has been established (Beck 2019) and (2) evaluating the behavior of the translocated group to determine if patterns are similar to those observed in conserved forest. First, we recorded the behavior (activity patterns, activity area, and diet) of the translocated focal group during the sixth year after translocation and compared it to reference values reported for howler monkey populations in conserved forest sites; we also compared the behavioral patterns with those observed 1 yr after the translocation (Shedden-González & Rodríguez-Luna 2010), to determine changes during the first years after translocation. Second, based on the results of previous studies, we determined the population trajectory during the first 14 yr after translocation. In addition, we wanted to gather some evidence to evaluate whether the seed-dispersal services provided by howler monkeys might be being restored at the site of translocation. To achieve this goal, we used the list of frugivore-dispersed tree species reported at the study site and identified those for which fruit-feeding by howler monkeys has been observed at the site.

2. MATERIALS AND METHODS

2.1. Study region

The study was carried out in the Los Tuxtlas region, specifically in the buffer zone of the Los Tuxtlas Biosphere Reserve (18° 26′ 43″ N, 95° 02′ 49″ W; 155 122 ha) in the Mexican state of Veracruz (Fig. 1). The region includes lowlands and a northwest–southeast oriented mountain chain; landscape and vegetation heterogeneity are high (e.g. tropical evergreen forest, secondary forest, mangroves, wetlands), and altitudes range from 0–1780 m (Castillo-Campos & Laborde 2004). Annual precipitation ranges from 3000–4500 mm in the northeast, and 1500–3500 mm in the southwest (Acebey et al. 2017). Historically, Los Tuxtlas had a rich mammalian fauna (Coates-Estrada & Estrada 1986). However, due to human activities (83% deforestation; Galán-Acedo et al. 2021), the region is now dominated by a mosaic of forest fragments embedded in an anthropogenic ma-

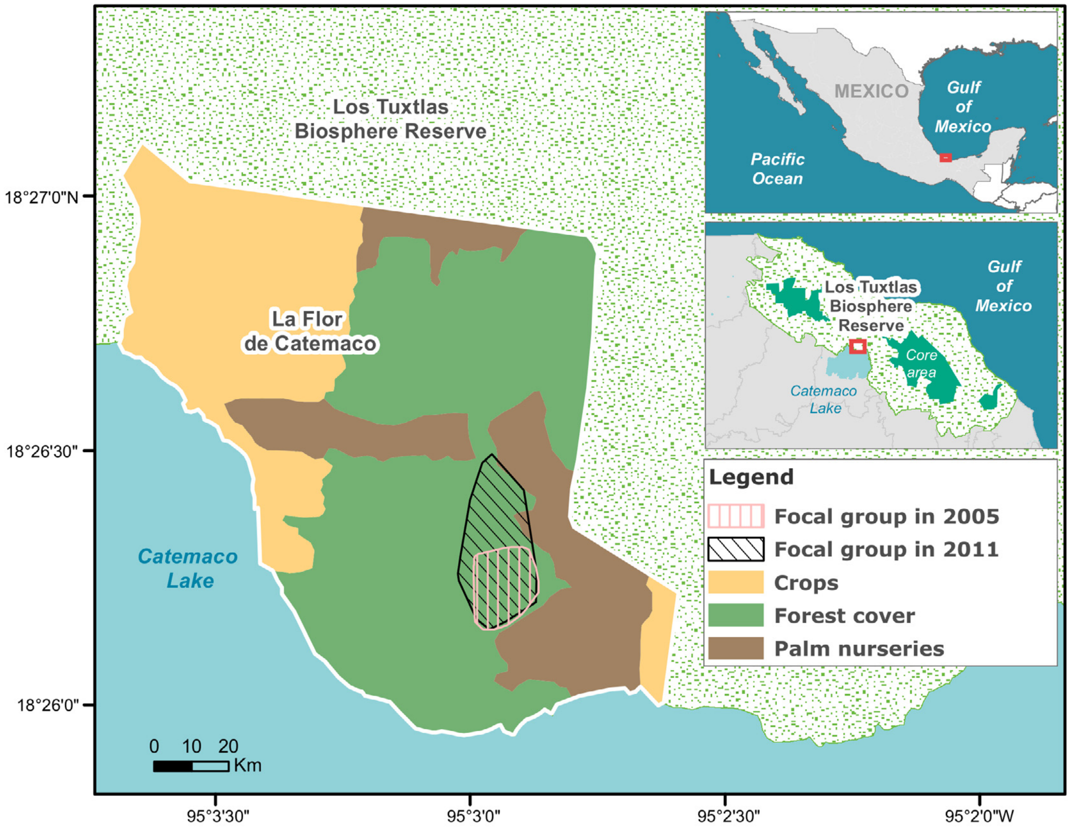

Fig. 1. Study site, the ranch 'La Flor de Catemaco' (white-bordered polygon), and smaller inset maps (top right corner) showing the location of the study region in Mexico (top) and the study site inside the Los Tuxtlas Biosphere Reserve (bottom; core areas dark green, buffer zone dotted). The large map shows the areas covered by forest, annual crops, and shade houses for the palm nurseries (brown areas); also shown are the activity areas of the focal primate group in 2005 (Year 1) and 2011 (Year 6; see Sections 2.3 & 2.4)

trix, and it is hence currently suffering faunal impoverishment, particularly of large mammals (Cristóbal-Azkarate et al. 2005, Dirzo et al. 2007).

2.2. Study site

Mexican howler monkeys *Alouatta palliata mexicana* were translocated into a 100 ha managed forest fragment, which is part of the ranch 'La Flor de Catemaco' (250 ha), located in the buffer zone of the Los Tuxtlas Biosphere Reserve (Fig. 1). The vegetation of the fragment is tropical evergreen forest and its understory is used for cultivating shade-grown plantations of parlour palm *Chamaedorea elegans*. The remaining area of the ranch is covered by a variety of annual crops and shade houses used as palm nurseries. After palm seedlings reach a certain size, they are transplanted from the nurseries into the understory of the forest fragment. All palm maintenance activities are designed to reduce impact on the environment but require constant human presence (Shedden-González & Rodríguez-Luna 2010). This site was selected for translocation because the owners had interest in the conservation of natural resources and the geographical location was within the natural distribution area of the species.

Several mammal species inhabited the study site at the time of translocation (e.g. coatis *Nasua narica*, Mexican hairy dwarf porcupines *Coendou mexicanus*, tamanduas *Tamandua mexicana*; Ceccarelli et al. 2020). Although the Los Tuxtlas region (including the Biosphere Reserve and surrounding areas) is the northern geographic distribution limit for Neotropical primates and 2 species inhabit the region (Mexican howler monkeys *A. p. mexicana* and spider monkeys *Ateles geoffroyi*), these primates were absent from the site.

2.3. Focal group

In September 2004, 4 individuals of *A. p. mexicana* (1 adult female, 1 adult male, 1 sub-adult female, and 1 sub-adult male), which constituted a family unit, were released into the study site as part of a primate translocation program managed by the Universidad Veracruzana, Mexico (Canales-Espinosa et al. 2011). Local people, ranch workers, and one of us (A.S.G.) confirmed that no monkeys were present at the study site before the translocation. Translocated monkeys had been captured in a degraded forest fragment located in Cascajal del Río, ~60 km south of the study site. This 4.9 ha isolated fragment was surrounded by cattle pastures and annual crops, and there were plans to remove the forest (Canales-Espinosa et al. 2011). After capture, the 4 animals were quarantined (35 d) and closely monitored until their release (Aguilar-Cucurachi et al. 2010, Shedden-González & Rodríguez-Luna 2010). The translocation process followed the guidelines of the IUCN (see Aguilar-Cucurachi et al. 2010), and some of the later published Translocation Tactics Classification System (i.e. animal release design, post-release animal management, environmental release design, and post-release environmental management; Batson et al. 2015). As part of a previous study (Shedden-González & Rodríguez-Luna 2010), the focal group was monitored for 8 mo (from September 2004 to December 2005, and from March to June 2005; 400 h of observation). We refer to the data of that study as 'Year 1'.

2.4. Behavior of the focal group 6 yr after translocation

Data collection for the present study took place between December 2010 and July 2011 (8 mo), and we refer to these data as 'Year 6'. By the time of our study, the focal group (same group as in Year 1, corroborated by one of us [A.S.G.]) consisted of 8 individuals: the 4 individuals of the initial family unit and 4 additional individuals. The composition of the group was 2 adult males, 2 adult females, 2 sub-adults of undetermined sex, and 2 infants.

We used the same data collection methods as in Year 1 (Shedden-González & Rodríguez-Luna 2010). Focal animal observations (Altmann 1974) were performed by 2 of us (I.V.B. and M.F.S.; inter-observer agreement: Cohen's Kappa test, $\kappa = 0.824$) on the 6 adult/sub-adult individuals (we excluded the 2 infants). Focal animals were continuously followed throughout 5 h periods (07:00–12:00 or 12:00–17:00 h), and changes in activity were recorded using time samples (in s). In total, we obtained 586 h of observation, homogenously distributed among the 6 individuals. We recorded activity (resting, locomotion, and feeding) and plant species and items (fruits, leaves, and flowers) consumed when feeding. Additionally, we georeferenced all trees used by the translocated group. With this information, we measured the area in which the monkeys were active during the study periods using the minimum convex polygon method in ArcGIS 10.4 (ESRI). We use the term 'activity area' rather than 'home range', as the minimum convex polygon method yields an empirical estimate of home range size, and additional sampling and calculations are required to obtain an accurate estimate (Vieira et al. 2019).

We estimated the monthly activity budget as the percentages of time spent on different activities. We also calculated the monthly percentage of time spent consuming different food items. The reference values for howler monkey populations in conserved forest were obtained from studies in the region of Los Tuxtlas (n = 10 studies; Table 1). We included studies carried out in areas ≥100 ha, with a duration ≥3 mo, which reported data on activity patterns, diet, and/or activity area. To compare parameter values between Year 1, Year 6, and reference values, we first estimated the mean and 95% confidence intervals. These descriptors were calculated for all variables except for the activity area for Years 1 and 6, where a single datum was obtained per year. We evaluated differences in the time invested in the 3 activities (resting, feeding, and locomotion), and dietary items (fruits and leaves) between Year 1, Year 6, and the reference values using generalized linear models (GLMs) fitted with binomial error distributions (adequate for proportions). We used the Akaike's information criterion (AIC) score to fit models (Burnham & Anderson 2002). We calculated the AIC weight (w_i) for each model, which ranges between 0 and 1 and can be interpreted as the probability that a model is the best one. For the selected models, we calculated the relationship between variables, extracting the p-value and slope from the GLM. The GLM was performed with the 'MuMIn' package (Barton 2020), and for fitting maximum likelihood models we used the 'bbmle' package (Bolker 2020) within the statistical program R v.3.2.0 (R Core Team 2013).

2.5. Reconstruction of the post-translocation population trajectory

To the best of our knowledge, 16 additional studies (scientific articles and theses; Table S1 in the Supplement at www.int-res.com/articles/suppl/n048p235_supp.pdf) on howler monkeys have been conducted at the study site between 2004 and 2021 (Aguilar-Cucurachi 2007, Shedden-González & Rodríguez-Luna 2010, Aguilar-Cucurachi et al. 2010, Cañadas Santiago 2014, Reynoso-Cruz 2014, Reynoso-Cruz et al. 2016, Cano-Huertes 2017, Cano-Huertes et al. 2017, Ceccarelli 2018, Maya-Lastra 2018, Rangel-Negrín et al. 2018, Cañadas Santiago et al. 2020, Ceccarelli et al. 2019, 2020, de la Torre et al. 2021, Rangel Negrín et al. 2021). These studies have focused on various aspects of howler monkey biology (behavior, endocrinology, reproduction, diet, and space use). We reviewed this literature and extracted information on the number of groups, individuals, group composition, and births to help us reconstruct the population trajectory of the translocated howler monkeys (it is im-

Table 1. Reference values of non-translocated populations of *Alouatta palliata mexicana* inhabiting conserved forest in the region of Los Tuxtlas. We included studies that were carried out in forests with areas ≥100 ha, had a duration ≥3 mo, and reported activity patterns (% of time spent resting [Rest.], feeding [Feed.], and in locomotion [Loc.]), diet (% of feeding time), and/or activity area (ha). EBT: Estación de Biología Tropical Los Tuxtlas (Los Tuxtlas Biological Station); dashes: data not reported

Site	Year	Months	Site size (ha)	Activity area	Activity patterns			Diet		Reference
					Rest.	Feed.	Loc.	Fruit	Leaves	
EBT Los Tuxtlas	1977–1978	12	700	60	–	–	–	51	49.3	Estrada & Coates-Estrada (1984), Estrada (1984)
EBT Los Tuxtlas	–	–	700	–	–	–	–	53	46	Estrada & Coates-Estrada (1986)
Balzapote Los Tuxtlas	1999	3	250	–	69	28	2.2	71.8	23.5	Juan-Solano et al. (2000)
Rancho Huber	2003–2004	12	244.1	40	78	14	7	46	49	Hervier (unpubl. data) in Cristóbal-Azkarate & Arroyo-Rodríguez (2007)
Rancho Huber	2006–2007	13	244.1	89.5	68.2	27.7	10.2	49.9	48.3	Dunn et al. (2009, 2010)
EBT Los Tuxtlas	2008	4	2000	12.5	–	–	–	–	–	Amato & Estrada (2010)
Montepio[a]	2009	10	230.6	15.94	72	14.7	13.3	41.1	58.3	Gómez-Espinosa et al. (2014)
					77.6	14.8	7.6	14.6	78.7	
Montepio[b]	2002–2003	14	100	8.5	46	11	9	–	–	Quintana-Morales et al. (2017)
				21	47	15	8.5	–	–	

[a] Includes separate data for wet (first row) and dry season (second row)

[b] Includes separate data for 2 howler monkey groups

portant to stress that this literature does not report migration data).

2.6. Potential seed-dispersal services

For tree species reported to occur at the study site (Cano-Huertes et al. 2017), we identified those that were registered as being used as fruit sources by howler monkeys during our focal observations, as well as in previous studies conducted at the study site (Shedden-González & Rodríguez-Luna 2010, Reynoso-Cruz 2014, Cano-Huertes et al. 2017). While frugivory by vertebrates does not always have seed dispersal as a consequence, many studies with howler monkeys have shown that *Alouatta* spp. are high-quality seed dispersers, either through defecation or seed-spitting, for most plant species used as fruit sources (reviewed in Arroyo-Rodríguez et al. 2015). Thus, we consider it highly unlikely, though not impossible, that howler monkeys are acting as seed predators for the plant species used for fruit-feeding in our study site. We also identified those tree species present at the study site that have been reported to be used as fruit sources by *Alouatta* in the Neotropics (Estrada & Coates-Estrada 1984, Wenny 1999, Dias & Rangel-Negrín 2015, Arroyo-Rodríguez et al. 2015, McKinney 2019). We think it is probable that those tree species are also being consumed (and their seeds dispersed) by howlers in our study site. While we recognize that this deduction is speculative, we believe that this list of potentially dispersed tree species can be valuable for future studies aiming at confirming this hypothesis.

3. RESULTS

3.1. Behavior of the focal group 6 yr after translocation

The average time (monthly mean ± SD) spent by howler monkeys resting, in locomotion, and feeding in Year 6 was 64.5 ± 10, 7.1 ± 2.2, and 21.4 ± 6.5%, respectively. The monkeys spent 57.8 ± 9.7% of their feeding time consuming fruits and 40.8 ± 8.9% eating leaves; the rest was spent on other minor items (flowers and bark). Comparing the activity patterns in Year 6 with those observed in Year 1 and the conserved forest, we found no differences, except for locomotion (Fig. 2, Table S2). In Year 6, the monkeys spent less time in locomotion than in Year 1 ($t = 0.37$, df = 2, $p < 0.01$; Fig. 2c). In terms of feeding items, in Year 6 the monkeys spent more time consuming fruit than in Year 1 (57.8 ± 9.7 vs. 40.2 ± 14.2%, respectively; $t = 1.52$, df = 2, $p < 0.05$; Fig. 2d, Table S2). As expected, given that howlers are folivore–frugivores, we observed a reverse trend in the time spent consuming leaves (Fig. 2e). Of the 100 ha of forest available in the study site, the focal group used 12 ha in Year 6, more than doubling its activity area when compared to Year 1 (5.5 ha; Fig. 1). However, the activity area in Year 6 was still smaller than the lower confidence limit estimated for the mean activity area of howler monkeys in conserved forests in the Los Tuxtlas region (Fig. 2f).

3.2. Post-translocation population trajectory

In 2004, as a result of the translocation, the population consisted of 4 individuals; no primates were present before the translocation. In March 2007, another group of howler monkeys, consisting of 3 females and 2 males, was released at the study site but was not monitored (Vélez del Burgo 2011, p. 53). During 2010–2011, the focal group consisted of 8 individuals, and we found a second group of 7 individuals. We also observed 2 solitary males living in the study site, yielding a total population size of 17 howler monkeys. In 2013, the population consisted of 3 different groups and a total of 25 howlers inhabiting the forest fragment. When the last studies were conducted in 2017–2018, the population consisted of 23 individuals: 20 individuals living in 3 groups and 3 solitary individuals (Table 2). The mean birth rate of the focal group was 0.51 ± 0.32 yr^{-1} (Table 2). It is important to note that Rangel-Negrín et al. (2018) reported that only 66.6% of births survived in the 2012–2017 period. Overall, the population increase was 18 individuals in 14 yr, i.e. a rate of 1.29 ind. yr^{-1}.

3.3. Potential seed-dispersal services

Howlers consumed the fruits of 16 native species from a total of 48 fleshy-fruited species found in the study site (Cano-Huertes et al. 2017). Additionally, 12 other native fleshy-fruited tree species present at the study site have been reported to be consumed by *Alouatta* spp. in the Neotropics (Table S3). Hence, the howler monkey population at the study site is very likely dispersing the seeds of 16 native tree species and potentially those of 28 native tree species (33–58% of all frugivore-dispersed native tree species found at the site).

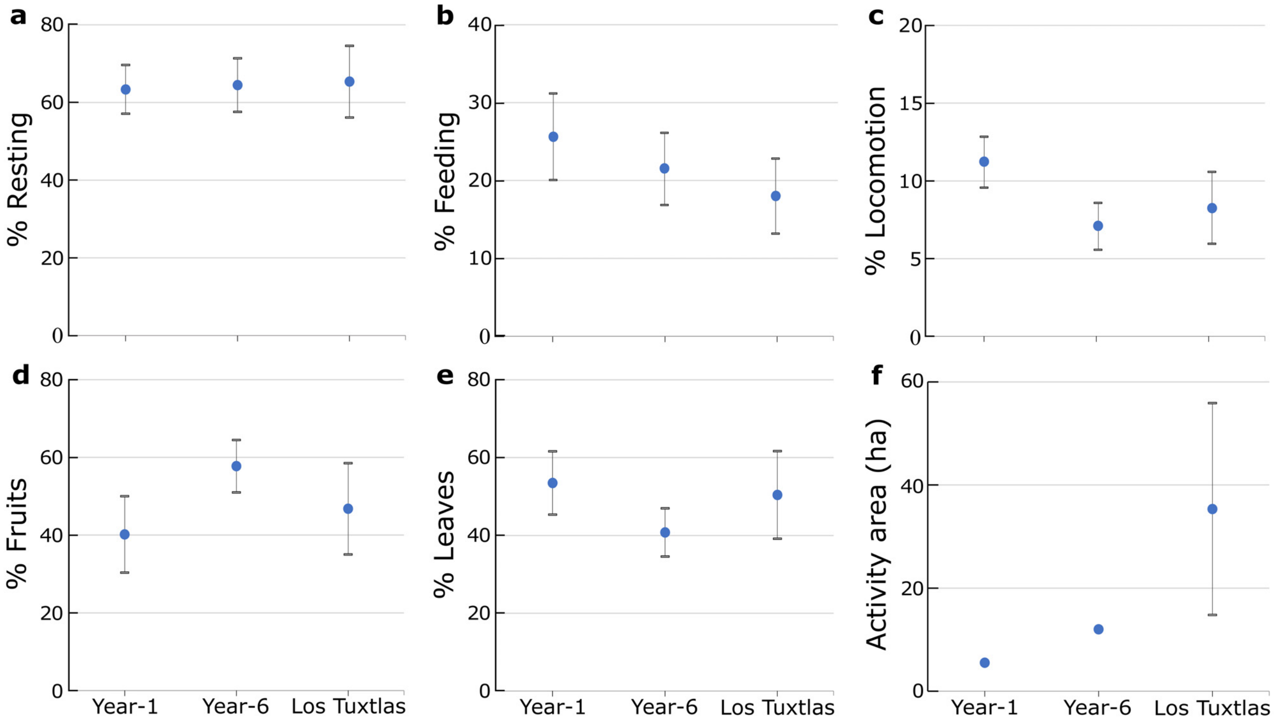

Fig. 2. (a–c) Activity pattern, (d,e) diet, and (f) activity area of Mexican howler monkeys, comparing the translocated group 6 yr after translocation (Year 6) with the same group immediately after translocation (Year 1) and with reference values for non-translocated populations of Mexican howler monkeys in conserved areas in the study region (Los Tuxtlas). Blue dots: mean values; error bars: 95 % confidence intervals. Year 1: 400 observation hours (Shedden-González & Rodríguez-Luna 2010); Year 6: 586 observation hours; Los Tuxtlas: includes data from 10 studies that were carried out in sites ≥100 ha in the Los Tuxtlas Biosphere Reserve, with a duration ≥3 mo (Table 1)

Table 2. Population trajectory reconstruction of the translocated howler monkeys based on the studies conducted at the study site (2004–2018). AM: adult males; AF: adult females; J: juveniles (including subadults); I: infants; (–) not reported

Year	Sampling effort (h)	No. of groups/ individuals reported	No. of groups studied/social composition	No. of births reported	Purpose of the study	Reference
2004	374	1/4	1/AM:2; AF:2	2	Behavior/stress (in pre-translocation and captivity)	Aguilar-Cucurachi (2007) Aguilar-Cucurachi et al. (2010)
2004–2005	400	1/4 ind.	1/AM:1; AF:1; J:2	1	Behavior/translocation	Shedden-González & Rodríguez-Luna (2010)
2010–2011	586	2/17	1/AM:2; AF:2; J:2; I:2	1	Behavior/post-monitoring	This study
2012–2013	–	2/19	2/AM:8; AF:5; J:3; I:2	3	Reproduction/stress	Cañadas-Santiago (2014)
2012–2013	603	2/–	2/AM:6; AF:3; J:4; I:3	–	Feeding	Reynoso-Cruz (2014)
2013	300	3/25	2/AM:2; AF:4; J:1; I:1	–	Feeding	Reynoso-Cruz et al. (2016)
2013–2015	1100	3/23	2/AF:7	8	Reproduction	Cano-Huertes (2017), Cano-Huertes et al. (2017), Días et al. (2018)
2014	1320	3/23	2/AM:6; AF:5	–	Endocrinology	Dias et al. (2017)
2016–2017	1712	3/24	2/AM:6; AF:7; I:4 1/AM:1; AF: 2	5	Spatial behavior	Ceccarelli et al. (2018, 2019, 2020, 2021)
2017–2018	888	1/23	2/AM:6; AF:7	–	Movement behavior	Maya-Lastra (2018)
2012–2017	–	–	2/AF:7	21[a]	Reproduction	Rangel-Negrín et al. 2018

[a] Sum of births reported from 2012–2017

4. DISCUSSION

Our study provides a long-term assessment of a translocation of Mexican howler monkeys into a rainforest fragment managed as an agroforest for the cultivation of an ornamental palm in the forest understory. We considered aspects of behavior, population growth, and the potential reestablishment of primate ecological functions, focusing on seed dispersal. Our results suggest that the translocation has been successful so far because (1) 6 yr after translocation the focal group had activity patterns similar to those reported for the species in conserved forest, even though the activity area was still below the values observed for conserved forest; (2) compared to the first year after translocation, during the sixth year the monkeys spent less time on locomotion and more time feeding on fruit, which can be indicative of more efficient foraging; and (3) the translocated population increased by 18 individuals during the first 14 yr. Additionally, the translocated monkeys ate the fruits of at least 16 frugivore-dispersed tree species and are very likely functioning as seed dispersers for those species. Furthermore, our results strongly suggest that certain agroforestry systems can be considered as potential target sites for translocation programs. Our findings have important management implications for long-term biodiversity conservation in tropical anthropogenic landscapes.

For over 50 yr, the region of Los Tuxtlas has experienced high rates of deforestation and fragmentation (von Thaden et al. 2018). Despite the Los Tuxtlas Biosphere Reserve protecting the last large remnants of tropical forest in the Gulf of Mexico (Guevara et al. 2004), >80% of the region's forest cover has been lost as a result of land-use change (Vega-Vela et al. 2018). Even though the region still harbors an extremely rich biodiversity, it is considered defaunated due to declining wildlife populations, in particular populations of large-bodied mammals (Dirzo et al. 2007, Zamora-Espinoza et al. 2021). Nevertheless, Mexican howler monkeys can be found inhabiting small forest remnants in the Los Tuxtlas fragmented-forest landscapes (Cristóbal-Azkarate et al. 2017, Galán-Acedo et al. 2021), as they are relatively resilient to anthropogenic disturbances (Dias & Rangel-Negrín 2015).

Despite their resilience, Mexican howlers are classified as Endangered and can suffer adverse effects in fragmented landscapes, including changes in their behavior and diet, and reduced genetic diversity (Melo-Carrillo et al. 2020). Furthermore, this subspecies has a very limited distribution, being endemic to southeastern Mexico (Cristóbal-Azkarate et al. 2005). As its habitat continues to shrink, population declines will likely increase in severity and frequency (Mandujano & Escobedo-Morales 2008). Under this scenario, translocations of individuals may become a necessary strategy to reintroduce the species where it has become locally extinct, to reinforce small populations, or to relocate groups with small chances of persisting over time. Our results show that, if adequately executed, translocation programs of Mexican howler monkeys can be successful, even when the target habitat is a forest managed for productive purposes.

There are several lines of evidence supporting the contention that the translocation has been successful so far. The translocated population showed normal activity patterns and increased at a rate comparable to that reported for the species in conserved forests of the region (Table 1). The population growth at La Flor (18 ind. in 14 yr) was high compared to the demographic change in a non-translocated population at Los Tuxtlas (2.4 ± 4.6 ind. in 11 yr for 10 groups; Cristóbal-Azkarate et al. 2017) Furthermore, the birth rate observed for the translocated population (0.51 ± 0.32 yr^{-1}) is consistent with other reports for the species (0.36–0.52 in Cristóbal-Azkarate et al. 2017; ~0.5 in Carrera-Sánchez et al. 2003; 0.62 in Cortés-Ortiz et al. 1994). A positive birth rate can indicate that the translocated howler monkeys have adapted properly to their release site and probably are in good nutritional condition (Rossi & dos Santos 2018). Also, the translocated focal group increased its activity area over time (Year 1: 5.5 ha; Year 6: 12 ha), with the last value reported (92 ha in 2018; Maya-Lastra 2018) being similar to non-translocated populations of howlers in conserved forests (Table 1). Other studies evaluating success of primate translocations have also found an increase in activity area over time (e.g. Campera et al. 2020).

However, although the translocation has been successful so far, continued monitoring will be necessary, as it is possible that the area of the managed forest fragment (100 ha) may limit future population growth or cause other negative effects associated with increased population densities (e.g. malnutrition, increased parasitism; Orihuela López et al. 2005, Galán-Acedo et al. 2021). To prevent or mitigate such effects, this habitat area could be enlarged (e.g. through forest restoration in adjacent properties) or the emigration of individuals could be facilitated (e.g. through the establishment of forest corridors connecting the ranch with other forest patches). We believe that both options are feasible, and some anecdotal information suggests that migration of individuals between the study site and nearby forest fragments has occurred (N. Maya Lastra pers. comm.).

In addition to establishing a self-sustaining population, this translocation is probably playing an important role in reestablishing ecological functions associated with howler monkeys, as shown in other studies (e.g. Genes et al. 2019). Due to their important role as seed dispersers, the loss of primates is known to have strong negative effects on the regeneration of tropical forests worldwide (Gardner et al. 2019), and howler monkeys are not an exception (Anzures-Dadda et al. 2011). Howlers are known to be effective seed dispersers for most plant species whose fruits they consume, and they are believed to be particularly important for large-seeded species, which are not dispersed by smaller frugivores such as birds (Arroyo-Rodríguez et al. 2015). In this regard, we found an increase of fruit consumption after translocation (Fig. 2), and several of the fruit species eaten by howlers in our study site have large seeds (≥15 mm; Table S3). We suggest that future studies aimed at quantifying the restoration of seed-dispersal services through the translocation of howler monkeys could focus on those plant species. We also propose that the translocation of Mexican howler monkeys may even be functionally compensating for the local extinction of the other large frugivorous primate, the spider monkey (Andresen et al. 2018). Spider monkeys are also very effective seed dispersers (di Fiore et al. 2010), but, unlike howlers, they are extremely sensitive to habitat loss. Spider monkeys usually disappear from all but the larger forest fragments (>100 ha); consequently, they are rarely found in the fragmented landscapes of the Los Tuxtlas region (Galán-Acedo et al. 2018).

Seed dispersal by howler monkeys in our study site, and other agroforests, can have at least 2 potentially beneficial effects. First, seed dispersal might contribute to the regeneration of other tree species that are used by local people when exploiting resources inside the agroforest, in addition to the main crop (e.g. timber, fruit trees) (Zárate et al. 2014). Second, if owners decide to stop palm production and leave the fragment as an ecological reserve, seed dispersal by howler monkeys might facilitate the natural regeneration of the forest (Andresen et al. 2018). Finally, frugivorous primates not only affect ecosystems through seed dispersal but also through many other ecological functions (Chapman et al. 2013), including some that may enhance the productivity of agroforests, such as the input and transport of nutrients (Stevenson & Guzmán-Caro 2010, Estrada et al. 2012). Those benefits may in turn foster positive attitudes and perceptions in landowners and the local communities (Hockings et al. 2017).

To be successful, any conservation project, including conservation translocations, must consider the human dimension (Marchini et al. 2019). The integration of socio-economic and ecological aspects is a key factor for achieving ‘multifunctional landscapes’ (Grass et al. 2019) that reconcile local needs with biodiversity conservation. Rural and indigenous communities inhabiting the Los Tuxtlas region strongly depend on natural resources, agricultural crops, and cattle ranching (Durand & Lazos 2008). Within the Biosphere Reserve, the communities' use of the land encompassing the buffer zone is somewhat restricted. However, agroforests that constitute alternative habitat for wildlife could be a feasible land-use option for both conservation and livelihood purposes. Such agroforests, when established in areas previously covered by more intense land uses (e.g. cattle pastures, annual crops) could increase the amount of available habitat for forest wildlife and promote connectivity at the landscape scale (Martin et al. 2020). Our study site, La Flor de Catemaco, is a successful example of such an agroforest.

In conclusion, the 14 yr history at La Flor de Catemaco gives us valuable insights about the translocation process. The evaluation of primate translocation projects over time is still an uncommon practice (Beck 2019), even though it provides key information for future translocations. We also showed that Mexican howler monkeys can be successfully translocated into forest fragments that are managed as agroforestry systems. Thus, we propose that agroforestry systems similar to the one studied here could be used as target habitat for wildlife translocation programs, thus contributing to biodiversity conservation in human-modified landscapes.

Availability of data and material: The data that support the findings of this study are available in the Supplement or from the corresponding author upon reasonable request.

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