Life in a fragment: evolution of foraging strategies of translocated collared brown lemurs, *Eulemur collaris*, over an 18-year period

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Short title: **Brown lemurs'** response to translocations

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Abstract

Whilst the drivers of primate persistence in forest fragments have been often considered at the population level, the strategies to persist in these habitats have been little investigated at the individual or group level. Considering the rapid variation of fragment characteristics over time, longitudinal data on primates living in fragmented habitats are necessary to understand the key elements for their persistence. Since translocated animals have to cope with unfamiliar areas and face unknown fluctuations in food abundance, they offer the opportunity to study the factors contributing to successful migration between fragments. Here, we illustrated the evolution of the foraging strategies of translocated collared brown lemurs (*Eulemur collaris*) over an 18-year period in the Mandena Conservation Zone, south-east Madagascar. Our aim was to explore the ability of these frugivorous lemurs to adjust to recently colonized fragmented forests. Although the lemurs remained mainly frugivorous throughout the study period, over the years we identified a reduction in the consumption of leaves and exotic/pioneer plant species. These adjustments were expected in frugivorous primates living in a degraded area, but we hypothesize that they may also reflect the initial need to cope with an unfamiliar environment after the translocation. Since fragmentation is often associated with the loss of large trees and native vegetation, we suggest that the availability of exotic and/or pioneer plant species can provide an easy-to-access, non-seasonal food resource and be a key factor for persistence during the initial stage of the recolonization.

Key words: *Eulemur collaris*, primate translocations, fragmentation, feeding adaptations, littoral forest

Research Highlights:

- Collared brown lemurs remained mainly frugivorous over a 18-year period after their translocation into a new forest fragment.
- Exotic and pioneer plant species facilitate persistence during the initial stage of the recolonization.

Introduction

Habitat fragmentation is widely recognized as one of the main menaces to species survival (Laurance et al., 2011; Laurance, Goosem, & Laurance, 2009; Laurance & Peres, 2006), and primates are no exception (Estrada et al., 2017). Several deleterious consequences are associated with fragmentation including a decrease in the available area, a reduction of habitat quality due to edge effects, and a reduction of the species' ability to disperse in its geographical range and reproduce (Laurance et al., 2007; Pfeifer et al., 2017). Although the sensitivity to fragmentation varies across species, for many animals it has dramatic consequences on population viability (Dirzo et al. 2014; Fahrig, 2003; Walker, Sunnucks, & Taylor, 2008). Thus, local extinctions of small populations existing in fragments are common (Fahrig & Merriam, 1994; Kindlmann & Burel, 2008). Persistence depends on the ability of dispersing individuals to move across the matrix between the fragments, as well as on species' social and ecological flexibility to cope with resource scarcity and variations (Boyle & Smith 2010; Marsh, 2003; Nowak & Lee, 2013; Schwitzer, Glatt, Nekaris, & Ganzhorn, 2011). In addition to the interruption of gene flow, non-genetic factors that may lead to rapid extinction in fragments include resource scarcity (Arroyo,Rodríguez, Mandujano, Benitez-Malvido, & Cuendefanton 2007; Robinson, 1998), food depletion and disease spread due to overcrowding (Gabriel, Gould, & Cook, 2018), greater exposure to climatic variations, demographic stochasticity, and poaching (Onderdonk & Chapman, 2000; Schmiegelow, Machtans, & Hannon, 1997).

The longer the habitat fragmentation has been present, the more the floristic composition, vegetation structure, and plant phenology cycles diverge among the forest patches (Arroyo-Rodríguez & Mandujano, 2006; Hill & Curran, 2003). For example, it has been demonstrated that the abundance and richness of large trees vary between forest fragments and this can affect the persistence of many primate species (Arroyo-Rodríguez & Mandujano, 2006; Arroyo-Rodríguez et al., 2007; Chapman, Naughton-Treves, Lawes, Wasserman, & Gillespie, 2007; Dunn, Cristobal-Azkarate, & Veà, 2009; Onderdonk & Chapman 2000). Since fruiting trees in tropical areas tend to be scarce and scattered in distribution, frugivorous primates are expected to be more vulnerable to fragmentation and disappear earlier than other **dietary guilds** (Di Fiore, Link, & Dew, 2008; González-

Zamora et al., 2009; Wallace, 2005). Species persistence may thus largely rest on the ability of the individuals to modify their diet in response to what is available (Bicca-Marquez, 2003; Dunn et al., 2009; Rivera & Calmé, 2006). This flexible response may include either an increase or a reduction in dietary diversity, a shift to locally abundant tree species, the consumption of exotic and secondary successional species such as vines or climbers or an increased consumption of leaves (Asensio, Cristóbal-Azkarate, Dias, Veà-Baro, & Rodriguez-Luna, 2007; Cristóbal-Azkarate & Arroyo-Rodríguez, 2007; de Luna et al., 2017; Dias, Rangel-Negrín, Coyohua-Fuentes, & Canales-Espinosa, 2014; González-Zamora et al., 2009; Irwin, 2008; Onderdonk & Chapman, 2000).

Exploring the long-term behavioral adjustment of translocated animals may offer promising insights on the abilities of a species to colonize new forest patches and thus to persist in a fragmented landscape. By definition, translocation involves moving wild animals from one part of their distributional range to another for various purposes (Griffith, Scott, Carpenter, & Reed,1989). In essence, animal translocations simulate a successful dispersal event to another fragment since the animals involved have not been exposed to humans or only for the very short time of the operation (Fischer & Lindenmayer, 2000; Strum, 2005). The ability of the animals to persist in the new area will depend on their ecological and behavioral plasticity. Similarly to dispersing animals moving across the matrix between the fragments, translocated primates have to cope with unfamiliar areas and need to face unknown fluctuations in food abundance or include new foods in their diet (Ostro, Silver, Koontz, & Young, 2000; Rodriguez-Luna, Domínguez-

Domínguez, Morales-Mávil, & Martínez-Morales, 2003; Silver & Marsh, 2003; Strum, 2005).

The lemurs of Madagascar are currently considered to be among the most threatened mammals in the world (Schwitzer et al., 2014). This group of strepsirrhines includes either strictly or mainly arboreal species, which makes them particularly vulnerable to habitat loss and fragmentation in a country where around half of the remaining forest (46 %) is less than 100 m away from its edge (Vieilledent et al., 2018). Over the last two decades, numerous studies have demonstrated the impact of habitat fragmentation on lemur species richness at the landscape level (Dunham, Erhart, Overdorff, & Wright, 2008; Ganzhorn & Eisenbeiß, 2001; Steffens & Lehman, 2018), their behavioural and ecological response within and between fragments (Donati et al., 2011; Campera et al., 2014; Eppley et al., 2017; Gould & Gabriel, 2015; Irwin, 2008; Irwin, Raharison, Raubenheimer, Chapman, & Rothman, 2015; Lehman, Rajaonson, & Day, 2006), and the genetic consequences of habitat fragmentation on their populations (Quéméré, Amelot, Pierson, Crouau-Roy, & Chikhi, 2012; Radespiel, Rakotondravony, & Chikhi, 2008; Sgarlata et al., 2018). Despite an overall negative effect of fragmentation on lemur persistence, several species have been shown to tolerate some levels of habitat degradation via shifts in activity patterns and in dietary choices (Donati et al., 2016; Irwin et al., 2010; Sato et al., 2016). Considering the wide variation between species and the rapid variation of habitat characteristics over time, multi-annual data on lemurs living in fragmented habitats are vital to understanding the key elements for their persistence in modified landscapes. However, while the drivers of lemur persistence in forest fragments have often been considered at the population level, there has been little investigation of the strategies to survive in these habitats at the individual or group level.

The post-release monitoring of a translocation of several groups of Endangered collared brown lemurs (*Eulemur collaris*) in the littoral forest of southern Madagascar offers an excellent opportunity to document the long-term development of dietary strategies of a strepsirrhine in an unfamiliar environment. In 2000-2001 the entire population of collared lemurs of the Mandena region was moved from a forest patch logged by charcoal makers to a recently protected but partially degraded forest fragment, the Mandena Conservation Zone (Donati, Ramanamanjato, Ravoahangy, & Vincelette, 2007a). The translocated population has now increased from the original 28 individuals relocated in 2000 to the 58 individuals counted in 2018 (Ramanamanjato unpublished data, 2018). Previously published data indicate that these lemurs were able to modify group size and several aspects of their time budget and ranging behaviour to cope with the partially degraded habitat in Mandena when compared to populations of collared brown lemurs living in **larger fragments** (Donati et al., 2011; Campera et al., 2014). However, these previous comparisons were based on specific time-windows, while a longitudinal analysis illustrating the evolution of the lemur foraging strategies since the beginning of their relocation was never conducted.

Here, we report the development of the foraging strategies of three groups of translocated collared brown lemurs over an 18-year period (2001-2018) to shed light on the ability of this medium-sized lemur to adjust to recently colonized fragmented forests. We made the following predictions:

- Since non-translocated individuals are mainly frugivorous (Donati, Bollen, Borgognini-Tarli, & Ganzhorn, 2007b) but fruiting trees are expected to be more difficult to locate in an unfamiliar area compared to leaves, we predicted the lemurs to be more folivorous during the initial **(three year)** post-release phase and increase frugivory over time. Leaf consumption would be also a primate response to a high level of habitat degradation (Chaves, Stoner, & Arroyo-Rodríguez, 2012; de Luna et al., 2017) characterizing the initial phase of the operation (Donati et al., 2011).

- Since the lemurs had to familiarize with the new area, we predicted dietary breadth, defined as the diversity of plant species in the diet, to show initial high values and decrease over time. This would be caused by the need to explore the new environment and balance the secondary component overload of leaves and other fall-back food (Dunn et al., 2010; MacArthur & Pianka, 1966). Improved ability to find preferred food species in the new habitat over time may also lead to a decrease of dietary breadth.

- Finally, we predicted exotic and/or pioneer plant species to have a large representation in the lemurs' diet during the initial **(three year)** post-release phase. The release area provides a complex mosaic of upland and swamp forest habitats, monodominant exotic species, old and new timber plantations (Eppley et al., 2017). Fast-growing plants may provide an easy to access, non-seasonal, and relatively large resource biomass (Eppley et al., 2017; Poorter, 1999) that can be important during the lemurs' initial familiarization with the release area.

Methods

Study site and species

This study was conducted in the littoral forests of the Mandena Conservation Zone (hereafter MCZ), 11 km North-West of Fort Dauphin (24°57'18''S 46°59'42''E), in south-eastern Madagascar (Fig. 1). This region is characterized by a tropical wet climate, with average monthly temperatures of 23°C (range: 18.2–25.9; n= 30), annual rainfall ranging from 1600–2480 mm, and no clear dry season (Vincelette, Theberge, & Randrihasipara, 2007). The MCZ is located on sandy soils at an altitude of 0–20 m above the sea level. The two largest forest fragments, M15 and M16, cover an area of 148 hectares of degraded littoral forest (Ganzhorn et al., 2007). Approximately 82 ha of swamp connect the two fragments but because the lemurs regularly use the swamp for travelling, feeding and resting, we considered these two fragments as a single area. M15/M16 are the two main forest fragments where collared lemurs are still present at this site (Donati et al., 2011). One of the study groups of collared brown lemurs (group C) use a fragment outside the MCZ (M20), which includes ca. 6 ha of heavily degraded forest, and is located northeast of the other two fragments (Ganzhorn et al., 2007).The average canopy height is 8.9 m and the understorey is dense (Rabenantoandro, Randriatafika, & Lowry II, 2007). Phenological records from MCZ (Campera et al., 2014) show that there is a distinct period of fruit abundance between November and April, while fruit availability is low from May to October.

Collared brown lemurs are arboreal strepsirrhines living in multi-male, multi-female groups (Donati et al., 2007b). Mean body mass is 2.15 ± 0.25 kg and mean body length is 46.1 ± 2.6 cm (n = 11). Median group size in intact littoral forest is 7 (range: 2–17; n =13), while in the degraded MCZ is 5 (range: 2–6; n = 9) (Campera et al. 2014; Donati et al., 2011). Mean home-range size is 58.9 ha (range: 34.5-83.2) in MCZ while it is 32.6 ha (range: 15.1-50.2) in the less degraded area of Ste Luce (Campera et al., 2014). This lemur species is cathemeral and its dietary regime is mainly frugivorous (Donati et al., 2007b). In addition to *E. collaris*, four nocturnal (*Microcebus ganzhorni*, *Cheirogaleus medius*, *Cheirogaleus major*, *Avahi meridionalis*), and one cathemeral lemur species (*Hapalemur meridionalis*) are found in MCZ.

The collared brown lemurs now living in the MCZ were relocated in 2000 and 2001 from a forest fragment heavily logged by charcoal makers about 3 km east of the release site (Donati et al., 2007a). The species was extirpated from the release area several years before the relocation due to hunting by humans while the site was unprotected. Since their relocation, the population in the MCZ has been monitored regularly and the lemurs have shown stable ranging areas during the last few years (Balestri et al., 2014; Campera et al., 2014; Donati et al. 2007a, 2011).

Observations

Diurnal ethological data were collected from 2001 to 2018 on three groups of collared brown lemurs with the exception of 2010 and 2015-2016 (Table 1). The group size ranged from 3 to 7 individuals for group A and group C and from 2 to 5 individuals for group B. We observed the same three groups each year until 2009 and then only two groups from 2011 to 2018, as Group B split up in 2010 and its members joined group A and C. Since nocturnal observations were not possible in the MCZ during most of the study period, the analysis was limited to the diurnal phase. Overall, we collected and analyzed 5,509 observation hours with an average of 196.79 h per group per year (range: 64-609 h). Observation sessions ranged from a minimum of 4 hours to 12 consecutive hours of data collection from dawn to dusk, while observation months ranged from 4 to 12 months per group per year (median: 7 months). Over the years, individual identification of each study animal was either made using nylon collars or, more often, using natural marks. In 2001, 2004, 2011, and 2017 one individual per group was radio-collared (TW-3, Biotrack, 29 g) to facilitate the localization of the groups. This study was conducted with the authorization of the Commission Tripartite of the Direction des Eaux et Forets de Madagascar, the Department of Animal Biology of Antananarivo University, the University of Pisa, and Oxford Brookes University. In accordance with the recommendations of Weatherall report, captures of lemurs were conducted entirely under anesthesia using a hypnotic (5 mg/kg of ketamine hydrochloride or tiletamine hydrochloride)(Cunningham et al., 2015). **The research also adheres to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-Human Primates.** Captures were carried out by experienced Malagasy technicians via a blow-pipe darting. All animals recovered from anesthesia within 1.5 hours. During the translocation the lemurs were kept in habituation cages for 3 weeks before their release (Donati et al., 2007a), while in subsequent years they were not moved from the capture area but followed until regaining full mobility (Campera et al., 2014). There were no injuries as a consequence of the captures.

Please, insert Table 1 here

Behavioral data were collected by the instantaneous sampling method with a 5-minute interval (Altman, 1974; Crook & Aldrich-Blake, 1968). Focal animals were chosen among the adult individuals at the beginning of each observation, balancing the time spent observing males and females. One focal individual was observed during each observation session, and substituted with the first visible individual of the same sex if lost. Instantaneous data collected consisted of animal activity, food type, feeding and resting trees. Activities included feeding (food ingestion), foraging (food exploration), resting, moving, social, and other activities. Food types were noted as fruits, unripe fruits, leaves, young leaves, flowers, invertebrates, and other (bark, stems, roots, mushrooms, decayed wood). Differentiation between unripe/ripe fruits and mature/young leaves was based on differences in color, size, and texture. We estimated lemur diet by using the proportion of feeding records, as the poor visibility conditions in dense littoral forests precluded a reliable quantification of the absolute amount of food items consumed. Although temporal measures of diet may produce significant distortions of actual food intake (Kurland & Gaulin, 1987; Zinner, 1999), since we focus on the relative proportion of food items over the years and not on the absolute quantification of food consumed, this method can be considered adequate for our purposes. The Shannon index was used to determine the annual dietary diversity of each group per year. This measure is particularly useful when comparing similar dietary regimes, as it considers both the number of food species and their evenness in the diet (Pielou, 1966).

JR and FR identified all plant species used for feeding by the lemurs over the whole study period. Exotic plant species, i.e. non-endemic, were then validated with a list of exotic and invasive species in Madagascar (Gérard, Ganzhorn, Kull, & Carrière, 2015). Pioneer species are characterized by the need for full light, and they do not establish in mature forest but only under canopy gaps or along forest edge.

Analysis

As a proxy of vegetation quality and primary productivity we used NDVI (Normalized Difference Vegetation Index), a satellite-based vegetation index that is derived from the red: near-infrared reflectance ratio. NDVI is a measure of photosynthetic activity, more specifically a measure of the absorbed photosynthetic active radiation, hence the energy used by plants for photosynthesis (Myneni, Hall, Sellers, & Marshak, 1995). NDVI has been widely used to study animal distribution and abundance, in relation to changes in vegetation phenology, quality and primary productivity (Pettorelli et al., 2005, 2011). We extracted the NDVI time series for MCZ using the MOD13Q1 dataset in Google Earth Engine (Gorelick et al., 2017). MOD13Q1 has a resolution of 250 m and spans from 2000 to present with intervals of 16 days. We drew a polygon encompassing MCZ, and extracted the average of all cells falling into the polygon for each 16-day interval from 2001 to 2018. We estimated the mean NDVI ($NDVI_{mn}$) and standard deviations ($NDVI_{sd}$) per year. The first was a measure of forest productivity, which in our case was used as a proxy of forest regeneration. The second was used as a proxy of seasonality in habitat primary productivity.

To reconstruct the annual dietary pattern of each lemur group the records of feeding activity on different food categories and plant species were weighted by the total number of feeding instantaneous records. **To minimize inconsistencies between years and observers we grouped for the analysis the observed food categories into broader categories. The category "fruits" included both ripe fruits and unripe fruits, "leaves" included both mature leaves and young leaves, while the category "other" included invertebrates, bark, stems, roots, mushrooms, and decayed wood**. To allow comparisons between the period immediately following the release with the subsequent periods we grouped the annual observations on each group within 7 biannual periods from 2001-2003 to 2017-2018. Since our unit of analysis is the annual average per group and we do not have all the 3 groups represented each year we decided to compare biannual periods rather than single years in this analysis. The first biannual period, **i.e. initial post-release period**, included in fact three years of data as we only have observations of one group for 2003 so this was merged with the previous two years.

To check whether the forest fragment of the MCZ has regenerated since it gained conservation status we ran a Pearson correlation between annual $NDVI_{mn}$ and years. To test for the effect of biannual periods, $NDVI_{mn}$, $NDVI_{sd}$, and group size on the dietary composition (proportions of fruits, leaves, flowers and other), number of food plants, and proportions of exotic and pioneer species in the diet, we ran a Generalized Linear Mixed Model using a Poisson error distribution and a log link function on the total feeding records. We also tested the same predictors on the annual dietary diversity, measured via Shannon index using a Gaussian error distribution and an identity link function. To account for variation in the effort taken per year, we included the total observation hours per group per year (log-transformed) as an offset term in the model. Because our data represent repeated measures over the years of several groups we used a model that could control for temporal autocorrelation of the residual structure. **Accounting for the temporal autocorrelation in the model residuals generally increases the precision of model parameter estimates (Mikkonen et al., 2008)**. We thus tested three different covariance matrices, the scaled identity, unstructured, and autoregressive (AR1) on the residual structure, and selected the latter as the one giving the lowest AICc. We specified in our outputs the residual covariance parameters with AR1 diagonal indicating the residual variance for each year and AR1 rho the residual correlation between two consecutive years. **We treated the three lemur groups as random intercepts**. To assess whether the model complexity was justified by an increase in goodness of fit, we compared the models controlled for temporal autocorrelation and random intercepts with their corresponding models without these terms using AICc. **We then ran a full model selection with all the fixed factors (including the null, intercept-only model) and selected the combination that resulted in the lowest AICc.** We performed all the analyses with SPSS v26.

Results

Forest condition

Between 2001 and 2018 the average NDVI_{mn} within the MCZ was 0.82 (SD: 0.01; n=18 years) while the average NDVI_{sd} was 0.03 (SD: 0.01; n=18 years). The NDVI_{mn} increased significantly over time (Pearson r = 0.64, n=18, p<0.01) while NDVI_{sd} was not significantly correlated with time (Pearson r = 0.12, n=18, p=0.680) nor with NDVI_{mn} (Pearson r = -0.10, n=18, p=0.733).

Proportions of food category

The three collared brown lemur groups were mainly frugivorous (median: 75%; quartiles: 64-81%; n=29 group-year) during the study periods, complementing their diet with flowers (median: 12%; quartiles: 3-17%), leaves (median: 8%; quartiles: 6-12%) and other items (median: 3%; quartiles: 2-6%) (Fig. 2). The annual proportions of fruits in the lemurs' diet did not differ significantly between the initial post-release period (2001-2003) and the other 6 biannual periods, nor it was correlated with NDVI_{mn} (productivity), NDVI_{sd} (seasonality), or group size (Table 2; model 1). Conversely, the annual proportions of leaves in the lemurs' diet was significantly higher during the first five years after the release and during 2017-18 compared to 2006-2014, while NDVI_{mn}, NDVI_{sd}, and group size did not enter the best model (Table 2; model 2). The annual proportions of flowers in the lemurs' diet did not differ significantly between the initial post-release period and the other biannual periods, nor it was significantly correlated with NDVI_{mn}, NDVI_{sd}, or group size (Table 2; model 3). Finally, the annual proportion of other items in the lemurs' diet was also not different between the initial post-release period (2001-2003) and the other 6 biannual periods, **except for the 2008-2009 period, when the animals consumed fewer of the items that we categorized as 'other'** (Table 2; model 4).

Please, insert Fig, 2 and Table 2 here

Diet diversity

The collared brown lemurs fed on a total of 155 different plant species between 2001 and 2018 with a median of 32 species per year/group (quartiles: 22-38; n=29) and a mean Shannon index of diversity of 2.72 (SD: 0.36; n=29)(Fig. 3). The annual number of species in the lemur diet increased from the initial years after the release to the subsequent biannual period and again in 2011-12 and 2017-18 (Table 3; model 1). The number of food species consumed by the lemurs was negatively correlated with forest productivity ($NDVI_{mn}$). The Shannon index of dietary diversity shows the same response of the number of species in the diet, with increases in 2004-05, 2011-12 and 2017-18 compared to the initial period after the release (Table 3; model 2). A strong negative effect of $NDVI_{mn}$ on the Shannon dietary diversity was also detected.

Please, insert Fig. 3 and Table 3 here

Use of exotic and pioneer species

The three preferred plant species consumed by the lemurs during biannual periods accounted on average for 33.22% of feeding time with the highest value in 2001-03 (43.03%) and the lowest in 2004-05 (22.98%) (Table 4). In the 2001-2003 post-release initial period the lemurs consumed the fruits of one exotic species (*Psydium guayava*) and the leaves of a pioneer species (*Dichapetalum* sp.) as two of the three most **frequently** consumed plant species. Over the entire study period, the three collared brown lemur groups spent on average 0.1% (median; quartiles: 0-1.3%) of their feeding time consuming exotic species and 5.1% (median; quartiles: 3.2-11%) on pioneer species (Fig. 4). The annual proportion of exotic species in the lemur diet was significantly higher during the initial period after the release compared to the following 8 years while no significant difference was detected in 2013-14 and 2017-18. The $NDVI_{mn}$ and $NDVI_{sd}$ **were both included** in the model but were not correlated with the proportions of exotic species in the lemur diet (Table 5; model 1). Finally, the annual proportion of pioneer species consumed by the lemurs was significantly higher during the initial period after the release compared to all the subsequent periods. $NDVI_{mn}$ positively affected the proportions of pioneer species in the diet (Table 5; model 2).

Please, insert Table 4, Fig. 4 and Table 5 here

Discussion

In recent years, translocations of animals within their habitat have been more commonly used as a conservation tool despite these operations are known to be problematic and costly (Seddon, Strauss, & Innes, 2012). In the 18 years following their relocation, the collared brown lemur groups of MCZ have significantly modified some aspects of their feeding ecology while others remained more stable. Since the translocated population has now doubled its original size (Ramanamanjato unpublished data, 2018), we can conclude that these strategies have allowed the lemurs to adapt to the new environment. To our knowledge, this is the longest post-release record of the feeding ecology of a relocated population of strepsirrhines. Previously published single-year comparisons with non-translocated groups indicate that the translocated lemurs in the MCZ modified their group size, their time budget, and their ranging behaviour (Campera et al., 2014; Donati et al., 2007a, 2011, 2016). This was interpreted as a strategy to cope with the partially degraded habitat in MCZ when compared to populations of collared brown lemurs living in less disturbed habitats. The longitudinal data that we show here suggest that single-year comparisons may not reflect the overall response to a dynamic habitat, such as a forest fragment. Using the $\mathrm{NDVI}_{\mathrm{mn}}$ as a proxy for forest regeneration we showed that the protection of the MCZ allowed an improvement of the vegetation over time. Some aspects of the lemur feeding ecology, such as dietary diversity and the use of exotic/pioneer species, appear to be related to this improvement, but potentially also to the gradual familiarisation of the lemurs with the release area. The proportions of leaves in the diet also varied over time showing high values after the release, but without a direct correlation with forest productivity or seasonality.

Our first prediction was that the three groups of collared brown lemurs would have relied more on leaves during the initial post-release phase and increase frugivory over time. Overall, the lemurs remained predominantly frugivorous over the study period confirming the reluctance of eastern species of brown lemur to shift to a more folivorous diet (Donati et al., 2007b, 2011; Overdorff, 1993; Sato et al., 2016), in contrast to what has been observed in western brown lemur populations (Colquhoun, 1997; Curtis & Zaramody, 1998; Rasmussen, 1999; Sussman, 1974). However, the annual proportion of leaves in the diet showed significantly higher values during the first five years after the release compared to the following years (with the exception of 2017-2018). Increasing low energy and/or more difficult to digest food in this mainly frugivorous species as a response to habitat degradation is a strategy in line with a previous comparison with populations living in more pristine habitats (Donati et al., 2011). It also matches with previous studies on other frugivorous or frugivorous-folivorous primates in fragmented habitats (Chaves et al., 2012; de Luna et al. 2017; Dunn et al., 2010; Felton et al., 2009; Irwin, 2008; Riley, 2007; Tutin, 1999; but see Bicca-Marquez, 2003; Cristobal-Azkarate & Arroyo-Rodrıguez, 2007). In translocated groups of *Alouatta palliata* at Agaltepec Island, Mexico, an increased consumption of non-fruit parts of plants such as leaves was also reported (Rodriguez-Luna et al., 2003).

The most likely reason for a higher consumption of leaves in the years after the release is the high level of degradation that characterized the MCZ before its declaration as protected area, in 2001. Due to the proximity to the town of Fort Dauphin, the fragments of Mandena were subject to heavy logging and charcoal production in the second half of the 1990s (Vincelette et al., 2007). Structural differences between the MCZ and the most intact fragments of littoral forests in south-eastern Madagascar, i.e. the Ste Luce area, indicate that at the time of its protection, the area represented a degraded form of the vegetation type found in Ste Luce (Rabenantoandro et al., 2007). This conclusion is also suggested by the vanishing of some tree families known to have been heavily logged in the MCZ (Rabenantoandro et al., 2007). Thus, the low density of large trees, a preferred target of selective logging, likely had an impact on fruit availability (Donati et al., 2011). However, we cannot exclude that the higher proportions of leaves in the diet also reflect some difficulties of translocated lemurs to adjust to an unfamiliar environment during the years immediately following their release (Silver & Marsh, 2003). Unfortunately, there are very few reports of post-release feeding ecology after translocation attempts of **strepsirrhines** and they often indicate mixed survival success. A study on reintroduction attempts of slow lorises (*Nycticebus* sp.) at Ciapus Primate Centre in Indonesia indicate that at least 11 out of 23 died on average 76 days after their release (Moore, Wihermanto, Nekaris, 2014). Reintroduced groups of black and white ruffed lemurs (*Varecia variegata variegata*) from captive-born animals from the Duke Lemur Center to the Betampona Reserve remained reliant on supplementary food up to two years after their release (Britt & Iambana, 2003). It is evident that reintroduced animals from captive stocks have to face more serious difficulties than wild individuals relocated to the MCZ from nearby forest patches (Britt et al., 2004). As for anthropoids, translocated baboons (*Papio anubis*) in Kenya were lightly provisioned with a commercial cattle feed for weeks after their release and during droughts (Strum, 2005).

Learning new resource locations within the complex environment of the tropical forest may also have represented a challenge for the wild animals relocated to the MCZ. Unfortunately, little is known about the memory abilities of lemurs, but recent studies indicate that strepsirrhines are able to encode items using a spatial framework and to remember multiple locations in a complex environment (Joly & Zimmermann, 2011; Rosati, Rodriguez, & Hare, 2017). The accuracy and response times of ring-tailed lemurs (*Lemur catta*) in serial ordering tasks are similar to monkeys (Merritt, MacLean, Jaffe, & Brannon, 2007) and they can implicitly learn spatial sequences (Drucker, Baghdoyan, & Brannon, 2016). The most frugivorous taxa appear to possess the most accurate spatial memory reflecting the need of mapping spatial and temporal variations of fruiting trees (Rosati et al., 2014; Rosati, 2017). Landmarks and traditional travel routes seem to be crucial to orientate and work out directions and distances (Trapanese, Meunier, & Masi, 2018). For example, in Ranomafana the main travel routes used by *Propithecus edwardsi* and *Eulemur rufus* to move from one food tree to the next were traditional travel routes (Erhart & Overdorff, 1999). These routes are probably learned over time as animals familiarize with their habitat to generate a network of landmarks and routes (Trapanese et al., 2018). After a translocation, released animals face the challenge of having to learn resource locations within the new environment, with the additional likelihood of being in a stressful situation that may slow down cognitive functions (Teixeira, De Azevedo, Mendl, Cipreste, & Young, 2007). Faecal-glucocorticoid levels in the MCZ's collared brown lemurs indicate high levels of stress compared to individuals living in more intact habitats, probably caused by limited food resources during the lean season (Balestri et al., 2014). It is thus possible that translocated lemurs at the MCZ may have relied on easy to locate but low energy food resources such as the leaves of the pioneer, light-loving vine *Dichapetalum* sp. while learning more efficient foraging routes in a partially degraded environment. Despite their **high** nitrogen content, the leaves of this vine are very low in carbohydrates and rich in fibres, so they do not represent a main food for the species living in intact habitats (Donati et al., 2007a).

Since the lemurs had to familiarize with the new area we predicted that their dietary breadth would show initial high values and decrease over time as they became more able to find preferred food species in the new environment. Overall, comparisons of dietary diversity between biannual periods showed significant fluctuations, suggesting a large variability that is likely to be explained by factors not captured among our predictors. However, during the immediate post-release years (2001-03) we found the lowest values of dietary breadth for both number of food species and dietary diversity (Fig. 3). This observation is not in line with the predictions of optimal foraging theory, that the animals would have increased their dietary breadth when consuming lower quality food such leaves (Chaves et al., 2012; Cristobal-Azkarate & Arroyo-Rodrıguez, 2007; Dunn et al., 2010; MacArthur & Pianka, 1966; but see de Luna et al., 2017). Although increasing dietary diversity may balance toxin or digestibility inhibitor overload (Freeland & Janzen, 1974; Glander, 1981), the groups may have had difficulties to locate food resources in the initial period after the release. We suggest that other strategies such as a reduction of the daily activity and daily path length may have actually compensated for a low energy and potentially slow to digest diet (Campera et al., 2014; Donati et al., 2011). More fine-grained data on energy balance and secondary compound intake are necessary before drawing conclusions on this aspect.

The low dietary breadth during the years following the translocation is not only associated with an increase in leaf eating, but also with an important contribution of exotic and pioneer species to the diet of the lemurs. In our best model, the annual proportion of exotic species in the lemur diet was significantly higher during the period after the release compared to the following years, although the effect was not significant in 2013-14 and 2017-18. A similar but stronger effect was recorded for pioneer, light-loving plant species with the period immediately after the release showing the higher values than any other period. Indeed, during the three years that followed the release, the three most **consumed** species in the translocated lemurs' diet included one exotic (*Psydium guayava*) and one pioneer species (*Dichapetalum* sp.), **that did not enter in the list in the subsequent 15**

year period (Table 4). This is consistent with a previous report indicating that despite collared brown lemurs in the MCZ being more likely to use both slow- and mid-growing plants, exotic and fast-growing/pioneer species were important during the lean season (Eppley et al., 2017). In 2001-03, the translocated lemurs were often observed moving to the periphery of forest fragments to feed on fruits of the exotic *Psidium guayava* (Campera et al., 2014; Donati et al., 2011) or on the fruits and flowers of the pioneer "*meramaintso*" (*Sarcolaena multiflora*: Campera et al., 2014; Eppley et al., 2017). The key role of exotic or pioneer species for primate survival in degraded, anthropogenic landscapes has been repeatedly shown **for** a large number of lemur species or genera including *Eulemur* (Donati et al., 2009; Schwitzer et al., 2007; Simmen, Bayart, Marez, & Hladik, 2007); *Lemur catta* (Cameron & Gould, 2013; Gould & Gabriel, 2015; Soma, 2006); *Hapalemur meridionalis* (Eppley et al., 2017); and *Propithecus diadema* (Irwin, 2008; Irwin et al., 2010). Additionally, this pattern has been found in the folivorous howler monkey, *Alouatta* sp. (Bicca-Marques & Calegaro-Marques, 1994; Bonilla-Sánchez, Serio-Silva, Pozo-Montuy, & Chapman, 2012; Zárate, Andresen, Estrada, & Seri-Silva, 2014) and the frugivorous chimpanzee, *Pan troglodytes* (Hockings & McLennan, 2012; McLennan & Hockings, 2014).

Considering the rapid variation of forest fragment characteristics over time, longitudinal data on primates living in fragmented habitats are vital to understanding the key elements for their persistence in modified landscapes and to planning future conservation actions (Cristóbal-Azkarate & Dunn, 2013; Ganzhorn et al., 2007; Marsh, 2003; Onderdonk & Chapman, 2000). Similarly to dispersing animals moving across the matrix between the fragments, translocated primates have to cope with unfamiliar areas and need to face unknown fluctuations in food abundance or include new food in their diet (Ostro et al., 2000; Rodriguez-Luna et al., 2003; Silver & Marsh, 2003; Strum, 2005). Here, we illustrated the evolution of the foraging strategies of translocated collared brown lemurs over an 18-year period to explore the ability of these frugivorous lemurs to adjust to recently colonized fragmented forests. In line with previous, single-year studies, the lemurs remained mainly frugivorous over the years thanks to adjustments to their group size, ranging pattern and activity pattern (Campera et al., 2014; Donati et al., 2007a, 2011, 2016). However, we identified an initially high consumption of leaves and exotic/pioneer plant species compared to the following years and to the levels observed in non-translocated lemurs. We hypothesize that these adjustments were caused by the degradation of the habitat, but they may also reflect some fine-tuning by the lemurs themselves in order to cope with an unfamiliar environment during the years that followed the release. Since fragmentation is often associated with the loss of large trees and native vegetation from within a habitat, our study confirms that the availability of predictable food sources and/or exotic species that can provide an easy-to-access, non-seasonal food resource may contribute to the settling of the lemurs during the initial stage of colonization (Eppley et al. 2017; Gould & Gabriel, 2015; Irwin et al., 2010). Within a framework of appropriate management strategies, plantations of fast-growing exotic or pioneer plants could replace open grasslands or edge areas and provide a non-optimal but stable resource to maximize lemur survival in degraded forest fragments.

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Table 1: Number of hours of observation, individual feeding records, and average size (median) of the three groups of *Eulemur collaris* observed in Mandena from 2001 to 2018 (grouped by biannual periods). The last row represents totals over the years or overall medians (group size). The groups were not observed in 2010 and 2015-2016.

Periods	**Observations hours**	**Feeding records**	**Group A**	**Group B**	**Group C**
2001-03	1,100	2,034	3	4	3
2004-05	893	1,850	3	5	3
2006-07	1,022	2,310	5	3	3
2008-09	856	1,376	4	2	4
2011-12	1,228	2,016	5		6
2013-14	444	542	5		6
2017-18	339	799	7		7
	5,882	**10,927**	**5**	**4**	**4**

Table 2: Best fitting Generalized linear mixed models predicting annual proportion of fruits, leaves, flowers, and other items in the diet of *Eulemur collaris* in Mandena, Madagascar, from 2001 to 2018. **AR1 Diagonal indicates the residual variance for each year and AR1 Rho the residual correlation between two consecutive years**. Bold indicates factors significant at P < 0.05. SE: standard error.

	Fixed Effects	Estimate	SE	Residual Effects	Estimate	SE
Fruits						
	2001-03 vs 2004-05	-0.64	0.20	**AR1 Diagonal**	**32.16**	**7.37**
	2001-03 vs 2006-07	0.18	0.19	AR1 Rho	-0.22	0.16
	2001-03 vs 2008-09	-0.44	0.22			
	2001-03 vs 2011-12	-0.07	0.23			
	2001-03 vs 2013-14	-0.59	0.29			
	2001-03 vs 2017-18	-0.44	0.42			
	$NDVI_{mn}$	5.10	15.59			
	$NDVI_{sd}$	6.33	13.73			
Leaves						
	2001-03 vs 2004-05	-0.17	0.12	**AR1 Diagonal**	**66.94**	**15.77**
	2001-03 vs 2006-07	**-0.36**	**0.17**	**AR1 Rho**	**0.97**	**0.01**
	2001-03 vs 2008-09	**-0.48**	**0.21**			
	2001-03 vs 2011-12	**-0.59**	**0.21**			
	2001-03 vs 2013-14	**-0.83**	**0.29**			
	2001-03 vs 2017-18	0.46	0.25			
Flowers						
	2001-03 vs 2004-05	0.07	0.78	**AR1 Diagonal**	**43.31**	**9.94**
	2001-03 vs 2006-07	0.44	0.75	**AR1 Rho**	**0.32**	**0.15**
	2001-03 vs 2008-09	0.01	0.81			
	2001-03 vs 2011-12	1.39	0.82			
	2001-03 vs 2013-14	0.14	1.09			
	2001-03 vs 2017-18	1.99	1.27			
	$NDVI_{mn}$	-35.13	48.17			
	$NDVI_{sd}$	-18.03	30.15			
Other						
	2001-03 vs 2004-05	0.09	0.32	**AR1 Diagonal**	**5.56**	**1.27**
	2001-03 vs 2006-07	-0.38	0.38	**AR1 Rho**	**0.43**	**0.13**
	2001-03 vs 2008-09	**-1.24**	**0.52**			
	2001-03 vs 2011-12	-0.57	0.48			
	2001-03 vs 2013-14	-1.92	0.99			
	2001-03 vs 2017-18	0.04	0.69			
	$NDVI_{mn}$	-23.86	20.91			
	$NDVI_{sd}$	-4.83	17.86			

Table 3: Best fitting Generalized linear mixed models predicting the annual number of food species and diversity (Shannon index) in the diet of *Eulemur collaris* in Mandena, Madagascar, from 2001 to 2018. **AR1 Diagonal indicates the residual variance for each year and AR1 Rho the residual correlation between two consecutive years**. Bold indicates factors significant at P < 0.05. SE: standard error.

	Fixed Effects	Estimate	SE	Residual Effects	Estimate	SE
Food Species						
	2001-03 vs 2004-05	**0.46**	**0.14**	**AR1 Diagonal**	**1.53**	**0.35**
	2001-03 vs 2006-07	0.01	0.16	AR1 Rho	-0.07	0.17
	2001-03 vs 2008-09	0.10	0.15			
	2001-03 vs 2011-12	**0.51**	**0.18**			
	2001-03 vs 2013-14	0.13	0.21			
	2001-03 vs 2017-18	**0.91**	**0.31**			
	NDVI_{mn}	**-34.01**	**11.37**			
	NDVI_{sd}	-8.47	8.90			
Diet diversity						
	2001-03 vs 2004-05	**0.50**	**0.19**	**AR1 Diagonal**	**0.09**	**0.03**
	2001-03 vs 2006-07	0.01	0.19	AR1 Rho	-0.09	0.25
	2001-03 vs 2008-09	-0.05	0.19			
	2001-03 vs 2011-12	**0.58**	**0.24**			
	2001-03 vs 2013-14	0.07	0.24			
	2001-03 vs 2017-18	**1.14**	**0.37**			
	NDVI_{mn}	**-45.74**	**14.70**			
	NDVI_{sd}	-23.11	11.45			

Table 4: Scientific name, Malagasy name, family, part eaten (frm = ripe fruits, fru = unripe fruits, flo = flowers, yle = young leaves), and percentage in the diet (%) of the three preferred plants in the diet of *Eulemur collaris* in Mandena, Madagascar, from 2001 to 2018.

Genus & species	**Malagasy name**	**Family**	**Part eaten**	**%**
2001-2003				
Uapaca littoralis	Voapaky vavy	Phyllanthaceae	frm,fru	20.33
Psydium guayava	Guavy	Myrtaceae	frm	12.69
Dichapetalum sp.	Vahiazo	Dichapetalaceae	yle	10.01
2004-2005				
Uapaca littoralis	Voapaky vavy	Phyllanthaceae	frm,fru	9.35
Pandanus dauphinensis	Voakoa	Pandanaceae	frm	7.73
Vitex chrysomalum	Nofotrako	Verbenaceae	frm,fru	5.90
2006-2007				
Uapaca littoralis	Voapaky vavy	Phyllanthaceae	frm,fru	23.97
Brexia sp.	Voakarepoky	Celastraceae	frm,fru	8.36
Canarium boivinii	Ramy	Burseraceae	frm	7.39
2008-2009				
Ravenala madagascariensis	Ravinala	Streliziaceae	flo	12.28
Vitex chrysomalum	Nofotrako	Verbenaceae	frm,fru	11.99
Uapaca littoralis	Voapaky vavy	Phyllanthaceae	frm,fru	7.63
2011-2012				
Brexia sp.	Voakarepoky	Celastraceae	frm,fru	11.86
Vepris elliotii	Ampoly	Rutaceae	frm,fru	8.03
Syzigium sp.	Rotry	Myrtaceae	frm,fru,flo	6.59
2013-2014				
Syzigium sp.	Rotry	Myrtaceae	frm,fru,flo	16.83
Vitex chrysomalum	Nofotrako	Verbenaceae	frm,fru	12.26
Pandanus dauphinensis	Voakoa	Pandanaceae	frm	11.29
2017-2018				
Ravenala madagascariensis	Ravinala	Streliziaceae	flo	11.76
Dichapetalum sp.	Vahiazo	Dichapetalaceae	yle	9.39
Vitex chrysomalum	Nofotrako	Verbenaceae	frm,fru	6.88

Table 5: Best fitting Generalized linear mixed models predicting annual proportion of exotic plant species and pioneer plant species in the diet of *Eulemur collaris* in Mandena, Madagascar, from 2001 to 2018. **AR1 Diagonal indicates the residual variance for each year and AR1 Rho the residual correlation between two consecutive years**. Bold indicates factors significant at $P < 0.05$. SE: standard error.

	Fixed Effects	Estimate	SE	Residual Effects	Estimate	SE
Exotic Species						
	2001-03 vs 2004-05	**-2.15**	**0.95**	**AR1 Diagonal**	**18.76**	**4.31**
	2001-03 vs 2006-07	**-3.49**	**1.79**	**AR1 Rho**	**0.32**	**0.15**
	2001-03 vs 2008-09	**-2.83**	**0.28**			
	2001-03 vs 2011-12	**-4.04**	**1.08**			
	2001-03 vs 2013-14	-3.99	2.51			
	2001-03 vs 2017-18	-4.22	4.03			
	$NDVI_{mn}$	16.22	31.32			
	$NDVI_{sd}$	-17.46	54.56			
Pioneer Species						
	2001-03 vs 2004-05	**-1.50**	**0.50**	**AR1 Diagonal**	**26.53**	**6.35**
	2001-03 vs 2006-07	**-1.83**	**0.62**	**AR1 Rho**	**0.58**	**0.10**
	2001-03 vs 2008-09	**-1.72**	**0.72**			
	2001-03 vs 2011-12	**-2.31**	**0.65**			
	2001-03 vs 2013-14	**-2.82**	**1.14**			
	2001-03 vs 2017-18	**-1.89**	**0.64**			
	$NDVI_{mn}$	**59.52**	**18.69**			
	$NDVI_{sd}$	40.02	21.65			

Figure legend

Figure 1: Location of the study site. North is up.

Figure 2: Proportions of feeding records spent by the translocated groups of *Eulemur collaris* eating fruits, leaves, flowers, and other items from 2001 to 2018. Values are medians. Error bars are 1st and 3rd quartiles. The groups were not observed in 2010 and 2015-2016.

Figure 3: Standardized residuals (controlled for log-transformed observation hours) of annual number of food plant species and dietary diversity (Shannon) of the translocated groups of *Eulemur collaris* from 2001 to 2018. Values are means and standard errors. The groups were not observed in 2010 and 2015-2016.

Figure 4: Proportions of feeding records spent by the translocated groups of *Eulemur collaris* eating exotic plant species and pioneer plant species from 2001 to 2018. Values are medians. Error bars are 1st and 3rd quartiles. The groups were not observed in 2010 and 2015-2016.