Population Dynamics of Nocturnal Lemurs in Littoral Forest Fragments: The Importance of Long-Term Monitoring

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ABSTRACT

Habitat loss and fragmentation pose a significant threat to many primate species worldwide, yet community level responses are complex and nuanced. Despite repeated calls from primatologists and the wider conservation community to increase monitoring initiatives that assess long-term population dynamics, such studies remain rare. Here we summarise results from a longitudinal study set in the littoral forests of southeast Madagascar. Littoral forests are a useful model for monitoring lemur population dynamics, as they are relatively well-studied and their highly fragmented nature enables the effect of forest size and anthropogenic impacts to be examined. This study focuses on three Endangered nocturnal lemur species – *Avahi meridionalis*, *Cheirogaleus thomasi* and *Microcebus tanosi* – across three forest fragments of different size and with different usage histories. Between 2011 and 2018, we walked 285km of line transect and recorded 1,968 lemur observations. Based on Distance Sampling analysis our results indicate that nocturnal lemurs respond to forest patch size and to levels of forest degradation in species-specific ways. The largest species, *A. meridionalis*, declined in density and encounter rate over time across the three study forests. *C. thomasi* populations appeared stable in all three fragments, with densities increasing in the most degraded forest. *M. tanosi* encounter rates were extremely low across all study fragments but were lowest in the most heavily degraded forest fragment. Our results emphasise the importance of localised pressures and species-specific responses on population dynamics. Monitoring population trends can provide an early warning signal of species loss and species-specific responses can inform crucial intervention strategies.

Keywords Nocturnal primate conservation, Population monitoring, Habitat fragmentation, *Avahi meridionalis*, *Cheirogaleus thomasi*, *Microcebus tanosi*

INTRODUCTION

Today, many primate species and populations exist in diminishing and fragmented habitats (Marsh et al. 2003; 2013; Gould et al. 2020). Across the tropics, habitat loss and forest fragmentation, driven largely by agricultural expansion and resource extraction, threatens approximately 60% of primate species with extinction (Estrada et al. 2017). Agricultural forecasts further predict increased spatial conflicts with 75% of primate species by the end of the 21st century (Dobrovolski et al. 2014). Whilst large-scale deforestation and habitat loss present a great threat to tropical biodiversity in general (Sala et al. 2000; Runyan and D'Odorico 2016; Estrada et al. 2017), the response of primate communities to anthropogenic disturbance and habitat fragmentation is complex (Marsh et al. 2013; de Almeida-Rocha et al. 2017; Kamilar and Beaudrot 2018; Gould et al. 2020). However, it is becoming ever clearer that the isolation of populations as a consequence of forest breakup generally has a strong negative effect over time, even in ecologically adaptable species (e.g. Gardner 2009; Holmes et al. 2013; Kling et al. 2020). Both habitat degradation and fragmentation have far-reaching effects and, besides limiting dispersal opportunities, can rapidly transform intact forest into unsuitable habitat (Nijman 2013; Farias et al. 2015; Bicca-Marques et al. 2020; Gould and Cowen 2020).

Edge phenomena associated with fragmentation can be pervasive, affecting environmental conditions, ecological relationships and modulating plant and animal communities deep into standing forest (Lovejoy 1986; Saunders et al. 1991; Estrada et al. 1999; Arroyo-Rodriguez and Mandujano 2009; Lehman et al. 2006). Fragmentation is also often associated with increased human accessibility, facilitating greater opportunity for illegal hunting, resource extraction and disease transmission (Laurance et al. 2006; 2015; Nunn et al. 2016; Benítez -Lopez et al. 2019). Yet, primate responses to fragmentation vary in the short term and the effects are not always adverse, as habitat change can provide initial ecological opportunity to some species (Raboy et al. 2004; Merker et al. 2005; Herrera et al. 2011; McLennan et al. 2017; Nekaris et al. 2017; Donati et al. 2020). Landscape level analyses have identified key functional traits (e.g. body size, diet, habitat requirements) and habitat characteristics (e.g. fragment size, connectivity, level of anthropogenic disturbance and resource patchiness) as important predictors for primate survival in fragmented landscapes (Isaac and Cowlishaw 2004; Eppley et al. 2020; Steffens et al. 2020). However, the specific nature and relevance of local conditions underscores the importance of documenting species- and population-specific responses (Steffens et al. 2020).

Today, Madagascar supports roughly one-fifth (114) of the world's 515 recognised primate species, with lemurs representing one of the world's most threatened vertebrate groups. Some 98% of lemur species are classified as being threatened with extinction (IUCN 2020) and 100 species are reported as experiencing population declines (Schwitzer et al. 2014). It is crucial to obtain reliable estimates of population size and density to understand how lemur communities are responding to intensifying anthropogenic threats and formulate robust conservation initiatives (e.g. Müller et al. 2000; Ganzhorn et al. 2007; Erhart and Overdorff 2008; Wright et al. 2012; Kling et al. 2020). Lemurs form highly nested assemblages, and, as in other primates, diversity and minimum viable population size are correlated with forest patch size, habitat complexity, adult body mass and dietary regime (Ganzhorn et al. 2000; Lehman et al. 2006; Eppley et al. 2020). Given that Madagascar's forests have experienced large-scale declines over the past century (Green and Sussman 1990; Harper et al. 2007), there is no doubting the importance of understanding both generalised and species-specific lemur responses (Marsh et al. 2013; Eppley et al. 2020; Gould et al. 2020). As of 2007, an estimated 80% of remaining Malagasy forest stood within 1 km of a forest edge (Harper et al. 2007) and while it is well documented that some lemur species can tolerate and use anthropogenic biomes (e.g. Ganzhorn and Abraham 1991; Eppley et al. 2015; Knoop et al. 2018), responses to habitat degradation vary, even among closely-related species (Lehman et al. 2006; 2006b; Ganzhorn et al. 2007; Wright et al. 2008).

The littoral forest formations of eastern Madagascar represent one of the most threatened ecosystems on the island (Schatz et al. 2000; Ganzhorn et al. 2001), with conservative estimates suggesting only 10% of the original forest cover remains (Consiglio et al. 2006; Vincelette et al. 2007; Temple et al. 2012). These humid, evergreen forests are adapted to low altitude (0-50 m a.s.l.), sandy substrates and support high levels of diversity and endemism (Lowry and Faber-Langendoen 1991; Lewis Environmental Consultants 1992). Furthermore, what little is left of this coastal forest is now severely fragmented, (Du Puy and Moat 1996) and continuity with lowland evergreen forests further inland is now almost entirely broken (de Gouvenain and Silander 2003). In the extreme southeast, several important littoral forest stands remain, with those in Sainte Luce considered to be amongst the most intact (Lowry and Faber-Langdoen 1991; Rabenantoandro et al. 2007; Temple et al. 2012). Today, the littoral forests of Sainte Luce consist of a series of 17 disconnected forest fragments set amidst a matrix of ericoid grassland, swamp and sparse exotic tree plantations (Virah-Sawmy et al. 2009). The remaining forests cover approximately 1,650 ha, with fragments ranging in size from ca. 7 ha to 368 ha. In the past, hunting and bushmeat consumption has been prevalent in the area (Bollen and Donati 2006), but appears to have abated in recent decades (G. Donati, pers. obs). Sainte Luce supports three strictly nocturnal lemur species: *Avahi meridionalis* (EN), *Cheirogaleus thomasi* (EN) and *Microcebus tanosi* (EN) and a single cathemeral species, *Eulemur collaris* (EN) (Donati et al. 2020b; 2020c; 2020d; Ganzhorn et al. 2020). A further two lemur species (*Cheirogaleus major* and *Hapalemur meridionalis*) have been reported from Sainte Luce previously (Ellis 2003; Ganzhorn et al. 2007; Campera et al. 2014), although sightings are unconfirmed. Whilst *E. collaris* occupies only a small number of forest fragments in Sainte Luce, plausibly the result of high historic hunting pressure (Hyde Roberts et al. 2020), *A. meridionalis*, a folivorous species (Norscia et al. 2011), and the two Cheirogaleids (*C. thomasi* and *M. tanosi*), both considered generalist omnivores (Lahann 2007; Donati et al. 2020c), are more ubiquitous and have been observed in all fragments surveyed to date (Hyde Roberts, pers. obs). Although the nature and magnitude of the threats facing these species are not fully understood, their distinct biological attributes (e.g. size and reproductive capacity) and ecological requirements (niche, diet and predator-prey relationships) (Lahann 2007; 2008; Norscia et al. 2011) likely shape different demographic responses to environmental pressures.

As a consequence of habitat destruction, it has been predicted that most remaining littoral forest fragments are now too small to sustain viable populations of forest-dependent species, such as lemurs, long-term (Cowlishaw 1999; Ganzhorn et al. 2000; Harper et al. 2007), provoking debate about the feasibility of conservation in fragments (Harcourt and Doherty 2005; Gibbons and Harcourt 2009). While there is now evidence that *Eulemur collaris* can travel between isolated fragments on rare occasions (Donati et al. 2007; Bertoncini et al. 2017; Hyde Roberts et al. 2020) and *Microcebus* species can use small shrubs and meagre vegetation to disperse, the separation between most forest patches in Sainte Luce is deemed a significant barrier for the strictly arboreal and nocturnal lemur species (Craul et al. 2009). In Sainte Luce, protected forest fragments are currently separated by distances of well over a kilometre and in some cases by large aquatic systems. Long-term monitoring studies are therefore critical to detect population level changes, especially among species with limited dispersal capacity, providing an early warning signal to conservationists. Furthermore, the ecological roles that primates such as lemurs play in maintaining ecosystem function underscores the importance of their survival in threatened forests (Chapman 1995; Chapman and Onderdonk 1998; Bollen et al. 2004; Chapman and Dunham 2018; Ramananjato et al. 2020).

In addition to the effects of fragmentation, degradation and diminishing patch size, mining initiatives in the region (QMM 2001; Vincelette 2003; Temple et al. 2012) are an additional threat to existing forest cover and biodiversity (Schatz et al. 2000; Bollen and Donati 2006; Watson et al. 2010; Goodman et al. 2019). Under current proposals, mining operations are anticipated to remove an estimated 66% of littoral forest in the southeast (Temple et al. 2012), including ca. 58% of existing forest cover in Sainte Luce, with the total clearance of 12 fragments. However, the mining project has financed and attracted much associated research and as a result, there is now a significant body of literature focusing on littoral biodiversity (Lowry and Faber-Langendoen 1991; Lewis Environmental Consultants 1992; Ganzhorn et al. 2007b). The history of the study area is very well documented (Vincelette 2003; Virah-Sawmy et al. 2009; Temple et al. 2012). Furthermore, the management regime of several forest fragments in Sainte Luce changed in 2015, with five fragments gaining official IUCN protected status (category IV), while two, also in the mining footprint, were designated as community resource forests. The collection of natural resources (e.g. firewood, construction materials, medicinal plants) in Sainte Luce is now limited to the community forests, with entry into the protected forests largely prohibited. While the effects of protected areas on wildlife communities and primates are far from clear (Beaudrot et al. 2016; Kamilar and Beaudrot 2018), this change provided an opportunity to assess the impact of local forest management policies on a well-studied lemur community and to assess the time over which such measures may manifest tangible impacts.

This study provides a longitudinal assessment of the nocturnal lemur community in the littoral forests of Sainte Luce and offers insight into the mechanisms driving population dynamics. This study aims to assess the impact of fragment size and forest management policy on long-term population survival. Based on previous findings, we offer the following predictions:

1. The study populations of all three nocturnal lemur species will be relatively stable over the study period, with larger forest fragments supporting larger sub-populations.
2. Species-specific demographic trends are likely discernible between forest fragments. Given their small size, broad diet, and fine branch niche, *Microcebus tanosi* will be least susceptible to the effects of habitat degradation and may be highly abundant within each fragment. Conversely, *Avahi meridionalis*, the largest and most conspicuous species, with a preference for tall large trees, will be most vulnerable and show negative population effects in both the smallest fragment and community use forest. *Cheirogaleus thomasi* sub-populations will be negatively impacted by habitat disturbance as resources vital to hibernation become scarce. Such differences may manifest in the variation seen in population data over time.
3. We hypothesise that the high levels of habitat degradation seen in the community forests since their designation in 2015 will have negatively impacted the local lemur community. In contrast, a positive population signal is expected within the protected fragments over the same period. All three nocturnal species will broadly exhibit similar responses in line with these overarching management interventions.

METHODS

Sainte Luce (24°46'52"S; 47°10'28"E) lies in Madagascar's humid bioclimatic zone in the southeastern coastal lowlands, ca. 45 km north of Tolagnaro/Fort Dauphin. The area receives an average annual rainfall of ca. 2690 mm, with temperatures relatively constant with a mean annual temperature of 28°C (Goodman et al. 1997, Vincelette 2007b). Littoral forest is recognised as a distinct phytogeographic unit (Ratsivalaka-Randriamanga 1987; Lowry and Faber-Langendoen 1991) and is often defined as a dense and humid lowland forest with a relatively open or non-continuous canopy (Bollen and Donati 2006; Consiglio et al. 2006). Average canopy height ranges between 10-15 m in Sainte Luce (Goodman et al. 1997) with emergent trees occasionally reaching 20 m and over. Today, the remaining fragments are degraded to various extents, the result of decades if not centuries of selective and non-selective resource extraction.

We collected data using a line transect methodology, with exact perpendicular distances and single observer configuration. Distance sampling is generally considered a key method for producing robust abundance and density estimates of wild plant and animal populations (Leopold 1933; Struhsaker 1981; Buckland et al. 2001). Specifically, line transect sampling (Thomas et al. 2010) has been central to the study of primate populations for at least half a century (e.g. Southwick and Cadigan 1972; Brugiere and Fleury 2000; Nijman and Menken 2005; Bicknell and Peres 2010). Furthermore, this method has been widely used to study lemurs in Madagascar (e.g. Johnson and Overdorff 1999; Ganzhorn et al. 2007; Meyler et al. 2012; Nguyen et al. 2013). We conducted surveys each month between January 2011 and December 2018, in four of the 17 Sainte Luce littoral forest fragments (Fig. 1). Forest fragment naming convention follows QIT Madagascar Mineral's (QMM) standard designation (Lowry and Faber-Langdoen 1991; Lewis Environmental Consultants 1992). We selected fragments S7, S8, S9 and S17 for study as they constitute the largest and most accessible patches of littoral forest and support representative lemur assemblages. We surveyed S17 only to confirm the presence/absence of lemur species and did not include this fragment in the long-term monitoring protocol.

The fragments are relatively clustered and situated close to the major human settlements, and as such, each has a different extractive resource history. Together, the study fragments exhibit a variety of broad physical attributes (differing in extent, tree species composition, canopy height and canopy cover) that may influence lemur population dynamics. We selected transects along established forest routes to minimise disturbance, so they vary in length in relation to the size and shape of the fragment. We established 16 transect routes across four study fragments, ranging in length from 220 m to 1,007 m (Table 1). With the exception of S17, all transects run perpendicular to the forest edge and are relatively evenly spaced (Fig. 1), guarding against the possibility of several transects being positioned by chance in areas of either high or low lemur density.

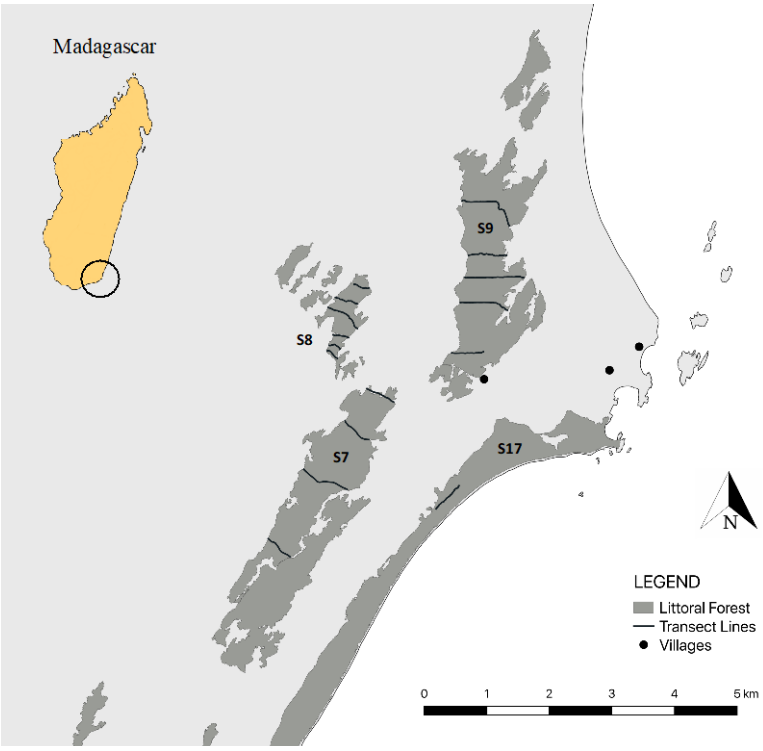
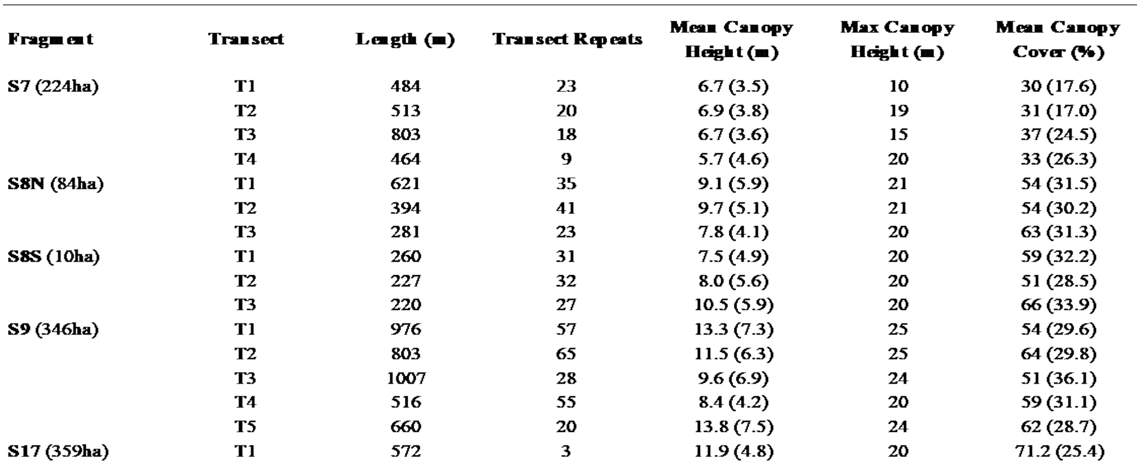


Fig. 1 The relative position of the four study forest fragments (S7, S8, S9 and S17) and 16 transects in southern Madagascar (UTM 38J 719448 mE; 7257491 mS). Fragment S8 is bisected by a road (RN 12). Fragment S17 has a single transect established to confirm the presence/absence of each lemur species and is not part of the regular monitoring schedule. Fragments S8, S9 and S17 received formal IUCN protection in 2015 while fragment S7 was designated as community resource forest.

Surveys followed a standardised protocol, beginning between 18.00 and 19.30pm. A small research group (maximum five people) followed a pre-determined transect route, walking 0.5-1 km per hour. Observer team composition changed continually over the course of the study, however, the continuous involvement of longstanding and fully trained local guides served to minimise observer bias across years (Buckland et al. 2001). We used torches to locate and identify lemurs at distance. We regularly alternated the direction in which we walked a transect, as recommended by Buckland et al. (2001). Although we scheduled transect routes to ensure equal coverage throughout the year, some transects became inaccessible at some times and in some weather conditions. We scrutinised all forest strata carefully, as the lemurs in Sainte Luce exhibit some degree of vertical separation (Lahann 2008). A single team member was responsible for recording data. Once an observation was made, we recorded a set of key parameters, including GPS fix and a unique-dated GPS code, observation time, species, the sex of the animal if possible, and the exact perpendicular distance from the transect at the nearest position (measured to the nearest cm using a 50 m tape). Once we made an observation, we carefully scrutinised the area for additional lemurs, to avoid disturbing unseen animals. For *Avahi meridionalis*, a pair or group living species, we noted the number of observed individuals and group spread in metres. We estimated the height of the animal and of the tree it was first observed in to the nearest meter, measured tree diameter at breast heigh (DBH) to the nearest millimetre, and estimated canopy cover directly above the initial lemur location.

We established forest fragment size using GIS Tools (Google Earth Pro v.7.3.3 and CNES / Airbus 2020 imagery) and measured transect lengths using a hand-held Garmin GPSmap 62s device. We measured forest characteristics along transects by recording canopy height and canopy cover at 10 m intervals. We measured canopy cover using a standard convex densiometer, with values rounded to the nearest percentage point. Canopy heights are estimates made by a single researcher in an attempt to minimise error.

Table 1 A description of fragment and line transect characteristics in Sainte Luce, Madagascar.



Fragment	**Transect**	**Length (m)**	**Transect Repeats**	**Mean Canopy Height (m)**	**Max Canopy Height (m)**	**Mean Canopy Cover (%)**
S7 (224ha)	T1	484	23	6.7 (3.5)	10	30 (17.6)
	T2	513	20	6.9 (3.8)	19	31 (17.0)
	T3	803	18	6.7 (3.6)	15	37 (24.5)
	T4	464	9	5.7 (4.6)	20	33 (26.3)
S8N (84ha)	T1	621	35	9.1 (5.9)	21	54 (31.5)
	T2	394	41	9.7 (5.1)	21	54 (30.2)
	T3	281	23	7.8 (4.1)	20	63 (31.3)
S8S (10ha)	T1	260	31	7.5 (4.9)	20	59 (32.2)
	T2	227	32	8.0 (5.6)	20	51 (28.5)
	T3	220	27	10.5 (5.9)	20	66 (33.9)
S9 (346ha)	T1	976	57	13.3 (7.3)	25	54 (29.6)
	T2	803	65	11.5 (6.3)	25	64 (29.8)
	T3	1007	28	9.6 (6.9)	24	51 (36.1)
	T4	516	55	8.4 (4.2)	20	59 (31.1)
	T5	660	20	13.8 (7.5)	24	62 (28.7)
S17 (359ha)	T1	572	3	11.9 (4.8)	20	71.2 (25.4)

Transect characteristics (canopy height and cover) recorded in November 2018. Values in parentheses represent standard deviation.

Statistical Analysis

We carried out descriptive population analysis using the software DISTANCE 7.3 and the CDS FORTRAN engine, based on the ‘Buckland’ line transect method (Thomas et al. 2010). The cheirogaleid species, *Cheirogaleus thomasi* and *Microcebus tanosi* are solitary foragers and we treated observations as independent. We treated observations of the indriid, *Avahi meridionalis*, as clusters. We adjusted the underlying data to account for the hibernation period of *C. thomasi* (Dausmann et al. 2003; Lahann 2008), excluding transect data from the beginning of May to the end of September for this species. We recorded measurements in metres (m) and hectares (ha) and set no multipliers. We excluded animal observations of +50 m from the transect prior to analysis and considered these as outliers (Buckland et al. 2001). These observations were often the result of animals being spotted across open areas and forest clearings, and on occasion in separate forest remnants. To estimate population size, we grouped data were into two-year sets to ensure a robust sample size, and modelled each species independently for each of the three main forest fragments, and then globally (all fragments combined). We tested all analytical model combinations (i.e. model definitions or key functions combined with adjustment terms) and selected models on the basis of Akaike Information Criterion (AIC) and Kolmogorov-Smirnov Goodness of Fit (GOF). Finally, we fitted models with varying truncation percentages to increase the accuracy of model fit and applied post-stratification techniques to reduce sampling bias (Fewster et al. 2009). Where the minimum number of observations required to accurately model detection function was not reached, we considered more useful encounter rates (Buckland et al. 2001; Ganzhorn et al. 2007).

We analysed the raw data (treated as year pairs for consistency with DISTANCE output) statistically using a Generalised Linear Mixed Model (GLMM) in SPSS v.26. We tested species individually. We fitted models with a Poisson error distribution and log link function to account for a count response variable (number of observations per transect). We treated variables ‘Year’, ‘Fragment’ and ‘Forest Protection’ as fixed effects, with the latter comparing the four-year periods pre- and post-protected status change. We also included the interaction between the two variables ‘Year’ and ‘Fragment’. We included the influence of transect placement in the forest fragments as a random effect. Finally, we log-transformed sampling effort and included it as an offset variable (Barelli et al. 2015). Analysis of S8 (a fragment bisected by a road) showed no significant difference in the total number of lemur observations between north and south, or between the number of *Avahi meridionalis* and *Microcebus tanosi* observations. As a result, we treated the fragment as a single patch in these cases. In contrast, we found a significant difference in the number of *Cheirogaleus thomasi* observations, so we analysed the fragment as two separate areas for this species. We set the level of statistical significance at 0.05, and n refers to sample size and N to population estimate in the remainder of the paper.

Ethical Note and Data Availability

Research was conducted with permission from the Malagasy Ministère de l'Environnement et du Dévelopment Durable (MEDD), formalised under an accord de siege and agreed biannually. Fieldwork complied with guidelines described by the American Society of Primatologists. Raw data are available from the corresponding author on reasonable request.

RESULTS

We completed 487 nocturnal transects during the study with 285 km of surveyed routes resulting in 1,968 lemur observations (*Avahi meridionalis* n = 1140; *Cheirogaleus thomasi* n = 627; *Microcebus tanosi* n = 186). We observed each of the three nocturnal species in all four study fragments. We found no evidence for the presence of either *Cheirogaleus major* or *Hapalemur meridionalis* in the study fragments.

Overall Population Estimates

The results of the population analysis (all study fragments combined) (Table 2) reveal a decline in the size of the *Avahi meridionalis* population between 2011 and 2014, falling sharply from an estimated 1281 individuals (95% CIs 793-2069) to 512 (95% CIs 325-806), a decline of 60.0%. Although the population rose slightly in 2015-2016, the downward trend appears to be continuing with the total population estimated at 480 individuals (95% CIs 348–663) in 2017-2018. Most of the *A. meridionalis* population resides in the largest fragment S9, and the decline in this sub-population drives the overall trend (Table 2, Fig. 2a). In contrast, the sub-population in S7 is extremely small despite the relatively large size of the forest. Results from the smallest fragment S8 (north and south sections pooled) show the sub-population here is again small (<100 individuals), but relatively stable. Modelled sub-population estimates for both S8 and S9 show consistent negative trends. Similarly, the number of estimated *A. meridionalis* groups (N_s) tracked the general population estimate (Table 2) for both sub-populations in S8 and S9, while the mean number of individuals per group (E_s) declined overall from 1.73 individuals/group to 1.40 individuals/group over the study.

Global population estimates for *Cheirogaleus thomasi* reveal a minor decline in the overall number of individuals between 2011-2016, followed by a rapid population increase from an estimated 827 (95%

CIs 639–1069) to 1291 individuals (95% CIs 970–717) in 2017-2018. The species appears to be relatively abundant throughout all three study fragments, with the largest sub-population now occurring in S7 (Table 2, Fig 2b). Population estimates and linear trends suggest that while the sub-population in S9 is relatively stable, those in both S7 and S8 have increased notably over the study. Sub-populations in S7 and S8 expanded rapidly in 2016-2018, increasing from an estimated 296 to 490 and from 81 to 199 individuals, respectively. In contrast, population estimates for *Microcebus tanosi* were complicated by the low number of observations made throughout the study. The total population estimate suggests that the *M. tanosi* population in Sainte Luce is very small but seems to have been relatively stable for most of the study (2011-2016), at around 200-280 individuals (Table 2). However, the overall population appears to have declined sharply in 2017-2018 (Table 2, Fig. 2c). The greatest proportion of the *M. tanosi* population in this study appears to again inhabit the largest fragment S9 and this sub-population largely determines the overall population trend. Estimates suggest a substantive global decline of 37% between 2015-2016 and 2017-2018. The number of direct *M. tanosi* observations made each year also shows a consistent decline.

Encounter Rates

Encounter rates for *Avahi meridionalis* mirror the general population trend, highlighting the severe decline during the first half of the study, before fluctuating in subsequent year groupings (Fig. 3d). *A. meridionalis* encounters increased incrementally in S8 since 2013-2014 (Figure 3a), reflecting a possible increase in the number of individuals occupying the fragment. Encounter rate in S7 was extremely low. Over the eight-year study, we observed this species in S7 only three times, with a single individual observed in 2013, a small group (three individuals) observed in 2014 and a singleton again seen in April 2016, although we also made several opportunistic sightings. Globally, *Cheirogaleus thomasi* showed a steady increase in encounter rate across the study (Fig. 3d). We observed a notable increase in encounter rate in fragment S7, while the sub-populations in the other fragments appear stable and show no consistent trend (Fig. 3b). Given the limited number of *M. tanosi* observations throughout the study, encounter rates provide a particularly useful metric for this species. Encounter rate for *M. tanosi* is low (maximum 1.15 individual/km in S9 in 2015-2016) but relatively stable over the study (Fig. 3d). Notably, encounter rate increased in S9 between 2011-2012 and 2015-2016 before dropping off (Fig. 3c).

Table 2 Population descriptives for three nocturnal lemur species in three forest fragments (S7, S8 and S9) in Sainte Luce, Madagascar, 2011-2018.

Species	**Year**	***Total Effort (m)***	***Number of Observations***	***Population Estimate***	***95% Lower Confidence Interval***	***95% Upper Confidence Interval***	***Estimated Number of Groups***	***Mean Group Size***	***Density of Animals / Ha***	***Density of Groups / Ha***	***Encounter Rate / Km***	***Detection Probability***	***Best Model Fit***	***Model***
Avahi meridionalis	2011-2012	104,310	362	1281	793	2069	740	1.73	2.062	1.190	3.38	0.54	0.943	Hazard Rate + Single Polynomial + 2.5% + PS
	2013-2014	61,696	90	512	325	806	303	1.64	0.824	0.502	1.41	0.55	0.752	Hazard Rate + Single Polynomial + 3% + PS
	2015-2016	66,441	108	692	442	1082	404	1.64	1.114	0.679	1.89	0.63	0.529	Hazard Rate + Single Polynomial + 1% + PS
	2017-2018	60,433	100	480	348	663	330	1.40	0.774	0.551	1.57	0.72	0.567	Hazard Rate + Single Polynomial + 5% + PS
Cheirogaleus thomasi	2011-2012	53,161	157	946	766	1168	–	–	1.524	–	2.95	0.39	0.833	Hazard Rate + Single Polynomial + PS
	2013-2014	39,942	129	876	658	1167	–	–	1.411	–	3.23	0.36	0.894	Hazard Rate + Single Polynomial + PS
	2015-2016	34,104	124	827	639	1069	–	–	1.332	–	3.46	0.58	0.881	Hazard Rate + Single Polynomial + 5% + PS
	2017-2018	36,537	156	1291	970	1717	–	–	2.079	–	3.83	0.61	0.940	Half Normal + COS + 10% + PS
Microcebus tanosi	2011-2012	104,310	67	243	183	324	–	–	0.394	–	0.59	0.40	0.685	Hazrad Rate + Single Polynomial + 7.5%
	2013-2014	61,696	46	208	157	275	–	–	0.340	–	0.71	0.76	0.685	Hazard Rate + Single Polynomial + 5%
	2015-2016	66,441	37	260	165	409	–	–	0.420	–	0.64	0.53	0.997	Hazard Rate + Single Polynomial + 2.5% + PS
	2017-2018	60,433	34	163	99	269	–	–	0.264	–	0.56	0.53	0.813	Half Normal + COS + PS

Results are based on pooled two-year datasets, increasing observation counts and estimate accuracy. Total survey area = 664 ha (S7 = 224 ha, S8 = 94 ha and S9 = 346 ha). The reduced effort attributed to *Cheirogaleus thomasi* is the result of excluded winter transects (May-Sept), when the species undergoes hibernation. Estimated number of groups calculated by population estimate / mean group size. Best model fit based on Kolmogorov-Smirnov test significance value. Model indicates key function series expansion, truncation values and whether post-stratification (PS) measures were included.

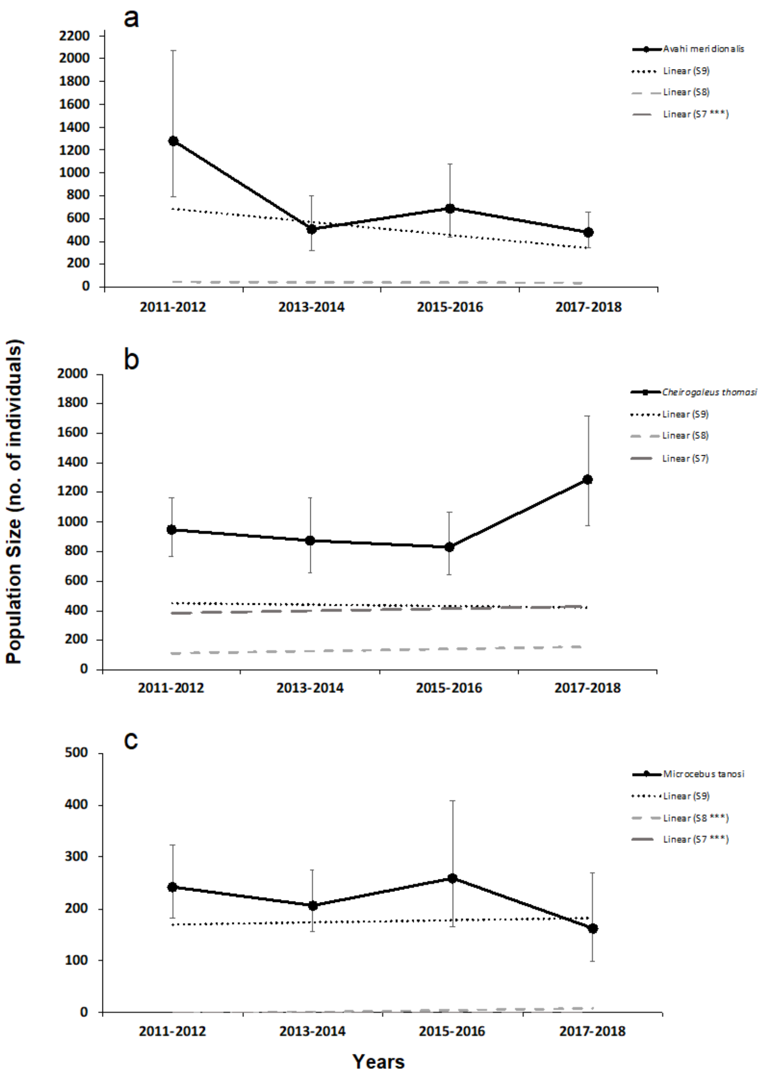


Fig. 2 Population trends of three nocturnal lemur species in the littoral forest fragments of Sainte Luce, Madagascar, based on distance sampling between 2011 and 2018. Data are combined into periods of two years to improve population estimates. **a**) *Avahi meridionalis*, **b**) *Cheirogaleus thomasi* and **c**) *Microcebus tanosi*. Black dots with a thick bold line indicate the global trend (combines S7, S8 and S9 data). *** represent cases where observations were too limited to produce reliable population estimates.

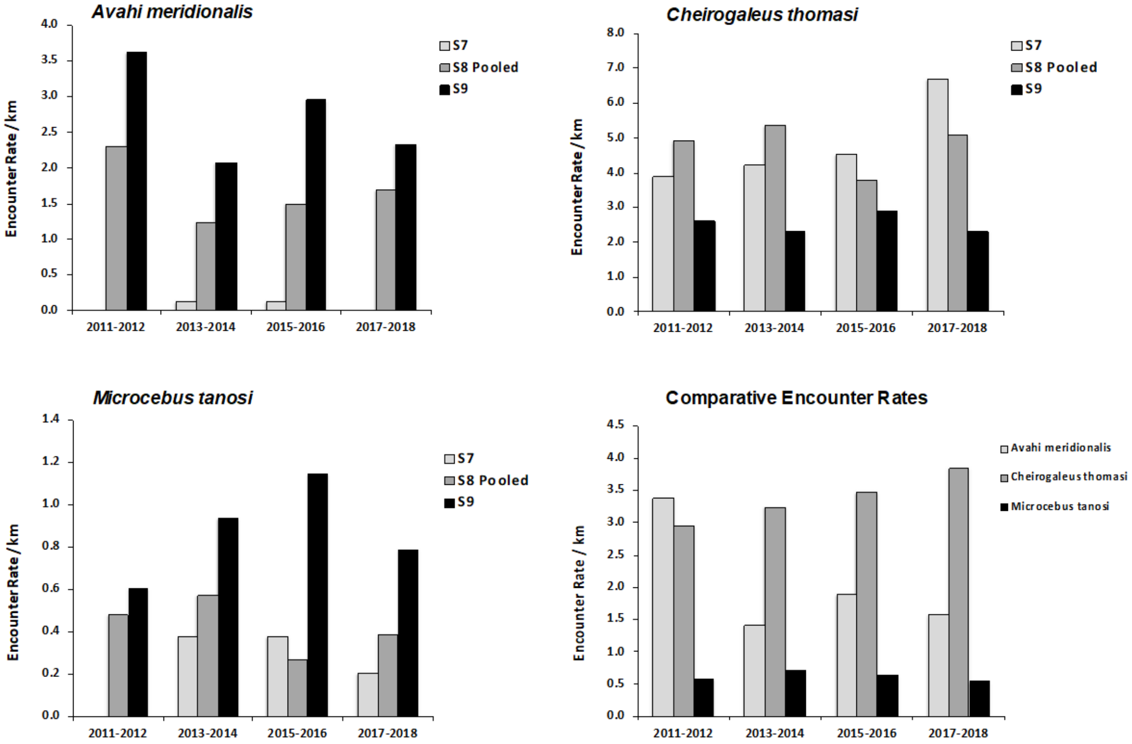


Fig. 3 Encounter rates for three nocturnal lemur species (*Avahi meridionalis*, *Cheirogaleus thomasi* and *Microcebus tanosi*) in the littoral forests fragments S7, S8 and S9 in Sainte Luce, Madagascar, between 2011 and 2018. Values for *Cheirogaleus thomasi* adjusted for seasonality. A global comparison of species' encounter rates, representing general population trends. Encounter rates based on the limited transect repeats for S17 are: *A. meridionalis* 7.6 groups/km (n = 3), *C. thomasi* 7.0 ind/km (n = 1) and *M. tanosi* 1.2 ind/km (n = 3).

Demographic changes

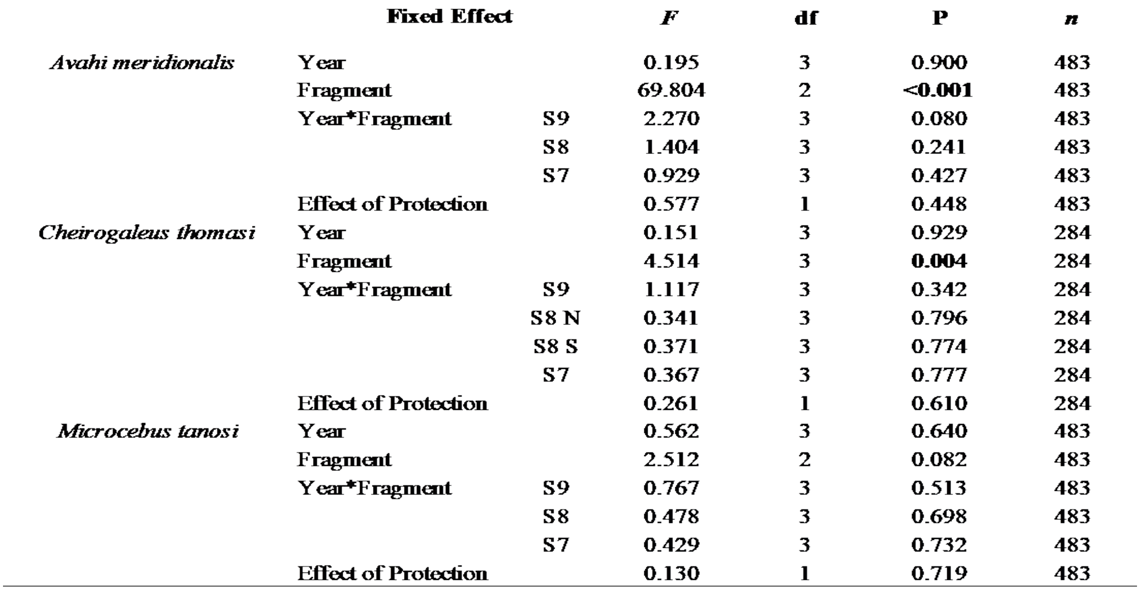
We found no significant difference in the overall number of *Avahi meridionalis* across the study (Table 3). However, *A. meridionalis* observations differed significantly between fragments, with significant pairwise comparisons between S7-S8, S7-S9 and S8-S9 (Table 4). The interaction between the fixed effects 'Year' and 'Fragment' was not significant for fragments S7, S8, or S9 (Table 3). Pairwise analysis revealed a significant reduction in observations between 2011-2012 and 2013-2014 (Table 4). We found no significant changes in the number of observations of *Cheirogaleus thomasi* between years. In contrast, the total number of observations was again significantly different between fragments (Table 3), with pairwise analysis showing significant differences between all fragment combinations except between fragments S7-

S8N and S8S-S9 (Table 4). The interaction between ‘Year’ and ‘Fragment’ was not significant (Table 3). We found no overall significant differences in the total number of *Microcebus tanosi* observations across time or between forest fragments (Table 3). Again, the interaction between fixed effects ‘Year’ and ‘Fragment’ was not significant (Table 3).

Effect of Forest Protection

We found no significant difference in the number of observations of any individual species when we compared the four years before and after the formal implementation of the protected areas (S8 and S9) and community resource zone (S7) in 2015 (Table 3). We found no significant interactions between individual forest fragments and the pre- and post-protective measures, either in each of the study species or in the lemur communities as a whole.

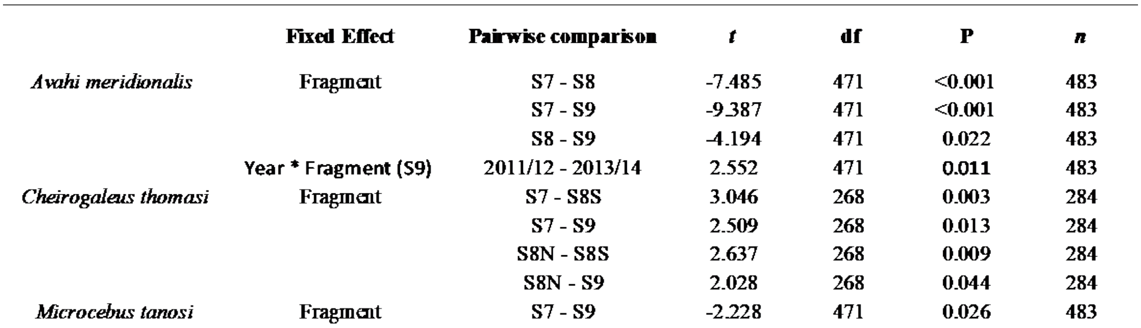
Table 3 Results of a type III test of GLMM fixed effects and interactions for three nocturnal lemur species in Sainte Luce, Madagascar, during an eight-year study (2011-2018)



	Fixed Effect		***F***	**df**	**P**	***n***
Avahi meridionalis	**Year**		**0.195**	**3**	**0.900**	**483**
	Fragment		**69.804**	**2**	**<0.001**	**483**
	Year*Fragment	**S9**	**2.270**	**3**	**0.080**	**483**
		S8	**1.404**	**3**	**0.241**	**483**
		S7	**0.929**	**3**	**0.427**	**483**
	Effect of Protection		**0.577**	**1**	**0.448**	**483**
Cheirogaleus thomasi	**Year**		**0.151**	**3**	**0.929**	**284**
	Fragment		**4.514**	**3**	**0.004**	**284**
	Year*Fragment	**S9**	**1.117**	**3**	**0.342**	**284**
		S8 N	**0.341**	**3**	**0.796**	**284**
		S8 S	**0.371**	**3**	**0.774**	**284**
		S7	**0.367**	**3**	**0.777**	**284**
	Effect of Protection		**0.261**	**1**	**0.610**	**284**
Microcebus tanosi	**Year**		**0.562**	**3**	**0.640**	**483**
	Fragment		**2.512**	**2**	**0.082**	**483**
	Year*Fragment	**S9**	**0.767**	**3**	**0.513**	**483**
		S8	**0.478**	**3**	**0.698**	**483**
		S7	**0.429**	**3**	**0.732**	**483**
	Effect of Protection		**0.130**	**1**	**0.719**	**483**

* Represents interactions between effects. ‘n’ indicates number of transect repeats.

Table 4 Pairwise comparisons based on GLMM model estimates showing only significant results



	Fixed Effect	Pairwise comparison	*t*	df	P	*n*
Avahi meridionalis	Fragment	S7 - S8	-7.485	471	<0.001	483
		S7 - S9	-9.387	471	<0.001	483
		S8 - S9	-4.194	471	0.022	483
	Year * Fragment (S9)	2011/12 - 2013/14	2.552	471	0.011	483
Cheirogaleus thomasi	Fragment	S7 - S8S	3.046	268	0.003	284
		S7 - S9	2.509	268	0.013	284
		S8N - S8S	2.637	268	0.009	284
		S8N - S9	2.028	268	0.044	284
Microcebus tanosi	Fragment	S7 - S9	-2.228	471	0.026	483

t values indicate direction of result. 'n' indicates number of transect repeats.

DISCUSSION

The results of this study confirm the dynamic nature of population-level processes, revealing different trends in each of the focal species across each of the study forest fragments. While in general all three species appear relatively stable; no single factor fully explains the variation in observed trends. Species demographics appear to fluctuate independently between fragments, irrespective of size, paralleling observations made by Ganzhorn et al. (2007) in nearby Mandena. These species-specific trends highlight the complexity of population dynamics in fragmented habitats and emphasise the need for carefully considered and species-specific conservation management strategies (Harrison and Bruna 1999). This analysis concludes that local effects have an important influence on nocturnal lemur population dynamics and that generalised predictions based on forest size, especially at small scales, may be too simplistic to describe community-level patterns. While forest patch size in general parameterises primate population size (e.g. Ganzhorn 2000; Harcourt and Doherty 2005), it does not necessarily determine short-term population trends. Instead, species demography appears to be highly specific and influenced by different anthropogenic pressures and local phenomena. However, the negative long-term effects of inbreeding depression may be inevitable in smaller isolated fragments, although such effects may be too subtle to detect accurately in broadly modelled population data (Montero et al. 2019).

This study confirms that the larger-bodied *Avahi meridionalis* is in imminent danger of extirpation in forest fragment S7 (Ganzhorn et al. 2007). Furthermore, the sub-population in S9 appears to have undergone a substantial decline between 2011-2014. This decline is mirrored in the smaller sub-population in S8, suggesting that a broader mechanism may be responsible, although the driver remains unclear. Mean group size also appears to have decreased over the study, most notably in S9, indicating a possible reduction in birth rate. Although further investigation is required to understand this phenomenon, it has also been observed in other lemur species (Erhart and Overdorff 2008). The limited number of observations in S7 is not easily explained by conventional factors associated with populations dynamics such as patch size or diet (Ganzhorn et al. 1995; 2000; Struhsaker 1997; Chapman et al. 2002; Lehman et al. 2006) given that floral diversity in the fragment remains high (S. Hyde Roberts, unpubl. report). In fact, the relatively large size of S7 and its proximity and connectivity to another large forest block (S6) suggests that these two fragments combined (436 ha) could support a relatively large sub-population. *Avahi meridionalis* persist in even tiny vestiges of forest (<10 ha) in both Sainte Luce (S. Hyde Roberts, pers. obs.) and Mandena (Ganzhorn et al. 2007). However, the forest structure in S7 is notably degraded, with lower average canopy height and coverage than in the other study fragments (Table 1). This observation supports the hypothesis that the population density of this species is positively correlated with the presence of larger trees (Ganzhorn et al. 2007; Norscia 2008).

As a folivore (Thalmann 2003; Norscia et al. 2011), it seems unlikely that limited food resources could have driven the decline of *Avahi meridionalis* between 2011-2014 given the high plant diversity in the area (Dumetz 1999; Cadotte et al. 2002; Consiglio et al. 2006). *Avahi meridionalis* is a known folivore generalist with only moderate selectivity (Norscia et al. 2011), although other *Avahi* species have been shown to be more selective (Thalmann 2001). It has also been postulated that the minimum area requirement for folivorous and omnivorous species may be smaller than for species with other dietary needs (e.g. frugivores) (Ganzhorn et al. 2000), with resources expected to be more evenly distributed and reliable. Furthermore, low-level forest disturbance, a notable characteristic of littoral forests, can potentially benefit some folivorous species (e.g. other *Avahi* spp.) by improving the nutritional quality of foliage (Chapman et al. 2002; Ganzhorn 1992; Ganzhorn 1995).

Although the designation of S7 as a community resource forest could be predicted to negatively impact lemur communities (de-Almeida-Rocha et al. 2017) affecting forest structure and increasing the number of woodsmen and potential hunters present in the forest, *Avahi meridionalis* appear to have been scarce in this fragment for far longer (Ganzhorn et al. 2007). The most parsimonious explanation for the anomalously small sub-population of *A. meridionalis* in S7 and the declines in both S8 and S9 is therefore a combination of historical and on-going hunting pressure. Similarly, the absence of *Eulemur collaris* from S7 is likewise attributed to hunting, and as the next largest and conspicuous species it is plausible that *A.*

meridionalis has been similarly depleted. Local elders (six individuals including the ex-village chief and local guides) estimated the disappearance of collared brown lemurs from the S6/S7 forests to be ca. 1960 and confirmed that hunting pressure was high in these forests until as recently as 2010. The finding that the sub-population of *A. meridionalis* in S7 has remained so low since at least 2004 (Ganzhorn et al. 2007) suggests that either the species is very slow to recover from severe historic exploitation or that some level of hunting pressure continues in the community resource forests. The recent severe degradation of the forest as a result of intense community harvesting could also be hindering species recovery, as large trees are removed, and forest structure is impacted (Norscia 2008). In light of these results, the Endangered *A. meridionalis* should be considered a priority species for conservation efforts in Sainte Luce.

We detected no significant change in the total number of *Cheirogaleus thomasi* over the study, indicating that the population as a whole in Sainte Luce is relatively stable. Despite this, the dynamics differ markedly between the forest fragments and the isolated sub-populations. In general, estimated sub-population size does not adhere to the expected pattern whereby a larger fragment supports a larger population (Harcourt and Doherty 2005). Fragment S7 currently supports a larger estimated population of *C. thomasi* than S9, despite being 122 ha smaller in size and S8 supports a substantial population but is only roughly a fifth of the size. Although larger forests should provide a greater quantity and diversity of resources, the effect of fragment size on population density is complicated by a range of other interacting environmental, ecological and genetic factors (e.g. Ramanamanjato and Ganzhorn 2001; Marsh 2003; Balko and Underwood 2005; Holmes et al. 2013). Notably, the sub-population of *C. thomasi* in S7 appears to be increasing despite intense logging and natural resource removal. This observation suggests that the species may tolerate moderate to severe forest degradation to some extent, as has been observed in other *Cheirogaleus* species (Hending et al. 2018; Steffens and Lehman 2018). However, this interpretation contrasts with the conclusion of Ganzhorn et al. (2007), who surmised that *Cheirogaleus* spp. responded negatively to habitat degradation. However, two distinct Cheirogaleid species (*C. major* and *C. thomasi*), now understood to exhibit specific responses, were considered jointly in that study, likely influencing the deduction.

Although there is no conclusive explanation for the unexpected positive trend for *Cheirogaleus thomasi* in fragment S7, the seemingly rapid increase in population size and the timing suggests the expansion is linked to local forest management policy. Given its degraded nature, S7 could be expected to exhibit relatively limited fruit availability and increased patchiness (Campera et al. 2014), however reduced competition for fruit resources from other fauni-frugivorous lemur species (e.g. *Eulemur collaris*) may be significant. Similarly, a shift towards a more invertebrate-based diet seems unlikely given the limited importance of invertebrates in the diet of *Cheirogaleus* spp. (Fietz and Ganzhorn 1999; Lahann 2007). Although degradation may be increasing this dietary resource (Corbin and Schmid 1995), there is no indication that the *Microcebus tanosi* sub-population is similarly benefiting from it as could be expected. Alternatively, a potential increase in the nutritional content of plant food resources, associated with habitat degradation and increased light levels may be a contributing factor (Ganzhorn 1992; Ganzhorn 1995; Chapman et al. 2002) as logging exposes understorey trees to increased levels of sunlight, which is positively correlated with fruit production (Ganzhorn 1995). Ultimately, however, continued degradation is likely to negatively impact the species in the long-term. The loss of large trees and sufficient sleeping sites may eventually reverse the positive population trends and increased temperatures associated with degraded habitats may begin to negatively impact hibernation patterns (Ganzhorn and Schmid 1998; Lehman et al. 2006b). Given that such an important sub-population exists in S7, within the proposed QMM mining footprint (Temple et al. 2012), future mitigation work will be required if substantial losses are to be avoided.

The sub-population of *Cheirogaleus thomasi* in S9 appears to be the most stable of the three studied, indicating that perhaps the fragment is the most ecologically balanced (Janson and Chapman 1999). The formal protection of the fragment appears to have had little impact on the sub-population in S9 so far. The S8 sub-population has also seemingly expanded in recent years, although it fluctuated over the study period. Although the exact driver of the trend is unclear, the sharp boundary between the forest edge and savannah-like matrix environment to the west of the fragment has been heavily planted with non-native trees, and particularly with *Grevillea robusta*. It is now common to see large numbers of *C. thomasi* feeding on flowers and nectar in these maturing plantations. Similar observations have also been made outside natural forest at Lokaro (S. Hyde Roberts, pers. obs.). These plantations likely provide a highly abundant and nutritious resource as the lemurs emerge from hibernation and although *G. robusta* can become invasive, capitalising on such resources could provide an additional management tool in future conservation efforts (Ganzhorn et al. 1991; Donati et al. 2020; Steffens 2020; Konersmann et al. 2021).

The *Microcebus tanosi* population in Sainte Luce appears to be small but stable with no significant overall change in the number of observations across the study, or in the number of observations made between forest fragments. However, population modelling was inhibited by the very low number of observations in both forest fragments S7 and S8. Both population estimates and encounter rates are much lower than for the other two nocturnal species, and for other *Microcebus* species in proximal littoral forests (Ganzhorn et al. 2007; Malone et al. 2013). The limited number of *M. tanosi* observations is surprising and we initially hypothesised that they would be the most abundant lemurs in Sainte Luce, given their small size, social structure, broad ecological niche and small home ranges (e.g. Radespiel 2000; Andrianasolo et al. 2006; Lahann 2007). *M. tanosi* is considered relatively tolerant of habitat disturbance (Andrianasolo et al. 2006) and is regularly observed in degraded habitats and forest edges in Sainte Luce and even around the research field station. Although our population estimates are based on a limited number of survey observations, they match earlier results (Ganzhorn et al. 2007). This species also seems to occur at very low densities in the Protected Area of Tsitongambarika, the large expanse of lowland rainforest to the west of our study site (Nguyen et al. 2013).

This study shows that distance sampling following the standard 'Buckland' method and using line transects and perpendicular distance is well suited to the study of larger nocturnal lemur species such as *Avahi* and *Cheirogaleus*, but is problematic for the study of *Microcebus*, at least in Sainte Luce. Modelling accuracy depends on generating sufficient sample sizes, which can be difficult for rare or low-density species (Thompson 2013), as appears to be the case for *Microcebus tanosi*. Furthermore, even under ideal conditions, the method produces relatively high standard errors, making small-scale population fluctuations difficult to identify, particularly when the number of observations is limited (Plumptre and Cox 2006). The method also relies on a series of crucial assumptions, including perfect detection of all animals at distance 0 m from the transect line and that animals do not appear again ahead of the survey team (Buckland et al. 2001). Although it is conceivable that we missed individual animals high in the canopy, the overall lack of observations suggests that double counting is not a critical problem in our study. Furthermore, measuring the exact distance between the transect and an observation using a tape measure may disturb other mouse lemur individuals nearby. To avoid this, other measurement techniques (e.g. laser range finders) could be trialled in the future. However, the longitudinal nature of the project and high survey effort also suggests that the low number of sightings is a valid representation of the *M. tanosi* population in Sainte Luce.

It is plausible that the line transects used in this study, and specifically their positioning, which bisect the forest fragments, are not wholly adequate for the accurate determination of the *Microcebus tanosi* population in the littoral forests. It is possible that we missed individuals foraging near or at the forest edge. However, given the highly fragmented nature and small size of the littoral forests, edge effects likely permeate entire fragments. Furthermore, the small size and agile nature of *M. tanosi* makes detection more problematic in dense forest, finding some accord with both Müller et al. (2000) and Radespiel et al. (2001) who speculate on the appropriateness of the line transects methodology for mouse lemurs. It is also becoming increasingly clear that the demographics of mouse lemur species vary considerably (e.g. Ganzhorn et al. 2007; Rakotondravony and Radespiel 2009; Schäffler and Kappeler 2014), adding to the difficulties associated with determining population size for certain species or populations (i.e those occurring at low densities). Additionally, whilst all *Microcebus* species are thought capable of entering short bouts of daily torpor during the winter months and reducing activity levels (Petter-Rousseaux 1980; Schmid 2000), the number of observations in this study was largely consistent throughout the year.

The designation of protected areas and community use zones in 2015 have so far shown no significant impact on lemur communities, although it is conceivable that the benefits of protecting S8 and S9 will take many years to manifest significantly in population data. These findings echo those of a recent global assessment of biodiversity in protected areas (Beaudrot et al. 2016), which found that of 24 primate study populations across Africa and southeast Asia, none were increasing. However, protected area management, enforcement and effectiveness is highly unequal between sites. The community forests of Sainte Luce present an unusual scenario given that resources are situated on land designated for mining and are viewed by the community at large as being only temporarily available. As such, comparisons with other community resource forests elsewhere are impractical. Furthermore, the combined threats from rapid unsustainable resource extraction and from mining make finding conservation solutions in the community forests particularly challenging.

The statuses now attributed to each forest fragment in Sainte Luce have been long proposed (Temple et al. 2012), but only during 2015 were formal measures introduced and practically enforced. Until this point, logging and resource collection was common practice across all fragments, and S7 was highly degraded by 2006 (G. Donati, pers. comm.). Once protection measures were introduced, logging and community use in the protected fragments ended abruptly, while resource collection and activity in the community forest increased (S. H. Roberts, pers. comm.). While the total number of lemur observations in the community resource zone has risen since 2015, due to increased numbers of *Cheirogaleus thomasi*, the future of this fragment and its lemur community remains bleak. The results of this study further emphasise the complex and species-specific response of lemur communities to habitat degradation and fragmentation (e.g. Merenlender et al. 1998; Lehman et al. 2006; Eppley et al. 2020; Gould et al. 2020), and that forest management policies can play an important role in conserving threatened lemurs (Gorenflo et al. 2011).

An additional source of variation in the dataset may stem from stochastic events. Over the course of this study, seven major tropical storms and cyclones passed within 100 km of Sainte Luce with the epicentre of three passing within 20 km (Cyclones Bingiza 2011, Dando 2012 and Harunga 2013). However, cyclones Bingiza, Giovanna (2012), Haruna (2013) and Enawo (2017) are the most likely storms to have had a detrimental impact on lemur populations, given both their proximity and severity. Cyclones cause severe negative impacts on lemur populations, causing direct damage to habitats, destroying important fruit crops (Ratsimbazafy et al. 2002), and potentially disrupting reproductive cycles (Wright 1999; Dunham et al. 2011).

In conclusion, this study demonstrates the importance of long-term population monitoring for lemurs and other nocturnal primates and highlights the critical importance of local phenomena (e.g. hunting pressure, habitat structure and connectivity, resource distribution) and forest management strategy for species conservation. Insights gained from long-term studies can provide early diagnosis of declines in vulnerable populations and help to pinpoint causal mechanisms. In the case of Sainte Luce, these results are particularly salient, as community demand for natural resources grows, putting additional pressure on remaining forests. Furthermore, proposed mining operations are expected to clear an estimated 58% of existing forest cover (Temple et al. 2012), further isolating lemur sub-populations. However, this study indicates that even modestly sized forest fragments (<100 ha) can provide vital refuges for threatened nocturnal lemur species and should not be overlooked in environmental planning. The natural dispersal of each of the three nocturnal species in this study is limited between isolated fragments and strategies must therefore attempt to maximise habitat connectivity to encourage dispersal between larger forest fragments. A range of conservation tools including habitat corridors, habitat restoration and translocations are likely to be necessary in the short- to medium-term future in order to maintain the viability of the lemur community in Sainte Luce.

Conflict of Interest: The authors declare that they have no conflict of interest.

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