The effect of habitat disturbance on the abundance of nocturnal lemur species on the Masoala Peninsula, north eastern Madagascar.

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ABSTRACT

Madagascar is one of the world's 'biodiversity hotspots'. The island's past and current rates of deforestation and habitat disturbance threaten its plethora of endemic biodiversity. On Madagascar, t*avy* (slash and burn agriculture), land conversion for rice cultivation, illegal hardwood logging and bushmeat hunting are the major contributors to habitat disturbance. Understanding species specific responses to habitat disturbance across different habitat types is crucial when designing conservation strategies. We surveyed three nocturnal lemur species in four forest types of varying habitat disturbance on the Masoala Peninsula, north eastern Madagascar. We present here updated abundance and density estimates for the Endangered

Avahi mooreorum and *Lepilemur scottorum,* and *Microcebus* sp. Distance sampling surveys were conducted on 11 transects, covering a total of 33km after repeated transect walks. We collected data on tree height, bole height, DBH, canopy cover and tree density using point quarter sampling to characterise the four forest types (primary lowland, primary littoral, selectively logged and agricultural mosaic). Median encounter rates by forest type ranged from 1-1.5 ind./km (*Microcebus* sp.), 0-1 ind./km (*Avahi mooreorum*) and 0-1 ind./km (*Lepilemur scottorum*). Species density estimates were calculated at 232.31 ind./km^2 (*Microcebus* sp.) and 121.21 ind./km^2 (*Avahi mooreorum*), while no density estimate is provided for *Lepilemur scottorum* due to a small sample size. *Microcebus* sp. were most tolerant to habitat disturbance, exhibiting no significant effect of forest type on abundance. Their small body size, omnivorous diet and generalised locomotion appear to allow them tolerate a variety of habitat disturbance. Whereas both *Avahi mooreorum* and *Lepilemur scottorum* showed significant effects of forest type on their respective abundance. This study suggests that the specialist locomotion and diet of *Avahi mooreorum* and *Lepilemur scottorum* makes them susceptible to the effects of increasing habitat disturbance.

Keywords: *Microcebus* sp., *Avahi mooreorum*, *Lepilemur scottorum.* anthropogenic disturbance, line transects, densities.

INTRODUCTION

Primate responses to habitat disturbance are often species and site specific (Fimbel, 1994), and many primates have been shown to be ecologically flexible and able to tolerate some level of habitat disturbance (Johns and Skorupa, 1987; Chapman and Lambert, 2000; Donati et al., 2011). Large bodied frugivorous species are considered to be most at risk from habitat disturbance, based on their reliance on larger trees which are patchily distributed, and higher ranging area per unit biomass (Johns, 1992; Arrigo-Nelson, 2006). On the contrary, small prosimians which consume insects, such as Dian’s tarsiers (*Tarsius dianae*; Merker and Mühlenberg, 2000), and Javan slow lorises (*Nycticebus javanicus*; Rode-Margono et al., 2014) have been observed at high abundances in agricultural mosaic habitats, and appear more tolerant. Folivorous species have also been observed to cope well with a low level of habitat disturbance, and in some cases show higher abundances in selectively logged areas due to increased leaf quality and productivity (Johns, 1988; Ganzhorn, 1995; Arroyo-Rodríguez and Dias, 2009). Much of the research which currently exists on primates in disturbed habitats is focussed on forest fragments or species responses in dichotomous situations, i.e. intact versus degraded areas, with research lacking comparing species responses across habitats which differ in the type of disturbance they experience (Irwin et al., 2010; Schwitzer et al., 2011). Just as there are few homogeneous intact forests, there are equally few homogeneous degraded areas, and the continuous use of anthropogenic zones makes them extremely dynamic ecosystems (Bennett et al., 2006).

Anthropogenic land use on Madagascar has resulted in the emergence of many heterogeneous habitats which vary largely in quality over a relatively small area (Herrera et al., 2011). Despite the large network of protected areas (Kaufman, 2006), many wildlife populations inhabit areas outside of these zones (Irwin et al., 2010; Schwitzer et al., 2011). Due to the limited financial and logistic resources of the parks' management to patrol and protect Madagascar's National Parks, increasingly local communities are encroaching on the parks, resulting in the alteration of these 'protected' habitats (Kull, 2002). Landscape alterations may have significant effects on species which reside in these changing habitats. 'Domino effects' of a changing habitat can include; dispersal, restricted locomotion, reduced food resources, reduction in suitable sleeping sites, increased hunting risk and increased parasite loads (Golden et al., 2011; 2014; Schwitzer et al., 2011; Junge et al., 2011; Lazdane et al. 2014; Balestri et al., 2014).

In recent years' research into lemur communities living in degraded habitats has increased exponentially (Irwin et al., 2010; Donati et al., 2011 Schwitzer et al., 2011; Tecot, 2013; Balestri et al., 2014; Campera et al., 2014). Studies into nocturnal lemur responses to habitat degradation have shown that they are ecologically flexible and largely tolerant to minor habitat changes (Lehman et al., 2006a; 2006b; Radespiel, 2007; Meyler et al., 2012). Mixed results have been observed for folivorous nocturnal lemurs (*Avahi* sp. and *Lepilemur* sp.) living in disturbed habitats. Whereas some species have been found at high abundance in disturbed areas (Ganzhorn, 1987, 1999; Norscia, 2008), others have been found at lower densities than their conspecifics in primary habitats (Randrianambinina et al., 2010; Lehman et al., 2006a). This can be attributed to their specialised locomotion and diet, as heavy disturbance can reduce or eradicate dispersal paths between populations (Ganzhorn, 1993; Lawes et al., 2000; Thalmann, 2003), and heavy tree cutting can ultimately limit leaf production and therefore dietary resources (Thalmann, 2003). Small insectivorous lemurs such as *Microcebus* sp. have been frequently observed in anthropogenic habitats, and particularly agricultural mosaic habitats, as these ecosystems often contain a high abundance of insects (Ganzhorn, 1987; Lehman et al., 2006b). Their small body size and generalised locomotion allows them to exploit a mixture of substrate sizes without causing major restriction to their movements (Radespiel, 2007).

This study aims to address some of the knowledge gaps which exist in nocturnal lemur responses to habitats differing in the type of disturbance. In particular, we aim to assess how differing habitat disturbance affects forest structure and composition, and in turn the abundance of nocturnal lemur species on the northwest Masoala Peninsula, northeastern Madagascar. We will measure the habitat characteristics of four forest areas of differing disturbance to characterise how different types of disturbance shape vegetation structure and composition. We will do so by measuring various habitat characteristics shown to affect the locomotion and resource availability of our study genera (Ganzhorn, 1989; Seiler et al., 2014). Tree height and bole height, for example, have been shown to be important structural characteristics for vertical clingers and leapers, and could be particularly important in areas where *Avahi* spp. and *Lepilemur* spp. are sympatric in terms of vertical niche separation (Thalmann, 2001).

Specifically, we aim to answer the following questions;

1) Do different types of habitat disturbance affect the abundance of nocturnal lemur species?

2) Which species are most affected, and what are the ecological correlates of lemur responses to varying habitat disturbance?

Currently the nocturnal species studied here have no population abundance estimates available on the IUCN Red List (IUCN, 2014). We will therefore present here updated estimates of abundance for *Microcebus* sp., *Avahi mooreorum* and *Lepilemur scottorum* on the Masoala Peninsula. The last nocturnal census was carried out on the Peninsula in 1994-1995, when plans were being made to create Masoala National Park (Sterling and Rakotoarison, 1998). However, many species classifications have changed since this time, and data on these species requires updating.

METHODS

Study Site & Species

The study was conducted on the north western coast of the Masoala Peninsula surrounding the village of Ambodiforaha (S15°42.728', E049°57.839'). Masoala National Park was gazetted as a National Park in 1997, the Park ranges in altitude from 0-1300m above sea level, and is a combination of lowland and high elevation humid forest, with some small areas of remaining littoral forest (Kremen et al., 1999; Schwitzer et al., 2013). Masoala National Park was contained for the conservation of biodiversity, and outside of the park boundary land was set aside for multiple resource use by local communities (Kremen et al., 1999). Annual rainfall in the park ranges from 2,200-7,000 mm and average yearly temperatures range from 21-24°C (Martinez, 2010). The Park has four distinct seasons 1) hot-rainy (January-March), 2) transitional cold (April-May), 3) cold rainy (June-August), and 4) hot dry (October- December) (Vasey, 2000).

Masoala National Park is home to a total of 10 species of lemur, 3 diurnal or cathemeral species; *Varecia rubra*, *Eulemur albifrons,* and *Hapalemur occidentalis*, and 7 nocturnal species; *Microcebus* sp., *Cheirogaleus major, Allocebus trichotis, Phaner furcifer, Lepilemur scottorum, Daubentonia madagascariensis,* and *Avahi mooreorum.* This region is recognised as an area of high floristic and faunal diversity and endemism. All nocturnal lemur species present at Masoala National Park were included in this study, although only *Microcebus* sp., *Avahi mooreorum*, *Lepilemur scottorum* and *Daubentonia madagascariensis* were observed (Table 1).

Vegetation Assessment

Nocturnal lemur censuses were carried out between 13 May and 25 June, 2014. Transects were marked within an area of “primary” lowland forest, an area of “primary” littoral forest, an area of agricultural mosaic forest used by local communities, and an area used predominantly for selective logging for construction materials by local communities. We categorised the different forest types (primary lowland, primary littoral, selectively logged and agricultural mosaic) based on their vegetation structure and anthropogenic uses, and although all habitats are heterogeneous, we grouped transects into study areas based on their main human use and structural characteristics (Herrera et al., 2011; Nekaris et al., 2014).

Data on habitat characteristics were collected using the point-quarter sampling method (Ganzhorn et al*.,* 2011). Botanical sampling was carried out along transect lines of 750m. Point-quarter samples were taken every 50m along the transect line, including the start and end point, to a depth of 3m. At each point quarter sample structural tree data was collected on all trees ≥5cm diameter at breast height (DBH). We chose a DBH of ≥5cm based on the small body weight (39.5g-47.9g) of *Microcebus* sp. and their inclusion in our surveys (Mittermeier et al., 2010). In order to standardise between the four forest types, and to allow for comparisons within this study, we applied the DBH ≥5cm to all forest types. Structural data collected in each forest type included; tree height (m), bole height (m), circumference at breast height (CBH; to be later converted to DBH), canopy cover (%), and tree density (Ganzhorn et al., 2007). All estimates for tree height, bole height and canopy cover were made by the same observer, to reduce inter-observer bias. Sampled trees were marked with flagging and vernacular names provided by the local field guide. Voucher specimens were collected for each tree identified. Specimens were deposited for scientific identification by botanists at the Parc Botanique et Zoologique Tsimbazaza in Antananarivo.

Lemur Surveys

We conducted surveys using the line-transect method of distance sampling with multiple observers (Buckland et al., 2001). In total we conducted 44 nocturnal surveys, equating to a total survey effort of 33km. We surveyed three transects of 750m in three of the study areas (primary lowland, selectively logged and agricultural mosaic forest) and two transects of 750m in one area (primary littoral forest), separated by a gap of 250m. Fewer trails were walked in the primary littoral forest due to limited availability of existing trails. We used pre-existing trails to minimize disturbance, and transects were marked every 25m with flagging tape. We surveyed transect routes slowly (0.25/0.5km per hour) either between 18:00-midnight or midnight-06:00 (Chapman et al., 1988; Norscia, 2008; Nekaris et al., 2014). Each line transect was repeated a total of 4 times over the study period (Rovero et al., 2006). We walked line transects with a 10m distance between team members, checked both sides of the transect line, and checked regularly behind ourselves to minimise our chances of missing an observation (Nekaris et al., 2014). Survey routes were not repeated more than once per week. We alternated the starting point on each repetition of a route to reduce bias (Fashing and Cords, 2000; Ross and Reeve, 2011).

As *Avahi mooreorum* is a pair-living taxon observations of >1 individual were considered to be a single cluster, although on occasions individuals were observed alone. Upon detection of a lemur cluster, data were collected on; the date, time (hour: minute), weather (rain or no rain), study area and transect number, GPS co-ordinate, species, cluster size and composition, perpendicular distance from line to group centre/individual, or distance from observer to individual (Fashing and Cords, 2000; Lehman et al., 2006a; Marshall et al., 2008; Meyler et al., 2012).

Abundance Metrics & Density Estimates

We estimated lemur abundance using median encounter rates (number of individual encounters/transect walk) of each taxon in each forest type. We also calculated mean species-specific cluster size (number of individuals/number of observations) by forest type. No statistical analyses were performed on *Daubentonia madagascariensis* due to a small sample size (n=1). Overall density estimates (number of individuals/ km^2) for *Microcebus* sp. (n=70) and *Avahi mooreorum* (n=51) were calculated by pooling all transects and repeats for each species. No density estimate is provided for *Lepilemur scottorum* due to a small sample size (n=20). The Buckland method of distance sampling was carried out using Distance 6.0 software (Buckland et al., 2001; 2010; Thomas et al., 2010). We truncated our data at 5% (Meyler et al., 2012). We chose the estimated strip width (ESW) which returned the lowest Akaike Information Criterion

(AIC) value and a high goodness-of-fit Chi-square (GOF Chi-p) value (Buckland et al., 2001).

Statistical Analyses

All forest structural variables were tested for normality using the Kolmogorov-Smirnov test. Any structural variables which deviated significantly from normality were log-transformed to render them normally distributed and allow parametric statistical tests. Analyses of variance (ANOVA) were used to compare habitat variables between the four forest types. Post-hoc Tukey Least Significance Difference (LSD) tests were used to identify which forest type contributed to the significant result. ANOVA were also implemented to investigate differences in animal-transect perpendicular detection distances between the forest types.

We used a General Linear Mixed Model (LMM) to investigate the effect of forest type, time and weather on encounter rates of *Microcebus* sp., *Avahi mooreorum* and *Lepilemur scottorum* (Dytham, 1999). “Encounter rate” was used as response variable, “forest type”, “time” (am or pm) as fixed effects, and “transect ID” as random effect. Before running the model, we tested the effect of “weather” on species mean encounter rates using a univariate ANOVA and found no significant effect; *Lepilemur scottorum* (F=0.106, df=1, p=0.746), *Avahi mooreorum* (F=0.66, df=1, 0.798), *Microcebus* sp. (F=0.143, df=1, p=0.707). As our sample size was small (n =24), we did not include weather in our LMM to decrease the degrees of freedom. There were no significant differences shown in perpendicular detection distances for all nocturnal lemur observations between forest types (F=0.123, df=3, p= 0.944), or in species-specific perpendicular detection distances between forest types; *Microcebus* sp. (F=1.368, df=3, p=0.300), *Avahi mooreorum* (F= 1.640, df=3, p=0.256), *Lepilemur scottorum* (F=

0.346, df=2, p= 0.721). We thus pooled the data to estimate overall densities. Residuals from our analyses were tested for normal distribution using the Kolmogorov-Smirnov test. Residuals from the *Lepilemur scottorum* LMM were not normally distributed. Despite this, we opt to still report the results of the LMM as the test is acknowledged to be quite robust to violations (Gellman and Hill, 2007). Post-hoc LSD tests were used to identify significant differences within fixed effects from the LMM's. All statistical analyses were carried out using SPSS 21.

RESULTS

Habitat Structure

No significant differences were shown in mean DBH between the four forest types ($F_{3,170}$= 2.597, p= 0.054). Mean tree height was significantly different between the four forest types ($F_{3,170}$= 15.344, p<0.001: Table 2). Post-hoc LSD tests showed mean tree height in the primary lowland forest was significantly higher than in the agricultural mosaic forest (p<0.001), and the primary littoral forest (p=0.026). Mean tree height in the selectively logged forest was significantly higher than in the agricultural mosaic forest (p<0.001), and was also significantly higher in the primary littoral forest than the agricultural mosaic forest (p<0.001). Significant differences were also revealed in the mean bole height between the four forest types ($F_{3,170}$=25.689, p<0.001). Post-hoc LSD tests revealed the mean bole height was significantly higher between three forest types, the primary lowland forest (p<0.001), primary littoral forest (p<0.001), selectively logged forest (p<0.001) and the agricultural mosaic forest, and in addition significantly higher in the primary littoral forest than the selectively logged forest (p=0.036).

Other habitat parameters which significantly differed between the four forest types included mean percentage canopy cover ($F_{3,170}$ =9.767, p<0.001), and mean tree density per ha ($F_{3,170}$ =7.782, p<0.001). Follow-up post-hoc LSD tests showed mean percentage canopy cover was significantly higher in the primary forest than the three other forest types; littoral forest (p=0.001), selectively logged forest (p=0.004) and the agricultural mosaic forest (p<0.001). Post-hoc LSD tests showed that mean tree density per ha was significantly lower in the agricultural mosaic forest than the three other forest types; primary forest (p=0.000), littoral forest (p<0.001) and selectively logged forest (p=0.001). We also observed variation in the floristic composition of the four forest types, although there were some species which overlapped between the study areas (Table 2). *Anisophyllea fallax* and *Garcinia commersonii* were the only two tree species which were present in more than one forest type.

Lemur abundance

A total of 142 individuals representing four nocturnal lemur species were observed; *Microcebus* sp. (n=70), *Avahi mooreorum* (n=51), *Lepilemur scottorum* (n=20) and *Daubentonia madagascariensis* (n=1). There were two instances in which the vocalisations of *Phaner furcifer* were heard in the primary lowland forest, although no individuals were observed. No direct sightings were made of *Cheirogaleus major* or *Allocebus trichotis* but we were informed of sightings of the two species (Table 1).

When data is pooled within sites, nocturnal lemur encounter rates and species richness was highest in the primary lowland forest and lowest in the agricultural mosaic forest (Table 3). Among the four forest types and between survey times we found no significant effect for either factor on *Microcebus* sp. encounter rates (forest type: $F_{3,36}$= 0.521 p=0.475; time: $F_{1,36}$ =1.078, p= 0.371), and the interaction between forest type and time also showed no significant effect on *Microcebus* sp. encounter rates ($F_{3,36}$= 0.044, *p*=0.988;). We found a significant effect of forest type on *Avahi mooreorum* encounter rates ($F_{3,36}$= 3.190, *p*=0.035). Both time and the interaction of time and forest type were found to have no significant effect on *Avahi mooreorum* encounter rates (time: $F_{1,36}$= 0.275, *p*= 0.603; forest type: $F_{3,36}$= 1.856, *p*=0.155). Follow up pairwise comparisons identified that *Avahi mooreorum* encounter rates were significantly higher in the primary lowland forest (*p*=0.008), and selectively logged forest (*p*=0.016) than in the agricultural mosaic forest (Table 3). Forest type was shown to have a strong significant effect on *Lepilemur scottorum* encounter rates also ($F_{3,36}$=5.542, *p*=0.003). Follow-up pairwise comparisons identified a significantly higher abundance of *Lepilemur scottorum* in primary lowland forest over the selectively logged forest (*p*=0.018) and the agricultural mosaic forest (*p*=0.001), and also a significantly higher abundance of *Lepilemur scottorum* in primary littoral forest over the agricultural mosaic forest (*p*=0.007) (Table 3). Time and the interaction between time and forest type were found to not be significant predictors of *Lepilemur scottorum* encounter rates ($F_{1,36}$= 3.586, *p*=0.066 and $F_{3,36}$=1.834, *p*=0.158).

Population Density

Population density estimates are provided for *Microcebus* sp. and *Avahi mooreorum* pooling all observations from the four forest types (Table 3). The half-normal key with cosine adjustments provided the lowest AIC for *Microcebus* sp. (AIC 161.26) and *Avahi mooreorum* (AIC 107.86) respectively, and in addition provided high goodness of fit values (*Microcebus* sp.= 0.650, *Avahi mooreorum*= 0.871 GOF Chi-p). The population density of *Microcebus* sp. was estimated at 232.31 individuals/km^2 (95% CI= 147.49-

365.92), while the population density of *Avahi mooreorum* was estimated at 121.21 individuals/km² (95% CI= 73.02- 201.20).

DISCUSSION

The primary lowland forest of the Masoala National Park exhibited the highest species richness of the four study areas. Structurally the primary forest exhibited the highest mean tree height, mean bole height, mean percentage canopy cover, and an intermediate tree density. These characteristics were lowest in the agricultural mosaic forest, as was lemur species richness, which is typical of areas with anthropogenic disturbance (Ganzhorn et al., 1997; Irwin et al., 2010; Schwitzer et al., 2011). The similarities observed in mean DBH between the four forest types is likely to be a consequence of the methods used to collect DBH which took trees of ≥5cm as the lowest value, rather than the standard ≥10cm DBH which is commonly used (Ganzhorn et al., 2007).

Both *Avahi mooreorum* and *Lepilemur scottorum* were observed at their highest abundance in the primary lowland forest, and at their lowest abundance in the agricultural mosaic forest. The structural characteristics of these two study areas, suggest that the abundance of the two lemur species is positively correlated with higher mean tree and bole heights, which are more frequently observed in areas of lower disturbance (Hitimana et al., 2004; Balko and Underwood, 2005; Malone et al., 2013). A similar pattern has been observed for these genera at sites across Madagascar (Herrera et al., 2011; Seiler et al., 2014). Both *A. mooreorum* and *L. scottorum* are vertical clingers and leapers (VCL's), this is a postural and locomotor "habit" in which the individual clings on to and leaps between predominantly vertical supports (Demes et al., 1996). It is an expensive form of locomotion (Warren and Crompton, 1998), in which the species often require large trees (in Madagascar trees with a DBH ≥5cm/10cm; Ganzhorn et al., 1999) to move around their habitat (Norscia, 2008). The space between the tree crown and ground is preferred for VCL's, meaning that increased tree and bole heights provide these two species with a greater space in which to navigate (Ganzhorn, 1989; Warren, 1997).

Food resource availability can significantly influence the occurrence and abundance of animal populations (Balko and Underwood, 2005). *Avahi* sp. and *Lepilemur* sp. are both dedicated folivores (Ganzhorn, 1985; Nash, 1998; Thalmann, 2001), where abundance is often positively correlated with the availability of preferred food tree species (Ganzhorn et al., 1997). Preferred tree species of *Avahi* sp. include *Harongana madagascariensis*, *Syzygium* sp. and *Symphonia* sp., which are often present in disturbed habitats (Ganzhorn, 1985; Lowry et al., 1997; Faulkner and Lehman, 2006). These were common in the selectively logged forest and agricultural mosaic forest on the Masoala Peninsula (Table 2), where *A. mooreorum* individuals were present at a relatively low abundance. The abundance of *Garcinia commersonii* and *Eugenia* sp. in the primary lowland forest were positively associated with the highest abundance of *A. mooreorum*. These tree species have been reported as feeding species of *A. laniger* elsewhere in eastern Madagascar (Ganzhorn, 1985; Harcourt, 1991). This positive association would suggest that these are preferred feeding tree species of *A. mooreorum*, but may be a rarer tree species which only occur at high densities in less disturbed habitats. In order to verify this hypothesis, a detailed comparative study of the feeding ecology of *A. mooreorum*, including nutritional analyses of food resources, across our different study habitats would be necessary.

Lepilemur scottorum appeared to be the species most affected by habitat disturbance, as they occurred at the lowest abundance of all species surveyed (other than *Daubentonia madagascariensis*). Tree species most commonly recorded to be consumed by *Lepilemur* sp. include *Grewia* sp., *Garcinia* sp., and *Mangifera* sp. (Ganzhorn, 2002; Seiler et al., 2014). *Lepilemur scottorum* abundance was highest in the primary lowland forest where *Garcinia commersonii* was abundant, perhaps influencing this species presence in this forest. *Dalbergia* sp. have also been recorded as a key dietary resource for *L. ruficaudatus* in western Madagascar (Ganzhorn, 2002). It may be that the continued illegal extraction of rosewood (*Dalbergia* sp.) is negatively impacting on *L. scottorum* abundance on the Masoala peninsula.

As two ecologically similar species, the potential for the occurrence of competition between sympatric *Avahi* sp. and *Lepilemur* sp. is high, particularly in disturbed habitats where the availability of high quality resources and habitat are decreased (Huey and Pianka, 1981). As *A. mooreorum* was observed at a higher abundance across all habitat types, there is a possibility that this species may outcompete *L. scottorum* in our study area. Additionally, our population density estimate for *A. mooreorum*, falls around the mid-range of density estimates for this genera (Ganzhorn, 1988; Norscia, 2008; Herrera et al., 2011), whereas our *L. scottorum* encounter rate falls on the lower end of encounter rates observed for other *Lepilemur* species (Schmid and Smolker, 1998; Irwin et al., 2000; Sterling and McFadden, 2000; Meyler et al., 2012). This hypothesis is currently only speculation, based on a short-term study on a small sample size. Long-term monitoring of the forest types and population dynamics of the nocturnal species in this study area would be necessary to confidently verify this hypothesis.

Microcebus sp. were observed in all four habitats, with no significant difference in their abundance between the four forest types. As a small-bodied omnivorous species, *Microcebus* spp. are flexible in terms of both their behavioural and feeding ecology, and as such are often abundant in secondary and anthropogenic habitats (Ganzhorn 1995; Lehman et al., 2006b; Dammhahn and Kappeler, 2008a; Lahann, 2007; Herrera et al., 2011). *Microcebus* spp. appear tolerant to varying habitat disturbance, and even extreme habitat alteration, they occur across a range of habitats including primary and secondary forests (Malone et al., 2013), and even pure garden habitats (Irwin et al., 2010). Their tolerance for habitat degradation has been attributed to morphological and behavioural adaptations in *Microcebus* sp. such as their small body size, diet and generalised locomotion.

Microcebus sp. small body size allows them to locomote easily through disturbed habitats despite low tree densities (Dammhahn and Kappeler, 2008b). At Masoala, *Microcebus* sp. were observed to use a range of supports for travelling including the small stems of *Afromomum angustifilium* in the agricultural mosaic forest, and larger tree crown branches up to heights of *ca.* 20m in the primary lowland forest. This illustrates the variety of supports they are able to exploit when compared with other more specialised species. *Microcebus* sp. omnivory facilitates their ability to tolerate habitat disturbance, they consume a mixture of insects, fruits, gums and flowers to varying degrees (Mittermeier et al., 2010). Agricultural and secondary habitats often provide high insect abundance (Losey and Vaughan, 2006), and a thick understorey which provides protection form aerial predators (Mittermeier et al., 2010). Primary forest may provide an "ideal" habitat for *Microcebus* sp., but they appear able to exploit the opportunities which anthropogenic habitats can present. This is exemplified by the density estimate of 232.31 individuals/km² observed in this study, which leans toward the top range of density estimates reported elsewhere across Madagascar for other *Microcebus* species (Ganzhorn, 1992; Lehman et al., 2006a; Meyler et al., 2012; IUCN, 2014).

We calculated population density estimates for our study species based on the average trail-to-animal distance method also employed by Sterling and Rakotoarison (1998) on the Masoala Peninsula. Density estimates were calculated based on our observations from the primary lowland forest, as this was the study habitat most comparable to the Iketra study site surveyed in 1994 (Sterling and Rakotoarison, 1998). We found higher density estimates at our study site for *Microcebus* sp., 69.4 ind./km^2 compared with 39 ind./km^2 (Sterling and Rakotoarison, 1998), and *A. mooreorum,* 93.8ind./km^2 compared with 25 ind./km^2 (Sterling and Rakotoarison, 1998). We calculated a lower density estimate for *L. scottorum*, 25.2 ind./km^2 compared with 33 ind./km^2 (Sterling and Rakotoarison, 1998). The higher density estimates observed for *Microcebus* sp. and *A. mooreorum* in this study from Sterling and Rakotoarison (1998) may be an indication of the success that the inception of Masoala National Park since 1997 has had on the populations of these species, where they are protected.

Whilst this paper focuses on the effect of habitat disturbance on lemur densities, another aspect to consider is the effect of hunting pressure. Hunting was not previously considered to be a huge threat to lemurs as many species were protected by *fady*, however in recent years, research has shown that hunting is now one of the major threats to the conservation of lemurs across Madagascar (Golden, 2009; Jenkins et al., 2011). Research shows that lemur species targeted for bushmeat are often the larger diurnal and cathemeral species, such as *Eulemur* sp., *Varecia* sp. and *Propithecus* sp.

(Razafimanahaka et al., 2012). Across the Masoala Peninsula and Makira Forest, hunting of the red ruffed lemur (*Varecia rubra*), and white-fronted brown lemur (*Eulemur albifrons*) using *laly* traps has been widely recorded (Golden, 2009; Borgersen, 2015). On Makira, Golden (2009) additionally recorded the hunting of a number of nocturnal lemur species including; *Avahi laniger*, *Lepilemur* sp., *Cheiroglaeus major*, *Daubentonia madagascariensis*, and *Microcebus* sp. In general, the reporting of nocturnal lemur hunting is less common than that of diurnal and cathemeral species, although detailed research on nocturnal lemur hunting is largely lacking.

Research on the hunting of nocturnal primates has shown the prevalence of their use as bush meat and in traditional medicine globally (Nekaris et al., 2010; Maldonado and Peck, 2014; Svensson and Friant, 2014; Svensson et al., 2015). Considering global patterns of bush meat hunting, it is likely that larger nocturnal species, such as *Avahi mooreorum* and *Lepilemur scottorum*, are at risk from hunting pressure, particularly in disturbed areas where high quality sleeping sites are generally less available (Seiler et al., 2013), making these species more visible and accessible to hunters.

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TABLES

Table 1

Table 1. Nocturnal lemurs present at Masoala National Park, northeastern Madagascar.

Common Name	Scientific name	Diet	IUCN Red List status	IUCN Red List Category	Observed in this study
Moore's woolly lemur	*Avahi mooreorum*	Folivore	Endangered	B1ab (iii,v)	Yes
Scott's sportive lemur	*Lepilemur scottorum*	Folivore	Endangered	B1ab (i,iii,v)	Yes
Mouse lemur	*Microcebus* sp.	Frugivore/ Insectivore	Unknown	N/A	Yes
Greater dwarf lemur	*Cheirogaleus major*	Frugivore/ Insectivore	Data deficient	N/A	No[ab]
Hairy-eared dwarf lemur	*Allocebus trichotis*	Frugivore/ Insectivore	Vulnerable	A2c+3c+4c	No[b]
Eastern fork-marked lemur	*Phaner furcifer*	Gummivore	Vulnerable	A2c+3c+4c	No*
Aye-aye	*Daubentonia madagascariensis*	Frugivore/ Insectivore	Endangered	A2cd + 4cd	Yes

[#] Body size is given as either XS (extra small), S (small), M (medium) or L (large). Estimated weights are given in parentheses based on weights in Mittermeier et al., 2010.

**Phaner furcifer* was not observed during the study, but vocalisations were heard on 2 occasions in the protected areas, which appeared to be coming from higher elevations.

[a] Other abundance surveys of *Cheirogaleus major* have not observed individuals between May and September as the species is known to enter torpor throughout these colder months in eastern Madagascar (Lehman et al., 2006c).

[b] The presence of *Cheirogaleus major* and *Allocebus trichotis* in our study area were confirmed by local tourist guides and residents who regularly live and work in the area. Sightings of these species were reported as rare and intermittent.

N/A given when data is not available.

Table 2

Table 2. Habitat Characteristics measured in vegetation surveys.

Habitat Parameter *n*	**Primary Lowland** 50	**Selectively Logged** 50	**Agricultural Mosaic** 40	**Primary Littoral** 30
Mean Tree Height (m) *	16.38 ± 9.51^{A,B}	15.80 ± 6.59^{C}	10.11 ± 8.15^{A,C,D}	13.96 ± 6.38^{B,D}
Mean Bole Height (m) *	9.99 ± 7.70^{E}	9.99 ± 5.65^{F,H}	3.92 ± 5.16^{E,F,G}	8.23 ± 5.39^{G,H}
Mean DBH (m)	15.15 ± 10.18	17.62 ± 10.47	17.86 ± 21.33	13.62 ± 8.53
Mean Canopy Cover (%) *	75.31 ± 14.29^{I}	69.89 ± 14.75^{J}	65.10 ± 19.47^{I,J,K}	68.13 ± 13.46^{K}
Tree Density (> 5cm DBH per ha) *	1568.60 ± 1994.14^{L}	1015.59 ± 1496.12^{M}	591.168 ± 1309.40^{L,M,N}	1725.08 ± 1626.21^{N}
Top 5 tree species	*Cryptocarya* sp.	*Anthostema madagascariensis*	*Harongana madagascariensis*	*Uapaca thouarsii*
	Homalium sp.	*Symphonia fasciculata*	*Albizia* sp.	*Anisophyllea fallax*
	Eugenia sp.	*Anisophyllea fallax*	*Mangifera indica*	*Polyscias sp.*
	Garcinia commersonii	*Garcinia commersonii*	*Anisophyllea fallax*	*Dracaena fontanesiana*
	Dracaena xiphophylla	*Diospyros* sp.	*Ravenala madagascariensis*	*Anthostema madagascariensis*

Habitat Parameters with significant differences based on one-way ANOVA tests are marked with *($p \leq$ 0.05). Means and standard deviations (±) are displayed. Cells with superscript letters in common differed significantly in LSD post-hoc comparisons. ($p \leq 0.05$).

n = sample size

Table 3

Table 3. Encounter rates of lemurs (individuals/ transect walk). Values are medians with upper and lower range in parentheses (min-max).

Forest Type	Transect walks	*Microcebus* sp.	*Lepilemur scottorum*	*Avahi mooreorum*	*Daubentonia madagascariensis*	Species richness
Primary Lowland	12	1 (0-9)	1 (0-3) ^{A,B}	1 (0-8) ^{D}	0 (0-1)	4
n		25	11	26	1	
Mean cluster size		1 ± 0	1.1 ± 0.32	1.73 ± 0.80	1 ± 0	
Selectively Logged	12	1 (0-3)	0 (0-2) ^{A}	1 (0-3) ^{E}	Absent	3
n		13	4	15		
Mean cluster size		1 ± 0	1 ± 0	1.15 ± 0.38	-	
Primary Littoral	8	1.5 (1-4)	1 (0-1) ^{C}	0.5 (0-3)	Absent	3
n		14	5	8		
Mean cluster size		1 ± 0	1 ± 0	1.6 ± 0.55	-	
Agricultural Mosaic	12	1 (0-5)	Absent $^{B.C}$	0 (0-1) ^{D,E}	Absent	2
n		18		2		
Mean cluster size		1.13 ± 0.34	-	1 ± 0	-	
n	44	70	20	51	1	4
Species density estimate (individuals/km^2)		232.31	-	121.21	-	-
95% lower-upper CI		147.49-365.92		73.02-201.20		
Estimated strip width		4.64	-	6.20	-	-
Cluster size		1.03	-	1.43		

Mean cluster size with standard deviation (±) is provided.

Species specific encounter rates with superscript letters in common differed significantly in pairwise comparisons from LMM ($p \leq 0.05$).

n= total number of individuals observed

Species density estimate, ESW and cluster size were calculated using Distance 6.0.

CI=confidence interval.