ARTICLE https://dx.doi.org/10.4314/mcd.v20i1.4

Distribution and habitat use by the eastern woolly lemur, *Avahi laniger* (Gmelin 1788), in the fragmented forests of the Ambohidray Protected Area, Central-Eastern Madagascar

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ABSTRACT

Lemurs are one of the key species for conservation in Madagascar. While much research has focused on diurnal lemurs, nocturnal species such as the eastern woolly lemur (*Avahi laniger*) remain understudied. To address this gap, we conducted a population and habitat study of *A. laniger* in the Ambohidray Protected Area (PA) of, in two forest zones: (i) core area, interior and (ii) buffer zone outside PA. Vegetation structure was assessed using 50 m × 2 m standard botanical plots. Six diurnal and nocturnal observations were conducted along ~1 km transects. The distance sampling method, specifically the Conventional Distance Sampling (CDS) approach, was used during nighttime observations to assess population density, which resulted in a total sampling effort of 38.7 km. To model how habitat variables, as well as distance, influence lemur detection probability, we use the Multiple Covariate Distance Sampling (MCDS) method. We observed 58 individuals and estimated a population density of 63 individuals/km² with our best MCDS fit model. Our model suggests preference for habitats with small crown diameter and semi-open canopy cover. Encounter rates were higher in the buffer zone (2.26 individuals/km) than in the core zone (1.03 individuals/km). *A. laniger* was detected in trees with a diameter at breast height (DBH) of 11–20 cm, a height of 9–16 m, and relatively small crowns. Vegetation structure, including DBH, tree height and plant diversity differed between zones. These findings suggest *A. laniger*'s adaptation is shaped by more than habitat structure, and that Ambohidray PA serves as a vital refuge for the species.

RÉSUMÉ

Les lémuriens jouent un rôle crucial dans les efforts de conservation à Madagascar. Cependant, les connaissances sur les lémuriens nocturnes, tels que *Avahi laniger*, restent limitées. Pour combler cette lacune, une étude écologique de cette espèce a été menée dans l'Aire Protégée d'Ambohidray. Cette étude s'est concentrée sur deux zones distinctes : le noyau dur et la zone tampon de l'aire protégée. La végétation a été analysée en établissant des parcelles standard de 50 m x 2 m dans les zones étudiées. Des observations directes diurnes et nocturnes le long de transects ont été réalisées. La méthode d'échantillonnage par distance (*distance sampling*), en particulier l'approche CDS (*Conventional Distance Sampling*), a été utilisée lors des observations nocturnes pour évaluer la densité de la population. La méthode MCDS (*Multiple Covariate Distance Sampling*) a été utilisée afin d'évaluer l'influence des variables de l'habitat ainsi que la distance sur les taux de rencontre afin d'améliorer la précision de l'estimation de la densité et d'évaluer son influence sur les taux de rencontre. Une densité de population de 63 individus/km² a été estimée à partir du nombre d'observation (n = 58) en utilisant le modèle le mieux ajusté. La visualisation graphique de la fonction de détection indique que l'espèce préfère un habitat caractérisé par des arbres avec un faible diamètre de la couronne associé à une couverture de canopée semi-ouverte. *A. laniger* était plus fréquemment rencontré dans la zone tampon (2,26 individus/km) que dans le noyau dur (1,03 individus/km). L'espèce a été le plus souvent observée dans des arbres ayant un diamètre à hauteur de poitrine (DHP) de 11 à 20 cm, une hauteur comprise entre 9 et 16 m, de faibles diamètres de couronne (<5 m) et une canopée semi-ouverte. Des différences dans la structure de la végétation

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Citation Raharinirina, H., Sambado, S., Richard, Y., Ravelojaona, R. N., Rakotomalala, Z. and Ratsoavina, F. M. 2025. Distribution and habitat use by the eastern woolly lemur, Avahi laniger (Gmelin 1788), in the fragmented forests of the Ambohidray Protected Area, Central-Eastern Madagascar. Madagascar Conservation & Development 20, 1: 32–40. <https://doi.org/10.4314/mcd.v20i1.4>

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University of Zurich
Winterthurerstrasse 190
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(DHP et hauteur maximale des arbres) ainsi que dans les indices de diversité (indice de Shannon = 3,8 vs. 3,3 ; Jaccard = 0,39 ; Sørensen = 0,24 et Bray-Curtis = 0,60) entre les zones ont été constatées. Le noyau dur présentait une diversité spécifique significativement plus élevée que la zone tampon. La hauteur des arbres était significativement plus grande dans le noyau dur tandis que le DHP des arbres y était plus faible. Ces résultats montrent que la Nouvelle Aire Protégée d'Ambohidray constitue un refuge pour *A. laniger* et suggèrent que l'adaptation de cette espèce aux habitats fragmentés est influencée non seulement par la structure de l'habitat, mais aussi par d'autres facteurs écologiques ou anthropiques. En fournissant ces informations, cette étude offre une base importante pour le suivi écologique de cette espèce dans cette aire protégée.

INTRODUCTION

Understanding the population dynamics and basic ecology of species is essential for the implementation of successful practices for their conservation (Courchamp et al. 2015), as well as for effective management of a protected area. The abundance and density measurements of an animal population can indicate species rarity and extinction risk (Purvis et al. 2000).With increasing anthropogenic pressures, such as increased land fragmentation and hunting, establishing population records as well as understanding the associated habitat will measure for the effects and outcomes of conservation strategies in the future (Gerber et al. 2012). Additionally, population viability assessments, including considerations of population size and fragmentation, are essential for evaluating the impact of these pressures on species survival (Frankham et al. 2014).

The Ambohidray PA is a protected area created in response to the Durban Vision ratified by the Malagasy government in September 2003 to triple the national surface area of protected areas. The objective of these PAs are: (i) to conserve all of Madagascar's unique biodiversity, (ii) to conserve the cultural heritage of the Malagasy, and (iii) to maintain ecological services and promote the sustainable use of natural resources for poverty reduction (Andriamalala and Gardner 2010). Ambohidray was officially created on May 5, 2015 (Decree N. 2015-808), and is classified as a Category V "Protected Landscape" according to the IUCN classification. Yet very few studies on the fauna and flora of Ambohidray have been carried out since its inauguration.

Lemurs are an emblematic group of fauna in Madagascar (Durbin 1999). However, given the fact that lemurs are tightly linked with their natural habitat (Eppley et al. 2020); they are very sensitive to fragmentation, hunting, and human disturbances (Rakotondravony and Rabenandrasana 2011, Hending et al. 2024). Recent anthropogenic activities such as deforestation for agriculture or gold mining has reduced forest cover by 40%, with an 80% reduction in Madagascar's central highlands forest between 1950–2000 (Harper et al. 2007). With these increased threats to lemur habitat, lemurs are among the key animals of conservation concern in Madagascar. Approximately 98% of lemur species are listed under an IUCN (2020) category of threat, making their conservation a global concern.

Despite the numerous studies on lemurs, the nocturnal species such as the eastern woolly lemur (*Avahi laniger*) are less studied, which is considered a neglected group of primates (Joly 2011). Avahi species are the only nocturnal lemur species belonging to the family Indriidae while *A. laniger* is native to the northern half of the Malagasy eastern humid forests (Mittermeier et al. 2023). *A. laniger* typically lives in monogamous family groups that maintain long-lasting bonds (Thalmann 2006). With a home range covering an area of one to two hectares (Ganzhorn et al. 1985), *A. laniger* can be sensitive to habitat fragmentation. However, studies suggest that *A. laniger* can tolerate some degree of forest fragmentation, though the extent of this tolerance remains unclear (Lehman et al. 2006, Rakotondratsimba et al. 2013). This ecological flexibility makes *A. laniger* a useful model for understanding how lemur species may respond to different levels of anthropogenic disturbance. Although primarily folivorous, *A. laniger* occasionally consumes fruits (Mittermeier et al. 2023), contributing modestly to seed dispersal and forest regeneration. Additionally, *A. laniger* serves as prey for native predators such as the fosa (*Cryptoprocta ferox*, Norsia & Borgognini-Tarli 2008) and nocturnal birds of prey (*Accipiter henstii*, Karpanty 2006), playing a vital role in sustaining the forest food web. Through population density surveillance, the threat status of *A. laniger* on the IUCN Red List was elevated from *Least Concern* (Rakotondratsimba et al. 2013) to *Vulnerable* in July 2013 (Schwitzer et al. 2013). This change in threat status suggests that the population dynamics of *A. laniger* are shifting. This species like all in the woolly lemur genus, has never been kept in captivity with any success (Mittermeier et al. 2023). Therefore, documenting the ecology and distribution of *A. laniger* is essential not only to guide future conservation actions and inform management strategies in the region but also to fill gap in scientific understanding.

This study focusses on the population of *Avahi laniger* within the Ambohidray PA in central eastern Madagascar. In this study, we focus on two key zones within the Ambohidray PA: the core and buffer zones. The core zone is strictly protected with minimal human disturbance, while the buffer zone allows certain economic activities, resulting in a higher level of anthropogenic pressure. These zones provide a valuable comparison for assessing the population and ecological dynamics of *A. laniger* under different disturbance regimes. The main objectives were to provide knowledge on the current population and ecological associations of *A. laniger* to help establish conservation policy for land managers and serve as a reference for future ecological monitoring. Specifically, we aimed to: (i) estimate the population density of *A. laniger* in the Ambohidray PA by incorporating habitat variables as covariates to improve the accuracy of the density model; (ii) assess patterns of spatial distribution of the species between the core and buffer zones; (iii) identify key tree species and structural characteristics (DBH, crown diameter, height, canopy cover) associated with *A. laniger* presence; and (iv) assess differences in habitat characteristics between the core and the buffer zone of the PA.

METHODS

FIELD METHODS. Study location. The study took place in the southern part of the Ambohidray PA in Central-Eastern Madagascar (E048°17' to 048°19', S18°34' to 18°37'). The Ambohidray PA has an IUCN conservation status of category V—a Protected Landscape—and is jointly managed by the Plant Biology and Ecology Department of the Faculty of Science (Mention Biologie et Écologie Végétales, MBEV), University of Antananarivo and the local community of Ambohidray referred as VOI Miray (*Vondron'olona Ifotony*, meaning "local community"). The Ambohidray PA is located between Moramanga and Ambatondrazaka and accessible 40 km north of Moramanga by following the national road 44 (Figure 1). The PA is made up of several forest blocks with a total area of 1,241 ha and a total perimeter of 22.15 km. The eastern part consists of continuous forest, whereas the central, northern, and western are fragmented, occupied by cultivated areas, rice paddies and degraded areas. The Ambohidray forest is classified as a tropical, hot, and humid environment with annual precipitation of approximately 1,681 mm. The average annual temperature is 18°C, with seasonal variations (wet season: October to April; Tadross et al. 2008). This complex evergreen forest is rich in tree and shrub species.

Study design. The Ambohidray PA is divided into four zones, with boundaries proposed by the managing organization, MBEV at the time of the PA's creation: core hard zone (here after as core zone), buffer zone, ecotourism zone, and peripheral zone Figure 2). This zonation was applied during our study. This study focuses on the differences between the core and buffer zones, representing two areas experiencing different anthropogenic disturbance pressure (core = lower, buffer = higher). The core zone is strictly protected, and biodiversity conservation is a priority. The buffer zone is an area where various economic activities are permitted but regulated to ensure better conservation of biodiversity and the sustainability of its use. This distinction is based on the official zoning of the protected area, which designates the core zone as strictly protected, prioritizing biodiversity conservation, and the buffer zone as a regulated area where certain economic activities are allowed to promote sustainable use of natural resources (COAP 2015, 2017). In addition to this zoning framework, our field observations confirmed this pattern. We recorded significantly more signs of human activity in the buffer zone, including rice fields, *Eucalyptus* plantations, and degraded areas, compared to the core zone. By comparing these zones, this study aims to assess the species' response to different environmental conditions and inform conservation strategies for the sustainable management of Ambohidray PA. We conducted this research in these locations for this study under permit number N. 087/21/MEDD/SG/DGGE/DAPRNE/SCBE.Re.

In each zone type, transects of approximately 1 km in length (Meyler et al. 2012) were installed following a north-south orientation. Every 50 m interval of the transect line was marked by a colored ribbon to facilitate their identification and orientation during observations. Each transect line was spaced at least 200 m apart (Meyler et al. 2012; Figure 2). In total, 13 transects were established, with eight transects in the core zone (453 ha) and five transects in the buffer zone (408.5 ha). Transects were planned based on field visits to assess forest continuity and accessibility and were finalized using QGIS, ensuring a minimum spacing of 200 m between them. Transect lines were established at least 24 hours prior to the first lemur observation to avoid any disturbances to the animals. The study took place from 26 June 2021 through 6 September 2021 during the dry season for the central Madagascar region.

LEMUR OBSERVATION. We used "Line-transect-distance sampling" (Buckland 2001, Meyler et al. 2012) to estimate the density of the *Avahi laniger* population across Ambohidray PA. This method involves the direct observation of lemurs along transect lines while considering the perpendicular distance between the animal and transect line. Over the course of our study, we visited each transect six times, three during the day and three during the night. For the density estimation, we used only the nighttime observation when *A. laniger* was active, which resulted in a total sampling effort of 38.7 km. Both nighttime and daytime observations are used to characterize the habitat preference of the species. Daytime observations took place either in the morning between 0730–1030 or in the afternoon between 1430–1730 and nighttime observations began around 1830. Lemur eyeshine was first detected using headlamps, followed by the use of a more powerful light to confirm species identity. Transect observations were conducted by a team of three people who walked each transect line at a slow pace of ~ 0.5 km/h. Visits to the same transect were separated by at least two days to minimize disturbance of the animal and its habitat (Buckland 2001). For each group of lemurs observed, we recorded the identity of the transect, and GPS

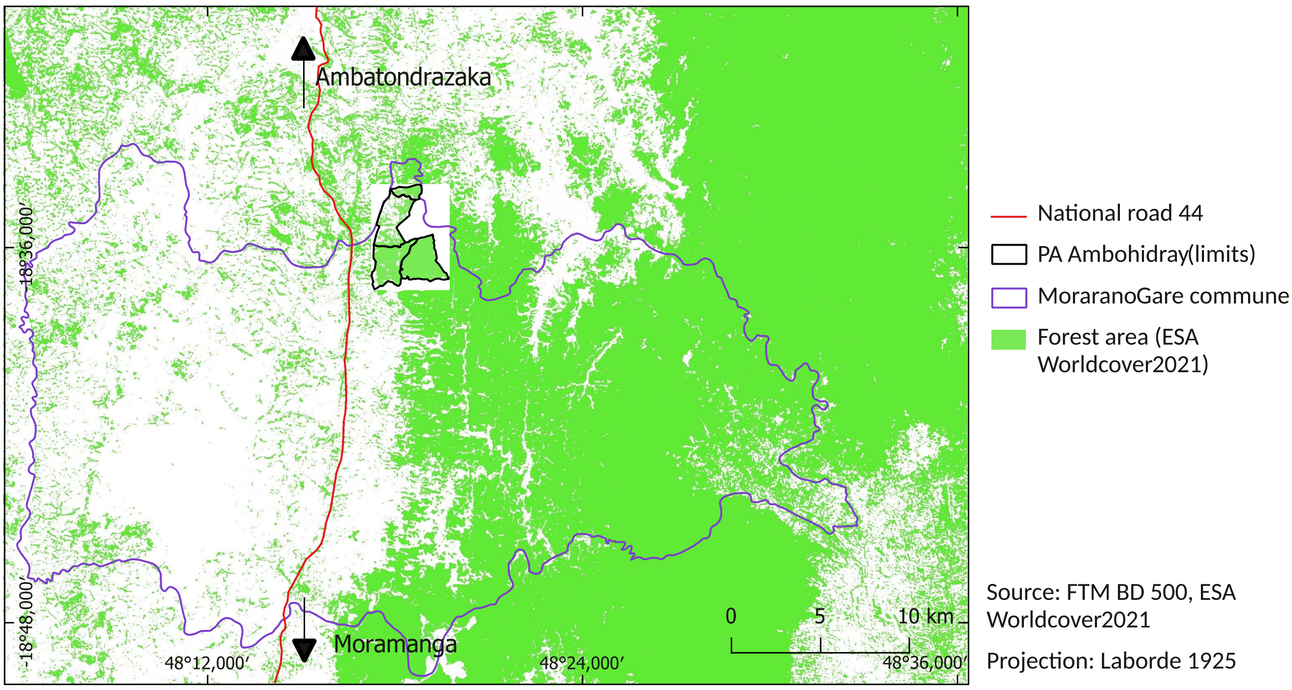

Figure 1. Geographic location of the Ambohidray Protected Area

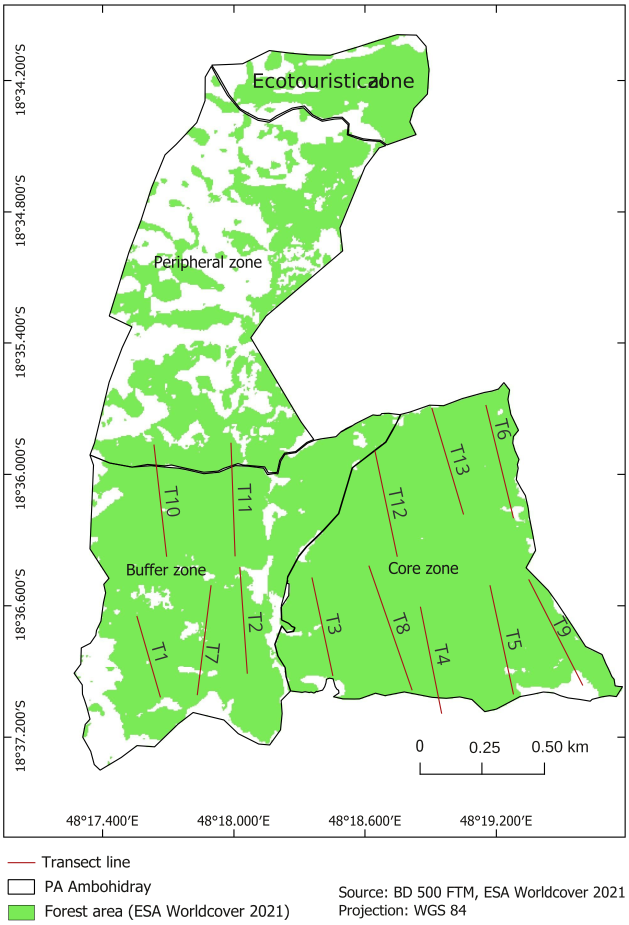

Figure 2. Ambohidray PA with its four management zones and transect lines (red lines labeled TN) implemented in the buffer zone and the core area).

coordinates of the observation point, as well as the species identities, and the estimated perpendicular distance between lemurs and transect line. Additionally, we marked the tree at the observation site for later habitat characterization.

CHARACTERIZATION OF HABITAT. To characterize the vegetation, we established standardized plots that were first divided into 50 m x 2 m “botanical plots” which were further subdivided into 2 m x 2 m subplots to facilitate data collection (Figure S1). The botanical plots were established every 150 m along each transect line, positioned 2 meters to the side of the transect line, to characterize the vegetation of the study area (Figure S2). This plot size and arrangement provide a practical balance between detail and field efficiency, allowing for effective detection of microhabitat variability along ecological gradients. Smaller, repeated plots are often preferred over fewer large plots for more accurate habitat characterization across heterogeneous environments (Dengler 2017).

Within each subplot (2 m x 2 m), vegetative habitat characteristics were documented. Specifically, we recorded the species identity, height, diameter of crown, and diameter at breast height (DBH) for all woody plants with a circumference at chest height (CBH) greater than 10 cm. Height measurements of the woody plants were categorized into seven height classes for analysis: 0–1 m, 1–2 m, 2–4 m, 4–8 m, 8–16 m, 16–32 m, and > 32 m (Daniels et al. 1992).. DBH estimates were subsequently grouped into five classes for analysis: 0–2.5 cm, 2.5–5 cm, 5–10 cm, 10–20 cm, 20–30 cm, and > 30 cm (Honoré Djadagna Ahy 2024). Crown diameter was estimated and assigned to one of four width categories: < 5 m, 5–10 m, 10–15 m and > 15 m (Mitchell et al. 1991). These classification systems were selected because they have been applied in tropical forest ecology studies (Boinski et al. 2002, Honoré Djadagna Ahy 2024), allowing for standard assessment of forest structure. Canopy cover was estimated following the protocols of Paletto and Tosi (2009) which consist of taking digital photographs of the canopy. Photos of the canopy were taken in the middle of each subplot with a digital camera (Powershot Sx50). Photos were analyzed with the open-source software Canopydigi developed by Goodenough and Goodenough (2012). This method has demonstrated to provide accurate and repeatable estimates of canopy density (Morales et al. 2016). The photos were converted to monochrome (BMP format) using ReaConverter Lite, and processed in Canopydigi to create "false color" images. Dark pixels representing the canopy were identified, and the software calculated the percentage of canopy cover. Additional details on how the photos were uploaded, transformed, and analyzed can be found in Supplement Text 1. The cover was classified into five groups: open (≤ 20%), relatively open (21–50%), semi-open (51–70%), relatively closed (71–90%), and closed (> 90%). Grouping canopy cover into categories allowed for a clearer ecological interpretation of habitat openness and facilitated comparisons across plots.

We used the same 50 m× 2 m botanical plots for *Avahi laniger* microhabitat characterization. Botanical plots were established at locations where the species was observed during both daytime and nighttime surveys. The tree supporting *A. laniger* was positioned at the center of the plot (Figure S2), and we recorded its species identity, height, crown diameter, and CBH. These plots were used solely for canopy cover estimation, with photos taken following the same methodology described above.

DATA ANALYSIS

Lemur density estimates. To estimate the density of *Avahi laniger* from transect observation, we applied the Conventional Distance Sampling (CDS) method (Buckland 2001), which models the detection probability as a function of the perpendicular distance from the transect line to each *A. laniger* sighting. The CDS method estimates animal density (*D*, individuals per km²) using the equation:

$$D = \frac{NT}{2(<*ESW)}$$

where NT is the number of detected animals, LT is the total transect length, and ESW is the effective strip width. To implement this method, we used the distance package in R Studio (version 4.1.1) (Miller et al. 2019, R Core Team 2021). Detection functions were modeled using different key functions (e.g., half-normal, uniform, exponential (Miller et al. 2019), and the best model was selected based on the lowest Akaike Information Criterion (AIC) (Akaike 1974). Data were truncated at 10% of the maximum observed distance to eliminate extreme values (Buckland 2001). The ESW was estimated, and model fit was both visually with Q-Q plots and statistically with the Cramér-von Mises test to evaluate how well the fitted detection function matched the observed data (Burnham et al. 2004, Miller et al. 2019). Variance and confidence intervals for density estimates were calculated from the fitted model.

We expanded the previous model to assess how detection probability varied with both distance and additional habitat covariates, including canopy cover, height, DBH and crown distance of the trees. These habitat variables were obtained through microhabitat characterization of *Avahi laniger*. We tested the multiple-covariate distance sampling (MCDS) models by first considering each variable individually, then combining two variables, and finally testing combinations of three variables (Buckland et al. 2004, Marques et al. 2007). The AIC was again applied to choose the best model, selecting the one with the lowest AIC score. Once the best-fit model was identified, we used it to estimate the population density of *A. laniger*. To understand how changes in the covariates influence detection probabilities, we generated visualizations of the detection functions based on the interaction of habitat variables (Marques et al. 2007).

Lemur distribution within core vs. buffer zone. As the number of observations was insufficient for accurate estimates, the CDS was not applied to compare density estimates or abundance between the core and buffer zones. Minimum of 40 observations was required for reliable effective strip width (ESW) and density estimates (Buckland et al. 2001). Instead, we used encounter rates (the number of individuals observed per kilometer surveyed) to compare the relative distribution of *A. laniger* between the two zones (Murphy et al. 2016). Mean encounter rates were calculated separately for each zone, and statistical comparisons were made using a one-way ANOVA to assess potential differences in lemur distribution across the core and buffer zones.

Habitat characteristic differences within core vs. buffer zones. The data used for this analysis were collected from botanical plots established along each transect in both the core and buffer zones. Based on these data, we first examined potential difference in the plant genera diversity of the two zones by calculating the Shannon diversity (Heusèrr, 1998) (i.e., alpha diversity within a site). We additionally applied the Hutcheson t-test to compare the Shannon diversity results between the core and buffer zones. To determine the dissimilarity between the two areas, we evaluated the beta diversity (i.e., between sites) using the Jaccard (1908), Sørensen (1948), and Bray-Curtis (1957) indices. Because some individuals were identified only to the genus level, these indices were calculated based on generic composition, which may underestimate species-level turnover. To examine how the association between habitat variables and the plant genera may vary between core and buffer zones, we used a linear mixed effects models with habitat variables as fixed effects and plant genera or species as a random effects.

RESULTS

AVAHI LANIGER POPULATION DENSITY. We observed 36 groups of *A. laniger* composed of 58 individuals (Core zone = 14 groups – 25 individuals and buffer zone = 22 groups – 33 individuals). Each group refers to a distinct sighting recorded during nocturnal surveys, and the number of individuals was based on direct visual confirmation. Using the CDS method, the best-fit model was the half-normal key function with no adjustment (Figure 3A) yielding an estimated density of 37 groups/km2 and 59 individuals/km2 for the entire study area (Table 1). When incorporating the habitat covariates with the CDS method (i.e., the MCDS models), the best-fit model to improve the detection function was a half-normal key function with no adjustments and the addition of crown diameter and canopy cover covariates (Figure 3B). From this best-fit model (Cramer-von Mises: test statistic = 0.08, p-value = 0.6), we obtained a density of 41 groups/km2 and 63 individuals/km2 (Table 1). Additional model summaries can be found in Table S1. The plot detection function indicates that the encounter rates peak where trees supporting *A. laniger* have a relatively small mean crown diameter (4 m in the dataset) and are associated with a semi-open canopy cover (64%) (Figure 3C). Certain combinations of these two covariates not present in the dataset produced irregular or "non-normal" detection curves. These were excluded from the interpretation, as they likely resulted from the model extrapolating beyond the observed data range.

SPATIAL DISTRIBUTION OF ENCOUNTER RATES IN CORE AND BUFFER ZONES. *Avahi laniger* was observed in all transects except on transect four (T4) in the core zone. Encounter rates varied among transects and differed significantly between zones (Table S2). The species was more frequently encountered in the buffer zone, where the mean encounter rate was higher (2.26 individuals/km) compared to the core zone (1.03 individuals/km) (ANOVA, t-test = 5, p = 0.01).

AVAHI LANIGER HABITAT PREFERENCE. The most common tree species that *A. laniger* were observed in were *Labourdonnaisia laciniata* (vernacular name: *Menahihy*), *Syzygium cuneifolium* (*Rotramena*), *Garcinia chapelieri* (*Fantsikahitra*), *Brexiella cymosa* (*Ranga*), *Syzygium cumini* (*Rotrafotsy*). Tree characteristics that had higher occurrences of *A. laniger* were trees with a DBH of 11–20 cm, max height between 9 and 16 m, little crown diameter < 5 m, and a canopy coverage that is semi-open or relatively open (Table S3).

VEGETATION ANALYSIS. From our vegetation survey of 2,805 tree observations in the core zone, and 1,405 tree observations in the buffer zone, we identified 110 unique plant genera (Table S4, core = 101 unique plant genera, buffer = 94 unique genera). The Shannon diversity was calculated to test the diversity of plant genera within each zone and then applied to the Hutcheson t-test, which found significant differences between plant genera in

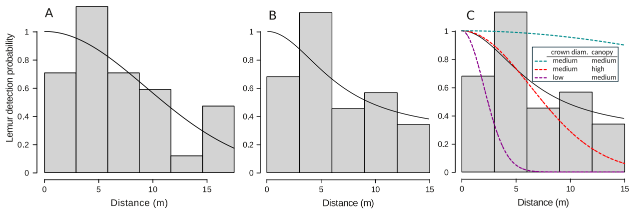

Figure 3. (A) The estimated conventional distance sampling (CDS) detection function for *Avahi laniger* based on the best-fit model. (B) The estimated multiple covariate distance sampling (MCDS) detection function for A. laniger based on the best-fit model. (C) Visualization of the detection function based on the interaction between the two habitats covariates (crown diameter and canopy cover).

Table 1. Best-fit detection model without (-) and with covariates for an area of 8.9 km² and covered area of ~ 1 km². (Model types are D = density per km², A = abundance in core zone, E = expected cluster size; the best-fit density estimate for cluster and individual *Avahi laniger* are in bold)

Model	Level	Covariates	Estimate	Se	Coeff variation	Lower & upper CI
D	Cluster	-	37.6	11.1	0.3	20.7 -68.5
A	Cluster	-	336.0	99.2	0.3	184.5 -611.7
D	Individual	-	60.0	15.2	0.3	36.0 -99.9
A	Individual	-	535.5	135.3	0.3	321.7 -891.4
E	NA	-	1.6	0.2	NA	1.2 -1.9
D	Cluster	Canopy cover + crown distance	41.2	14.6	0.4	20.2 -84.0
A	Cluster	Canopy cover + crown distance	367.8	130.4	0.4	180.5 - 749.4
D	Individual	Canopy cover + crown distance	63.9	24.1	0.4	30.2 -135.4
A	Individual	Canopy cover + crown distance	570.5	215.1	0.4	269.5 - 1208.1
E	NA	Canopy cover + crown distance	1.6	0.2	NA	1.1 - 2.0

the core and buffer zone (t-statistic = -8.93, df = 535.05, p-value < 0.001). The buffer is less diverse than the core zone (3.3 vs. 3.8, respectively). The dissimilarity metrics (Jaccard = 0.39, Sørensen = 0.24, Bray-Curtis = 0.60) are greater than zero and suggest differences in plant diversity between the core and buffer zones. The linear mixed effects models testing the association of habitat variables by zone (with genus as a random effects) found evidence of differences in plant characteristics between the core and buffer zones. For the fixed effects, tree DBH and maximum height were significantly different between the zones (Table S5). The strongest relationship was for maximum tree height with the core zone having significantly taller trees than the buffer zone (genus fixed effects: estimate = 0.56, se = 0.16, df = 1629.73, t-statistic = 3.51, p-value < 0.001). The next strongest relationship was between tree DBH with the core zone having lower tree DBH than the buffer zone (genus fixed effects: -0.87, se = 0.32, df = 1617.6, t-statistic = -2.75, p-value < 0.01). We did not find significant differences in tree crown distances between zones (Table S5). Similarly, canopy cover percentages showed little variation, with the core area averaging 64.2% and the buffer zone 64.7%, both exhibiting a semi-open canopy.

DISCUSSION

This study provides updated information on the current population status of *Avahi laniger* in the Ambohidray PA, intended to support conservation planning and management decisions. Our study found an estimated density of 41 groups/km2 and 63 individuals/km2 with our best-fit MCDS model. The result of the multiple covariates distance sampling allows us to know the potential habitat preference of *A. laniger*, which is a combination of small crown diameter and semi-open canopy cover. Notably, in our study, the occurrence of *A. laniger* was higher in the buffer zone compared to the core zone.

When compared to other regions of Madagascar, the estimated density of 63 individuals/km² in the Ambohidray PA is relatively high. Previous studies that employed similar methods to estimate *Avahi laniger* populations have reported densities ranging from 13 to 41 individuals/km² (Rakotondratsimba et al. 2013, Sabin 2013, Rakotomalala et al. 2017). However, these studies were conducted in forests across Madagascar, each subject to varying levels of anthropogenic pressures. In general, *A. laniger* appears to reach higher population densities in fragmented or disturbed forests compared to large, intact forest areas. For example, in the Ankadivory Classified Forest (Tsinjoarivo-Ambatolampy), a relatively small forest fragment of less than 20 ha and under significant anthropogenic pressure, Rakotomalala and collaborators (2017) reported a density of 31.98 ± 9.05 individuals/km². Similarly, in the VOI forest of Ambodiriana Manompana, a predominantly primary forest covering 2.25 km², Sabin (2013) estimated a density of 41 individuals/km². In contrast, Rakotondratsimba and collaborators (2013) recorded a much lower density of only 13 individuals/km² in the extensive (~8,000 ha) and largely undisturbed humid evergreen forest of Torotorofotsy. An exception to this trend is found in the Ambatovy–Analamay forest, where extremely high densities of 235 and 172 individuals/km² were recorded in plots with natural forest in good condition, and 140 individuals/km² in a degraded plot (Ralison 2010). Although large-scale mining was planned for the area, extraction activities had not yet resumed at the time of the inventory; however, road construction linked to the project had already begun, providing access to the forest plots. This area is where a large scale mining activities have been occurring. These findings suggest that *A. laniger* may reach higher densities in disturbed or fragmented forests. However, this apparent pattern may be influenced by methodological and ecological biases (Buckland 2001) related to forest size, disturbance level, and transect coverage. In smaller forests like Ambohidray, transects may cover a larger proportion of the total area, increasing the likelihood of detection and potentially inflating density estimates. Furthermore, habitat fragmentation can concentrate individuals in the remaining patches of suitable habitat (Irwin et al. 2010), leading to artificially high local densities that reflect habitat limitation rather than true preference.

In our study, *Avahi laniger* was encountered more frequently in the buffer zone, although it was also present in the core. The lack of strong negative response to forest degradation resembles the pattern observed in forest remnants of north-eastern Madagascar (Schüßler et al. 2018). This suggests that *A. laniger* may be more sensitive to habitat area than to degradation level. In contrast, on the Masoala Peninsula, *Avahi mooreorum* showed significant differences in abundance across distinct forest types (Sawyer et al. 2017). Its specialized locomotion and dietary requirements may make it more vulnerable to habitat disturbance. However, it is important to note that the comparison in that study was between clearly different forest types, while our study focused on varying levels of disturbance within a single forest type. The results of these studies suggest that *A. laniger* can thrive in general fragmented habitats, and similar patterns were observed in the Ambohidray PA, where the species displayed relatively high densities and a preference for the buffer zone. However, the sensitivity of population density estimates to factors such as fragmentation, forest type, and sampling methods warrants further investigation.

We were able to detect higher occurrences of *Avahi laniger* individuals in trees that had a DBH of 11–20 cm, max tree height between 9 and 16 m, small crown diameters, and a canopy coverage that is semi-open or relatively open. The woody plants most commonly used by *A. laniger* in our observations—such as *Syzigium* spp. (*rotrafotsy* and *rotramena*), *Garcinia chapelieri* (*fatsikahitra*), and *Labourdonnaisia laciniata* (*menahihy*)—have also been reported as componients of its diet (Harcourt 1991, Ganzhorn et al. 1985, Faulkner and Lehman 2006). Previous studies have documented that *A. laniger* typically rests on vertical tree trunks supported by thin branches at heights ranging from 5 to 10 m (Harcourt 1991) and more generally at heights ranging from 2 to 10 m (Ganzhorn et al. 1985). Furthermore, Ganzhorn (1989) reported that trees where *A. laniger* were found in the National Park Analamazoatra had a mean DBH of 15.62 cm, a mean height of 9.17 m, and a mean crown diameter of 3.11 m. Interestingly, the trees used by *A. laniger* in Ambohidray PA do not appear to have distinct characteristics compared to those in other localities. This suggests that the species may demonstrate flexibility in its habitat use, potentially adapting to various types of trees across different regions.

We were able to detect a significant difference in plant diversity between core and buffer zones (3.8 vs. 3.3, respectively). Beta diversity metrics also indicated differences between the zones (Bray-Curtis = 0.60, Jaccard = 0.39, Sørensen = 0.24), but these differences varied in magnitude across the indices. The linear mixed-effects models indicated significant differences in tree characteristics between zones, with taller trees in the core zone and trees with larger DBH in the buffer zone. The canopy cover percentages were nearly identical between the zones, with both exhibiting a semi-open canopy. No significant differences were observed in tree crown diameter between the zones. Although the core zone has taller trees overall, particularly within the preferred height range of *Avahi laniger* (11–20 m), the species shows a preference for the buffer zone. This preference may seem surprising, as the core zone contains more trees of the preferred height range for this species. The density and distribution of lemurs are influenced by factors beyond vegetation characteristics, including food availability, competition, predation pressure, and habitat disturbance. The presence of the species in both habitat types with higher encounter rates in the buffer zone despite the significant difference in plant diversity, may indicate that the species can tolerate variation in plant diversity between habitats (Norscia et al. 2006). This magnitude of difference of plant diversity may not be large enough also to be spatial patterns of the species. Additionally, higher light levels and limited temperature variation in the buffer zone likely improve leaf quality (Ganzhorn 1995), making it a more valuable food source for folivores. Coexisting species like *A. laniger* and *Indri indri* exhibit different activity patterns, allowing them to share similar habitats (Ganzhorn 1989), while competition with nocturnal lemurs such as *Lepilemur* spp. for food quality and habitat selection (Ganzhorn 1993, Thalmann 2001, Ralison 2010) may push *A. laniger* to fragmented habitats near edges. Although habitat fragmentation happen in the buffer zone, *A. laniger* may occasionally use these areas to reduce competition for resources making the buffer zone a refuge for the species.

How land is managed can be informed by ecological studies that focus on key species important to the cultural and ecological characteristics of Madagascar. Our findings serve as a reference for future ecological monitoring as anthropogenic pressures increase throughout Madagascar's landscape, particularly affecting species such as the *Avahi laniger*. Variation in abundance across the species' range is likely linked to habitat characteristics, such as canopy cover and tree height, which influence the species' fitness responses. Despite these differences in tree characteristics, they do not seem to affect *A. laniger*'s occurrence, suggesting the species can tolerate a range of tree characteristics. Although there are differences in plant diversity between the two zones, these metrics may change over time due to forest degradation or conservation efforts, which could influence habitat suitability for *A. laniger*. Continuous monitoring is essential to understand how these dynamics impact the species' distribution over the long term.

Although our study was able to achieve some of the objectives we sought to address, there is additional methods that could fill remaining knowledge gaps. An important aspect of an ecological study is understanding how a species can respond to seasonal changes which can alter their food preferences and behavior. Because of logistical constraints, our study took place only during the dry season. Many lemur species, including *Avahi laniger* are active throughout the year (Harcourt 1991). However extending the study into the rain season, when more food is available in Madagascar's rainforest (Campera et al. 2021) would allow for a more comprehensive understanding of *A. laniger* population dynamics. As the transition from *Least Concern* to *Vulnerable* on the ICUN Red List suggests, this species is experiencing population-level threats that may be the result of habitat change from anthropogenic pressures such as conversion of land to agriculture or mining activities. A more nuanced study that takes into consideration the type and magnitude of anthropogenic stress on lemur habitat and populations may be more appropriate to inform policy on land management and conservation. Also, *A. laniger* does not represent all lemur species in the Ambohidray PA, and other considerations beyond our results should be incorporated into non-*A. laniger* ecological studies such as those focused on *Propithecus diadema*, *Indri indri*, *Hapalemur griseus*, *Eulemur fulvus*, Lepilemur *mustelinus*, *Cheirogaleus* spp., and *Microcebus* spp.

IMPLICATIONS FOR CONSERVATION MANAGEMENT. The higher density of *Avahi laniger* in the buffer zone compared to the core zone suggests that this area could play a critical role in species conservation. Given that the buffer zone is subject to anthropogenic pressures, such as human disturbance and habitat fragmentation, effective management strategies could focus on enhancing the ecological conditions within these zones. For example, management efforts could prioritize reducing disturbances in the buffer zone to maintain its role as a refuge for *A. laniger*. Moreover, the distinct tree characteristics observed in both zones- such as tree height and DBH- indicate the importance of maintaining diverse tree structures for the species' habitat. Forest restoration initiatives that focus on promoting a variety of tree sizes and canopy cover in degraded areas may improve the suitability of the landscape for *A. laniger*, especially in the buffer zone where the species seems to thrive. Finally, continuous monitoring of the species' distribution and habitat use in both the core and buffer zones is crucial for assessing the effectiveness of conservation measures over time. By tracking how changes in vegetation structure, fragmentation, and human activity impact the species, management practices can be adapted to ensure *A. laniger*'s persistence in the Ambohidray NA.

ACKNOWLEDGEMENTS

HR and SS want to thank the Coding 4 Conservation and E2M2 communities for their feedback on the project. We especially thank and recognize Dr. Cara Brooks who led both programs and contributed greatly to the manuscript including figure making, analyses, and feedback on multiple drafts. The authors thank the community of Ambohidray (VOI Miray) and the Plant Biology and Ecology Department at the University of Antananarivo, the managers of the Ambohidray PA for the approval of the project and the reception at site. HR acknowledges the Department of Animal Biology, University of Antananarivo. HR also acknowledges VolkswagenStiftung for financial, technical, and logistical support in the realization and presentation of this work.

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Supplemental Text 1

Additional information regarding sampling design and techniques

Sampling results from the impossibility of collecting data over the entire area studied. For the present study, it is based on the establishment of transect lines installed so as to cover the majority of the study area. The latter was divided into two sampling areas according to the level of anthropogenic pressure exerted on the environment, which is defined as all the disturbances caused by humans and their activities (Irwin et al. 2010). For this, the zoning of the protected area already established was used: the core zone, a strictly protected zone, hence less human disturbance and the buffer zone, zone where various economic activities are permitted, hence a stronger disturbance.

Transects of approximately 1 km are installed in all existing forest blocks in a more or less parallel manner following the north direction of the compass. Each transect is spaced at least 200 m apart to avoid counting errors. Thus, 13 transects were obtained including 8 transects located in the core zone and 5 transects in the buffer zone, giving a total length of 12.9 km (Figure 2, Figure S1, S2). Transect lines are placed at least 24 hours before the start of the first observation to avoid any disturbance to the animals. Each 50 m interval of the transect line was marked with a colored ribbon to facilitate their identification and orientation during observations.

Additional Information regarding Canopydigi

Estimating the degree of canopy cover is important to see the relationship between a species and its habitat (Goodenough and Goodenough 2012). The photographic method is the most precise method to provide canopy cover estimates and is applied in this study (Paletto and Tosi 2009). The photos of the canopy were taken in the middle of each subplot (25 2 x 2 m) using a digit camera. These images are then analyzed with the free software Canopydigi developed by Goodenough and Goodenough (2012).

The images taken at the plots are polychrome and in JPEG format, while the software Canopydigi uses monochrome images with different shades of grey (256 shades of gray; 0 for black, 255 for white) and in BMP format. The free and open-source software ReaConverter Lite has been used for conversion. These monochrome images are converted into "false color" images by Canopydigi, in which dark pixels colored blue represent the canopy and pixels colored in red represent the sky. The user then chooses a threshold that is closest to the corresponding monochrome image. Finally, the software makes an automatic calculation and thus gives the percentage of canopy cover from these false color images. Once the canopy cover percentages are interpreted, they are classified into canopy groups designed by Ganzhorn et al. (1985): open (canopy coverage ≤ 20%), relatively open (21 – 50 %), semi-open (51 – 70 %), relatively closed (71 – 90 %), and closed (> 90 %).

Raharinirina, H., Sambado, S., Richard, Y., Ravelojaona, R. N., Rakotomalala, Z. and Ratsoavina, F. M. 2025. Distribution and habitat use by the eastern woolly lemur, Avahi laniger (Gmelin 1788), in the fragmented forests of the Ambohidray Protected Area, Central-Eastern Madagascar. Madagascar Conservation & Development 20, 1: 32–40. Supplementary Material. https://doi.org/10.4314/mcd.v20i1.4

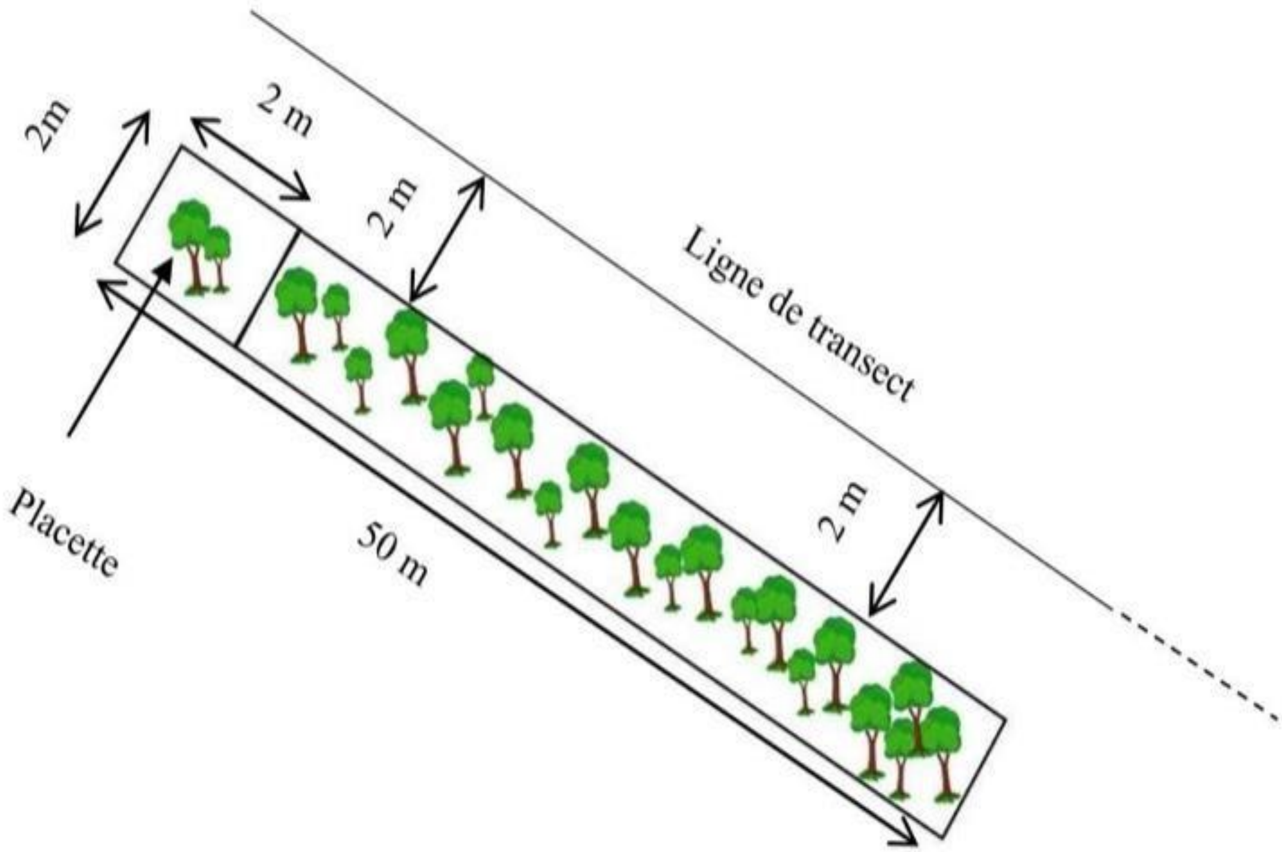

Figure S1. Diagram showing the device of the botanical plot used for the study of the habitat using the transect method by Braun-Blanquet (1995). (*Ligne de transect* for transect line, *placette* for small plots)

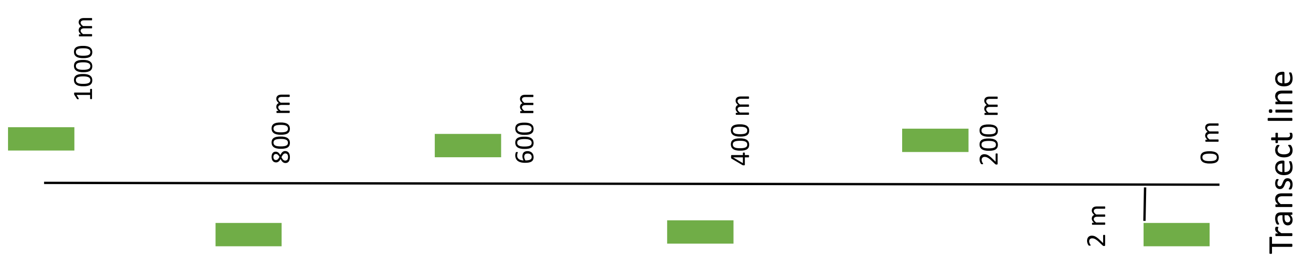

Figure S2. Schematic representation of vegetation plot sampling.

Raharinirina, H., Sambado, S., Richard, Y., Ravelojaona, R. N., Rakotomalala, Z. and Ratsoavina, F. M. 2025. Distribution and habitat use by the eastern woolly lemur, Avahi laniger (Gmelin 1788), in the fragmented forests of the Ambohidray Protected Area, Central-Eastern Madagascar. Madagascar Conservation & Development 20, 1: 32–40. Supplementary Material. https://doi.org/10.4314/mcd.v20i1.4

Table S1. Results from the density estimation models of *Avahi laniger*.

Key Function & Adj	Formula	CvM	Pa hat	se Pa hat	delta AIC
Half-normal	~1	0.67	0.63	0.10	0.00
Hazard-rate	~1	0.72	0.66	0.13	1.50
Half-normal with cosine adjustment term of order 2	~1	0.73	0.68	0.22	1.89
Half-normal with Hermite polynomial adjustment term of order 4	~1	0.71	0.66	0.19	1.95
Half-normal with simple polynomial adjustment term of order 4	~1	0.67	0.63	0.15	1.99
Hazard-rate with Hermite polynomial adjustment term of order 4	~1	0.72	0.66	0.20	3.50
Hazard-rate with simple polynomial adjustment term of order 4	~1	0.72	0.66	0.15	3.50
Hazard-rate with cosine adjustment term of order 2	~1	0.72	0.66	0.24	3.50
Half-normal with cosine adjustment terms of order 2,3	~1	0.66	0.63	0.22	3.66
Half-normal with simple polynomial adjustment terms of order 4,6	~1	0.68	0.63	0.21	3.92
Half-normal with Hermite polynomial adjustment terms of order 4,6	~1	0.71	0.66	0.23	3.96
Hazard-rate with simple polynomial adjustment terms of order 4,6	~1	0.72	0.68	0.18	5.40
Hazard-rate with Hermite polynomial adjustment terms of order 4,6	~1	0.70	0.65	0.22	5.45
Hazard-rate with cosine adjustment terms of order 2,3	~1	0.70	0.65	0.23	5.46
Half-normal	~scale_crown + scale_canopy	0.75	0.63	0.14	0.00
Half-normal	~scale_crown + scale_DBH	0.75	0.61	0.63	1.57
Half-normal	~crown_dist_m	0.87	0.73	0.16	1.97
Half-normal	~scale_crown + scale_canopy + scale_height	0.75	0.63	0.17	2.00
Half-normal	~1	0.67	0.79	0.13	2.94
Half-normal	~scale_crown + scale_canopy + scale_DBH	0.70	0.61	0.76	3.47
Half-normal	~scale_crown + scale_height	0.82	0.74	0.25	3.84
Half-normal	~zone	0.68	0.77	0.16	3.89
Half-normal	~max_height_m	0.71	0.75	0.12	3.95
Half-normal	~canopy_cover	0.66	0.77	0.13	3.96
Half-normal	~DBH_cm	0.70	0.82	0.15	4.67
Half-normal	~scale_canopy + scale_DBH	0.87	0.77	0.16	5.00

Raharinirina, H., Sambado, S., Richard, Y., Ravelojaona, R. N., Rakotomalala, Z. and Ratsoavina, F. M. 2025. Distribution and habitat use by the eastern woolly lemur, Avahi laniger (Gmelin 1788), in the fragmented forests of the Ambohidray Protected Area, Central-Eastern Madagascar. Madagascar Conservation & Development 20, 1: 32–40. Supplementary Material. https://doi.org/10.4314/mcd.v20i1.4

Table S2. Total number of *Avahi laniger* on individual transects detected across the field season by forest zone.

Zone	**Transect #**	**Number of *A. laniger* (nighttime)**	**Encounter rates (number of individuals / km)**
CORE	T3	3	1.05
	T4	0	0
	T5	5	1.66
	T6	5	1.66
	T8	2	0.57
	T9	7	2.33
	T12	1	0.33
	T13	2	0.66
BUFFER	T1	4	1.66
	T2	4	1.33
	T7	10	3.33
	T10	6	2
	T11	9	3

Raharinirina, H., Sambado, S., Richard, Y., Ravelojaona, R. N., Rakotomalala, Z. and Ratsoavina, F. M. 2025. Distribution and habitat use by the eastern woolly lemur, Avahi laniger (Gmelin 1788), in the fragmented forests of the Ambohidray Protected Area, Central-Eastern Madagascar. Madagascar Conservation & Development 20, 1: 32–40. Supplementary Material. https://doi.org/10.4314/mcd.v20i1.4

Table S3. Observed group of *Avahi laniger* in tree habitats across the study period. (daytime and nighttime observation, n= 39 observations)

Characteristics	Classifications	Observed lemurs
DBH class (cm)	2.5 – 5	0
	6 – 10	7
	11 – 20	24
	21 – 30	5
	> 30	3
Height class (m)	2 – 4	0
	5 – 8	9
	9 – 16	26
	17 – 32	1
Canopy cover (%)	Open (< 20%)	0
	Relatively open (21-50%)	3
	Semi-open (51-70%)	26
	Relatively closed (71-90%)	7
	Closed (>90%)	0
Crown diameter (m)	Little (<5)	22
	Medium (5 – 10)	12
	Big (> 10)	

Raharinirina, H., Sambado, S., Richard, Y., Ravelojaona, R. N., Rakotomalala, Z. and Ratsoavina, F. M. 2025. Distribution and habitat use by the eastern woolly lemur, Avahi laniger (Gmelin 1788), in the fragmented forests of the Ambohidray Protected Area, Central-Eastern Madagascar. Madagascar Conservation & Development 20, 1: 32–40. Supplementary Material. https://doi.org/10.4314/mcd.v20i1.4

Table S4. Counts of observed trees by zone (identified at the genus level)

Family	Genus	Number of trees in CORE	Number of trees in BUFFER ZONE
ANACARDIACEAE	*Baronia*	9	1
	Micronychia	3	
ANNONACEAE	*Xylopia*	47	19
APHLOIACEAE	*Aphloia*	4	1
APOCYNACEAE	*Mascarenhasia*	10	4
ARALIACEAE	*Neocussonia*	1	1
ARECACEAE	*Dypsis*	5	
	Phloga (Dypsis)	1	
ASPARAGACEAE	*Dracaena*	22	1
ASTERACEAE	*Brachylaena*	15	
	Erigeron	16	
	Helichrysum	26	
ASTEROPEIACEAE	*Asteropeia*	17	2
BIGNONIACEAE	*Phyllarthron*	1	
BURSERACEAE	*Canarium*	12	4
CANNABACEAE	*Trema*	40	4
CELASTRACEAE	*Brexiella*	72	39
CLUSIACEAE	*Garcinia*	74	16
	Symphonia	34	6
CUNONIACEAE	*Weinmannia*	2	
EBENACEAE	*Diospyros*	18	5
ERICACEAE	*Philippia (Erica)*	2	
	Vaccinium	6	1
EUPHORBIACEAE	*Croton*	14	1
	Macaranga	15	3
FABACEAE	*Albizia*	29	6
	Cadia	4	
	Dalbergia	6	3
	Entada	23	3

Family	Genus	Number of trees in CORE	Number of trees in BUFFER ZONE
	Phylloxylon	3	
	Viguieranthus	3	23
GENTIANACEAE	*Anthocleista*	14	1
HERNANDIACEAE	*Hernandia*	8	4
HYPERICACEAE	*Harungana*	7	1
	Psorospermum	1	1
LAURACEAE	*Aspidostemon*	10	
	Cryptocarya	78	27
	Ocotea	34	8
MALVACEAE	*Dombeya*	48	12
MORACEAE	*Ficus*	1	1
	Streblus	14	1
MYRICACEAE	*Morella (Myrica)*	1	
MYRTACEAE	*Eucalyptus*	1	
	Eugenia	37	17
	Psidium	2	
	Syzygium	172	35
PITTOSPORACEAE	*Pittosporum*	19	1
PROTEACEAE	*Dilobeia*	2	3
PUTRANJIVACEAE	*Drypetes*	20	2
RUBIACEAE	*Coffea*	2	1
	Gaertnera	8	
	Hyperacanthus	1	1
	Ixora	7	
	Peponidium	6	
	Psychotria	2	1
	Saldinia	1	
	Tarenna	5	1
RUTACEAE	*Vepris*	6	4
	Zanthoxylum	1	

Family	Genus	Number of trees in CORE	Number of trees in BUFFER ZONE
SALICACEAE	*Homalium*	10	1
	Scolopia	4	11
SAPINDACEAE	*Plagioscyphus*	17	
	Tina	21	7
	Tinopsis	21	
SAPOTACEAE	*Gambeya*	45	23
	Labourdonnaisia	47	53
SARCOLAENACEAE	*Rhodolaena*	19	
	Sarcolaena	24	
SOLANACEAE	*Solanum*	8	1
STILBACEAE	*Nuxia*	7	5
VIOLACEAE	*Rinorea*	1	
ANACARDIACEAE	*Baronia*	9	1
	Micronychia	3	
ANNONACEAE	*Xylopia*	47	19
APHLOIACEAE	*Aphloia*	4	1
APOCYNACEAE	*Mascarenhasia*	10	4
ARALIACEAE	*Neocussonia*	1	1
ARECACEAE	*Dypsis*	5	
	Phloga (Dypsis)	1	
ASPARAGACEAE	*Dracaena*	22	1
ASTERACEAE	*Brachylaena*	15	
	Erigeron	16	
	Helichrysum	26	
ASTEROPEIACEAE	*Asteropeia*	17	2
BIGNONIACEAE	*Phyllarthron*	1	
Total number of trees		**1,266**	**366**
Number of families		**39**	**32**
Number of genera		**71**	**46**

Table S5. Linear mixed effect model results for habitat characteristics per zone. Three separate models were ran (model 1 = DBH ~ zone, model 2 = Crown distance ~ zone, model 3: Max height ~ zone) with the random effect genera.

	DBH	Crown distance	Max height
Buffer Zone	8.39 (0.42)	2.39 (0.10)	6.55 (0.19)
Core Zone	7.56 (0.34)	2.40 (0.08)	7.12 (0.15)
SD (Intercept sci_name)	2.42	0.51	1.00
SD (Observations)	4.94	1.30	2.52
Number of observations	1632	1632	1632
R2 Marg.	0.004	0.000	0.008
R2 Cond.	0.197	0.133	0.143
AIC	9967.5	5601.4	7751.5
BIC	9989.1	5622.9	7773.1
ICC	0.2	0.1	0.1
RMSE	4.86	1.28	2.48

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