

Diversity and altitudinal distribution of lemurs on the eastern slopes of the Marojejy Massif

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Abstract

We conducted a census of lemurs in the Parc National de Marojejy between 2 October and 15 November 2021 at five sites along an elevational transect from 480 to 1880 m and across a range of vegetation formations. This transect was in parallel to a similar one conducted in 1996 and following the same dates and field techniques, which included standard line transects varying in length from 150 to 1000 m during the day and night and noting all lemur observed. Nine species of lemurs were identified, including one diurnal species (*Propithecus candidus*), three cathemeral species (*Haplemur occidentalis*, *Eulemur albifrons*, and *E. rubriventer*), and five nocturnal species (*Avahi laniger*, *Cheirogaleus crossleyi*, *Microcebus lehilahytsara*, *Lepilemur seali*, and *Allocebus trichotis*). The local presence of *Daubentonia madagascariensis* was reported by the local guides, but this species nor signs of its presence were not observed during the 2021 survey. Species richness by elevational zone were quite similar based on the results from 1996 and 2021, with the highest species richness in the elevational range from 750 to 1300 m and lowest at 1880 m, which can be explained by elevational differences in meteorological gradients and available food resources. However, the main differences between both studies is the presence of *Daubentonia madagascariensis* and *Phaner furcifer* in 1996 and not in 2021 and observations of *Allocebus trichotis* in 2021 and not in 1996. Lemur abundance was notably higher in 1996 than in 2021; an explanation for this general pattern is difficult to discern but is presumably related to changes in vegetation structure associated with the passage of local cyclones or more general patterns of climatic

change. The occurrence in the Marojejy forests of some lemur species of high conservation importance makes the park a critical locality for the conservation of these animals; hence, the need to maintain its world heritage site status.

Key words: lemurs, census, Marojejy, 1996 and 2021, community trends, conservation

Résumé détaillé

Le Parc National de Marojejy attire bon nombre de visiteurs grâce à l'aspect verdoyant et la topographique de la forêt et surtout la présence de la faune endémique de la région. Ce parc constitue un des refuges des espèces de lémuriens du Nord-est de Madagascar, avec la présence des cinq familles endémiques de Madagascar.

Afin d'évaluer le changement éventuel de la communauté de lémuriens du parc au cours des 25 dernières années, un inventaire biologique tenant compte des sites d'étude en 1996 a été réalisé entre le 2 octobre et le 15 novembre 2021. Les inventaires ont été menés dans cinq sites de différentes altitudes au sein du parc, le long d'un gradient altitudinal de 480 à 1880 m. Pour pouvoir faire la comparaison, les approches utilisées en 1996 ont été gardées autant que possible (sites d'inventaire, méthodes, dates). En effet, la méthode de transect a été utilisée tout en essayant de noter les espèces de lémuriens diurnes et nocturnes rencontrées ou entendues le long de ce transect pour connaître la richesse spécifique et estimer la densité de la population. En termes de traitement de données, la courbe cumulative des espèces permet d'exprimer la valeur de l'effort de l'échantillonnage pour chaque site ; l'indice kilométrique d'abondance permet de mesurer l'abondance relative des espèces le long d'un trajet et d'estimer la densité.

Un total de neuf espèces de lémuriens a été recensé dans le parc en 2021 dont une espèce diurne (*Propithecus candidus*), trois espèces cathémérales (*Eulemur rubriventer*, *Eulemur albifrons* et *Haplemur occidentalis*) et cinq espèces nocturnes (*Microcebus lehilahytsara*, *Allocebus trichotis*, *Cheirogaleus crossleyi*, *Lepilemur seali* et *Avahi laniger*). La présence de *Daubentonia madagascariensis* dans le parc a été signalée par les guides locaux. Le nombre

maximum d'espèces par zone d'élévation est de neuf à 1300 m.

Les deux études (1996 et 2021) ont presque donné les mêmes résultats en termes de richesse spécifique par zone d'altitude, avec plus de concentration de lémuriens à 750 et 1300 m, alors que la richesse est faible à 1880 m. De plus, la distribution de ces espèces varie le long du gradient altitudinal. Ce phénomène pourrait être expliqué par la variation des aspects météorologiques et celle des formations végétales suivant l'altitude. Dans l'intervalle entre les deux études, certains changements ont eu lieu dans la taxonomie des espèces de lémuriens présents à Marojejy.

La principale différence de ces deux études est la présence/absence de *Daubentonia madagascariensis*, de *Phaner furcifer* et de *Allocebus trichotis* : les deux premières espèces ont été trouvées en 1996 et la dernière étant en 2021. De plus, la communauté lémurienne du parc était plus abondante en 1996 qu'en 2021 ; une explication de ce schéma général est difficile à trouver mais elle est probablement liée à des changements dans la structure de la végétation associés au passage des cyclones dans la région ou à des schémas plus généraux de changement climatique. La présence de certaines espèces de lémuriens à haute importance de conservation sur le massif de Marojejy fait du parc un habitat critique à fort intérêt pour la conservation de ces espèces, d'où la nécessité de le garder dans le réseau de sites patrimoniaux mondiaux.

Mots clés : lémuriens, recensement, Marojejy, 1996 et 2021, dynamique de la communauté, conservation

Introduction

About half of Madagascar's forest cover was lost in the 20th century and the remaining forest habitat covers about 15% of the island (McConnell & Kull, 2014; Waeber *et al.*, 2020). One important protected area with reference to its exceptional biodiversity is the Parc National de Marojejy, which in 2007 was designated as part of a UNESCO World Heritage Site. The Marojejy Massif covers an elevational range varied between 75 to 2132 m, which contributes to its varied and diverse flora and fauna (Goodman, 2000; Goodman *et al.*, 2018).

The Parc National de Marojejy is a relatively large block of nearly continuous forest dominated by numerous peaks, the main culminating at 2130 m. The massif has different vegetation formations, ranging from lowland moist evergreen forest to

montane grassland (following the classification of Gautier *et al.*, 2018), and subjected to the action of humid ascending air currents from the Indian Ocean, which generate precipitation (Humbert, 1965). Marojejy attracts numerous tourists due to its extraordinary landscapes, excellent trail system, and unique plants and animals. Ecotourism contributes to the protection of the park's biota and the economic development of local guides and regional inhabitants.

Differentiated from other regions of eastern Madagascar by its exceptionally rich biodiversity and high rates of endemism, the Parc National de Marojejy constitutes one of the last refuges for lemur species in northeastern Madagascar. The five endemic families of Malagasy lemurs are known across the broad elevational gradient of the park, and include 11 known species (Goodman *et al.*, 2018).

Lemurs at Marojejy are subject to specific threats, including the natural perturbation of forest such as cyclones, human destruction of their habitats by logging of selected woods, illegal exploitation, swidden agriculture (often referred to as slash-and-burn), and hunting (Patel, 2007; Loudon *et al.*, 2017). It is important to mention that certain species of lemurs with a distribution area below 50,000 km² are sensitive to disturbance of their habitat, and these taxa require intact forests to survive. Indeed, such taxa are good indicators of the quality of the forest ecosystem (Ganzhorn, 1999).

In 2010, Marojejy was incorporated into a UNESCO World Heritage Site known as Ala Atsinanana or rainforests of the east and composed of a series of disjunct protected areas. Subsequently, associated with different human pressures, Marojejy and other sites making up the World Heritage Site were placed on the list of World Heritage sites in danger. As a result, important efforts are being made to advance local conservation and remove the park from this ranking. Up-to-date scientific information is essential to the protected area manager, Madagascar National Parks, to fulfill their mission in terms of management and conservation.

The aim of this study is to survey lemur populations along an elevational gradient in the eastern portion of the Parc National de Marojejy, which is the zone visited by most tourists, and to compare our results with a parallel inventory conducted in 1996 along the same transect by Sterling and McFadden (2000), providing a window into possible changes in the lemur community of the park over 25 years.

Methods

Study area

Our study zone in the Parc National de Marojejy was along the eastern slopes, specifically the area used for tourist visits and in five different altitudinal zones: 480 m (Site 1), 750 m (Site 2), 1300 m (Site 3), 1550 m (Site 4), and 1880 m (Site 5). The following main forest vegetational types have been recognized on the massif: lowland moist evergreen forests (below 800 m), medium altitude moist evergreen forests (800-1400 m), high altitude moist evergreen forest (1400-1800 m), and ericoid montane thickets (above 1800 m) (Gautier, 2018). For different parameters on the vegetational structure of the five sites and relation to altitude see Tahinarivony (2023a, herein). In the Marojejy forest, the vertical structure is formed by arborescent strata including large trees over 25 m high, an upper stratum between 15 and 25 m, a middle stratum between 5 and 15 m high (sometimes very dense), and a lower stratum less than 5 m high with young trees and bushes forming a variable shrub layer intermingled with lianas.

Census methods

For this study, the survey methods used by Sterling and McFadden (2000) were applied. The field work was conducted between 2 October and 15 November 2021 and included five sites in different elevation zones within the park, and across a gradient from 480 to 1880 m. For each site, an elevational swath centered at the research camp of about 150 m was surveyed.

The standard line transect method was used, which consisted of noting all the species of diurnal and nocturnal lemurs observed along a transect. Observations were made on pre-existing or newly established trails. Each transect varied in length from 150 to 1000 m and during a transect period were traveled slowly, at a speed of about 1 km per hour. In certain elevational zones the topography was rather abrupt and at such sites it was difficult to find trails of notable length and falling within the elevational zone. The number of transect trails installed per site varied from three to six. Three to eleven replicates per transect were conducted. Geographic coordinates from each transect point were recorded (Figure 1) and the specific details are presented in Appendix 1. The duration of sampling per site was six days and seven nights. The observations were made during the peak of lemur activity, that is to say diurnal surveys were conducted between 5h00 to 11h00 and from 14h00 to 16h00 in the afternoon and nocturnal surveys

from 18h30 to dawn. At night, headlamps were used to locate lemurs and once found a high intensity flashlight for species identification. Observations were made by a primatologist (RR) accompanied by a local guide.

During each encounter with an individual lemur or group of lemurs, the following parameters were noted: species name, date and time of observation, GPS coordinates, elevation (based on GPS reading), number of individuals, perpendicular distance of the animal(s) from the transect trail, estimated height of the animal(s) above ground, animal activity, and, when possible, composition of the group (number, age, and sex).

Also, all lemur sightings outside of the transect work by RR or team other researchers were noted. Any signs of lemur presence such as nests and feeding holes of Aye-aye (*Daubentonia madagascariensis*) were noted.

Species accumulation curves

Species accumulation curves provide insight into the relationship between sampling effort and the number of taxa recorded within each elevational zone. More specifically, if the sampling effort was sufficient to infer the number of locally occurring lemur species towards the end of each site survey, the curve reaches an asymptote. The number of species encountered for each 24-hour period of observation at each study site, separating diurnal and nocturnal periods, was used to construct these curves. Species noted outside of the transects are not considered in the tabulation of these data.

Encounter rates

The encounter rates of each species were estimated by dividing the number of individuals observed with the distance (km) surveyed.

Abundance and density

The estimation of lemur species abundance and density were based on the results of transect observations. To calculate lemur abundance, we employed the Index of Kilometric Abundance (IKA) for each species. IKA is a commonly used measure in wildlife studies because it allows direct comparisons of species abundance at different locations or over time (Vincent *et al.*, 1991; Buckland *et al.*, 1993). In our case, it represents the ratio of the total number of individuals observed along the transect to the total length of the transect inventoried in each elevational zone.

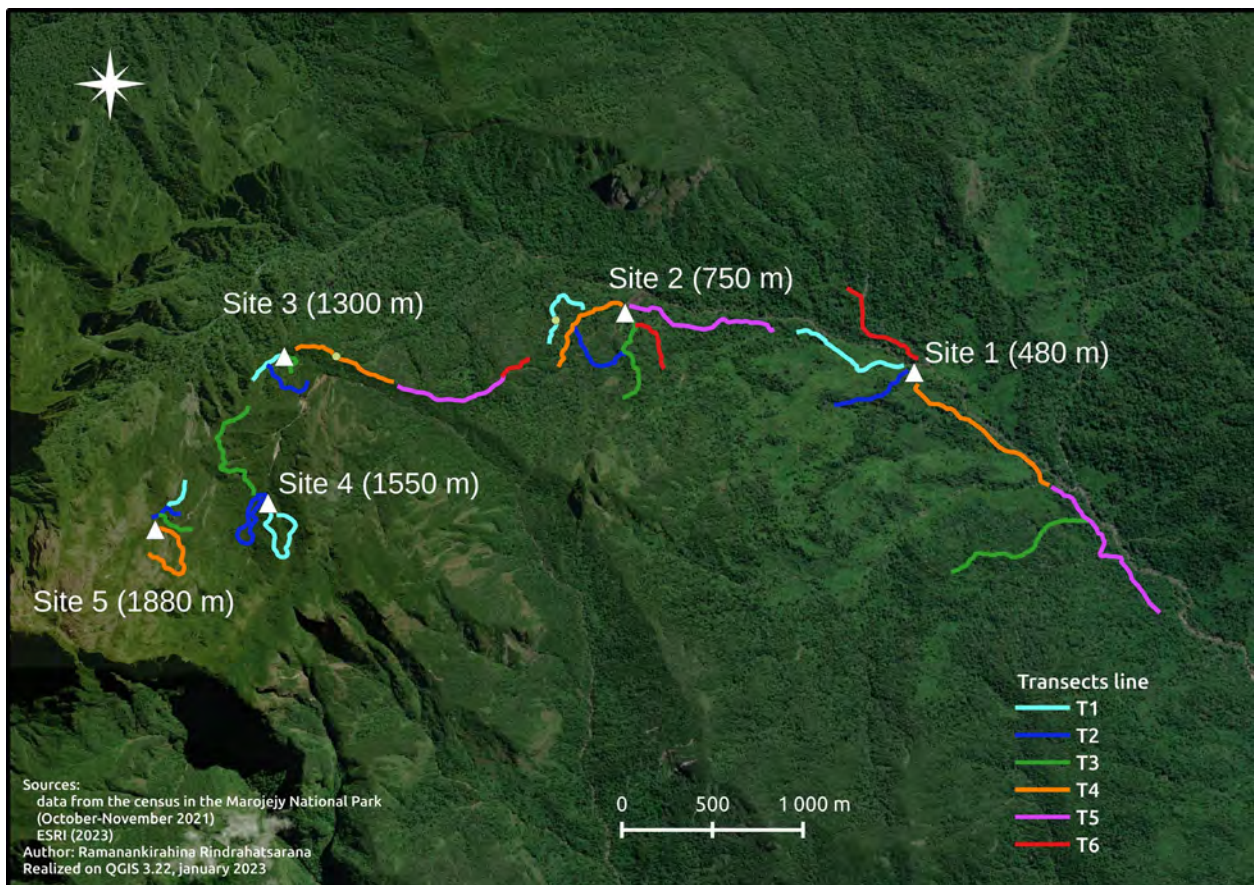


Figure 1. Transects established at each site in the Parc National de Marojejy during the 2021 inventory of the eastern slopes. The details of each trail system per transect site are given in Appendix 1.

Transect line sampling is one of the simplest counting methods for estimating population density of primates (Whitesides *et al.*, 1988) and calculated based on the following equation:

$$D = N/2WL$$

with D: density estimated

N: total number of individuals of a given species

W: perpendicular distance (in m) of individuals observed from the transect

L: total length (in m) of the transect

Results

Species accounts

A total of nine species of lemurs were identified during the 2021 survey, including one diurnal species (*Propithecus candidus*), three cathemeral species (*Hapalemur occidentalis*, *Eulemur albifrons*, and *E. rubriventer*), and five nocturnal species (*Avahi laniger*, *Cheirogaleus crossleyi*, *Microcebus lehilahytsara*, *Lepilemur seali*, and *Allocebus trichotis*)

Table 1. Species richness by elevational zone for transect and general observation data along the eastern slopes of the Parc National de Marojejy from 2 October to 15 November 2021.

Family	Species	Status IUCN	Occurrence in different elevational zones				
			Site 1 (480 m)	Site 2 (750 m)	Site 3 (1300 m)	Site 4 (1550 m)	Site 5 (1880 m)
Cheirogaleidae	<i>Allocebus trichotis</i>	Endangered			X	X	
	<i>Cheirogaleus crossleyi</i>	Vulnerable	X	X	X	X	X
	<i>Microcebus lehilahytsara</i>	Near Threatened	X	X	X	X [§]	X
Lepilemuridae	<i>Lepilemur seali</i>	Vulnerable	X	X	X		
Lemuridae	<i>Eulemur albifrons</i>	Vulnerable	X	X	X*	X	
	<i>Eulemur rubriventer</i>	Vulnerable	X*	X	X	X	
	<i>Hapalemur occidentalis</i>	Vulnerable	X	X	X*		
Indriidae	<i>Propithecus candidus</i>	Critically Endangered		X	X	X	X [§]
	<i>Avahi laniger</i>	Vulnerable		X	X		
Total number of species			6	8	9	6	3

*Species heard but not seen in this elevational zone.

§ Species observed by a member team of survey.

Table 2. A comparison of species present by elevational zone for transect and general observation data for an elevational transect of five sites in the Parc National de Marojejy from 2 October to 15 November 2021 and compared to a parallel transect conducted in 1996 (Sterling & McFadden, 2000). The study zones are the same between the two inventories, although the elevations of the five sites reported in Goodman (2000) are slightly different and associated with advances in GPS technology over the past decades. These aspects are presented in finer detail in Goodman *et al.* (2023, herein).

Species	Survey 2021					Survey 1996				
	Site 1 (480 m)	Site 2 (750 m)	Site 3 (1300 m)	Site 4 (1550 m)	Site 5 (1880 m)	Site 1 (450 m)	Site 2 (775 m)	Site 3 (1250 m)	Site 4 (1625 m)	Site 5 (1875 m)
<i>Allocebus trichotis</i>			X	X						
<i>Cheirogaleus crossleyi</i>	X	X	X	X	X	X	X	X	X	
<i>Microcebus lehilahytsara</i>	X	X	X	X [§]	X	X	X	X	X	X
<i>Phaner furcifer</i>						X*				
<i>Lepilemur seali</i>	X	X	X			X	X	X	X	
<i>Eulemur albifrons</i>	X	X	X*	X		X	X	X	X	
<i>Eulemur rubriventer</i>	X*	X	X	X		X*	X	X	X	
<i>Hapalemur occidentalis</i>	X	X	X*			X	X	X	X	
<i>Propithecus candidus</i>		X	X	X	X [§]			X	X	X
<i>Avahi laniger</i>		X	X			X	X	X		
<i>Daubentonia madagascariensis</i>						X	X	X	X	X
Total number of species	6	8	9	6	2	8	8	9	8	3

*Species heard but not seen in this elevational zone.

§ Species observed by a member team of survey.

Table 3. Number of individuals seen per kilometer transect for diurnal and cathemeral primate species in the Parc National de Marojejy. Detection distance is the mean distance (\pm standard deviation) perpendicular to the trail on which lemurs were seen. The different trails (T) surveyed per site are listed and with coordinates in Appendix I. Key to species names -- *Ea*: *Eulemur albifrons*, *Er*: *E. rubriventer*, *Ho*: *Hapalemur occidentalis*, and *Pc*: *Propithecus candidus*.

Elevation and site	Total length (m)	Number of individuals per species				Total species
		<i>Ea</i>	<i>Er</i>	<i>Ho</i>	<i>Pc</i>	
480 m (Site 1)						
T1	1400	0	0	1.4	0	1
T2	1000	0	0	2	0	1
T3	2000	5	0	1	0	2
T4	4000	0	0	1.3	0	1
T5	4000	1	0	2	0	2
T6	2400	0	0	0	0	0
Detection distance		5.3 \pm 2.08	-	5.4 \pm 2.85	-	
Total number of observations		3	-	19	-	
750 m (Site 2)						
T1	1000	4	0	0	0	1
T2	1000	0	0	0	0	0
T3	2400	3.8	1.3	0	0	2
T4	1875	0	0	0	2.7	1
T5	3000	3.7	0	2	0	2
T6	350	0	0	0	0	0
Detection distance	-	3.4 \pm 3.86	4*	3.3 \pm 0.55	3	-
Total number of observations		14	1	3	2	
1300 m (Site 3)						
T1	675	0	0	0	0	0
T2	1125	0	0	0	0	0
T3	1225	0	2.5	0	0	1
T4	2700	0	0	0	0	0
T5	2800	0	1.4	0	1.4	2
T6	200	0	0	0	0	0
Detection distance		-	5.5 \pm 2.42	-	5.5 \pm 3.54	
Total number of observations		-	4	-	2	
1550 m (Site 4)						
T1	3400	0	0	0	0.6	1
T2	2925	0	1.4	0	0	1
T3	5400	0	0	0	0	0
Detection distance		-	6.5 \pm 3.46	-	10*	
Total number of observations		-	2	-	1	
1880 m (Site 5)						
T1	900	0	0	0	0	0
T2	225	0	0	0	0	0
T3	1000	0	0	0	0	0
T4	1350	0	0	0	0	0
Detection distance		-	-	-	-	
Total number of observations		-	-	-	-	
Mean group size across sites		5.8 \pm 3.21	3.3 \pm 0.76	2.9 \pm 1.86	3.2 \pm 1.62	

* Single sighting at this elevation.

Table 4. Number of individuals of different nocturnal lemur species seen per kilometer of transect trail in the Parc National de Marojejy. Detection distance is the mean distance (\pm standard deviation) perpendicular to the trail on which lemurs were seen. The different trails (T) surveyed per site are listed and with coordinates in Appendix I. Key to species names -- *Al*: *Avahi laniger*, *Ls*: *Lepilemur seali*, *Ml*: *Microcebus lehilahytsara*, *Cc*: *Cheirogaleus crossleyi*, and *At*: *Allocebus trichotis*.

Elevation and site	Total length (m)	Number of individuals per species					Total species
		<i>Al</i>	<i>Ls</i>	<i>Ml</i>	<i>Cc</i>	<i>At</i>	
480 m (Site 1)							
T1	700	0	0	2.9	0	0	1
T2	500	0	0	6	2	0	2
T3	2000	0	0	2.5	1	0	2
T4	2000	0	0.5	2	1.5	0	2
T5	2000	0	0	1	1.5	0	2
T6	1200	0	0	1.7	2.5	0	2
Detection distance		-	6*	4.8 \pm 3.31	6.1 \pm 2.24	-	
Total number of observations		-	1	17	9	-	
750 m (Site 2)							
T1	1000	2	0	0	1	0	2
T2	1000	0	1	0	2	0	2
T3	1200	0	0	0	2.5	0	1
T4	1250	0	0	0.8	1.6	0	2
T5	2000	0	0	0	1	0	1
T6	700	0	0	0	2.9	0	1
Detection distance		6*	0*	4*	6.5 \pm 2.14	-	
Total number of observations		1	1	1	12	-	
1300 m (Site 3)							
T1	900	0	1.1	1.1	0	0	2
T2	1500	0	0	0.7	0.7	0.7	3
T3	700	0	1.4	2.9	0	0	2
T4	2025	1	0	1.5	0.5	0	3
T5	2800	0	0.3	2.5	1.1	0	3
T6	100	0	0	0	0	0	0
Detection distance		4*	4.1 \pm 3.54	3.1 \pm 1.23	2.3 \pm 2.65	3*	
Total number of observations		1	3	9	4	1	
1550 m (Site 4)							
T1	1700	0	0	0	0	0.6	1
T2	1950	0	0	0	0.5	0.5	2
T3	2700	0	0	0	1.1	0.4	2
Detection distance		-	-	-	4.5 \pm 1.86	3.7 \pm 0.64	
Total number of observations		-	-	-	3	3	
1880 m (Site 5)							
T1	1125	0	0	0.9	0.9	0	2
T2	900	0	0	0	0	0	0
T3	500	0	0	0	0	0	0
T4	1350	0	0	1.5	0	0	1
Detection distance		-	-	2.3 \pm 0.63	3*	-	
Total number of observations		-	-	3	1	-	

* Single sighting at this elevation.

(Table 1). Despite the absence of *Daubentonia madagascariensis* direct observations of feeding traces during the 2021 survey, its presence at the site was reported by local guides. Lemur densities were distinctly low in the highest elevational zone at 1880 m, where only three species were observed. In contrast, the zone at 1300 m contained all nine censused species, of which eight species were observed and one was only heard (*E. albifrons*). In comparison to the results of the 1996 survey conducted by Sterling and McFadden (2000), some differences in the presence and absence of lemur

species in each elevational zone were noted (Table 2); these are discussed below.

A total of 82.1 km of transect were utilized for diurnal surveys (Table 3) and 31.8 km for nocturnal surveys (Table 4). The chance of encountering an individual or group of lemurs decreases with increasing elevation. Of the 137 encounters, including 37.2% during the day and 62.8% at night, contacts were more numerous at the first two sites (480 and 750 m), fewer at sites 3 and 4 (1300 and 1550 m), and the lowest at the highest site (1880 m).

Characteristics of observed lemur species

Family Cheirogaleidae

Allocebus trichotis

This species, Hairy-eared Dwarf Lemur, is similar in size to mouse lemurs of the genus *Microcebus* but distinguished based on its bushy ears (Mittermeier *et al.*, 2010). It was observed only in two elevational zones, with one individual at 1300 m, and three individuals at 1550 m; the recorded elevational range was from 1370 to 1560 m. The species frequented the middle vertical forest stratum between 5 and 8 m off the ground.

Cheirogaleus crossleyi

After the revision of Groves (2000), this species known as Crossley's Dwarf Lemur is recognized as distinct from *Cheirogaleus major* based on the warm reddish fur color on the dorsum, gray underside that turns creamy-colored near the mid-ventral line, yellowish coloration on the face that extends above the eyes, black eye rings, dark fur on the ears, and a pointed nose. This species was observed in the five elevational zones, across the range from 375 to 1725 m, with more individuals in the two lower sites. They frequent the middle forest stratum, at an average height of 8.8 m. Two individuals in the same tree or in the immediate vicinity of one another were observed on four occasions.

Microcebus lehilahytsara

According to Poelstra *et al.* (2020) and Schüßler *et al.* (2020) and based on recent phylogeographic and morphological studies, we considered the *Microcebus* occurring at Marojejy as *M. lehilahytsara*, for which *M. mittermeieri* is considered a synonym.

This species, known as Goodman's Mouse Lemur, is the smallest mouse lemur in the Andasibe and surrounding regions and weighing on average 48 g (range 38-64 g) for males and 45 g (range 30-54 g) for females (Kappeler *et al.*, 2005). The hair coloration is yellowish under each eye and along the mandible, which extends ventrally to the neck. A light-colored patch occurs on the dorsal portion of the rostrum to slightly behind the eyes.

This species was present at the five elevational sites and across the range from 320 to 1885 m. At 1550 m, we did not observe this species during the transect surveys, but another member of the research team reported seeing a single individual. This species was distinctly more common at the three lower elevational sites. It was found in a range

of different topographic habitats (ridge, slope, and valley) and frequented the lower vertical strata, from 1 to 11 m, particularly in small trees and on lianas.

Family Lepilemuridae

Lepilemur seali

With a homogeneous light chocolate-brown to reddish-brown color pattern, *Lepilemur seali* or Seal's Sportive Lemur is a large-sized member of the genus. Brownish-gray colored fur covers its face, hands, feet, and tail. This species differs from its closest relatives based on genetic measures (*L. mustelinus*) and geographic distance (*L. wrighti*) (Louis *et al.*, 2006a).

Lepilemur seali was not frequently observed during the 2021 survey, with a total of five individuals at 480 m and 750 m, and three individuals at 1300 m, across an elevational range from 485 to 1400 m. It frequented the middle forest stratum, at an average height of 10 m, and used medium sized trees. No nesting hole of this species was observed during the 2021 survey.

Family Lemuridae

Eulemur albifrons

This species, also known as the White-headed Brown Lemur, shows sexual dimorphism in pelage coloration. The forehead of the male is white or cream-colored and females have black faces, light beards, and a brown to gray-brown dorsum (Mittermeier *et al.*, 2010). *Eulemur albifrons* was observed in the lower two elevational zones and across range from 340 to 895 m. The average group size was six individuals and varied from two to 11 individuals composed of adults, subadults, young, and babies. These animals exploit the middle forest stratum, at an average height of 8.5 m.

Eulemur rubriventer

Eulemur rubriventer or Red-bellied Lemur has a thick body pelage with deep chestnut brown fur color. Typically, fur covers the ears. The face is black, and behind each eye a patch of exposed skin displays a faint teardrop pattern that is more pronounced in males (Mittermeier *et al.*, 2010). This species was observed at 750 m, 1300 m, and 1550 m and heard at 480 m. This species was observed in the forest at an average height off the ground of 6.5 m. Groups were generally composed of three individuals, including an adult male and female, and a subadult or a young individual.

Haplemur occidentalis

This species, also known as the Western Lesser Bamboo Lemur, was only observed in the first two elevational zones, 480 and 750 m; at 1300 m it was heard vocalizing. The number of individuals in a group was around four, with two adult individuals, a young of the previous year, and a juvenile. However, a group of eight individuals was observed at 480 m. This species used the middle forest stratum at an average height of 6 m and generally associated with bamboo formations. This species was observed in different topographic settings (slope, valley, and ridge), but was more frequent on slopes or in low lying areas where herbaceous vegetation was denser.

Family Indriidae

Propithecus candidus

The fur of *Propithecus candidus*, also known as the Silky Sifaka, is long, silky, and largely whitish and often with a yellow tinge, except for some individuals where silvery gray tints on the crown, limbs, and back (Mittermeier *et al.*, 2010). This species was

observed in three elevational zones, 750 m, 1300 m, and 1550 m, and spanning an elevational range from 805 to 1645 m. The average group size was three individuals composed of two adults and a subadult or a young individual. One individual was observed at 1880 m by a team member and outside of the transect counts.

Avahi laniger

Avahi laniger or Eastern Woolly Lemur has a rufous brown tail. The back of the thighs have prominent white patches that serve as identifying field marks. The face is brown and there are light bands above the eyes. Based on phylogeographic and morphologic studies, several new species have been described from eastern Madagascar (Zaramody *et al.*, 2006, Andriantompohavana *et al.*, 2007). *Avahi laniger* was only observed two times during the 2021 survey, at 750 m and 1300 m. They were in pairs and often seen on medium-sized trees at the average height of 11 m. At 1300 m they were often heard or seen around the camp.

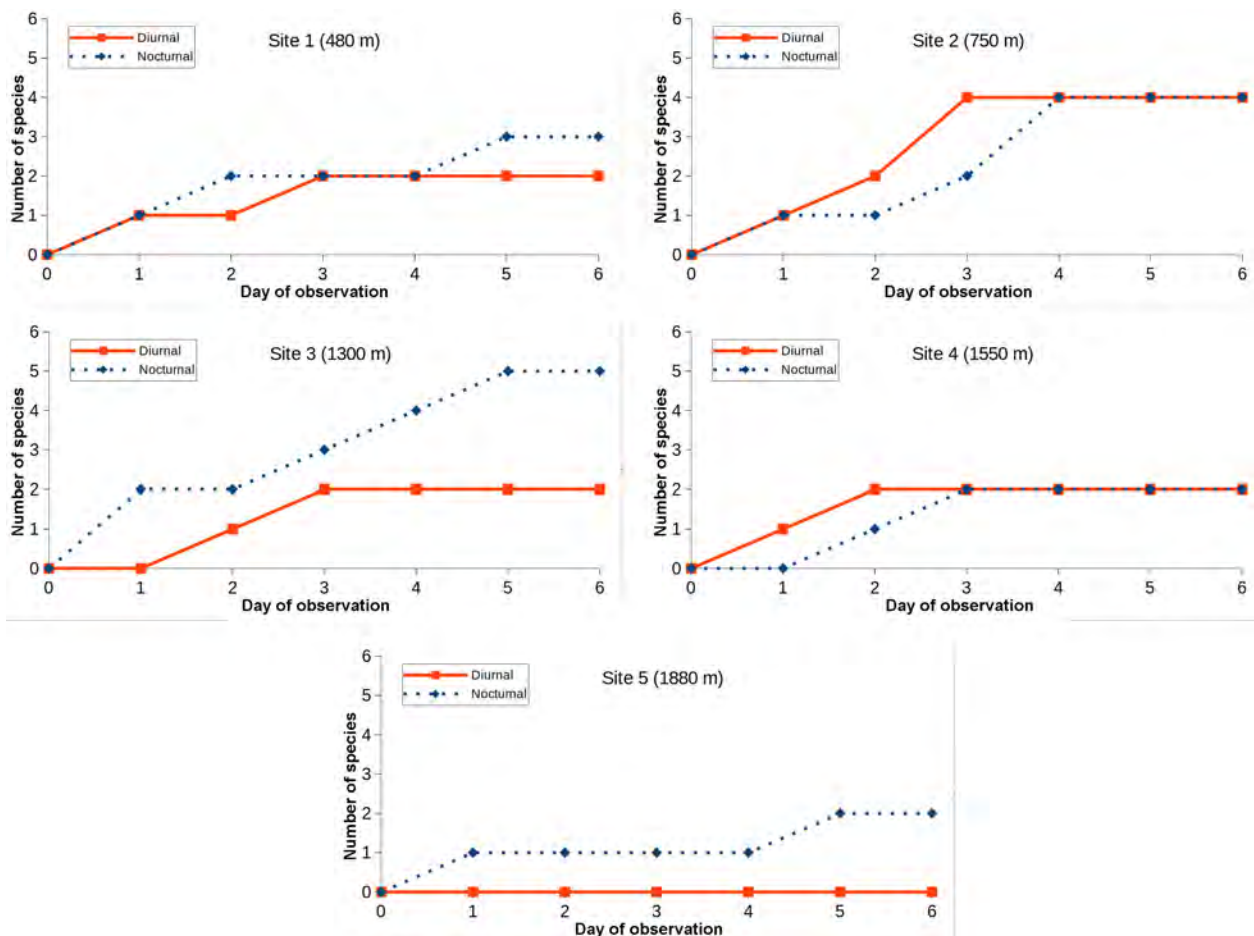


Figure 2. Species accumulation curves for lemur species at five sites along the eastern slopes of the Parc National de Marojejy and separated for each site by diurnal (including cathemeral species) and nocturnal taxa.

Table 5. Absolute density estimates of lemurs in individuals per km² along the eastern slopes of the Parc National de Marojejy.

Species	Density (individuals/km ²)				
	Site 1 (480 m)	Site 2 (750 m)	Site 3 (1300 m)	Site 4 (1550 m)	Site 5 (1880 m)
<i>Allocebus trichotis</i>			5	8	
<i>Cheirogaleus crossleyi</i>	12	12	6	9	7
<i>Microcebus lehilahytsara</i>	14	4	15		13
<i>Lepilemur seali</i>	3		5		
<i>Eulemur albifrons</i>	9	22			
<i>Eulemur rubriventer</i>		6	11	6	
<i>Hapalemur occidentalis</i>	17	11			
<i>Avahi laniger</i>		5	6		
<i>Propithecus candidus</i>		12	5	2	

Abundance and density

The number of sightings of lemurs per kilometer of transect is presented in Tables 3 (diurnal) and 4 (nocturnal). Table 5 summarizes the density of each species at each study site. The densities of nocturnal lemurs vary from 3 to 15 individuals per km² and for diurnal species from 2 to 22 individuals per km². The highest lemur densities were recorded at Sites 2 (750 m) and 3 (1300 m) and across an elevational range from 600 to 1400 m.

Species accumulation curves

The cumulative number of species encountered at a given site increases with the number of sampling days (Figure 2). For several sites, the curves tend to reach an asymptote at the end of an inventory session within a given elevational zone. The principal exception was for nocturnal species at 480 m, 1300 m, and 1880 m, where a previously unrecorded species was recorded on the 5th survey night. For the other sites, no new species was found after the 3rd day for diurnal and cathemeral lemurs and after the 4th day for nocturnal lemurs. In a good portion of the cases, most species recorded for a site were found during the first days of survey.

Discussion

Nine lemur species were recorded during our 2021 survey of five elevational zones on the Marojejy Massif, with sites ranging from 480 to 1880 m. Species richness varies along the elevational gradient. Given that Sterling and McFadden (2000) in 1996 conducted a parallel elevational transect of lemurs at the same sites and employed the same sampling techniques, we focus here mainly on the comparison of the results between the two studies.

Changes in lemur taxonomy over the past 25 years

In recent years, molecular analyses of lemur samples obtained during field surveys have intensified, especially for nocturnal species. The number of recognized species has increased significantly. These different studies have resulted in differences in species name used by Sterling and McFadden (2000) and are presented in this section.

In 1996, three species of *Microcebus* were recognized on Madagascar: *M. murinus*, *M. rufus*, and *M. myoxinus* (Mittermeier *et al.*, 1994; Schmid & Kappeler, 1994; Atsalis *et al.*, 1996). Sterling and McFadden (2000) recorded on Marojejy of a reddish mouse lemur that they named *M. rufus*. Subsequent molecular and morphological analyses revealed that the eastern moist evergreen forests of Madagascar hold several, all allopatric, species of *Microcebus* (Yoder *et al.*, 2000; Kappeler *et al.*, 2005; Louis *et al.*, 2006b; Radespiel *et al.*, 2008; Poelstra *et al.*, 2020; Schüßler *et al.*, 2020). Based on these analyses and our survey results, the mouse lemur observed in the Parc National de Marojejy was *M. lehilahytsara*.

Two species of *Cheirogaleus*, *C. medius* and *C. major* on Madagascar (Mittermeier *et al.*, 1994), were recognized when Sterling and McFadden (2000) put together their Marojejy survey results. Morphological and genetic analyses revealed several other species occur in the eastern forest area (Groves, 2000; Hapke *et al.*, 2005; Mittermeier *et al.*, 2010). *Cheirogaleus crossleyi* is the species occurring in the park.

As for *Lepilemur*, seven species of sportive lemur were recognized in 1994 (Mittermeier *et al.*, 1994). Those numbers increased to 25 species, 15 of which were described in or after 2006 (Andriaholinirina *et al.*, 2006; Louis *et al.*, 2006a; Rabarivola *et al.*, 2006; Craul *et al.*, 2007; Lei *et al.*, 2008; Mittermeier *et al.*, 2008). *Lepilemur seali* inhabits the northern part

of what was previously considered *L. mustelinus*'s former range and is the taxon that occurs in Marojejy.

Formerly, *Hapalemur griseus* was recognized to have three subspecies: *H. g. alaotrensis*, *H. g. griseus*, and *H. g. occidentalis*. The form *Hapalemur g. griseus* reported by Sterling and McFadden (2000) at Marojejy was thought to occupy a major part of the eastern forest. Rumppler *et al.* (2002) and Rabarivola *et al.* (2007) established new distribution ranges of *H. griseus* subspecies and confirm the presence of *H. griseus occidentalis* in the northeastern region. Groves (2001) subsequently elevated *occidentalis* to full species.

The promotion of subspecies to full species occurred with two other taxa that Sterling and McFadden (2000) reported from Marojejy: *Propithecus diadema candidus* to *P. candidus* (Mayor *et al.*, 2004) and *Eulemur fulvus albifrons* to *E. albifrons* (Groves, 2001).

Species richness

Species richness per the five elevational zones were similar between the 1996 and 2021 surveys (Table 2). The high diversity in the mid-elevation sites and the homogeneity of the lemur population in the lower-elevation site are consistent between the two studies.

Species observations

Excluding changes in lemur taxonomy over the past 25 years described above, the main differences between species reported by Sterling and McFadden (2000) and our survey results are differences in the presence or absence of three species: *Daubentonia madagascariensis*, *Phaner furcifer*, and *Allocebus trichotis*.

We found *A. trichotis* on four occasions during the 2021 survey; a species also known from the northwestern slopes of Marojejy (Goodman & Raselimanana, 2002). This species was not recorded by Sterling and McFadden (2000) during their 1996 field observations on eastern slopes of the massif. This absence of this species during the 1996 survey is presumably associated with chance and its relative rarity.

Sterling and McFadden (2000) reported *D. madagascariensis* and *P. furcifer* during the 1996 survey, but these two species were not recorded in 2021. Feeding signs of *Daubentonia* were reported in 1996 (Sterling & McFadden, 2000), but no such signs were found during the 2021 survey. Given the relatively wide distribution of this species, albeit low

density, it is almost certain that it still occurs along the eastern slopes of the Marojejy Massif.

Presence of *P. furcifer* in the park as reported by Sterling and McFadden (2000) was based at the lowest-lying site and based on vocalization. This species is easily recognizable by their loud call and known in numerous forests of northeastern Madagascar from near sea-level to 1000 m (Mittermeier *et al.*, 2010). However, during our 2021 investigation, this species was not heard or seen.

Abundances

When comparing the estimates of lemur densities for the 1996 and 2021 surveys, they were higher for the 480, 750, and 1300 m sites than at the 1550 and 1880 m sites. This pattern can be explained in elevational differences in meteorological variables, vegetation, food resources, and a pattern well known along elevational transects of lemurs (Goodman & Ganzhorn, 2004).

The measured abundance of certain lemur species between the two surveys are in certain cases rather different and in general higher in 1996 than in 2021, particularly for the 480 and 750 m sites 1 and 2. The differences might be explained by degradation of forest habitats, but for the portion of the eastern slopes of the Marojejy Massif that were surveyed, specifically the Manantenina River watershed, there is no evidence of such anthropogenic pressures (Tahinarivony, 2023b, herein).

Hunting is one of the problems of lemur survival in the northeastern portion of Madagascar. Lemur bushmeat is served in some restaurants in Andapa and Sambava and the origin of these animals is unknown. It is possible that differences in the lemur densities calculated from the 1996 and 2021 surveys are the result of hunting pressure. Local guides that worked with the 2021 team affirmed the presence of lemur hunting in the area and mentioned that nocturnal lemurs are dislodged into their roosting holes and poached. For diurnal lemur species, hunters no longer use traps for subduing these animals, but other methods such as guns. On several occasions along the Manantenina-summit tourist trail, notable fleeing behaviors of some diurnal species, specifically *Eulemur albifrons* and *Propithecus candidus*, were noticed during the 2021 survey, which would indicate continued human hunting pressure as known in the past (Duckworth *et al.*, 1995).

Conclusion

Our study revealed the presence of nine lemur species along the eastern slopes of the Marojejy National Park, which is the area visited on a regular basis by tourists. The distribution of these species shows some elevational variation. Comparisons of our 2021 study results at the five same sites surveyed in 1996 by Sterling and McFadden (2000), with survey techniques and the same portion of the calendar year held in parallel, showed some differences in the species recorded. Most important in this regard is that in 2021 we did not find two species on the massif, *Phaner furcifer* and *Daubentonia madagascariensis*, reported from the 1996 survey. We also added a species, *Allocebus trichotis*, not previously reported from the eastern slopes of the massif.

Seven of the eight locally occurring species found during the 2021 inventory are listed by IUCN as threatened: Critically Endangered (*Propithecus candidus*), Endangered (*A. trichotis*), and Vulnerable (*Lepilemur seali*, *Eulemur albifrons*, *E. rubriventer*, *Hapalemur occidentalis*, and *Cheirogaleus crossleyi*). These results highlight the Parc National de Marojejy as a site of high conservation importance.

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Appendix I. GPS coordinates of different transect trails.

Sites	Transect	Long	Lat
Site 1	T1 S1	49.77480157	-14.43726854
Site 1	T1 S1	49.77463436	-14.43731287
Site 1	T1 S1	49.77438401	-14.43729349
Site 1	T1 S1	49.77423595	-14.43722944
Site 1	T1 S1	49.77403208	-14.43719223
Site 1	T1 S1	49.77401333	-14.43722829
Site 1	T1 S1	49.77389334	-14.43711919
Site 1	T1 S1	49.77385703	-14.43697436
Site 1	T1 S1	49.77384706	-14.43710087
Site 1	T1 S1	49.77372618	-14.43715448
Site 1	T1 S1	49.7736803	-14.43706384
Site 1	T1 S1	49.77347598	-14.43710797
Site 1	T1 S1	49.77321557	-14.43723318
Site 1	T1 S1	49.77312247	-14.43729597
Site 1	T1 S1	49.77306651	-14.43734992
Site 1	T1 S1	49.77295476	-14.4374307
Site 1	T1 S1	49.77306651	-14.43734992
Site 1	T1 S1	49.77295476	-14.4374307
Site 1	T1 S1	49.77283388	-14.43748431
Site 1	T1 S1	49.77261116	-14.43750123
Site 1	T1 S1	49.77249107	-14.4374102
Site 1	T1 S1	49.77251959	-14.43728379
Site 1	T1 S1	49.77255704	-14.43722071
Site 1	T1 S1	49.77227952	-14.43708367
Site 1	T1 S1	49.77227981	-14.43702943
Site 1	T1 S1	49.77228021	-14.43695711
Site 1	T1 S1	49.77204871	-14.43688359
Site 1	T1 S1	49.77188239	-14.43676521
Site 1	T1 S1	49.77153146	-14.43648314
Site 1	T1 S1	49.77140199	-14.43641015
Site 1	T1 S1	49.77112491	-14.43619175
Site 1	T1 S1	49.77093995	-14.43609135
Site 1	T1 S1	49.77089431	-14.43595551
Site 1	T1 S1	49.77051555	-14.4356733
Site 1	T1 S1	49.77039526	-14.43561844
Site 1	T1 S1	49.77022835	-14.43560853
Site 1	T1 S1	49.77015434	-14.43557198
Site 1	T1 S1	49.77002508	-14.43546283
Site 1	T1 S1	49.76992354	-14.4353719
Site 1	T1 S1	49.76983977	-14.4354257
Site 1	T1 S1	49.76976576	-14.43538916
Site 1	T1 S1	49.76973744	-14.43547941
Site 1	T1 S1	49.7695239	-14.43551445
Site 1	T2 S1	49.77504121	-14.43755002
Site 1	T2 S1	49.77488292	-14.43765768
Site 1	T2 S1	49.77469682	-14.43776519
Site 1	T2 S1	49.774631	-14.43792757
Site 1	T2 S1	49.77454657	-14.43809888
Site 1	T2 S1	49.77429573	-14.4381699
Site 1	T2 S1	49.77420228	-14.43829597
Site 1	T2 S1	49.77411751	-14.43853057
Site 1	T2 S1	49.77395923	-14.43863822
Site 1	T2 S1	49.77378215	-14.43879098
Site 1	T2 S1	49.77356876	-14.43879891
Site 1	T2 S1	49.77337342	-14.43889733
Site 1	T2 S1	49.77320601	-14.43897782
Site 1	T2 S1	49.77295556	-14.43897651
Site 1	T2 S1	49.77272367	-14.43897531
Site 1	T2 S1	49.772501	-14.43898319
Site 1	T2 S1	49.77230576	-14.43906353
Site 1	T2 S1	49.77213835	-14.43914402
Site 1	T2 S1	49.7718135	-14.43917848
Site 1	T2 S1	49.77159971	-14.43925873
Site 1	T2 S1	49.77145135	-14.43924891
Site 1	T3 S1	49.78443357	-14.44516501
Site 1	T3 S1	49.78425732	-14.4451641
Site 1	T3 S1	49.78401619	-14.44515381

Sites	Transect	Long	Lat
Site 1	T3 S1	49.78381202	-14.44517084
Site 1	T3 S1	49.78351533	-14.44514219
Site 1	T3 S1	49.78338527	-14.44517768
Site 1	T3 S1	49.78319999	-14.44513152
Site 1	T3 S1	49.78304211	-14.44516687
Site 1	T3 S1	49.78280058	-14.4452289
Site 1	T3 S1	49.78259612	-14.44530016
Site 1	T3 S1	49.78238247	-14.4453533
Site 1	T3 S1	49.78223332	-14.44548812
Site 1	T3 S1	49.78212117	-14.44564122
Site 1	T3 S1	49.78194418	-14.4457759
Site 1	T3 S1	49.78190634	-14.44591131
Site 1	T3 S1	49.78180351	-14.44605541
Site 1	T3 S1	49.78165382	-14.44628967
Site 1	T3 S1	49.78165298	-14.44644335
Site 1	T3 S1	49.78152223	-14.44660539
Site 1	T3 S1	49.78138259	-14.44669507
Site 1	T3 S1	49.7811315	-14.44681129
Site 1	T3 S1	49.78102882	-14.44692827
Site 1	T3 S1	49.78082445	-14.44698145
Site 1	T3 S1	49.78066646	-14.44703488
Site 1	T3 S1	49.78046234	-14.44704286
Site 1	T3 S1	49.78028673	-14.44692443
Site 1	T3 S1	49.7801016	-14.44685115
Site 1	T3 S1	49.77986965	-14.44685899
Site 1	T3 S1	49.77968398	-14.44688515
Site 1	T3 S1	49.77947956	-14.44694737
Site 1	T3 S1	49.77924805	-14.44687385
Site 1	T3 S1	49.77898832	-14.44687251
Site 1	T3 S1	49.77884009	-14.44683558
Site 1	T3 S1	49.77858959	-14.44684332
Site 1	T3 S1	49.77848637	-14.44705974
Site 1	T3 S1	49.77830958	-14.44715827
Site 1	T3 S1	49.7781691	-14.44740161
Site 1	T3 S1	49.7780573	-14.44749143
Site 1	T3 S1	49.77787138	-14.44756279
Site 1	T3 S1	49.77766656	-14.44769732
Site 1	T3 S1	49.77743421	-14.44777747
Site 1	T4 S1	49.7756125	-14.43824906
Site 1	T4 S1	49.77551885	-14.43841129
Site 1	T4 S1	49.77599877	-14.43885674
Site 1	T4 S1	49.77628454	-14.43918365
Site 1	T4 S1	49.77673895	-14.43920409
Site 1	T4 S1	49.77695185	-14.43928656
Site 1	T4 S1	49.7771273	-14.4394321
Site 1	T4 S1	49.7773407	-14.43942417
Site 1	T4 S1	49.77750717	-14.43951543
Site 1	T4 S1	49.77782047	-14.43989673
Site 1	T4 S1	49.77826517	-14.43999847
Site 1	T4 S1	49.77879183	-14.44038088
Site 1	T4 S1	49.77902279	-14.44055383
Site 1	T4 S1	49.77943764	-14.44102605
Site 1	T4 S1	49.77968676	-14.44127142
Site 1	T4 S1	49.7798252	-14.44139869
Site 1	T4 S1	49.78014883	-14.4415902
Site 1	T4 S1	49.78045459	-14.44165506
Site 1	T4 S1	49.78061223	-14.44166492
Site 1	T4 S1	49.78089002	-14.44175676
Site 1	T4 S1	49.78109325	-14.44191148
Site 1	T4 S1	49.78125933	-14.44207506
Site 1	T4 S1	49.78147199	-14.44220272
Site 1	T4 S1	49.78163812	-14.44235725
Site 1	T4 S1	49.78189583	-14.44272922
Site 1	T4 S1	49.78194942	-14.44310917
Site 1	T4 S1	49.7821714	-14.44322784
Site 1	T4 S1	49.7822917	-14.4432827

Appendix I. (continued)

Sites	Transect	Long	Lat
Site 1	T5 S1	49.78256885	-14.44349205
Site 1	T5 S1	49.782763	-14.44361057
Site 1	T5 S1	49.78298504	-14.44372019
Site 1	T5 S1	49.78311402	-14.44388358
Site 1	T5 S1	49.7833551	-14.4439029
Site 1	T5 S1	49.78356771	-14.4440396
Site 1	T5 S1	49.78384314	-14.44456533
Site 1	T5 S1	49.78398149	-14.44471068
Site 1	T5 S1	49.78411008	-14.44494638
Site 1	T5 S1	49.78428574	-14.44505577
Site 1	T5 S1	49.7844983	-14.4452015
Site 1	T5 S1	49.7845996	-14.44533762
Site 1	T5 S1	49.7847839	-14.44556457
Site 1	T5 S1	49.78485688	-14.44579094
Site 1	T5 S1	49.78506974	-14.44588244
Site 1	T5 S1	49.78511494	-14.44609963
Site 1	T5 S1	49.78519769	-14.44623565
Site 1	T5 S1	49.78515961	-14.44641625
Site 1	T5 S1	49.78507514	-14.44659662
Site 1	T5 S1	49.7849437	-14.44688521
Site 1	T5 S1	49.7850452	-14.44698518
Site 1	T5 S1	49.7852773	-14.44695021
Site 1	T5 S1	49.78554602	-14.44700584
Site 1	T5 S1	49.78572236	-14.44698867
Site 1	T5 S1	49.78608369	-14.44707189
Site 1	T5 S1	49.78604546	-14.44727961
Site 1	T5 S1	49.78627599	-14.44753391
Site 1	T5 S1	49.78645096	-14.44776985
Site 1	T5 S1	49.78654284	-14.44793304
Site 1	T5 S1	49.78656959	-14.44813205
Site 1	T5 S1	49.78675394	-14.44834996
Site 1	T5 S1	49.78692013	-14.44849545
Site 1	T5 S1	49.78702128	-14.44865869
Site 1	T5 S1	49.78716872	-14.44884025
Site 1	T5 S1	49.78729742	-14.44905787
Site 1	T5 S1	49.78753654	-14.44943877
Site 1	T5 S1	49.787592	-14.44947522
Site 1	T5 S1	49.78794274	-14.44980246
Site 1	T6 S1	49.77554595	-14.43684754
Site 1	T6 S1	49.77537933	-14.43678339
Site 1	T6 S1	49.7751022	-14.43657404
Site 1	T6 S1	49.77514014	-14.43642056
Site 1	T6 S1	49.77491866	-14.43621149
Site 1	T6 S1	49.7747517	-14.43621062
Site 1	T6 S1	49.7745393	-14.43603776
Site 1	T6 S1	49.77432641	-14.4359553
Site 1	T6 S1	49.77397477	-14.43579979
Site 1	T6 S1	49.77341848	-14.4357517
Site 1	T6 S1	49.77315916	-14.43567803
Site 1	T6 S1	49.77280866	-14.43531461
Site 1	T6 S1	49.77278242	-14.4350252
Site 1	T6 S1	49.77279304	-14.43478118
Site 1	T6 S1	49.77280345	-14.43457332
Site 1	T6 S1	49.77272477	-14.43369605
Site 1	T6 S1	49.77250285	-14.43356833
Site 1	T6 S1	49.77233629	-14.43349515
Site 1	T6 S1	49.77208679	-14.43332209
Site 2	T1 S2	49.75846465	-14.43427227
Site 2	T1 S2	49.75842855	-14.43409128
Site 2	T1 S2	49.75815966	-14.43407179
Site 2	T1 S2	49.75792797	-14.43403441
Site 2	T1 S2	49.75773379	-14.43392491
Site 2	T1 S2	49.75761436	-14.43371636
Site 2	T1 S2	49.75748501	-14.43362528
Site 2	T1 S2	49.75722469	-14.43373239
Site 2	T1 S2	49.75721456	-14.43388601

Sites	Transect	Long	Lat
Site 2	T1 S2	49.75707483	-14.43399375
Site 2	T1 S2	49.75691604	-14.43419179
Site 2	T1 S2	49.75686881	-14.43434522
Site 2	T1 S2	49.75689588	-14.43448096
Site 2	T1 S2	49.75699666	-14.43470749
Site 2	T1 S2	49.75709728	-14.43496113
Site 2	T1 S2	49.75712411	-14.43514207
Site 2	T1 S2	49.75703035	-14.43532237
Site 2	T1 S2	49.75682528	-14.43550208
Site 2	T1 S2	49.75688003	-14.43566509
Site 2	T1 S2	49.75677725	-14.43580014
Site 2	T1 S2	49.75675749	-14.43601699
Site 2	T2 S2	49.75806921	-14.43532784
Site 2	T2 S2	49.75818839	-14.43558159
Site 2	T2 S2	49.75827107	-14.43572666
Site 2	T2 S2	49.75833565	-14.43579028
Site 2	T2 S2	49.75834332	-14.43607959
Site 2	T2 S2	49.75847213	-14.4362701
Site 2	T2 S2	49.75857356	-14.43637912
Site 2	T2 S2	49.75865614	-14.43654227
Site 2	T2 S2	49.75868306	-14.43670512
Site 2	T2 S2	49.75885825	-14.43689588
Site 2	T2 S2	49.75887615	-14.43701349
Site 2	T2 S2	49.75902371	-14.43716795
Site 2	T2 S2	49.75922732	-14.43725038
Site 2	T2 S2	49.75940346	-14.43726938
Site 2	T2 S2	49.75964493	-14.43721642
Site 2	T2 S2	49.75976556	-14.43720801
Site 2	T2 S2	49.75997028	-14.43709157
Site 2	T2 S2	49.76013709	-14.43711957
Site 2	T2 S2	49.76011046	-14.43690247
Site 2	T2 S2	49.76046459	-14.43660602
Site 2	T2 S2	49.76060352	-14.43664291
Site 2	T3 S2	49.76060977	-14.43886673
Site 2	T3 S2	49.76077713	-14.43879529
Site 2	T3 S2	49.76096324	-14.4386878
Site 2	T3 S2	49.76114921	-14.43860741
Site 2	T3 S2	49.76126147	-14.43843625
Site 2	T3 S2	49.76133672	-14.43824681
Site 2	T3 S2	49.76136555	-14.43806616
Site 2	T3 S2	49.76130162	-14.43788503
Site 2	T3 S2	49.76133305	-14.43769535
Site 2	T3 S2	49.76126727	-14.43738766
Site 2	T3 S2	49.76109118	-14.43735962
Site 2	T3 S2	49.76103668	-14.43715141
Site 2	T3 S2	49.76103798	-14.43691639
Site 2	T3 S2	49.76092797	-14.43668077
Site 2	T3 S2	49.76082619	-14.43663504
Site 2	T3 S2	49.76064103	-14.43657079
Site 2	T3 S2	49.76051217	-14.43638931
Site 2	T3 S2	49.76060567	-14.43625421
Site 2	T3 S2	49.76075529	-14.43603804
Site 2	T3 S2	49.76091292	-14.43604791
Site 2	T3 S2	49.76089572	-14.43580374
Site 2	T3 S2	49.76105556	-14.43541587
Site 2	T3 S2	49.76120427	-14.43536241
Site 2	T3 S2	49.76106698	-14.43502722
Site 2	T4 S2	49.76040429	-14.43409264
Site 2	T4 S2	49.76030256	-14.43403786
Site 2	T4 S2	49.76005217	-14.43402751
Site 2	T4 S2	49.75989429	-14.43406284
Site 2	T4 S2	49.75966145	-14.43423337
Site 2	T4 S2	49.75949409	-14.43430481
Site 2	T4 S2	49.75930838	-14.43433999
Site 2	T4 S2	49.75907639	-14.43435685
Site 2	T4 S2	49.75900143	-14.43449205

Appendix I. (continued)

Sites	Transect	Long	Lat
Site 2	T4 S2	49.75877852	-14.43454512
Site 2	T4 S2	49.75852748	-14.43465227
Site 2	T4 S2	49.75830471	-14.43467822
Site 2	T4 S2	49.75823858	-14.43489483
Site 2	T4 S2	49.75815425	-14.43504806
Site 2	T4 S2	49.75793093	-14.43517344
Site 2	T4 S2	49.75793906	-14.4353814
Site 2	T4 S2	49.75777114	-14.43555227
Site 2	T4 S2	49.75762168	-14.43574132
Site 2	T4 S2	49.75771308	-14.43598587
Site 2	T4 S2	49.75766657	-14.43616642
Site 2	T4 S2	49.75755309	-14.43640086
Site 2	T4 S2	49.75742258	-14.43651769
Site 2	T4 S2	49.75738442	-14.43670732
Site 2	T4 S2	49.7575227	-14.43686173
Site 2	T4 S2	49.75734546	-14.43704159
Site 2	T4 S2	49.75727036	-14.43720391
Site 2	T5 S2	49.76095095	-14.43420399
Site 2	T5 S2	49.76162717	-14.43437026
Site 2	T5 S2	49.76186813	-14.43440768
Site 2	T5 S2	49.76199884	-14.43425469
Site 2	T5 S2	49.76241574	-14.43434728
Site 2	T5 S2	49.76254425	-14.43459203
Site 2	T5 S2	49.76269176	-14.43475552
Site 2	T5 S2	49.76308836	-14.43516439
Site 2	T5 S2	49.76379311	-14.43520424
Site 2	T5 S2	49.76427479	-14.43532429
Site 2	T5 S2	49.76470112	-14.4353898
Site 2	T5 S2	49.76489621	-14.43533658
Site 2	T5 S2	49.76510047	-14.43530149
Site 2	T5 S2	49.76550146	-14.43491488
Site 2	T5 S2	49.7656966	-14.43485262
Site 2	T5 S2	49.76589972	-14.43502544
Site 2	T5 S2	49.76615963	-14.43499064
Site 2	T5 S2	49.76635457	-14.43496454
Site 2	T5 S2	49.76661404	-14.4350111
Site 2	T5 S2	49.76684623	-14.43495808
Site 2	T5 S2	49.76705907	-14.43504959
Site 2	T5 S2	49.76728178	-14.43503267
Site 2	T5 S2	49.76747652	-14.43504273
Site 2	T5 S2	49.76768961	-14.43508904
Site 2	T5 S2	49.7679211	-14.43516257
Site 2	T5 S2	49.76800369	-14.43532572
Site 2	T5 S2	49.7680957	-14.4354618
Site 2	T5 S2	49.7681701	-14.43542603
Site 2	T6 S2	49.76126092	-14.43518192
Site 2	T6 S2	49.76144663	-14.43514673
Site 2	T6 S2	49.76167797	-14.43524738
Site 2	T6 S2	49.76181706	-14.43525715
Site 2	T6 S2	49.76194571	-14.43547479
Site 2	T6 S2	49.76221426	-14.43555755
Site 2	T6 S2	49.76231444	-14.43589255
Site 2	T6 S2	49.76236047	-14.43595607
Site 2	T6 S2	49.76232237	-14.43613667
Site 2	T6 S2	49.76237662	-14.43639007
Site 2	T6 S2	49.7623668	-14.43648945
Site 2	T6 S2	49.76251366	-14.43677046
Site 2	T6 S2	49.76246643	-14.43692389
Site 2	T6 S2	49.76248378	-14.43714093
Site 2	T6 S2	49.76257559	-14.43731317
Site 3	T1 S3	49.74298811	-14.43673045
Site 3	T1 S3	49.74277436	-14.43680163
Site 3	T1 S3	49.74262504	-14.43696355
Site 3	T1 S3	49.74245762	-14.43704401
Site 3	T1 S3	49.742253	-14.43714236
Site 3	T1 S3	49.7421314	-14.4373225
Site 3	T1 S3	49.74198228	-14.43744827

Sites	Transect	Long	Lat
Site 3	T1 S3	49.74180523	-14.43759196
Site 3	T1 S3	49.74176727	-14.43774543
Site 3	T1 S3	49.74161789	-14.43791639
Site 3	T2 S3	49.74238215	-14.4372696
Site 3	T2 S3	49.74252072	-14.43736978
Site 3	T2 S3	49.74251104	-14.43744205
Site 3	T2 S3	49.74260207	-14.43774988
Site 3	T2 S3	49.74280558	-14.43785041
Site 3	T2 S3	49.74295323	-14.43798679
Site 3	T2 S3	49.74302637	-14.43817701
Site 3	T2 S3	49.74303503	-14.43828554
Site 3	T2 S3	49.74324766	-14.43841323
Site 3	T2 S3	49.74344306	-14.43830579
Site 3	T2 S3	49.74363704	-14.43845146
Site 3	T2 S3	49.74386832	-14.43856117
Site 3	T2 S3	49.74400746	-14.43856191
Site 3	T2 S3	49.74420285	-14.43845448
Site 3	T2 S3	49.74429642	-14.43831034
Site 3	T2 S3	49.74434381	-14.4381298
Site 3	T3 S3	49.74335878	-14.437957
Site 3	T3 S3	49.74351601	-14.4368779
Site 3	T3 S3	49.74370157	-14.43686985
Site 3	T3 S3	49.74381181	-14.43706027
Site 3	T3 S3	49.74365352	-14.43716791
Site 3	T3 S3	49.74347657	-14.43729352
Site 3	T3 S3	49.74350359	-14.4374383
Site 3	T3 S3	49.74352158	-14.43753783
Site 3	T4 S3	49.74384359	-14.43635534
Site 3	T4 S3	49.74405754	-14.436248
Site 3	T4 S3	49.74428928	-14.43627636
Site 3	T4 S3	49.74449334	-14.43627744
Site 3	T4 S3	49.74472538	-14.43625156
Site 3	T4 S3	49.74494764	-14.43631602
Site 3	T4 S3	49.74515191	-14.43628095
Site 3	T4 S3	49.74533666	-14.43641753
Site 3	T4 S3	49.74559577	-14.43652738
Site 3	T4 S3	49.74566931	-14.43664529
Site 3	T4 S3	49.74601109	-14.43690022
Site 3	T4 S3	49.74620553	-14.43696454
Site 3	T4 S3	49.74640949	-14.4369837
Site 3	T4 S3	49.74664077	-14.43709341
Site 3	T4 S3	49.74685376	-14.43715782
Site 3	T4 S3	49.7470194	-14.43739373
Site 3	T4 S3	49.74716726	-14.43749395
Site 3	T4 S3	49.74735216	-14.43760341
Site 3	T4 S3	49.74758355	-14.43769504
Site 3	T4 S3	49.74781529	-14.43772339
Site 3	T4 S3	49.74800019	-14.43783285
Site 3	T4 S3	49.74824091	-14.43791549
Site 3	T4 S3	49.74845369	-14.43801605
Site 3	T4 S3	49.74867605	-14.43806243
Site 3	T5 S3	49.74907339	-14.43833573
Site 3	T5 S3	49.7492398	-14.43843605
Site 3	T5 S3	49.74942511	-14.4384732
Site 3	T5 S3	49.74970313	-14.43851987
Site 3	T5 S3	49.74991602	-14.43860236
Site 3	T5 S3	49.75013853	-14.43862162
Site 3	T5 S3	49.75031472	-14.43863159
Site 3	T5 S3	49.75051843	-14.43869595
Site 3	T5 S3	49.75066644	-14.43876905
Site 3	T5 S3	49.75084177	-14.4389327
Site 3	T5 S3	49.75103616	-14.43900604
Site 3	T5 S3	49.7512681	-14.43899823
Site 3	T5 S3	49.75148154	-14.43898128
Site 3	T5 S3	49.75168566	-14.43897332
Site 3	T5 S3	49.7519173	-14.43901975
Site 3	T5 S3	49.75213059	-14.43902992

Appendix I. (continued)

Sites	Transect	Long	Lat
Site 3	T5 S3	49.75237161	-14.43905831
Site 3	T5 S3	49.75249255	-14.43899568
Site 3	T5 S3	49.75269717	-14.43889732
Site 3	T5 S3	49.75292024	-14.43881714
Site 3	T5 S3	49.75307848	-14.43871854
Site 3	T5 S3	49.75332917	-14.43867467
Site 3	T5 S3	49.75348711	-14.43863031
Site 3	T5 S3	49.75368261	-14.43850478
Site 3	T5 S3	49.75385985	-14.43832492
Site 3	T5 S3	49.75403674	-14.43820834
Site 3	T5 S3	49.75422286	-14.43810085
Site 3	T5 S3	49.75437213	-14.43794796
Site 3	T5 S3	49.75441034	-14.43774929
Site 3	T6 S3	49.75438261	-14.43773106
Site 3	T6 S3	49.75464414	-14.43740701
Site 3	T6 S3	49.7547742	-14.43737154
Site 3	T6 S3	49.75503417	-14.43732771
Site 3	T6 S3	49.75525683	-14.43731985
Site 3	T6 S3	49.755351	-14.43706723
Site 3	T6 S3	49.75564832	-14.4369784
Site 3	T6 S3	49.75564857	-14.4369332
Site 4	T1 S4	49.74241583	-14.4444835
Site 4	T1 S4	49.74245217	-14.44461929
Site 4	T1 S4	49.7425061	-14.44492693
Site 4	T1 S4	49.74246849	-14.44501713
Site 4	T1 S4	49.74235611	-14.44520636
Site 4	T1 S4	49.74216993	-14.44532288
Site 4	T1 S4	49.74222513	-14.44540454
Site 4	T1 S4	49.74238186	-14.44557713
Site 4	T1 S4	49.74253899	-14.4456774
Site 4	T1 S4	49.74266774	-14.44587696
Site 4	T1 S4	49.74270398	-14.44603083
Site 4	T1 S4	49.74265683	-14.44616618
Site 4	T1 S4	49.7426359	-14.44659093
Site 4	T1 S4	49.74277417	-14.44674535
Site 4	T1 S4	49.74283814	-14.44691744
Site 4	T1 S4	49.74298595	-14.44702671
Site 4	T1 S4	49.74318997	-14.44703684
Site 4	T1 S4	49.7433577	-14.44690214
Site 4	T1 S4	49.74333078	-14.44673928
Site 4	T1 S4	49.74323889	-14.44658511
Site 4	T1 S4	49.74336977	-14.44640501
Site 4	T1 S4	49.74341706	-14.44624255
Site 4	T1 S4	49.74346461	-14.44603489
Site 4	T1 S4	49.74341909	-14.44588097
Site 4	T1 S4	49.74354971	-14.44574607
Site 4	T1 S4	49.74363371	-14.44565612
Site 4	T1 S4	49.74376489	-14.44542179
Site 4	T1 S4	49.74371015	-14.44525878
Site 4	T1 S4	49.74358104	-14.4451225
Site 4	T1 S4	49.74338701	-14.44498587
Site 4	T1 S4	49.743276	-14.44493104
Site 4	T1 S4	49.74322131	-14.44475899
Site 4	T1 S4	49.74309079	-14.44487581
Site 4	T1 S4	49.74288667	-14.44488376
Site 4	T2 S4	49.74184342	-14.44400134
Site 4	T2 S4	49.74163899	-14.44406353
Site 4	T2 S4	49.74149909	-14.44419837
Site 4	T2 S4	49.74147035	-14.44436094
Site 4	T2 S4	49.74133942	-14.44455007
Site 4	T2 S4	49.74130094	-14.44479394
Site 4	T2 S4	49.74130028	-14.44491145
Site 4	T2 S4	49.74133647	-14.44507436
Site 4	T2 S4	49.74136369	-14.44518298
Site 4	T2 S4	49.74125126	-14.44538126
Site 4	T2 S4	49.7410557	-14.44551581
Site 4	T2 S4	49.74084185	-14.44560506

Sites	Transect	Long	Lat
Site 4	T2 S4	49.7408131	-14.44576762
Site 4	T2 S4	49.74073818	-14.44589378
Site 4	T2 S4	49.74084832	-14.44610228
Site 4	T2 S4	49.74096805	-14.4462566
Site 4	T2 S4	49.74116249	-14.44632091
Site 4	T2 S4	49.74135718	-14.44634003
Site 4	T2 S4	49.74152486	-14.44621437
Site 4	T2 S4	49.74157261	-14.44597056
Site 4	T2 S4	49.74159147	-14.44591642
Site 4	T2 S4	49.74139749	-14.44577075
Site 4	T2 S4	49.74144478	-14.44560828
Site 4	T2 S4	49.7414644	-14.44541855
Site 4	T2 S4	49.74157627	-14.44531971
Site 4	T2 S4	49.7416884	-14.44517568
Site 4	T2 S4	49.74176321	-14.4450676
Site 4	T2 S4	49.74154141	-14.44492178
Site 4	T2 S4	49.74150501	-14.44479503
Site 4	T2 S4	49.74165409	-14.44467831
Site 4	T2 S4	49.74171983	-14.44453402
Site 4	T2 S4	49.74185036	-14.4444172
Site 4	T2 S4	49.74192558	-14.44423681
Site 4	T2 S4	49.74212109	-14.4441113
Site 4	T2 S4	49.74227933	-14.4440127
Site 4	T2 S4	49.74225242	-14.44384985
Site 4	T2 S4	49.74201125	-14.44384856
Site 4	T2 S4	49.74180703	-14.44387459
Site 4	T3 S4	49.74160362	-14.44375598
Site 4	T3 S4	49.74161371	-14.4436114
Site 4	T3 S4	49.74155886	-14.44346647
Site 4	T3 S4	49.74135602	-14.44324844
Site 4	T3 S4	49.7413473	-14.44314895
Site 4	T3 S4	49.74113456	-14.44303934
Site 4	T3 S4	49.74113578	-14.44282239
Site 4	T3 S4	49.74121004	-14.44281375
Site 4	T3 S4	49.74118333	-14.44261473
Site 4	T3 S4	49.74096081	-14.44259547
Site 4	T3 S4	49.7407199	-14.44254898
Site 4	T3 S4	49.74056195	-14.44259333
Site 4	T3 S4	49.74038531	-14.44266471
Site 4	T3 S4	49.74020957	-14.44257337
Site 4	T3 S4	49.73995933	-14.44253588
Site 4	T3 S4	49.73987666	-14.4423908
Site 4	T3 S4	49.74004408	-14.44231033
Site 4	T3 S4	49.74016533	-14.44219347
Site 4	T3 S4	49.74001789	-14.44202092
Site 4	T3 S4	49.74004698	-14.44179509
Site 4	T3 S4	49.74003883	-14.44159617
Site 4	T3 S4	49.73987268	-14.44145064
Site 4	T3 S4	49.73985499	-14.44129687
Site 4	T3 S4	49.73982834	-14.44108882
Site 4	T3 S4	49.73967151	-14.4409343
Site 4	T3 S4	49.73982043	-14.4408447
Site 4	T3 S4	49.73997924	-14.44064668
Site 4	T3 S4	49.74002679	-14.44043902
Site 4	T3 S4	49.74007434	-14.44023136
Site 4	T3 S4	49.74025103	-14.44015094
Site 4	T3 S4	49.74040923	-14.44006139
Site 4	T3 S4	49.74058542	-14.44007137
Site 4	T3 S4	49.74067868	-14.43998147
Site 4	T3 S4	49.74092046	-14.43987429
Site 4	T3 S4	49.74092051	-14.43986525
Site 4	T3 S4	49.74125596	-14.43959585
Site 4	T3 S4	49.74130331	-14.43942435
Site 5	T1 S5	49.7372121	-14.44444663
Site 5	T1 S5	49.73732438	-14.44427548
Site 5	T1 S5	49.73753778	-14.44426758
Site 5	T1 S5	49.73771432	-14.44421429

Appendix I. (continued)

Sites	Transect	Long	Lat
Site 5	T1 S5	49.73784505	-14.44406132
Site 5	T1 S5	49.73796625	-14.44395349
Site 5	T1 S5	49.73800448	-14.44375482
Site 5	T1 S5	49.7380612	-14.44356529
Site 5	T1 S5	49.738053	-14.44337541
Site 5	T1 S5	49.73808184	-14.44319477
Site 5	T2 S5	49.73648562	-14.44496704
Site 5	T2 S5	49.73683872	-14.44486046
Site 5	T2 S5	49.73692302	-14.44471628
Site 5	T2 S5	49.73721154	-14.44454607
Site 5	T2 S5	49.73722143	-14.44443764
Site 5	T2 S5	49.73733187	-14.44459191
Site 5	T2 S5	49.73741449	-14.44474603
Site 5	T2 S5	49.73756244	-14.44482818
Site 5	T2 S5	49.73776662	-14.44481119
Site 5	T3 S5	49.73685712	-14.44488768
Site 5	T3 S5	49.73707943	-14.44494311
Site 5	T3 S5	49.73706909	-14.44513289
Site 5	T3 S5	49.73720756	-14.44525115
Site 5	T3 S5	49.73734583	-14.44540556
Site 5	T3 S5	49.73752192	-14.44543362
Site 5	T3 S5	49.73771616	-14.4455341
Site 5	T3 S5	49.73783603	-14.4456613
Site 5	T3 S5	49.73798475	-14.44560786
Site 5	T3 S5	49.73816105	-14.44559976
Site 5	T3 S5	49.73836512	-14.44560086
Site 5	T4 S5	49.73686252	-14.44557473

Sites	Transect	Long	Lat
Site 5	T4 S5	49.736983	-14.44559345
Site 5	T4 S5	49.73712178	-14.44565747
Site 5	T4 S5	49.73733487	-14.44570381
Site 5	T4 S5	49.73748268	-14.44581308
Site 5	T4 S5	49.7376027	-14.44591316
Site 5	T4 S5	49.73775046	-14.44603147
Site 5	T4 S5	49.73775861	-14.44623039
Site 5	T4 S5	49.73780387	-14.4464295
Site 5	T4 S5	49.73797925	-14.44658412
Site 5	T4 S5	49.7379875	-14.44676496
Site 5	T4 S5	49.73795865	-14.4469456
Site 5	T4 S5	49.73790198	-14.44712609
Site 5	T4 S5	49.73789168	-14.44730683
Site 5	T4 S5	49.73804846	-14.44747038
Site 5	T4 S5	49.73803806	-14.4476692
Site 5	T4 S5	49.73795356	-14.44784954
Site 5	T4 S5	49.73778618	-14.44792096
Site 5	T4 S5	49.73757324	-14.44784751
Site 5	T4 S5	49.73740704	-14.44771102
Site 5	T4 S5	49.73728701	-14.44761094
Site 5	T4 S5	49.73710144	-14.44761898
Site 5	T4 S5	49.73700954	-14.44746482
Site 5	T4 S5	49.73698309	-14.4472206
Site 5	T4 S5	49.73688106	-14.44722006
Site 5	T4 S5	49.73666868	-14.44704716
Site 5	T4 S5	49.73644605	-14.44704597
Site 5	T4 S5	49.73629835	-14.44691862