Behaviour and Ecology of Male Aye-Ayes (*Daubentonia madagascariensis*) in the Kianjavato Classified Forest, South-Eastern Madagascar

Doménico Roger Randimbiharirinirina^a Brigitte M. Raharivololona^a
Melissa T.R. Hawkins^b Cynthia L. Frasier^b Ryan R. Culligan^b
Timothy M. Sefczek^c Richard Randriamampionona^d
Edward E. Louis Jr.^{b, d}

^aMention Anthropobiologie et Développement Durable, Domaine Sciences et Technologie, Université d'Antananarivo, Antananarivo, Madagascar; ^bBill and Berniece Grewcock Center for Conservation and Research, Department of Conservation Genetics, Omaha's Henry Doorly Zoo and Aquarium, Omaha, NE, USA; ^cDepartment of Anthropology, Ohio State University, Columbus, OH, USA; ^dMadagascar Biodiversity Partnership, Manakambahiny, Antananarivo, Madagascar

Keywords

Activity budget · Diet · Home range · Nocturnal strepsirrhines · Primate · Territory

Abstract

Previous studies found that aye-ayes (*Daubentonia madagascariensis*) consume a variety of non-invertebrate resources, supporting the hypothesis that aye-ayes are too large-bodied to focus feeding efforts on insects. However, these conclusions were based on introduced populations, with little known about aye-aye behaviour and ecology in its natural habitat. This study investigates activity budgets, diet, and home range/territories of 2 male aye-ayes in the Kianjavato Classified Forest, a disturbed forest in south-eastern Madagascar, from October 2013 to October 2014. We used radiotelemetry and focal-animal sampling methods to collect behavioural data. We recorded GPS coordinates of the focal animal every 20 min, calculating the home range size for each individual. Results showed that male aye-ayes spent most of their time feeding and travelling. Their feeding time primarily focussed on larvae and adult insects from various substrates, and to a lesser extent *Canarium* spp. seeds. Home range sizes of the 2 males varied between individuals, overlapped greatly, and appeared to be related to the location of females. Our findings indicate that aye-aye behaviours are strongly indicative of insect-centric feeding ecology.

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Introduction

Insectivorous primates are typically associated with certain ecological expectations. Insectivores are expected to be small-bodied because invertebrates are not available in large enough quantities to support the necessary energetic demands of primates larger than 500 g [Kay, 1975; Gaulin, 1979; McGrew, 2001; Raubenheimer and Rothman, 2013; McGrew, 2014]. Additionally, primates relying on insects need to hunt their prey across a large area as invertebrate prey species are rare throughout the environment [Milton and May, 1976; Gaulin, 1979]. Increased territory ultimately results in an increase in foraging and travelling times as the primate hunts for its food [Clutton-Brock and Harvey, 1977]. It is unusual for any species to maintain a body size over 500 g and overcome the challenges of being predominantly insectivorous.

Aye-ayes were initially described as insectivores despite having an average body size of 2.5 kg, deemed too large to subsist primarily on invertebrates [Petter and Peyriras, 1970; Kay, 1975; Clutton-Brock and Harvey, 1977; Petter, 1977; Iwano and Iwakawa, 1988]. It has been suggested that the aye-aye's unusual, derived traits, including an elongated, thin, highly flexible middle finger and continuously growing incisors, and unique percussive foraging behaviours allow it to subsist mainly on invertebrates despite its large body size [Cartmill, 1974; Gaulin, 1979; Martin, 1990; Erickson, 1991; Simons, 1995; Erickson et al., 1998].

Other studies contradict the notion that aye-ayes are predominantly insectivorous, instead suggesting a degree of omnivory [Sterling, 1993a, 1994a] or granivory [Iwano and Iwakawa, 1988; Iwano, 1991]. The most significant studies on the behaviour and ecology of the aye-aye have been carried out in artificially established populations introduced in the late 1960s to the island of Nosy Mangabe, in north-eastern Madagascar [Sterling, 1993a; Sterling et al., 1994]. The diet of these animals consisted mainly of seeds from *Canarium* spp. (Burseraceae), cankerous growths, larvae, and nectar from flowers of *Ravenala madagascariensis* (Strelitziaceae) [Iwano and Iwakawa, 1988; Sterling, 1993a, 1994a]. Other researchers, focusing on aye-ayes introduced to the Mananara-Nord Biosphere Reserve (11 ha), on the east coast of Madagascar, found that nectar from the flowers of travellers' palm (*R. madagascariensis*) was the dominant food source during the dry season [Ancrenaz et al., 1994]. Further studies in Mananara-Nord Biosphere Reserve found the major diet composition was coconut flesh and milk, followed by larvae and *Terminalia* nuts, complemented by a variety of other foods [Andriamasimanana, 1994].

In addition to expanding the dietary repertoire of this species, these introduced populations had large home ranges [Sterling, 1993a, 1994a; Sterling et al., 1994] and high frequencies of foraging and travelling activity [Sterling, 1993a; Andriamasimanana, 1994; Sterling et al., 1994], both of which are expected of primates relying on insects for food. However, large home ranges and relatively high levels of foraging and travelling are also common for omnivores and frugivores [Milton and May, 1976; Clutton-Brock and Harvey, 1977]. Despite previous studies advancing our understanding of aye-aye behaviour and ecology, basic biological data on natural populations are still lacking [Schwitzer et al., 2013].

Our goal was to determine whether behaviours of naturally occurring aye-ayes were similar to previously reported behaviours of introduced populations. We studied the time budget, home range, and feeding time of 2 male aye-ayes for 1 year in

Fig. 1. Map showing the study site of *Daubentonia madagascariensis* in the Kianjavato Classified Forest, in south-eastern Madagascar, from October 2013 to October 2014 (modified from BD500 FTM 2007 and Holmes et al. [2016]).

Kianjavato Commune, located in south-eastern Madagascar. Our main goal was to determine whether the aye-aye's behaviours were focused on invertebrate or *Canarium* feeding. We predicted that (1) aye-ayes would spend the majority of their foraging and feeding time extracting and consuming invertebrates, and (2) aye-ayes would spend most of their activity budget feeding and travelling. Lastly, as male home range is often associated with distribution of solitary fertile females, a key resource, we predicted (3) male aye-ayes would maximize their access to this resource by having a range distribution pattern similar to that observed by Sterling [1993b] at Nosy Mangabe, with large overlapping male home ranges and smaller female home ranges.

Methods

Study Site

We conducted this study in the Kianjavato Classified Forest (KCF hereafter), in south-eastern Madagascar (21°17'–21°27' S and 47°47'–47°58' E; Fig. 1). This forest is degraded/secondary lowland rain forest, covers an area of 4,875 ha and ranges in elevation from 193 to 291 m above sea level. The KCF is composed of a conglomeration of agricultural subsistence farming, a coffee plantation (approx. 150 ha) managed by the Centre National pour la Recherche Appliquée sur le Développement Rural or FOFIFA, and a non-protected classified forest (4,725 ha) which is a sec-

ondary forest interrupted by bamboo [Manjaribe et al., 2013]. Our study area covered the Tsi-tola, Ambatovaky and Sangasanga forests which are local names for the 3 mountain ranges within the KCF. The natural vegetation surrounding Kianjavato is a low elevation, humid, evergreen forest dominated by *Anthostema* (Euphorbiaceae) and trees from the family Myristicaceae [Far-amalala, 1988]. Due to slash-and-burn agricultural practices, the KCF's landscape is classified as degraded and secondary; it is humid, lowland rainforest [Manjaribe et al., 2013].

Behavioural Data Collection

Lemurs were captured via a CO₂ projection rifle with approximately 10 mg/kg of Telazol (Fort Dodge Animal Health, Fort Dodge, IA, USA). Once immobilized, we attached VHF radiocollars to them (Advanced Telemetry Systems[®], Isanti, MN, USA, model No.: R410) to allow us to follow the animals via radiotelemetry [Honest and MacDonald, 2011]. All animal handling procedures followed protocols set by the Malagasy regulatory parties for the ethical treatment of non-human primates. Moreover, all interactions with the study subjects abided by Omaha's Henry Doorly Zoo and Aquarium's Institutional Animal Care and Use Committee guidelines (97-001, 12-101).

From October 2013 to October 2014, we monitored 2 male aye-ayes, KIAN13.7 and KIAN13.12, referred henceforth by their nicknames, "Dera" and "Zeppelin", respectively. We followed 1 individual Monday through Thursday each week, and switched between the 2 focal animals weekly. Focal follows were initiated as the animals emerged from their nests and then terminated at 2:00 a.m. at the latest. We collected behavioural data for an average of 5.5 h per night ($\sigma = 0.51$). We used the focal animal sampling method to collect behavioural data [Altmann, 1974], recording the following activities every 5 min: feeding, travelling, resting (non-sleeping, stationary), and self-grooming. We used binoculars to observe the animal as it extracted its food. The behavioural category "feeding" includes the extraction time as well as the time spent consuming the food. After the animal had left the food source, we checked the site to determine, to the best of our ability, the food type. Additional behaviours were also collected (such as vocalization and aggression). In addition, we recorded the animal's height in the forest, tree species occupied and diameter at breast height of the said tree, and GPS coordinates (using the WGS 1984 coordinate system) of all feeding sites for each individual, as well as for the localities of the focal animal every 20 min; these are referred to as non-feedGPS locations because they occurred during resting, travelling and other non-feeding events. To determine whether male home ranges were based on reproductive opportunities or resource distribution, we also collected sleep site GPS locations on 1 female aye-aye, KIAN11.6, referred to henceforth by the nickname "Bozy," from October 2013 to October 2014. Every 2 months we took a 2-week break.

Data Analysis and Statistics

We evaluated activity budgets and time budgets for both males. The activity budget was evaluated by calculating the average percentage of each activity every hour. The time budget was determined by comparing the relative frequency of each activity over the course of the study. We conducted the same analysis to identify the diet composition of the 2 individuals, to determine the proportion of time spent foraging on different food sources, and to investigate the patterns of habitat use by the animals.

We used Excel stat 2015 for our statistical tests. A Shapiro-Wilkes test ($\alpha = 0.05$) showed that data were not normally distributed ($W = 0.145$, $df = 420$, $p = 0.004$); therefore, we used non-parametric tests. We used a Mann-Whitney U test (1) to compare behaviours between the 2 individuals to determine whether there were any significant differences in daily activity and (2) to compare the general time budget of the 2 individuals. We conducted a z-test in Stat box 6.5 for a comparison of 2 proportions to examine whether the spatial distribution of food sources influenced the distribution of the 2 male aye-ayes. We also performed the z-test to compare: (1) the percentage of the feeding GPS locations to the other non-feeding GPS locations recorded for localities within each individual home range and (2) the percentage of feeding GPS locations by each individual inside the overlap of their home ranges compared to the feeding GPS locations outside the overlap of their respective home ranges.

We used the minimum convex polygon and the kernel density estimate (KDE) methods to map and estimate the size of both males' home ranges. The minimum convex polygon method

Fig. 2. Daily activity budget for 2 male aye-ayes, Dera (**a**) and Zeppelin (**b**), at the Kianjavato Classified Forest from October 2013 to October 2014.

serves to determine the area used by the animal by connecting all the most external locations occupied to form a polygon with convex angles [Mohr, 1947]. Conversely, the KDE method allows us to calculate a magnitude per unit area from point or polyline feature using a kernel function to fit a smoothly tapered surface to each point or polyline. Only the points or portions of a line that fall within the neighbourhood are considered in calculating density; 3 levels (10, 50, and 95%) should be considered to estimate home range size on KDE [Worton, 1989]. We calculated the area used by each individual in ArcMap v10.4.1.

Fig. 3. Proportion of different activities for the 2 male aye-ayes (Zeppelin and Dera) at the Kianjavato Classified Forest from October 2013 to October 2014.

Results

Activity Budgets

We followed the 2 male aye-ayes for a total of 373.5 h, with 198 h (over 44 nights) spent on Dera and 175.5 h (over 33 nights) spent on Zeppelin. During the dry season, both animals left their nests at $18 \text{ h} \pm 5 \text{ min}$, and during the rainy season, the 2 male aye-ayes left their nests later, at $18 \text{ h} \pm 30 \text{ min}$.

The Mann-Whitney U test found that there was no significant difference between the daily activity of Dera and Zeppelin ($df = 146$, $U = 38$, $p = 0.63$). During the first 2 h after the emergence from the nest, the most frequent behaviours were self-grooming, then moving, and finally feeding (Fig. 2a, b). From 19:00 h until we left the animals, anywhere between 00:00 and 02:00 a.m., the most frequent behaviours were travelling and feeding, with resting and self-grooming rounding out the rest of the aye-ayes' activities (Fig. 2a, b).

Time Budget

A Mann-Whitney U test showed that there were no significant differences between the proportion of each type of activity across the entire study of the 2 males ($U = 24$, $df = 128$, $p = 0.34$). The 2 animals spent most of their time feeding (38.53% for Dera and 34.16% for Zeppelin) and travelling (39.94% for Dera and 40.35% for Zeppelin). Both males were also recorded resting (13.35% for Zeppelin and 11.52% for Dera) and self-grooming (8.06% for Zeppelin and 8.13% for Dera; Fig. 3). We never observed either grooming or playing between the 2 individuals.

Feeding Time and Food Sources

The 2 individuals primarily consumed 4 types of food: larvae, seeds of *Canarium globosum*, *Canarium compressum* and *Canarium lamianum* (Burseraceae), together referred to as *Canarium* spp., nectar from *R. madagascariensis* (Strelitziaceae), and adult insects. Due to the difficulty in identifying invertebrates, insect prey classification was not specified.

Fig. 4. Proportion of feeding time per item by the 2 male aye-ayes (Zeppelin and Dera) at the Kianjavato Classified Forest from October 2013 to October 2014.

Table 1. Percentage of behaviour records spent on exploration for larvae and insect sources by the 2 male aye-ayes (Zeppelin and Dera) at the Kianjavato Classified Forest from October 2013 to October 2014

Food source	Zeppelin	Dera
Larvae		
Branch of partially dead wood	47	51
Dead wood	53	39
Trunk of <i>Bambusa vulgaris</i> adult	0	10
Insects		
Dry flower of <i>Ravenala madagascariensis</i>	42	4
Axil of <i>Dyopsis linea</i>	58	96

Dera spent 45.36% of his feeding time accessing and consuming larvae, 24.54% eating *Canarium* seeds and 21.76% eating insects. Zeppelin spent 58.7% of his feeding time consuming larvae, 33.85% eating *Canarium* seeds and 6.06% eating insects. Both males fed on nectar from *R. madagascariensis* for only a small portion of their feeding time (Fig. 4).

Zeppelin extracted larvae from dead wood and from dead branches on live trees an equal amount of the time, while Dera extracted larvae from dead branches on live trees more frequently. Additionally, Dera sought grubs in adult trunks of *Bambusa vulgaris* (Poaceae) for 10% of his foraging time (Table 1).

In general, the 2 individuals searched for insects on dead flowers of *R. madagascariensis* and on the axil of *Dyopsis linea* (Arecaceae) or “Hovana.” While Zeppelin searched for insects slightly more often on the axil of *D. linea* than in the dead flowers of *R. madagascariensis*, Dera almost exclusively investigated *D. linea* (Table 1).

Table 2. Home range size of the 2 male aye-ayes (Dera and Zeppelin) and 1 female (Bozy, nesting site data only) using the kernel density estimation (KDE) and the minimum convex polygon (MCP) methods at the Kianjavato Classified Forest from October 2013 to October 2014

Aye-aye	KDE, ha			MCP, ha	
	10%	50%	95%	all data	nesting site data
Bozy	–	–	–	98.20	98.2
Dera	5.98	74.36	285	973.12	870.9
Zeppelin	35.63	148.88	265.77	821.55	597.5

Table 3. Percentage of behaviour records spent feeding on food items within the male aye-ayes’ (Zeppelin and Dera) home range at the Kianjavato Classified Forest from October 2013 to October 2014

Food type	Ambatovaky forest	Tsitola forest	Sangasanga forest
Zeppelin			
Larvae	18.30	40.40	–
<i>Canarium</i> spp.	12.53	21.32	–
Insects	2.00	4.06	–
Nectar from <i>Ravenala madagascariensis</i>	0.40	1.00	–
Dera			
Larvae	10.20	15.00	20.16
<i>Canarium</i> spp.	4.15	10.00	11.40
Insects	1.56	4.10	16.10
Nectar from <i>Ravenala madagascariensis</i>	1.00	1.33	5.00

Home range, KDE

During our study period, Dera’s home range sizes were 5.98 ha (level 10%), 74.36 ha (level 50%), and 285 ha (level 95%). Zeppelin’s home range was 35.63 ha (level 10%), 148.88 ha (level 50%), and 265.77 ha (level 95%) (Table 2).

Home Range, Minimum Convex Polygon

Using all data, Dera’s and Zeppelin’s home ranges were 973.12 and 821.55 ha, respectively, while the female Bozy occupied only 98.2 ha, based on only sleeping site data (Table 2). The territory of both males overlapped greatly. Zeppelin’s home range encompassed the Tsitola and Ambatovaky forests, whereas that of Dera extended from Tsitola forest to the Sangasanga forest (Fig. 5a, b). The size of the overlap of Dera and Zeppelin’s ranges was 460.13 ha. Dera’s territory almost entirely overlapped Bozy’s (covering approx. 95 ha).

Nesting Site Data

Using the GPS point for nesting site, Dera’s and Zeppelin’s home range sizes were 870.9 and 597.5 ha, respectively, while the female Bozy occupied only 98.2 ha (Table 2). The territory of both males still overlapped greatly. The size of the overlap

Fig. 5. Map showing home ranges of the 2 male aye-ayes Zeppelin and Dera (a), nesting sites of the female Bozy and the 2 males Zeppelin and Dera (b), and the distribution of food sources exploited by each individual aye-aye (c) within the overlapped territory in the Kianjavato Classified Forest from October 2013 to October 2014.

Table 4. Percentage of feeding GPS locations and non-feeding GPS locations within home ranges of both male aye-ayes (Zeppelin and Dera) at the Kianjavato Classified Forest from October 2013 to October 2014

	Zeppelin	Dera
Percentage of feeding GPS locations	48.13	59.40
Percentage of non-feeding GPS locations	51.87	40.60

Table 5. Percentage of feeding GPS locations and non-feeding GPS locations inside and outside the overlapped area of both male aye-ayes (Zeppelin and Dera) within their home ranges at the Kianjavato Classified Forest from October 2013 to October 2014

	Zeppelin	Dera
Percentage of feeding GPS locations outside the overlap	45.45	48.45
Percentage of non-feeding GPS locations inside the overlap	54.55	51.55

between Dera and Zeppelin was 370.5 ha, while the size of the overlap between Dera and Bozy was 94.9 ha. Bozy’s and Zeppelin’s home ranges did not overlap at all. We observed that the home range size based on nesting site data of male aye-ayes is larger than those of the female at the KCF.

Ranging Pattern and Spatial Dispersion of Food Sources

Zeppelin spent nearly two thirds of his foraging time (67%) in Tsitola and the rest (33%) in Ambatovaky. Dera spent about half of his foraging time (52.66%) in Sangasanga, 30.43% at Tsitola, and 16.91% at Ambatovaky. In Tsitola, Zeppelin spent most of his feeding time on larvae and *Canarium* seeds. While in Sangasanga, Dera mainly focussed feeding time on larvae and insects, followed by *Canarium* seeds. Nectar consumption always represented the least amount of foraging time by both individuals in all forest patches (all details provided in Table 3 and Fig. 5c).

Within Zeppelin’s home range, the percentage of feeding GPS locations was significantly lower than that of other non-feeding GPS locations (z-test, $z = -11.26$, $p = 0.00$). We observed the same findings within Dera’s home range (z-test, $z = -5.90$, $p = 0.00$; Table 4). The percentage of feeding GPS locations by each individual inside the overlap did not differ from that of individual feeding locations outside the overlap (in their respective home ranges; for Zeppelin: z-test, $z = 1.35$, $p = 0.09$; for Dera: z-test, $z = 0.56$, $p = 0.29$; Table 5).

Discussion

The large body size of aye-ayes led some to argue they are not predominantly insectivorous [Kay, 1975; Iwano and Iwakawa, 1988; Sterling, 1993a, 1994a]. Our findings suggest that aye-ayes can accommodate an insectivorous lifestyle because of

their radical morphological adaptations, as mentioned by Gaulin [1979]. Not only did the aye-ayes spend the majority of their time feeding and travelling, covering large home ranges, but the majority of Dera's and Zeppelin's feeding times were spent on invertebrates, with a particular emphasis on larvae. Invertebrates, as well as the aye-ayes' second most consumed resource, *Canarium* seeds, are nutrient rich, and contain large quantities of lipids, protein and carbohydrates [Hladik and Charles-Dominique, 1974; Sailer et al., 1985; Dasilva, 1992; Morland, 1993; Sterling, 1993a, 1994a]. This high-quality diet perhaps allows aye-ayes to maintain their large body size despite Kay's threshold [Kay, 1975]. It is possible that the greater time spent accessing and consuming invertebrates, as opposed to the other available resources, is due to this food item being structurally defended and necessitating a greater amount of time to extract a single larva. However, *Canarium* seeds are also a structurally defended resource and require aye-ayes to manipulate the food stuff before consumption as well [Iwano and Iwakawa, 1988; Iwano, 1991; Sterling, 1994a]. We cannot definitively identify aye-ayes as insectivorous as we lack consumption rates and resource abundance data to show preferential use of invertebrates compared to other resources. Instead, taken in conjunction with previous research on aye-ayes, our results indicate that this species has a very flexible diet.

Feeding Times and Food Sources

Our first prediction was that the majority of feeding time would be comprised of invertebrate feeding for aye-ayes in the KCF. Both males spent most of their time accessing and consuming larvae, with *Canarium* seeds and adult insects rounding out the rest of the feeding time. Compared to aye-ayes in Mananara-Nord Biosphere Reserve and on the island of Nosy Mangabe, the feeding behaviours of the KCF aye-ayes vary considerably. In the Mananara-Nord Biosphere Reserve, coconut flesh and milk, grubs and *Terminalia* (Combretaceae) seeds made up the bulk of the diet [Andriamasimanana, 1994]. In another part of the Mananara-Nord Biosphere Reserve (degraded forest consisting of grazing land and plantations), nectar from *R. madagascariensis* was the most consumed food item [Ancrenaz et al., 1994]. On Nosy Mangabe, the aye-aye mainly consumed *Canarium* seeds, cankerous growth, larvae, and nectar from flowers of *R. madagascariensis* [Sterling, 1993a, 1994a].

The differences between our resource feeding time results and those of other studies, when taken in combination, suggest that aye-ayes are more adaptable than we anticipated. The aye-aye is distributed throughout much of Madagascar and survives in various habitat types such as primary rain forests, deciduous forests, secondary forests, plantations, dry scrub forests, coconut groves and mangrove swamps [Ancrenaz et al., 1994; Andriamasimanana, 1994]. Sussman et al. [1985] reported that lemur activity, especially feeding behaviours, depends on the food availability (annually and seasonally) in its habitat. Consequently, aye-aye diets may be flexible as food availability might differ from one habitat type to another. This could explain the dietary variation across the aye-aye's range. It also suggests that the aye-aye's feeding adaptations, while clearly intended for invertebrate foraging, do not limit their ability to consume a variety of other resources.

In the KCF, the aye-aye searched for grubs in dead wood, dead branches in living trees, and in bamboo stalks, but rarely from live wood; we never observed foraging on lianas. During our study period, we heard the crunching sounds from both individuals when they fed on *Canarium* seeds. We inferred this as evidence of seed con-

sumption as the locules were empty upon investigation, rather than searching for larvae inside seeds. This is not to say larvae were not present in *Canarium* seeds at the KCF. Aye-ayes consume larvae and insects from a variety of plant families [see Andriamasimanana, 1994, and Sterling, 1993b, 1994b]; therefore, substrate use for invertebrate feeding may vary across different habitat types. For example, in the Mananara-Nord Biosphere Reserve, the aye-aye extracted larvae from trunks or branches of trees [Andriamasimanana, 1994], whereas, on Nosy Mangabe, the aye-aye foraged for grubs from fallen dead wood, dead branches on a living tree, living trees, dead and living lianas, tree bark, and inside parasitized seeds [Sterling, 1993a, 1994a]. More recently, Sefczek et al. [2017] identified live trees as the most frequently utilized substrate for invertebrate consumption by aye-ayes in the continuous forest tracks of Mantadia National Park and Torotorofotsy Ramsar Site. This again speaks to the aye-aye's adaptability to various environments.

Activity Budget

Our second prediction was that aye-ayes would exhibit high activity levels, feeding and travelling most often. We discovered up to 80% of the 2 male aye-ayes' waking time expenditures consisted of travelling and feeding, with only a small amount of active hours spent resting. Compared to other lemur species, *D. madagascariensis* are very active as Sterling [1993a; Sterling et al., 1994] and Andriamasimanana [1994] also reported. The aye-aye's high levels of activity across their home range could be related to the high nutritional quality of its diet [Hladik and Charles-Dominique, 1974; Dasilva, 1992; Morland, 1993]. Because our observations stopped at 2 a.m., it is possible that the aye-aye's activity levels are skewed toward feeding and travelling. Resting and self-grooming may increase later in the night, after 2 a.m.

Both aye-ayes spent most of their time feeding and travelling between the hours of 19:00 and 1:00 a.m. However, the first hour of activity is different for the 2 males. Dera spent most of the first hour of observation self-grooming, while Zeppelin typically spent the first hour of observation resting (Fig. 2). Additionally, the last hour of observation was typically spent feeding by Dera and resting by Zeppelin (Fig. 2). This may be due to differences in territory, Dera having a more continuous parcel of forest that requires or allows for continued searching for food, while Zeppelin, in a more degraded forest patch, is limited by how much food is available in his home range. Alternatively, it is possible Zeppelin is expending more energy searching for food in his degraded habitat, necessitating a resting period.

Home Ranges

Our last prediction was that male aye-aye home ranges in the KCF would be closely associated with female distribution. As in Sterling [1993b], male home ranges were large and overlapping, whereas the female's home range was smaller. However, both sexes' home ranges were greater at the KCF (home range was estimated using all GPS data and nesting GPS data). On Nosy Mangabe, male territories ranged from 125 to 215 ha, and those of females varied from 30 to 40 ha [Sterling, 1993a, 1994b], whereas the aye-aye territories of the KFC, based solely on sleeping sites, were between 597 and 870 ha for males and approximately 98 ha for the female. The largest calculated home range for all data was 973 ha for Dera and 821 ha for Zeppelin. This difference in home range size is perhaps due to the limited size of Nosy Mangabe, approximately 500 ha [Sterling, 1993a, 1994b].

Food distribution did not appear to affect the space use of either male aye-ayes in the KCF. Zeppelin primarily used the Tsitola forest for feeding, while Dera exploited the Sangasanga forest. Dera often came to the surrounding area of Tsitola to forage, whereas Zeppelin never frequented Sangasanga. The main core of the overlap of both males' home ranges was located in the surrounding area of Ambatovaky forest. The percentage of feeding GPS locations for each individual (Dera and Zeppelin) inside their overlapping territories did not differ from the percentage of feeding GPS locations outside their overlapping ranges. It is possible male aye-ayes are not forced to focus on food availability because their main resources, invertebrates and *Canarium* seed endosperm, are inaccessible for most other animal species. Larvae are contained within a variety of substrates including deadwood, live trees and bamboo, making them cryptic and difficult to access. Similarly, *Canarium* produce a hard seed coat that most Malagasy animals cannot crack open to use as a food resource [Sterling, 1993a, 1994b]. Thus, the unique adaptations of continuously growing fused canines and incisors and elongated, flexible digits allow the aye-aye to exploit these resources, which other potential competitors lack.

It is apparent that access to females plays an important role in the spatial distribution of male aye-ayes, as previously suggested [Sterling, 1993a; Sterling et al., 1994]. We found that male aye-aye home ranges are larger than those of females, and the male ranges overlapped greatly with each other. Dera's territory overlapped almost entirely with that of the female Bozy. Greater home range sizes in males compared to females are common among non-human primates. For example, subadult and adult male orang-utans (*Pongo pygmaeus*) in Sumatran swamp forest, South-East Asia, had at least a territory of 2,500 ha whereas adult females used a minimum estimated home range of 850 ha [Singleton and van Schaik, 2001]. There are similar findings in male *Galago senegalensis*, where the distribution of males is strongly influenced by female distribution; female ranging, on the other hand, depends on the distribution of vegetative resources [Bearder and Martin, 1980].

Aye-aye food choices and territories in the KCF differed from those of the introduced population inhabiting the island of Nosy-Mangabe. If habitat permits, an individual aye-aye may prefer to occupy a large home range, which may be more linked to access to either females or food distribution, depending on the sex of the individual. Therefore, results from this study are not only significant to our understanding of aye-aye behaviour and ecology in a natural habitat; but are useful to strengthen the conservation plan of this flagship Malagasy species.

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Disclosure Statement

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