

## Habitat use by the endemic Malagasy bat *Hipposideros commersoni* in a littoral forest

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We investigated habitat use by the endemic Malagasy bat *Hipposideros commersoni* in evergreen littoral rainforest during the wet season in 2006, in order to better inform conservation guidelines. We used radiotracking to locate roosting and foraging sites. Roosts, typically  $5.4 \pm 0.2$  m from the ground, were always occupied by single bats and were found on branches of trees with a diameter at breast height of  $8.2 \pm 0.7$  cm. Home range size was  $31.8 \pm 9.2$  ha for males and  $41.7 \pm 12.9$  ha for females. Roosts were always located within the foraging areas and only five (5.4%) of the 91 located were situated outside the sheltered littoral forest. Foraging bats made greatest use of natural, sheltered littoral forest and relatively few foraging sorties occurred beyond the forest edge. Females were not trapped during January and may undergo local movements at that time. There are no known caves in the vicinity of the study area and *H. commersoni* roosted only on trees. Previous studies in Madagascar have highlighted the importance of caves for bats and we now extend this to include tree roosts, within the evergreen rainforest.

*Key words:* forest dependency, habitat use, *Hipposideros commersoni*, home range, Madagascar, radiotracking, Tampolo

### INTRODUCTION

Disturbance to key roosting and foraging habitats is a major threat to 15.8% of the 1,150 bat species categorized as threatened on the IUCN Red List (IUCN, 2012). However, habitat requirements of bats are relatively poorly understood because they use a variety of habitat types for roosting and foraging, and are also able to fly considerable distances in a relatively short time. Knowledge of how bat species interact with their habitats, both on temporal and spatial scales, is therefore required to assist the development of conservation strategies (Ball, 2002; Mickleburgh *et al.*, 2002; Warren and Witter, 2002).

Most Malagasy bats roost in natural rock cavities or artificial cavities in buildings (Racey *et al.*, 2009), but a few, like *Myzopoda aurita* and *Pteropus rufus*, use vegetation (Ralisata *et al.*, 2015 and MacKinnon *et al.*, 2003, respectively). Although cavity roosts feature prominently in bat surveys on the island, there are relatively few studies on the ecology

of roosting bats (Cardiff, 2006; Olsson *et al.*, 2006). Foraging habitats are similarly poorly described for Malagasy bats, but Goodman *et al.* (2005) suggested that most species in the west of the island are not forest-dependent because roosts were located in sites lacking significant intact forest cover. In contrast, in eastern Madagascar, where there are fewer caves and crevices, it is of interest to determine the relative dependency of bats on the remaining rainforests.

*Hipposideros commersoni*, with a body mass of ca. 73 g and a forearm length of ca. 94 mm (Goodman, 2011), is the largest insectivorous bat in Madagascar. Although once thought to occur in mainland Africa, where it was described as a perch hunter (Vaughan, 1977), recent taxonomic refinements classify it as a Malagasy endemic (Simmons, 2005) and refer the African species to *Hipposideros vittatus* (Monadjem *et al.*, 2010). Widely distributed throughout the island, except on the central highlands, the species is classified as Near Threatened on the IUCN Red List because of habitat loss and its exploitation as bushmeat, as hunting is widely

reported (Goodman, 2006; Andriafidison *et al.*, 2008; Goodman *et al.*, 2008). Females from the south of the dry region in western Madagascar are smaller in size than those from the north, but there is no difference for males (Ranivo and Goodman, 2007). In western Madagascar, the species is thought to be tolerant of forest degradation because it frequently uses habitats at the interface between natural forest and agriculture (Goodman *et al.*, 2005; Kofoky *et al.*, 2007).

*Hipposideros commersoni* roosts in large colonies in caves in the west of Madagascar but in the east it is reported to roost individually in large trees (Raharinantenaina *et al.*, 2008). Other studies in the east have detected this species in forests in which no suitable cave-roosting habitats are known (Russ *et al.*, 2003; Ifticène *et al.*, 2005). Differences in the roosting ecology of this species may therefore make populations in areas without caves more susceptible to forest degradation.

In this study, we used radiotracking to assess the habitat use of *H. commersoni* in humid littoral forest where no caves are known. We aimed (1) to locate the roosts and estimate the area used by foraging

bats and (2) to determine habitat preferences of bats within these areas. We hypothesised that *H. commersoni* would use all the habitat types in proportion to their availability for roosting and foraging.

## MATERIALS AND METHODS

### *Study Period and Area*

The study was conducted in the new protected area of Tampolo (17°17'S, 49°24'E) in Toamasina Province, eastern Madagascar (Fig. 1) during three periods of fieldwork in 2006: 20 January–11 February, 18 March–28 April and 21 November–19 December. There is no clear dry season in the area but the rainfall is lower between April and November than in other parts of the year (Fig. 2). Mean annual rainfall is 2,712 mm and mean annual temperature is 24°C (Rajoelison, 1997). Coastal forests on a sandy substrate, often referred to as littoral forests, are one of the most threatened vegetation types in Madagascar with only 10.3% of the original total area remaining (Consiglio *et al.*, 2006). The vegetation in the 675 ha of littoral forest in Tampolo, at less than 10 m a.s.l. (Ratsirarson and Goodman, 1998, 2005; Consiglio *et al.*, 2006) was classified into four types by Rajoelison (1997): sea-inundated, sheltered, mixed and marsh. The sea-inundated forest is closest to the sea, comprised of small trees that protect the rest of the forest from the wind. The more sheltered natural littoral forest is similar to the lowland

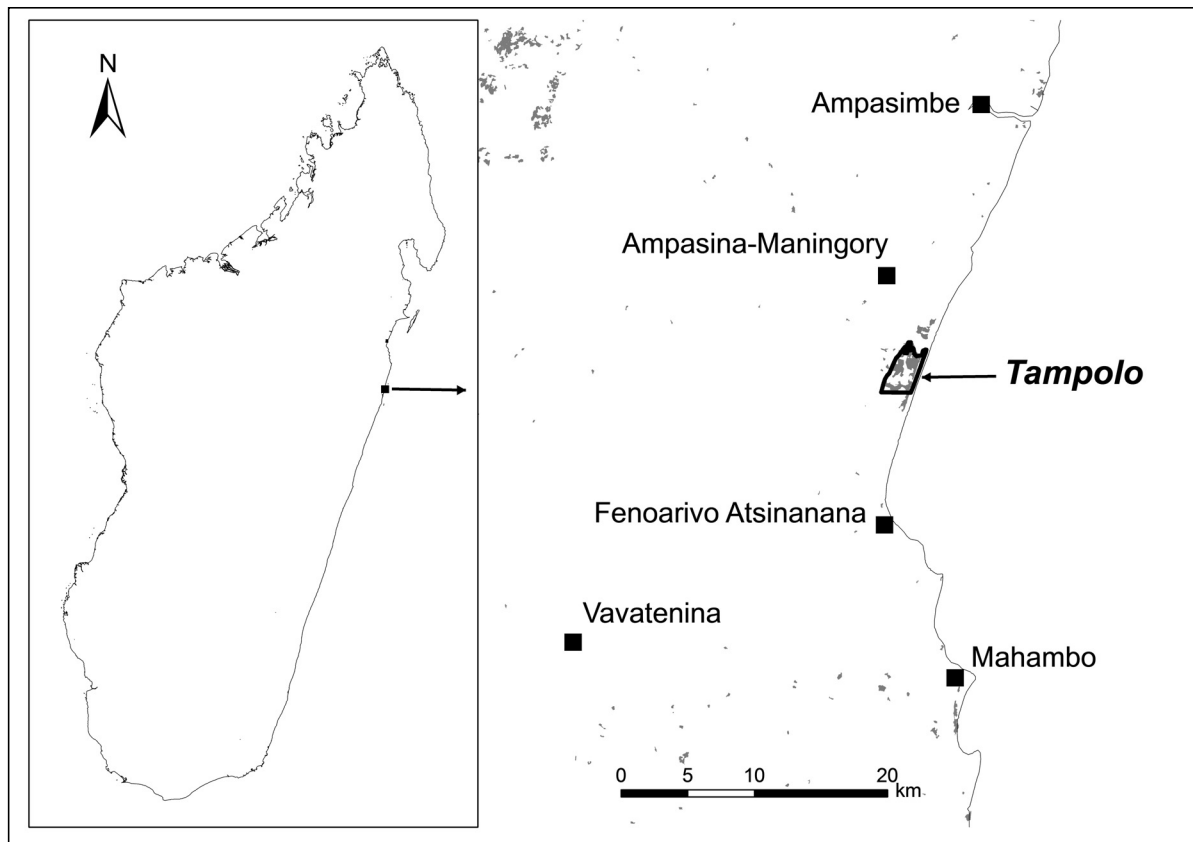


FIG. 1. Maps of Madagascar showing location of Tampolo protected area and nearby towns and cities in eastern Madagascar

evergreen humid rainforest in its structure and species composition (Rajoelison, 1997). Common tree species include *Harungana madagascariensis*, *Ocotea cymosa*, *Stephanostegia capuronii* and *Uapaca ferruginea* (Ratsirarson and Goodman, 1998, 2005). Following timber exploitation between 1956 and 1980, exotic trees, mostly *Aucoumea klaineana*, were planted in some areas to maintain the physical structure of the forest and now constitute the mixed forest. Marsh forest is associated with the waterways within the littoral forest, is mainly comprised of *Pandanus* spp. and *Typhonodorum lindleyanum* and is the least represented habitat type in Tampolo (Rajoelison, 1997; Ratsirarson and Goodman, 2005). A preliminary study of the vegetation during this study showed that the mean diameter (dbh) of the trees in Tampolo were  $9.7 \pm 0.3$  cm, ranging from 5 to 67 cm, with a mean height of  $7.6 \pm 0.1$  m with a maximum of 30 m. In total, we measured 748 trees. The edges of the protected area are bounded by anthropogenically impacted landscapes, dominated by rice fields, villages and scattered plantations of fruit trees (mainly litchis, grapefruits and mangos).

**Bat Capture and Handling**

*Hipposideros commersoni* were captured with mist nets set at ground level to 3.5 m across trails within all four vegetation types of the reserve and at the edge between forest and agriculture. We used 6 to 12 m mist nets, with 36 mm mesh. One to five mist nets were set for three hours after sunset depending on the number of personnel available. Sex and age were determined following Racey (2009) and Brunet-Rossini and Wilkinson (2009), and the body mass was determined with a 100 or 300 g Pesola spring balance for each captured bat. Twenty-two adults were fitted with a radiotracker attached to the dorsal pelage between the shoulders with Torbot Bonding Cement (Torbot Group Inc., Cranston, Rhode Island, USA). Four models of transmitters were used: LB-2, LB-2N, PD-2C, and BD-2A

(Holohil Systems, Carp, Ontario, Canada) weighing 0.32–1.80 g and with a battery life expectancy of 12 days (model LB-2N) to four months (model BD-2A). All transmitters weighed less than 5% of the bats’ body mass (Aldridge and Brigham, 1988). Individuals fitted with radiotransmitters were released at the capture site and tracking began two days later.

**Radiotracking**

Output from the transmitters was monitored with Regal 2000 receivers (Titely Electronics, Stones Corner, Queensland, Australia) for models LB-2, LB-2N and PD-2C and with TRX-48S (Wildlife Materials International Inc., Illinois USA) for the BD-2A transmitters. Both receiver types were used with 3-element Yagi antennae. Roosting bats were located during the day using the homing-in method (White and Garrott, 1990, Russo *et al.*, 2002), whereby the observer followed the direction from which the signal is strongest until the bat was observed directly. The geographic location of the roost was recorded using a GPS (Garmin eTrex, Garmin International Inc., Kansas, USA). Roost characteristics (tree height, diameter at breast height and species) and height of the bat were also noted.

The positions of active bats at night (hereafter called fixes) were located using the triangulation method (Kenward, 2001): two teams of field workers (two persons in each), who were in continuous contact with one another using hand-held FM-radios, simultaneously recorded information on the direction and strength of the signal as well as time and position of the observers every five min (Kenward, 2001; Bontadina *et al.*, 2002). Bats that were stationary for more than 15 min were approached as close as possible, and often observed directly, by following existing paths. Fixes from triangulation were calculated from the bearings and the observers’ positions using Map Source software (Version 6.0, Garmin). Normal tracking sessions lasted three h after a bat left the roost. Twice a week, four bats

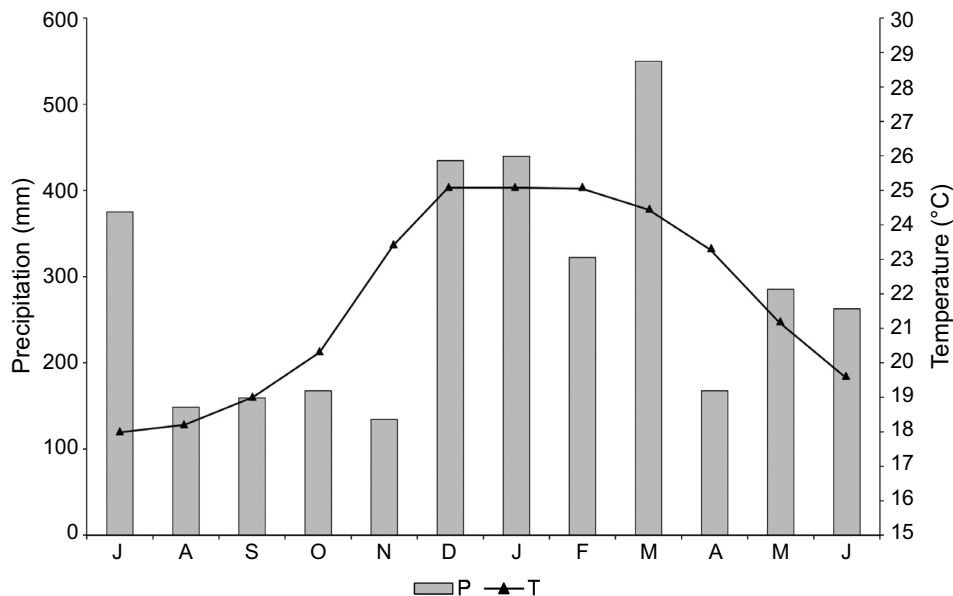


FIG. 2. Climate diagram for Tampolo protected area as collected by the Water and Forests Department of the Ecole Supérieure des Sciences Agronomiques, University of Antananarivo, between January 2005 and December 2007. Bars represent the monthly rainfall (P) and the line represents the mean monthly temperature (T)

were tracked successively for three hours each from 18:00 h to 06:00 h.

The precision of the fixes was estimated with the location error method (Zimmerman and Powell, 1995): the linear distances between actual and estimated locations of test transmitters were measured. Tests were conducted when finding the roost sites during the day and with a person moving with the transmitter at night.

### Ranging Behavior and Habitat Use

Home range analyses were conducted with the Animal Movement extension of ArcView 3.2™ (Hooge and Eichenlaub, 1997). The home range of one bat was defined as the minimum convex polygon joining its outermost positions (100% MCP) including roost sites and fixes. The number of fixes required to establish a home range is defined as the lowest number where plots of the size of home range vs. the number of fixes had approached an asymptote (Harris *et al.*, 1990; Kenward, 1992). If this minimum number was not reached, the bat was not included in the analyses of home range and habitat preference.

The maximum foraging distance was determined as the distance between the roost site and the furthest fix for each tracking session (Bontadina *et al.*, 2002). The core area is the part of the range where most of the bats' activity is concentrated (Wray *et al.*, 1992). The proportion of fixes considered to form the core area was determined by plotting the percentage of fixes used against the home range size on a utilization plot (Ford and Krumme, 1979) and determining the inflexion point of the curve (Kenward, 1992; O'Donnell, 2001).

The available area for all the bats in the study site, defining the limits of the study area, was determined by the MCP joining the outermost positions of all bats for which enough fixes were recorded. The areas of every habitat category falling within the study area and each individual MCP were calculated using ArcView GIS. The habitat category at each fix was also determined for each bat. Habitat preferences within the range of the study population and within each individual range were analyzed with compositional analysis (Aebischer *et al.*, 1993) using Microsoft Excel macro Compos Analysis version 6.2 plus (Smith, 2005). In this analysis, data are converted into proportions and MANOVA techniques are used to compare the use of each habitat to its availability and the rank order between habitats (Smith, 2006). In the results, the sign >>> indicates a significant difference in ranking compared with >. Apart from Compositional Analysis, all statistics were run on SPSS 15.0. Mean values are given with  $\pm$  one standard error (SE) unless otherwise specified.

## RESULTS

### Bat Capture and Tracking

A total of 31 *H. commersoni* were captured during the study. The number of bats captured per net per capture session during the three field visits did not vary significantly (Kruskal-Wallis  $H = 1.0$ ,  $P = 0.5$ ). However, there was a change in observed sex ratio across seasons. All 11 individuals captured in January–February were males, ten adults and one juvenile. In contrast, 12 of the 16 bats captured in

March–April (75%) were females. The same proportion was observed in November–December (three females out of four bats captured). A flying juvenile was present in February (a single male, weighing 31 g and with a forearm of 83.4 mm) and March–April (a single male, FA = 92.5 mm, W = 43.7 g and three females, FA = 81.8–88.3 mm, W = 35.5–39 g). No juveniles were caught in December.

There was no significant difference between the body masses of the male individuals captured during each field visit (Fig. 3;  $F_{2, 11} = 1.6$ ,  $P = 0.2$ ). In contrast, adult females captured in March–April were significantly heavier than those captured in November–December ( $F_{1, 10} = 5.6$ ,  $P < 0.05$  — Fig. 3). Overall, adult males were significantly larger than adult females considering their body masses ( $F_{1, 24} = 20.5$ ,  $P < 0.001$ ) and forearm lengths ( $F_{1, 24} = 62.7$ ,  $P < 0.001$ ).

Of the total of 22 bats fitted with radio transmitters, incremental plots showed that total MCP area for each individual bat was reached from 50 fixes (Fig. 4). Therefore, only bats with more than 50 recorded fixes were included in subsequent analyses (Table 1). This threshold was reached for only nine of our 22 radio-tagged bats (40.9%). For all bats, radiotracking stopped either because the tag fell off (31.8%), the bat could not be found in the study area for over one week (50%), or the fieldwork session had to be terminated for logistical reasons (18.2%). Overall accuracy of the fixes was estimated to  $97.8 \pm 14.8$  m.

### Roost Sites and Foraging Ranges

By following tagged bats, a total of 91 day roosts were located, of which 13 were used two to four

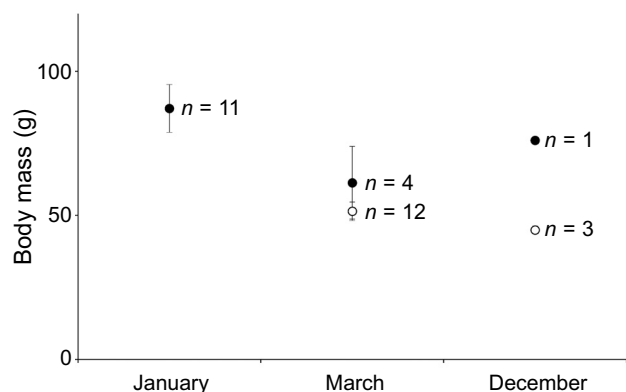


FIG. 3. Body mass ( $\pm$  SE) variation of male (filled circles) and female (empty circles) *H. commersoni* captured in Tampolo protected area during three field visits (January, March and December 2006)

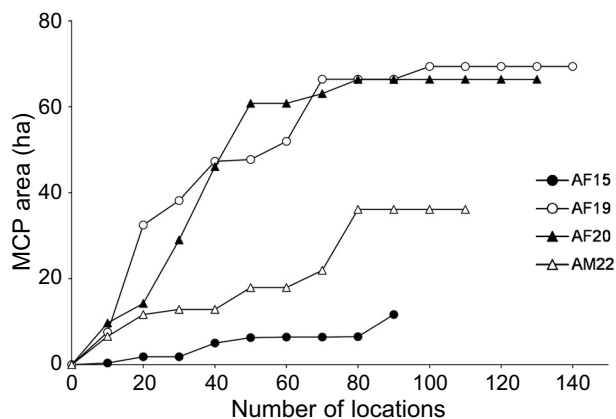


FIG. 4. Cumulative area of Minimum Convex Polygons (MCPs) with the number of fixes for four individuals with the highest total number of fixes. MCP area approached an asymptote with 50 locations for AF15 and AF20, 70 locations for AM22 and 80 locations for AF19

times by the same individual. Only five were found outside the littoral forest. At all roosts, *H. commersoni* were found during the day hanging alone on small branches and twigs of trees of  $8.2 \pm 0.7$  cm dbh, at  $5.4 \pm 0.2$  m from the ground, generally near open areas or trails. Roost heights correlated positively with tree height ( $r^2 = 0.7$ ,  $n = 87$ ,  $P < 0.001$ ). Bats used 52 different tree species for roosting; the most common were *Uapaca ferruginea*, *Canarium boivinii*, *Diospyros* sp., *Gaertnera* sp. and *Erythroxylum corymbosum*. No untagged roosting bat was observed during this survey.

Across all study periods, the mean home range areas (100% MCP) were  $31.8 \pm 9.2$  ha for males and  $41.7 \pm 12.9$  ha for females; the mean distance between the two furthest points of the home range (the span) were respectively  $1004.5 \pm 233.2$  m and  $1138.4 \pm 250.8$  m. Roost sites were located within the foraging areas of all individuals (Fig. 5). Core

areas, where 85% of the locations were recorded, were  $15.2 \pm 7.4$  ha for males and  $32.3 \pm 8.7$  ha for females and also included the roost sites except for one roost. Home ranges of two males captured on the same night at the same location in March overlapped only by 0.03%. In contrast, one female (AF17) had a high proportion of its range (79.5%) and core area (84.4%) overlapping with another (AF19) (Table 2).

#### Activity Patterns

Throughout the study, tagged bats began to forage  $26.8 \pm 2.2$  minutes after sunset. However, one male captured in December left the roost four hours after sunset while the females did not change their behavior. Moreover, of all the females tagged during this period, none could be located in the study area after mid-December.

Bats foraged around the roost sites for an average of three hours after sunset, and then flew to more distant sites before returning to the area of the roost site after midnight. They were also active before dawn (Fig. 6). Respectively, 56, 551 and 80 locations were recorded in January–February, March–April and November–December. The mean distance between roost and foraging locations was  $313.9 \pm 15.3$  m, with a maximum of 1.6 km. There were no significant difference between the distances travelled by males and females ( $F_{1,685} = 0.3$ ,  $P = 0.6$ ). The total area used by the tracked bats was 416.3 ha, which defines the total range in the habitat preference analysis.

#### Habitat Preference

The total range used by *H. commersoni* in Tampolo was comprised of 59.7% sheltered littoral

TABLE 1. Details of each the 11 individuals of *H. commersoni* radiotracked in Tampolo protected area during three field surveys in 2006 for which > 50 fixes were obtained

Period	ID <sup>a</sup>	Body mass (g)	Tag type	Date captured	No. of days	No. of roosts	No. of fixes
Jan–Feb	AM11	104	LB-2N	01 Feb	7	4	56
Mar–Apr	AF20	56	PD-2C	19 Mar	35	16	141
	AF17	47	LB-2N	26 Mar	16	6	70
	AM22	57	LB-2N	26 Mar	14	6	99
	AF19	55.5	PD-2C	26 Mar	33	16	146
	AM18	98	PD-2C	26 Mar	14	4	65
	AF15	71	LB-2N	10 Apr	13	7	101
Nov–Dec	AF21	52.5	PD-2C	22 Apr	6	1	86
	AM23	76	LB-2	11 Dec	7	6	80

<sup>a</sup> — AF: adult female, AM: adult male

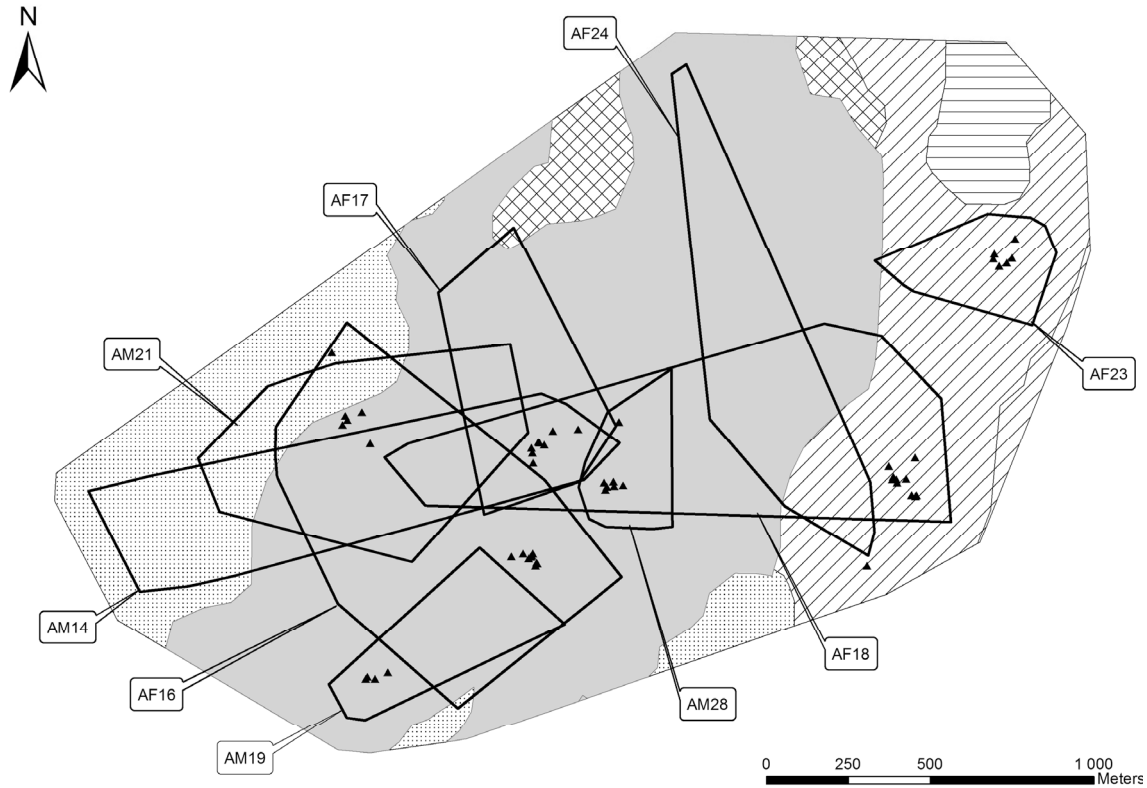


FIG. 5. Distributions of day roosts of tagged *H. commersoni* in Tampolo protected area in 2006 in relation to available habitats and showing the home ranges of radiotracked bats. Sea-inundated forest is hatched diagonally while mixed forest is hatched horizontally. Sheltered littoral forest is in grey and marshes are cross-hatched. Stippled areas represent agriculture

forest, 14.4% agriculture land, 19.3% sea-inundated forest, 3.6 % marsh forest and 3.1% of mixed forest. For all located roost sites, 62.6% were within the sheltered littoral forest, 31.8% in the sea-inundated forest and only 5.4% on the trees within the agriculture area. None of the individual home ranges contained marsh or mixed forests, therefore these habitats were not included in the analysis. At the scale of home ranges, the sheltered littoral forest was significantly the most used habitat for foraging (Compositional analysis,  $\lambda = 0.3$ ,  $\chi^2_2 = 10.9$ ,  $P < 0.01$ , randomisation  $P = 0.03$ . Rank: sheltered

littoral forest >>> agricultural land > sea-inundated forest). At the individual level, comparison of the habitat composition of home ranges (100% MCP) against habitat at each location confirmed the preference for the sheltered littoral forest although this preference was not significant (Compositional analysis,  $\lambda = 0.5$ ,  $\chi^2_2 = 6.3$ ,  $P < 0.05$ , randomisation  $P = 0.09$ ; Rank: sheltered littoral forest > agricultural land > sea-inundated forest). All tracked bats used the sheltered littoral forest, three exclusively so. Individual bats using agriculture areas were not located in the temporarily inundated forest, and vice versa.

TABLE 2. Percentage overlap between the home ranges and core areas of four *H. commersoni* captured on the same night (26 March 2006) at the same site in Tampolo protected area. Table should be read as follows: 1.4% of the home range of AM18 overlapped with that of AF17

ID <sup>a</sup>	Home range (100% MCP)				Core area (85% MCP)			
	AM18	AM22	AF17	AF19	AM18	AM22	AF17	AF19
AM18	–	0.0	1.4	1.5	–	0.0	1.6	0.1
AM22	0.0	–	2.4	16.6	0.0	–	0.0	0.0
AF17	2.8	9.5	–	79.5	4.1	0.0	–	84.4
AF19	0.5	11.0	12.50	–	–	0.1	0.0	10.3

<sup>a</sup> — AF: adult female, AM: adult male

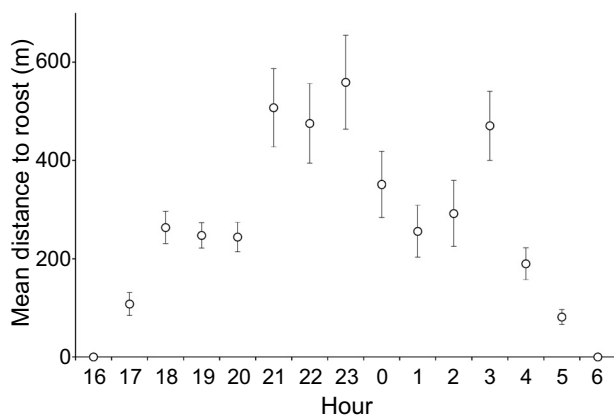


FIG. 6. Mean ( $\pm$  SE) distances of *H. commersoni* ( $n = 687$  fixes from nine bats) from the roost sites of the day to the foraging locations in Tampolo protected area

## DISCUSSION

This study of habitat use by *H. commersoni* in Tampolo reveals three major features in observed activity and roosting behaviour. Overall, this species prefers to roost and forage in sheltered littoral forest. Although females exploit a larger home range than males, the difference is not significant. Males were present throughout the study but females were captured only in March–April and November–December.

Our results for *H. commersoni* foraging in forests, and along forest edges, are consistent with those from western Madagascar (Kofoky *et al.*, 2007). They differ however in our eastern study area where this species makes significant use of relatively intact forest vegetation. In limestone areas of Madagascar, *H. commersoni* roosts in large colonies in sinkholes (Goodman, 2006) and caves (Cardiff, 2006; Goodman, 2011). In contrast, in lowland areas of the east, individuals roost individually in well-spaced out locations in trees. This contrast highlights the need to conduct radiotracking studies of habitat use by *H. commersoni* in sites where it roosts in caves.

Like its congeners in mainland Africa (Vaughan, 1977; McWilliam, 1982; Churchill *et al.*, 1997; Cotterill and Fergusson, 1999), and other observations in Madagascar (Olsson *et al.*, 2006; Kofoky *et al.*, 2007), *H. commersoni* did not occur consistently in Tampolo throughout the period of this study. In Tampolo, no cave was located but females were present during the austral summer (March–April and November–December in our study). Future studies are required to quantify patterns of activity

and occurrences throughout the year. As revealed in studies of congeners in mainland Africa (Monadjem *et al.*, 2010), it is likely that seasonal patterns of activity in *H. commersoni* depend on prevailing climatic and trophic conditions.

The presence of a flying juvenile in early February, together with adult females and flying juveniles in March suggest a probable January birth pulse. Females were not caught in the nets in January either because they were not foraging (albeit still resident), or because they may have moved to a maternity roost (as revealed in mainland Africa for *H. vittatus*, previously classified as *H. commersoni*, by McWilliam 1982 and Cotterill and Fergusson 1999). Also in mainland Africa, Cumming and Bernard (1997) showed that insectivorous bats commonly give birth a month before the peak rainfall while insect abundance peaks a month after the rainfall peak. With an average lactation of six weeks, young bats are thus weaned during the period of peak insect abundance.

Males' body masses were generally higher than the mean reported by Peterson *et al.* (1995) of 56.6 g (range: 39.8–68 g). The difference is likely to be explained by the fat deposits observed in bats captured in April 2004 in Tampolo (Ifticène *et al.*, 2005) and also reported from southern Madagascar (Goodman, 2006). The accumulated fat provides energy reserves when foraging conditions are not favorable, or to enable the bats to fly to other sites with caves. For the Namibian *H. vittatus*, previously classified as *H. commersoni*, fat deposits are metabolized during the cold season when prey availability is low (Churchill *et al.*, 1997).

Two of the tree species (*C. boivinii* and *Diospyros* sp.) most frequently used by roosting *H. commersoni* are among the most commonly exploited by local people (Rajoelison, 1997). In contrast, plantations of introduced trees, such as *Aucoumea klaineana*, were rarely used for roosting. These introduced trees are likely to change the microclimatic conditions in the area where they are planted and might also affect insect abundance and diversity, and thus the presence of bats.

The maximum home range size of *H. commersoni* recorded during this study was 69.4 ha. However, the fact that one individual (AM22) was not found in the study area for four days during its tracking period, before it returned to the study site, suggests that the foraging range may be larger. The species may undergo local movements between Tampolo and forests or caves further afield. Consequently, small forest fragments persisting around

Tampolo may be important areas for conservation, as they provide connectivity between Tampolo and neighboring areas used by the bats.

The study by Vaughan (1977) of the mainland species of *Hipposideros* (now reclassified as *H. vittatus*) revealed that this species relies on a ‘fly-catcher’ foraging strategy. It consists of short flights (less than 20% of the total foraging time) from a perch to catch flying insects. This foraging tactic presumably reduces energy expenditure during flight, as postulated by Vaughan (1977). Such fly-catching behavior was observed on a single occasion for *H. commersoni* in our study area.

Globally, islands and caves are top priorities for bat conservation (Mickleburgh *et al.*, 2002; Furey and Racey, 2016). The findings from this study provide evidence suggesting that native forest, sheltered littoral forest in particular, also provides important roosting and foraging habitat for *H. commersoni* in a landscape lacking caves. For bat conservation in Madagascar, forest conservation may be as important as protection of caves. Besides *H. commersoni*, the most threatened endemic bat species, *Pteropus rufus*, is also forest-dependent.

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