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DO BATS NEED TREES? HABITAT USE OF TWO MALAGASY HIPPOSIDERID BATS *TRIAENOPS FURCULUS* AND *T. MENAMENA* IN THE DRY SOUTHWEST

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ABSTRACT - Habitat degradation and loss threaten the survival of many bat species. Recent studies in Madagascar however have found some species are present in areas of low forest cover even though their echolocation calls and wing morphology suggest they are able to forage in forests. The present study investigated habitat use and prey selection in two sympatric hipposiderid bats, *Triaenops furculus* and *T. menamena*, in the dry southwest of Madagascar. The study colony occupied a cave in limestone karst surrounded by intact spiny bush and several secondary or degraded habitats. We used bat detectors and radio-tracking to determine habitat use, and faecal analysis and invertebrate sampling to assess prey selection. Spiny bush, the dominant habitat type in the study area, was used less than predicted from its availability, based on satellite imagery and ground-based habitat mapping. Areas containing large trees were used by radiotracked bats in approximate proportion to their availability and acoustic sampling revealed highest bat activity in this habitat. The radio-tracked individuals used agricultural land more than expected from its availability. A significant difference was found in the proportion of Lepidoptera in the faeces of the two species, with *T furculus* showing a preference for moths. *Triaenops furculus* also selected Coleoptera, whereas *T. menamena* preferred mainly Hemiptera. While this study did not identify a strong association with forested habitats in *T. furculus* or *T. menamena*, it remains to be established whether the bats forage in a sub-optimal habitat due to their preference for roosting in the nearby karst caves.

Key words: habitat use, prey selection, hipposiderid bats, radiotracking, Madagascar

RIASSUNTO - I ***pipistrelli necessitano di alberi? Uso dello habitat di* Triaenops furculus *e* T. menamena *in ambienti secchi del Madagascar sud occidentale***. Il degrado e la perdita di habitat minacciano la sopravvivenza di molte specie di pipistrelli. Recenti studi in Madagascar hanno trovato che alcune specie sono presenti in aree con scarsa copertura forestale, anche se le loro ecolocalizzazioni e la loro morfologia alare suggeriscono che sono in grado di utilizzare i boschi per il foraggiamento. Nel presente studio sono esaminati l'uso dell'habitat e la selezione delle prede di due pipistrelli simpatrici, *Triaenops furculus* e *T. menamena*., in ambienti secchi del Madagascar sud occidentale. La colonia studiata occupava una grotta carsica calcarea, circondata da boscaglia spinosa intatta e diversi habitat secondari o degradati. Il bat detector e la tecnica del radio-tracking erano utilizzati per valutare l'uso dell'habitat, mentre la selezione delle prede era determinata sulla base dei dati ottenuti dall'analisi delle feci e dai campionamenti sulla disponibilità di invertebrati. Le zone con cespugli spinosi bassi (< 2 m), habitat dominante nell'area di studio, erano sottoutilizzate rispetto alla loro disponibilità. Le aree con grandi alberi erano usate dai pipistrelli radiomarcati approssimativamente in proporzione alla loro disponibilità, mentre i rilevamenti delle ecolocalizzazioni evidenziavano una più elevata attività in questo ambiente. I pipistrelli radiomarcati utilizzavano l'ambiente agricolo in proporzione maggiore alla sua disponibilità. Il consumo di Lepidotteri differiva tra le due specie, con *T. furculus* che mostrava preferenza per le tarme. *T. furculus* selezionava anche i Coleotteri, *T. menamena* preferiva principalmente gli Emitteri. Anche se questo studio non ha evidenziato una marcata associazione tra le due specie di pipistrelli e gli habitat forestali, resta da stabilire se entrambe foraggiano in habitat sub-ottimali a causa della vicinanza di grotte carsiche utilizzate come *roost*.

Parole chiave: uso dell'habitat, selezione delle prede, pipistrelli ipposideridi, *radiotracking*, Madagascar

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INTRODUCTION

Deforestation has been identified as one of the biggest threats to global biodiversity (Brooks et al. 2002; Seabloom et al. 2002; Gaston et al. 2003). Biodiversity hotspots, areas of great species diversity and richness with often high levels of endemism, tend to coincide with poverty and anthropogenic pressure on natural resources (Fisher and Christopher 2007). Madagascar, one of the hottest hotspots for biodiversity, is no exception (Ganzhorn 2001). Although estimates vary, at least 40% and perhaps even over 80% of the original forest cover has been lost (Du Puy and Moat 1998; Harper et al. 2007; Hanski et al. 2007). In order to mitigate the impacts of deforestation on biodiversity, it is important to identify species that are most susceptible and to determine those that should be priorities for conservation action (Scott et al. 2006).

The southern dry forests of Madagascar have been identified as high priority areas for conservation, although it is feared that for many animal populations this may come too late as many ecosystems have degraded beyond the possibility of recovery (Seddon et al. 2000; Ganzhorn et al. 2001). The impact of forest degradation on bats in Madagascar is poorly understood; some authors have suggested a low dependence on intact forest (Goodman et al. 2005), but there is evidence that certain species require forested habitats to forage (Randrianandriananina et al. 2006; Kofoky et al. 2007). Randrianandriaina et al. (2006) also found that even though taxon richness was greatest in forest habitats (in eastern Madagascar), bat activity was highest in plantations and on agricultural land.

Bat species richness varies regionally in Madagascar, with the highest number of species reported from the dry region of the western domain rather than from the humid east (Bayliss and Hayes 1999; Goodman 1999; Goodman et al. 2005; Randrianandriananina et al. 2006). This is possibly because of the greater availability of roosting sites associated with the limestone karst regions of the west (Eger and Mitchell 2003; Goodman et al. 2005). Another suggested reason is that the availability of insect prey may be greater in the dry forests and spiny bush than in the eastern humid forests (Eger and Mitchell 2003).

Three insectivorous species in the genus *Triaenops* (Hipposideridae) have been described from Madagascar: *T. auritus, T. furculus* and *T. menamena* (previously *T. rufus*) (Peterson et al. 1995; Goodman and Ranivo 2009). *Triaenops auritus* is limited to the northernmost part of Madagascar whilst *T. furculus* occurs in the west and south west. *Triaenops menamena* is more widely distributed, occurring throughout the west and into the humid regions of the northeast (Peterson et al. 1995; Bennett and Russ 2001; Goodman et al. 2005). The precise habitat requirements for many Malagasy bat species are poorly understood, however wing morphology and the characteristic echolocation calls can provide an indication to the structure of the preferred habitat and prey types (Barclay 1986; Jones 1990; Norberg 1998). *Triaenops* bats have a relatively low aspect ratio and wing-loading (Peterson et al. 1995), and emit low energy frequency modulated (FM) calls with maximum amplitude at around 100 kHz (Bennett and Russ 2001), and could therefore be expected to fly close to vegetation. Kofoky et al. (2007) found *T. menamena* foraging close to forest edges, and in clearings. Surveys carried out in the dry regions of Madagascar found *T. furculus* and *T. menamena* roosting in caves in areas without extensive formations of intact forest and this led to the suggestion that neither species is forest dependant (Goodman et al. 2005).

The aim of the present study was to investigate the habitat use and preferred prey of *T. furculus* and *T. menamena*, in an attempt to identify some of the conservation needs of these species in the dry southwest of Madagascar.

STUDY AREA

This study was conducted over two periods in the field (six weeks in April-May and five weeks in June-July 2006) in and around the village of St Augustin (S23˚34’ E43˚46’) in the Toliara province of southwestern Madagascar. The study area experiences a dry, tropical climate with most rain falling between December and March and an average daily temperature of 20-25 ˚C during the austral winter (May-September). St. Augustin lies on the edge of the deciduous, dry southern forest and scrubland. This vegetation type encompasses over 100000 km^2, retains substantial primary vegetation cover, and is poorly protected (Du Puy and Moat 1998). The study was limited to a 3 km^2 area with the day roost located in a limestone cave at its centre. Of this, dry forest and scrub (‘spiny bush’) with a canopy height of < 2 m was the dominant habitat type, encompassing approximately 65% of the surface area. Other prominent habitats were ‘mangroves’ (5%), a riparian zone (8%) mostly comprising of, and here grouped together under, ‘agricultural land’ (5%) dominated by rice paddies, and 'forest' habitat (7%) containing taller trees that form a non-continuous canopy > 3 m high, found on the edge of the limestone karst formation and in the valleys. The remaining area comprised of bare sand (5%) and the 'village' itself (10%). Extent of each habitat was assessed using satellite imagery (Google Earth, ©DigitalGlobe, Terrametrics, Google) and ground-based habitat mapping. The village of St. Augustin has a dense concentration of simple dwellings and a few outlying houses; there is very little vegetation in the village itself, apart from some fruit trees. The study area experiences continuous, low level anthropogenic impact in the form of fire-wood gathering and goat grazing, and all of the natural habitat can be described as moderately degraded.

METHODS

Bat activity in the different habitat types was measured using acoustic recording stations. Over a total of 42 nights of recording, 14 recordings (each consisting of five 15 minute blocks) were made in the 'spiny bush' habitat; 14 recording were made in the 'forest' habitat, as this type of habitat was scattered around the study area in small disconnected patches. Six to seven recordings were made in each of the other habitats (mangroves, n = 6; village, n = 6; agriculture, n = 7). No recordings were made in the 'bare sand' habitat, as no bats were observed foraging in this habitat during reconnaissance walks conducted carrying a bat detector. Bat calls were recorded onto a minidisk (Sony Minidisk, Tokyo, Japan) in 15 minute blocks, hourly between 18.00 and 22.15 hours using a Batbox Duet (Stag Electronics, UK) heterodyne and frequency division bat detector set on the frequency of *Triaenops* calls (100 kHz) and secured onto a pole, at a height of 1.5 m. In addition, aerial insects were caught simultaneously to the acoustic sampling on 37 occasions, using a Malaise trap. *Triaenops* bats were commonly observed foraging at the height of 3-5 metres, but it was not possible to suspend the traps at such a height due to the lack of suitable trees and the difficulty in securing tall poles in the hard substrate. Instead, the hem of the trap was set at a height of one metre, and the trap was deployed from 18.00 to 23.00 h in the vicinity of each acoustic recording point. The invertebrates were stored in 70% ethanol and later identified to the level of order using Scholtz and Holm (1985) and Chinery (1993). One-way ANOVA was used to compare numbers of insects caught between the two collecting periods, and from the different habitat types.

The number and duration of *Triaenops* calls was later noted from each recording, and an attempt was made to differentiate between *T. furculus* and *T. menamena* calls by measuring the frequency of maximum amplitude, using BatSound v 3.1 software (Petterson Elektronik AB, Uppsala, Sweden). In Madagascar, the call frequencies of *Triaenops* spp. overlap, and there appears to be some regional variation. For this reason, calls were recorded from known individuals to determine the parameters for identifying the species: *T. furculus* frequency of maximum amplitude (FMA) 100.2 ± 0.2 kHz (n = 18), *T. menamena* FMA 95.8 ± 0.1 kHz (n = 21). An attempt was made to separate the frequency division *Triaenops* calls recorded at the acoustic sampling sites into *T. furculus* and *T. menamena* so that those with a FMA at or below 97 kHz were identified as *T. menamena* calls, and those above as *T. furculus*. A total of 71 randomly selected calls were thus analysed. Count data on *Triaenops* passes, determined as a distinct sequence of calls, were used to investigate habitat preferences of the bats. As the data were not normally distributed, the non-parametric Kruskal-Wallis test was performed on the total number of *Triaenops* passes (recorded in each type of habitat), using habitat as a factor. The resulting *H* statistic was adjusted for ties to account for the large number of zero values. A linear regression model was used to determine whether there was a correlation between the number (abundance) of insects caught and that of bat passes recorded. An ANOVA was used to determine the significance of the model findings.

In order to obtain individuals for radio-tracking, a 6-metre mist net was deployed at the entrance to the cave on nine separate occasions between April and July 2006. The cave had two entrances, the larger one 2.5 m high and 4 m wide, and the smaller one as high but only 2 m wide. The interior of the cave consisted of a large hall around 4-5 m high and 6x4 m in area; at one end of the cave, at a height of 2 m, was a small opening leading to the main roosting area. The bats presumably roosted deep inside this cavity, as no signal was received from the transmitters once the bats had entered inside. Outside the cavity, a large mound of guano had been deposited, suggesting either that the roost had been in use for a long time, or that it once contained many more bats. The total number of bats in this roost was estimated to be 200-250 individuals; in addition to *Triaenops furculus* and *T. menamena, Myotis gleni* and *M. manavi* were captured in the mist net. In total, nine male and two female *T. furculus* were fitted with LB-2N transmitters for bats (Holohil Systems Ltd., Ontario, Canada) with a battery-life of 12 days. The transmitters were attached between the shoulder blades of the bats using skin-bond (Torbot Bonding Cement, Torbot Group Inc., Cranston (RI), USA). The weight of the transmitter (0.37 g) did not exceed 5% of the body weight of the animals, each of them weighing 7.5 g or more. The tagged individuals were tracked from emergence to when they returned to roost, or were lost, each night while the battery on the transmitters lasted. Location of the tracked animal was determined either by estimating direction and distance to observer from the strength of the signal, or where two observers were present, by using standard triangulation techniques (White and Garrott 1990). To record the locations, eTrex Venture® GPS device (Garmin Ltd., Hampshire, UK) was used. The observed animal locations were then assigned to different habitat categories (see above), using satellite imagery (Google Earth, ©DigitalGlobe, Terrametrics, Google) and ground-based habitat mapping carried out in the field. Chi-square test was used to compare observed animal locations with expected ones based on proportional availability of each habitat type.

Faecal pellets were collected from caught bats held in cotton bags. The pellets were placed in sample vials filled with ethanol 90% and stored for later analysis. A total of 200 faecal pellets, collected from 10 individuals from each species (*T. furculus* and *T. menamena*) were analysed for dietary composition. The arthropod fragments were identified to the level of order with the aid of several identification guides (Scholtz and Holm 1985; Delvare and Aberlenc 1989; Shiel et al. 1997; Ranaivoson and Andrianaivoarivelo 2004).

The dietary preference of the bats was assessed using Ivlev's electivity index (E_i). This gives a measure of the level of preference or avoidance the bats are showing for each insect order consumed, and was calculated using the formula:

$$E_i = \frac{r_i - n_i}{r_i + n_i}$$

where r_i = percentage of order i in the diet, and n_i = percentage of order i in the environment. This measure (E_i) takes a value ranging from -1 (strong avoidance) through to +1 (strong preference) (Krebs 1989). The Mann-Whitney test was used to assess whether the diets of the two species differed significantly.

RESULTS

A total of 515 *Triaenops* calls were recorded across the 47 recording stations over 42 nights. Separating the calls into *T. furculus* and *T. menamena* was not possible in 40% of cases; of the 71 calls downloaded for analysis, only 42 were identified as belonging to one or the other species. Of the 42 identified calls, 30 belonged to *T. furculus*, and were recorded in all sampled habitats. *Triaenops menamena* calls (n = 12) were only recorded in habitats containing trees, or in the mangroves. In the statistical analysis, all calls were grouped together. The majority (n = 403) of all calls recorded came from one station, located in a small clearing surrounded by trees ('forest'). Overall, the stations located in 'forest' habitat (N = 14) had the highest number of calls recorded (90% of the total number, or 57% if the station with most recordings is excluded from the sample). However, the Kruskal-Wallis test revealed no significant difference in number of bat passes recorded in different habitats (H = 8.31, p = 0.081 (adjusted for ties), df = 4). No correlation was found between insect abundance and bat passes (r = 0.062, F = 0.139, p = 0.223 df = 37).

In over 60 nights of tracking, a total of 104 data points were obtained on the location of five of the 11 individuals fitted with transmitters. The remaining six bats were lost during the first night of tracking, and never found again. It was thought these individuals may have switched to a different day roost, and despite nightly searches none of them returned to the day roost cave while the transmitters remained viable. Day-time searches conducted in the surrounding area did not reveal additional roosting sites. Of the recorded bat locations, 10 were on a boundary between two habitat types, and were therefore excluded from the analysis. When all data were grouped together, a chi-square test revealed that the bat locations differed significantly from expected (X^2 = 264.86, p < 0.001, df = 93). Tracked bats were located in the spiny bush less frequently than expected, more locations were recorded in agricultural areas than expected,and visits to forest habitats were recorded approximately corresponding to availability (Tab. 1). The maximum distance travelled by the bats from the roost was 1681 m and was recorded for one of the males; the other bats travelled to a distance of 670-1486 m from the roost.

The difference in numbers of insects caught during the two collecting periods was not statistically significant (F = 2.85, df = 36, p = 0.100) and these data were combined in subsequent analyses. The number of insects caught during the different nights of sampling varied greatly (Fig. 1), and the difference in numbers collected from different habitat types was not statistically significant (F = 1.073, df = 36, p = 0.385).

The faecal analysis indicated that *T. furculus* and *T. menamena* consume insect prey mainly from the same three orders (Coleoptera, Hemiptera and Lepidoptera). A significant difference was found in the proportion of Lepidoptera in their diet, which was much higher in *T. furculus* (W = 134.5, df = 9, p = 0.028). Also, *T. furculus* was found to consume prey from the order Diptera which was absent in the faecal samples collected from *T. menamena* (Fig. 2). No differences were apparent in the diet of males and females. The Ivlev's electivity index based on the percentage of each order in the diet and its availability in the environment suggested that *T. furculus* strongly selected for Coleoptera, whereas *T. menamena* showed high preference for Hemiptera (Tab. 2).

DISCUSSION

Radio tracking bats at St. Augustin in southern Madagascar proved to be difficult and only 3 of the 11 individuals provided us with enough data to analyse. Notwithstanding the caveat of a small sample size, it appeared that the bats spent little time in the dry bush habitat, despite it being the most com-

Table 1 - Proportional availability of the different habitat types in the study area, and observed use by the radio-tracked individuals (proportion of total number of fixes recorded).

Habitat type	Available	Observed use
Spiny bush	65.0	19.10
Mangrove	5.00	0.00
Agriculture	8.00	47.90
Forest	7.00	6.40
Sand	5.00	22.30
Village	10.00	4.30

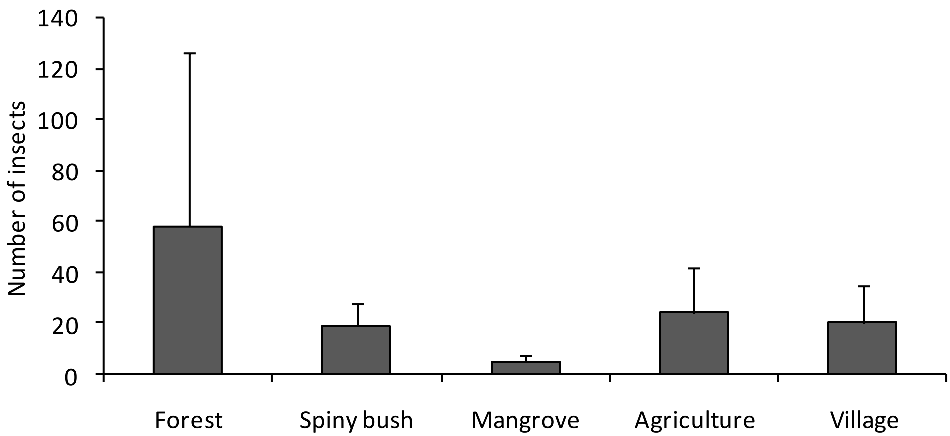

Figure 1 - Number of insects (± SE) caught over a total of 37 nights, using Malaise traps, in different habitat types.

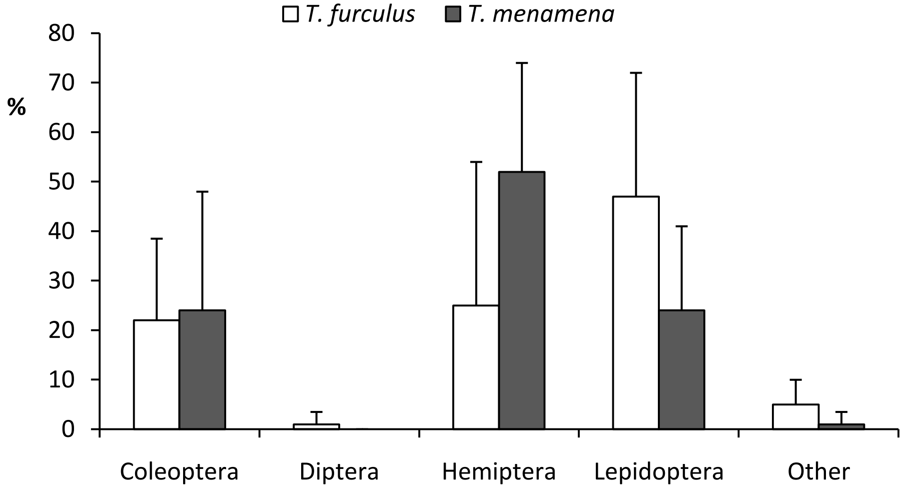

Figure 2 - Mean percentage of insect fragments (± SE) by Order, found in a total of 200 faecal pellets analysed for prey items. ‘Other’ includes remains of Homoptera and Heteroptera. Total number of fragments identified in *T. furculus* and *T. menamena* samples were 446 and 332, respectively.

Table 2 - Dietary selection by *T. furculus* and *T. menamena*, comparing prey consumption determined from faecal analysis on pellets collected from 20 individuals to prey availability, determined by invertebrate sampling over 37 nights of trapping. A high positive *D* value indicates strong selection for a prey order.

Insect Order	Ivlev’s electivity index (D)	
	T. furculus	*T. menamena*
Coleoptera	0.836	0.187
Diptera	-0.960	-
Hemiptera	0.760	0.857
Lepidoptera	0.329	-0.026

mon vegetation type in the study area,and areas of farmland were used disproportionately by the bats. *Triaenops furculus* has an echolocation and wing morphology typical of a bat that is adapted to fly and forage in or near vegetation. The low incidence of *T. furculus* feeding in the spiny bush habitat might be explained by the low availability of prey in these areas. Two of the tracked bats were found foraging in the spiny bush habitat each night of tracking; two bats foraged almost exclusively in the agricultural and riparian habitat, and visited areas with tall trees on their way to and from their foraging sites. Similarly, bats located in the bare sand habitats were commuting from the roost to their foraging sites, probably foraging opportunistically on the way; the high incidence of 'fixes' recorded in this type of habitat can be explained by the fact that it was the common habitat in the vicinity of the day roost. While no bats were observed foraging in this habitat during the reconnaissance walks using bat detectors, acoustic sampling of the 'bare sand' habitat in areas further away from the day roost and in areas not connected to known foraging habitats may have clarified whether or not the bats chose to forage in this habitat.

The apparent difference in foraging habitat selection between the tracked bats may reflect individual preference, or a difference in food availability, as the bats found foraging in the fields were tracked in June-July, during the austral winter. Riparian zones are known for being an abundant food source for insectivorous bats, even in disturbed habitats (Lloyd et al. 2006). However, insect abundance did not appear to fluctuate between the two periods in the field, although temperatures were noticeably higher and more thunderstorms and heavy rain occurred during April-May.

In contrast, the acoustic sampling results did not reflect a preference for agricultural or riparian habitats; highest numbers of bat passes were recorded in spiny bush and habitats containing tall trees. Although the number of recorded calls that were assigned to each species was low, the results suggest that *T. furculus* is less selective of its foraging habitat, whereas *T. menamena* may have a preference for habitats containing trees. However, the small sample size makes this inconclusive. In addition to being flexible in the types of habitat they use, *Triaenops* bats may also be able to switch prey according to seasonal changes in abundance. Razakarivony et al. (2005) analysed stomach contents of *T. menamena* and found remains of insects from the orders Isoptera, Hymenoptera, Coleoptera and Lepidoptera. They suggest that Isoptera may be a seasonally abundant food source that the bats exploit opportunistically (Razakarivony et al. 2005). In the present study, comparison between dietary compositions in the two species revealed a significant difference only in the proportion of Lepidoptera, which was higher in *T. furculus*. Diptera were the most common order found in the Malaise trap samples, and although both species seemed to avoid it, *T. furculus* faecal pellets contained some remains of Diptera whereas these were completely absent in *T. menamena* faeces. The apparent selection of Coleoptera by *T. furculus* may present a bias in the sampling method used for the capture of invertebrates; furthermore, the hard chitinous remains of Coleoptera are better preserved and easily identified in faecal samples. Based on the findings of the present study, it appears that *T. furculus* consumes prey from various different orders, and is less selective in its choice of foraging habitat than *T. menamena* which was observed only in habitats containing trees and found selecting prey mainly from the Order Hemiptera.

While the findings of the present study do not indicate a strong forest dependency in *T. menamena* or *T. furculus*, it remains unknown how the continuing habitat degradation around the St Augustin area will affect the long term survival of the colony. Further, more in-depth studies are required to establish the relative importance of the different habitat types to the bats. Often, the impact of habitat degra-dation and loss on animals can only be detected after considerable time has elapsed (Brooks et al. 1999; Ewers and Didham 2006). It is certain that soil erosion brought on by the grazing goats and tree felling, as well as the overall degradation and loss of the spiny bush habitat will have a negative impact on the diversity and abundance of wildlife, as well as reduce the resource base available to the inhabitants of St Augustin. In order to mitigate the impact of goat grazing, some areas would benefit from fencing to exclude the goats. To obtain fuel wood from a sustainable source, and to reduce the desertification in the area surrounding the village of St. Augustin, trees should be planted around the surviving shrubbery. Coppicing could be introduced to ensure a continuous supply of wood.

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