# Bats and the Loss of Tree Canopy in African Woodlands

By: M. Brock Fenton, David H. M. Cumming, I. L. Rautenbach, Graeme S. Cumming, Meg S. Cumming, Gavin Ford, Russell D. Taylor, Jenna Dunlop, Mark D. Hovorka, Dave S. Johnston, Christine V. Portfors, Matina C. Kalcounis, and  Zaccheus Mahlanga

**\*\*\*Note: Figures may be missing from this format of the document**

## Abstract:
We studied the activity patterns, abundance, diversity, and diets of bats, along with the abundance of nocturnal volant insects, at 30 sites in Miombo woodland in northern Zimbabwe. The woodland at 50% of the sites had been disturbed by high elephant densities to the extent that the tree canopy was greatly reduced. The tree canopy was intact at the other sites. Intact and impacted sites differed significantly in tree (>3 m tall;> 15 cm basal diameter) and shrub (1–3 m tall; <1 m tall) diversity and cover. At each site we used ultraviolet lights to sample insects and mist nets and bat detectors to sample bats. To assess their diets we collected and analyzed feces from captured bats. We caught 343 bats representing the families Pteropodidae (1 species), Vespertilionidae (11 species), and Molossidae (3 species). The molossids and vespertilionids are all aerial feeders taking airborne insects. Bat species richness, abundance, and activity were greater at intact than at impacted sites, but these differences were statistically significant only at adjacent sites (<5 km apart) not at more distant intact and impacted sites (>20 km apart). At the adjacent sites we caught a significantly greater proportion of small (<10 g) bats at intact than at impacted sites. These data and a significantly greater proportion of Scotophilus species (>10 g) caught during the early evening at intact than at impacted sites suggested that the removal of canopy trees affected roost availability for the bats. Although larger species may have commuted between intact and impacted sites, smaller species did not. In contrast, the availability of prey did not appear to have been significantly affected by the removal of the canopy trees, as indicated by the light-trap catches of insects and the bats' diets. Most bats ate mainly beetles and moths, the most abundant insects sampled at the ultraviolet lights. Our findings suggest that aerial-feeding bats such as vespertilionids and molossids do not appear to be useful indicators of disturbance in this habitat, even in the face of significant loss of tree canopy.

Muriélagos y la Pérdida del Dosel de Arboles en Bosques Africanos
Estudiamos los patrones de actividad, abundancia, diversidad y dietas de murciélagos, al igual que la abundancia de insectos voladores nocturnos en 30 sitios en el bosque de Miombo al norte de Zimbabwe. El bosque ha sido impactado en un 50% de los sitios por densidades altas de elefantes, a tal grado que el dosel de los árboles ha sido reducido grandemente. El dosel estuvo intacto en los otros sitios. Sitios intactos e impactados difieren significativamente en diversidad

y cobertura de árboles (>3m de altura;> 15 cm de diámetro basal) y arbustos (1–3 m de altura; <1m de altura). En cada sitio usamos luz ultravioleta para muestrear insectos y redes y detectores de murciélagos para muestrear murciélagos. Para determinar sus dietas, colectamos y analizamos heces de los murciélagos capturados. Capturamos 343 murciélagos representando a las familias Pteropodidae (1 especie), Vespertilionidae (11 especies) y Molossidae (3 especies). Los molósidos y vespertiliónidos son todos consumidores aéreos, alimentándose de insectos voladores. La riqueza de especies, abundancia y actividad de murciélagos fue mayor en sitios intactos, pero estas diferencias fueron estadísticamente significativas solo en sitios intactos e impactados adyacentes (>5 km aparte) pero no cuando eran mas distantes (>20 km aparte). En sitios adyacentes capturamos una proporción significativamente mayor de murciélagos pequeños (<10 g) en sitios intactos que en sitios impactados. Estos datos y una proporción significativamente mayor de especies de Scotophilus (>10 g) durante el atardecer en sitios intactos comparados con sitios impactados sugiere que la remoción del dosel afecta la viabilidad de perchas para los murciélagos. A pesar de que especies mas grandes podrían viajar diariamente entre sitios intactos e impactados, las especies pequeñas no lo hicieron. En contraste, la viabilidad de presas aparentemente no fue significativamente afectada por la remoción del dosel, a como lo indicaron la captura de insectos en trampas de luz y las dietas de los murciélagos. La mayoría de los murciélagos se alimentaron principalmente de escarabajos y mariposas nocturnas, siendo los insectos mas abundantes capturados en las trampas de luz ultravioleta. Nuestros resultados sugieren que los murciélagos de alimentación aérea como son los vespertiliónidos y molósidos, no aparentan ser indicadores útiles de disturbación en este tipo de hábitat, a pesar de una evidente pérdida significativa del dosel.

## Article:
### Introduction
The removal of trees from a woodland is an obvious and dramatic disturbance that can reduce biodiversity and change the structure of the ecosystem (Huston 1994). The actual impact of this disturbance on biodiversity, however, depends on the scale of the disturbance (Petraitis et al. 1989) and the capacity of the affected species to adapt to the changing conditions. The size and mobility of bats, like other mammals, influences their susceptibility to disturbance, partly because larger species tend to have bigger home ranges than smaller ones (Fenton 1997). For bats, disturbances such as tree removal may affect some species without causing a loss in the numbers of species in a community or altering patterns of distribution. Flight permits bats to move considerable distances quickly and efficiently (de la Cueva et al. 1995), giving them access to a variety of habitats to meet their requirements for food and roosts. This means that roosts and food need not be in the same immediate area, and some species of bats that forage along the edges of forest habitat may benefit from the disruption of woodlands. The same generalities apply to birds, although flight allows many migratory species to continue to use forest patches in otherwise disturbed landscapes. In reality, low reproductive success in these patches may mean that they are population sinks (Robinson et al. 1995).

Much of sub-Saharan Africa is covered by savannah woodlands (White 1983) that support a large and diverse bat fauna (Fenton & Rautenbach, in press). Expanding human populations in Africa affect savannah woodlands through urbanization, expansion of agricultural activity, and the collection of firewood (World Resources 1990–1991). Miombo woodlands are species-rich and dominated by broad-leaved deciduous trees, especially those in the genus *Brachystegia*.

These woodlands cover much of southern central Africa, from Tanzania to Zimbabwe and Angola to Mozambique (White 1983). Like some other ecosystems (Huston 1993), these woodlands have high biodiversity but their soils have low potential for agricultural productivity. At least 40 species of bat have been reported from Miombo woodlands (Smithers 1983), including fruit-eating and insect-eating species that roost in trees, caves, and rock crevices. Throughout their range, Miombo woodlands are being destroyed by expanding human and elephant populations that are increasingly confined to smaller areas (Cumming et al. 1997). In less than 30 years the combination of high elephant densities and fire has resulted in the change from closed-canopy Miombo woodland to open grassland and thicket in some areas (Anderson & Walker 1974;Guy 1981;McShane 1987;Lewis 1991;Swanepoel 1993).

We examined the effects of woodland disturbance on bats in Miombo woodlands in northern Zimbabwe by comparing bat species richness, abundance, activity, and diet and insect abundance between two kinds of sites. We used 15 intact sites where the tree canopy was present and 15 disturbed sites where it had been largely destroyed. Although the differences in these situations were obvious at the time of our study (Fig. 1), in 1965 all of the sites had been within closed-canopy Miombo woodland (Cumming et al. 1997). We assessed the importance of woodland canopy cover on the species richness and abundance of bats.
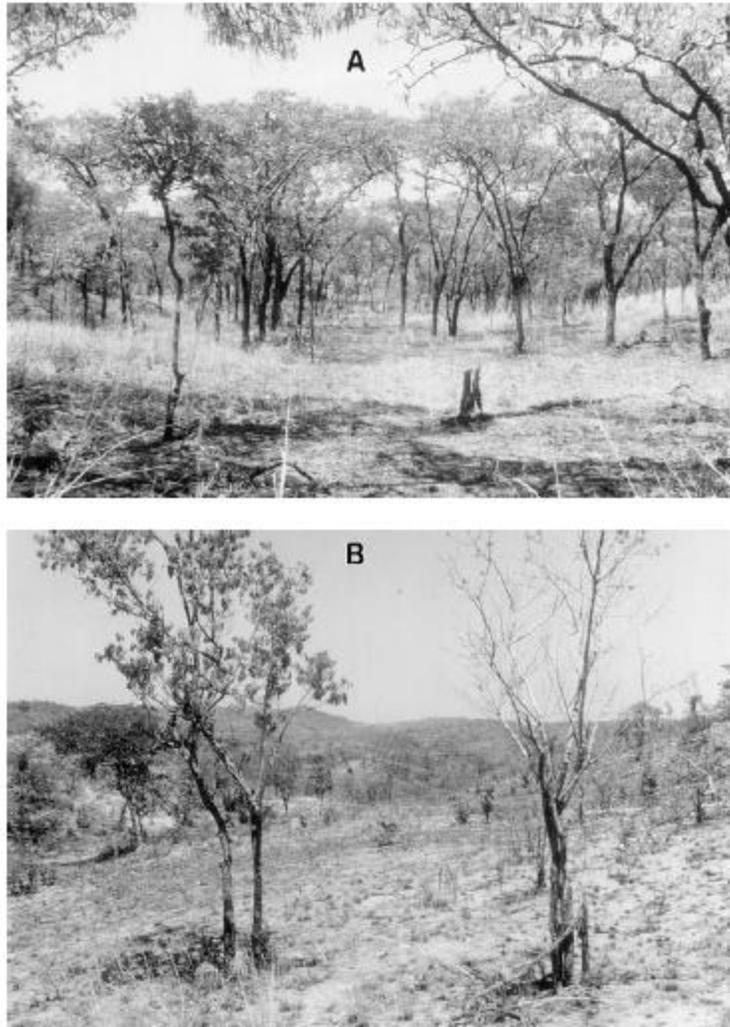
**Figure 1** Two photographs illustrate intact (a) and impacted (b) woodlands from the Mana area.

### *Study Area and Methods*

Our sites were located in northern Zimbabwe (Fig. 2), near the crests of ridges in undulating terrain. Specifically, in the Mana area 18 sites were located on either side of a game fence, providing adjacent (separated by less than 5 km) impacted and intact sites that were within the daily travel distance of some of the bats we caught (Fenton & Rautenbach 1986). Six other impacted sites (Matusadona area) were separated from 6 intact sites (Kanyati area) by at least 20 km, probably beyond the normal commuting range of most of the study species. In the Mana area the impacted sites were on the north side of the game fence that marks the southern boundary of Mana Pools National Park, whereas the intact sites were in the adjacent Hurungwe Communal Lands just south of the national park. The Kanyati area sites (intact) were separated by the Sanyati gorge from the impacted sites in the southeastern part of Matusadona National Park. The game fence, which had been used to restrict the movement of wildlife and thus sleeping sickness, is an artificial barrier to wildlife movement, whereas the Sanyati River gorge is a natural barrier. These boundaries allowed us to compare the bats of the intact and impacted Miombo woodland

(Fig. 1). All sites were 800–1200 m above sea level and located on comparable geological formation and soils (Cumming et al. 1997).
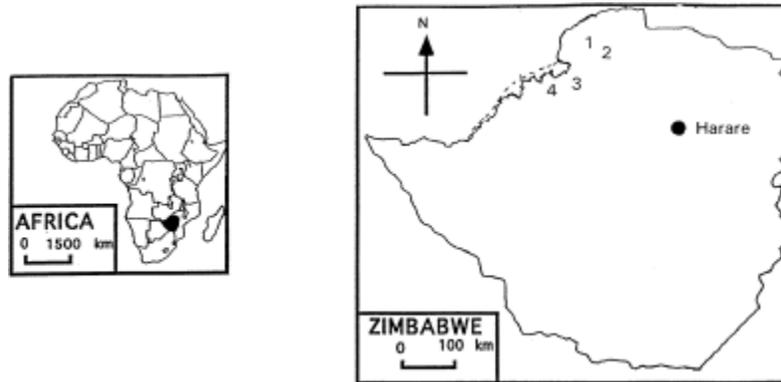


**Figure 2** The study area, showing the general locations of the groups of sites: 1, Mana area impacted; 2, Mana area intact; 3, Kanyati intact; and 4, Matusadona impacted.

We conducted our field work between 15 November and 3 December 1994. Where we sampled bats there were significant differences between intact and impacted sites in both the numbers of species and the densities of trees and shrubs (Table 1). The details and results of vegetation sampling are provided in Cumming et al. (1997), but canopy trees were significantly less diverse and occurred at lower densities at impacted than at intact sites (Table 1).

**Table 1 A comparison of the numbers of species ($N_{sp}$) and densities of trees and shrubs in intact ($n= 15$) and impacted ($n= 15$) woodlands at study sites in northern Zimbabwe. [a]**

| Group/Taxon | Intact (mean $\pm$ 1 SE) | Impacted (mean $\pm$ 1 SE) | p |
|---|---|---|---|
| Species of canopy trees[b] | 25.53 $\pm$ 0.96 | 11.17 $\pm$ 0.8 | <0.001 |
| Species of shrubs[c] | 35.60 $\pm$ 1.81 | 35.53 $\pm$ 2.77 | >0.05 |
| Tree density[b] | 408.00 $\pm$ 39.85 | 245.00 $\pm$ 70.90 | <0.05 |
| Tree density[d] | 193.78 $\pm$ 19.86 | 56.00 $\pm$ 22.01 | <0.001 |
| Shrub density[e] | 257.80 $\pm$ 44.86 | 1412.00 $\pm$ 209.54 | <0.001 |
| Shrub density[f] | 3482.62 $\pm$ 391.91 | 6029.33 $\pm$ 724.44 | <0.01 |

[a] Data from Cumming et al. (1997).
[b] >3 m tall.
[c] <3 m tall.
[d] Basal diameter >15 cm.
[e] 1–3 m tall.
[f] <1 m tall.

At each site we sampled flying bats with macro mist nets (Rautenbach 1985) kept open from 1830 to 2330 hours. The nets were tended continuously, and for each captured bat we recorded the time of capture, species, gender, forearm length (±1 mm), and body mass (±0.1 g). Bat activity was monitored for 4 minutes every 30 minutes by echolocation calls, 1 minute each at 20, 30, 40, and 60 kHz with either an Ultrasound Advice Mini-2 or an Anabat II bat detector. By using the frequency cursor in the computer display, we treated the Anabat output as if the detector were tuned to 20, 30, 40, and 60 kHz. Bat traffic was quantified as "bat passes" (Fenton 1970), with one bat pass being the flight of an echolocating bat through the airspace sampled by the microphone.

To assess the diets of bats, the first five of any species caught on any night were placed individually in numbered cloth bags and held there for at least 60 minutes, usually enough time for us to obtain fecal samples from them (Buchler 1975). Feces were collected from the bags and placed in 10-mL, straight-sided glass vials with rubber stoppers. Approximately 1 mL of a 70% ethanol, 30% glycerine solution was added as a softening agent. The softened samples were placed in glass petrie dishes, teased apart with fine probes, and examined under a 6X–50X binocular dissecting microscope. A maximum of five stools was analyzed from any individual bat. Insect remains in the feces were identified to order by comparisons with illustrations in Scholtz and Holm (1985) and to insects obtained in our samples from each site. After the insect parts had been identified, we estimated the percent volume for each order as per Whitaker (1988).

We collected insect samples using two types of light traps, ultraviolet (UV) lights and white lights. The UV lights were used concurrently with bat sampling (1830–2330 hours). Two light traps were used at each sampling site: a 12-V white fluorescent neon tube suspended above a dish of soapy water and turned on from 1900 to 2030 hours and a 12-V ultraviolet neon tube suspended under a white sheet spread over a tripod of poles 1 m long. The UV light was turned on for the first 15 minutes of each 30-minute period (starting at 1830 hours). An observer collected insects from the sheet for up to 5 minutes, starting 10 minutes after the light had been turned on. Insects were collected from the sheets and placed in wide-mouthed killing jars. Insects from the UV samples were sorted by size class and order. Means usually are shown as ±1 standard deviation.

Although there have been changes in the names of some bats in our study (e.g., *Tadarida pumila*, also known as *Chaerophon pumila*), at the species level there is general agreement about the taxonomy of bats of southern Africa (Smithers 1983). Our work suggests that bats in the genus *Scotophilus* are an exception. Here the names in current use have been changed: for example, the *Scotophilus nigrita* of Hayman and Hill (1971) is now *Scotophilus dinganii*, and the smaller *S. leucogaster* is now *S. borbonicus*. We caught two distinct forms of the smaller species, one with a pale whitish venter (presumably *S. borbonicus*) and another with a bright yellow venter (referred to as *Scotophilus*"other"). It is not clear which name would apply to this species or if it is a different taxon.

### Results
We captured 343 bats, representing 15 species from three families (1 Pteropodidae, 11 Vespertilionidae, and 3 Molossidae;Table 2). All the adult females we captured were pregnant, lactating, or post-lactating, suggesting resident, reproducing populations. We caught 235 bats (11 species) in the Mana area and 108 (10 species) in the Kanyati and Matusadona areas (Table 2). Four species were caught in all three areas (*Scotophilus borbonicus*, *Scotophilus* other, *Nycticeius schlieffeni*, and *Eptesicus capensis*); the frugivore (*Epomophorus wahlbergi*) was caught at only two sites in intact woodland in the Mana area.

**Table 2 A summary of the numbers and species of bats captured at study sites in northern Zimbabwe. ***

| Species of bats | Mana Area Intact (9) | Mana Area Impacted (9) | Kanyati Intact (6) | Matusadona Impacted (6) | Totals Intact (15) | Totals Impacted (15) | Overall (30) |
|---|---|---|---|---|---|---|---|
| Epomophorus wahlbergi | 2 | 0 | 0 | 0 | 2 | 0 | 2 |
| Pipistrellus nanus | 1 | 0 | 0 | 0 | 1 | 0 | 1 |
| Pipistrellus rusticus | 5 | 1 | 0 | 5 | 5 | 6 | 11 |
| Pipistrellus rueppellii | 0 | 0 | 3 | 0 | 3 | 0 | 3 |
| Pipistrellus kuhlii | 0 | 0 | 0 | 1 | 0 | 1 | 1 |
| Eptesicus capensis | 16 | 9 | 16 | 20 | 32 | 29 | 61 |
| Eptesicus melckorum | 0 | 0 | 1 | 0 | 1 | 0 | 1 |
| Eptesicus zuluensis | 1 | 0 | 0 | 0 | 1 | 0 | 1 |
| Scotophilus dingani | 2 | 1 | 0 | 1 | 2 | 2 | 4 |
| Scotophilus borbonicus | 95 | 66 | 10 | 4 | 105 | 70 | 175 |
| Scotophilus "other" | 15 | 0 | 7 | 15 | 22 | 15 | 37 |
| Nycticeius schlieffeni | 11 | 1 | 5 | 3 | 16 | 4 | 20 |
| Tadarida nigeriae | 2 | 0 | 0 | 0 | 2 | 0 | 2 |
| Tadarida pumila | 7 | 0 | 0 | 0 | 7 | 0 | 7 |
| Tadarida condylura | 0 | 0 | 0 | 17 | 0 | 17 | 17 |
| Totals | 157 | 78 | 42 | 66 | 199 | 144 | 343 |

*Number of sites are in parentheses under site status.

When the data for all intact and impacted sites were compared, there were no significant differences in the species richness (number of species), numbers of bats, or bat activity between the two kinds of sites (Table 3). At the adjacent intact and impacted sites (Mana area), however, bats were significantly more diverse, more abundant, and more active at intact than at impacted sites (Table 3). These differences did not emerge in the comparison of intact and impacted sites that were more distant from one another ($>20$ km; Kanyati and Matusadona areas). The bats at the intact and impacted sites in the Mana area were significantly different in other ways. There we caught significantly more (sign test $z = 3.0$, $p < 0.002$) *Scotophilus* in the first 2 hours after dark at intact than at impacted sites, but not 2–4 hours after dark ($z = 1.3$, $p < 0.09$). These differences did not appear between the Kanyati (intact) and Matusadona (impacted) sites (first 2 hours, $z = 0.1$, $p > 0.8$; second 2 hours $z = 1.52$, $p > 0.64$). In the Mana area species of bats weighing less than 10 g constituted 22% of the catch ($n = 150$) at intact sites, compared to 13% ($n = 77$) at impacted sites, differences that are significant ($t = 3.24$, df $= 2$; $p < 0.05$). Again, this difference was not evident between the Kanyati and Matusadona sites.

**Table 3 A comparison of the incidences of bats and insects between impacted and intact Miombo sites.**

| Variable | Intact (mean ± SE) | Impacted (mean ± SE) | Statistics |
|---|---|---|---|
| Mana and Matusadona sites | | | Wilcoxan signed rank ($W, p$) |
| Bat species richness[a] | 3.88 ± 2.27 | 2.17 ± 1.79 | 1.70, 0.09 |
| Bat captures[b] | 13.27 ± 8.34 | 9.67 ± 9.87 | 1.01, 0.31 |
| Bat activity[c] | 13.07 ± 11.15 | 7.33 ± 6.07 | 1.45, 0.15 |
| Insects, all orders[d] | 240.46 ± 84.79 | 239.06 ± 124.82 | 0.23, 0.82 |
| Beetles[e] | 42.13 ± 29.96 | 86.40 ± 95.15 | 1.11, 0.27 |
| Moths[f] | 143.73 ± 54.12 | 118.13 ± 56.86 | 1.31, 0.19 |
| Mana sites | | | Paired $t$ test ($t$, df, $p$) |
| Bat species richness[a] | 4.33 ± 2.50 | 1.33 ± 0.87 | 3.18, 8, 0.01 |
| Bat captures[b] | 17.44 ± 8.02 | 8.67 ± 10.94 | 2.29, 8, 0.05 |
| Bat activity[c] | 14.78 ± 9.31 | 4.78 ± 5.07 | 3.08, 8, 0.02 |
| Insects, all orders[d] | 248.77 ± 94.88 | 230.88 ± 88.52 | 0.48, 8, 0.65 |
| Beetles[e] | 46.22 ± 38.10 | 57.67 ± 34.76 | 0.58, 8, 0.58 |
| Moths[f] | 146.11 ± 61.53 | 136.22 ± 58.04 | 0.52, 8, 0.62 |

[a] Number of species.
[b] Number of individuals.
[c] Number of bat passes.
[d] Number of insects.
[e] Number of beetles.
[f] Number of moths.

There were no significant differences in the numbers of insects (all orders), beetles, and moths attracted to the lights at intact and impacted sites, whether all sites are considered or only those in the Mana area (Table 3). Beetles and moths were the most abundant insects in our samples, and an analysis of 802 fecal pellets from 189 bats (11 species) revealed that most bats ate mainly beetles and moths. Some bats also ate a variety of other insects, including embiopterans, mantids, dipterans, and hymenopterans (Table 4). Beetles constituted more than 50% of the insects eaten by five of the six species for which we obtained larger samples (Table 4). Two species of *Scotophilus*, in particular, tended to feed more on beetles, whereas one of the two common smaller species (≈5 g), *Eptesicus capensis*, fed mainly on beetles; the other, *Nycticeius schlieffeni*, ate beetles, moths, and flies (Table 4). Among the 10- to 25-g bats, the *Scotophilus* fed more on beetles, whereas *Tadarida pumila* ate more moths. Species for which we have smaller samples showed the same general trend, although two species (*Pipistrellus rueppellii* and *Eptesicus zuluensis*) ate only moths (Table 4). The presence of beetles and moths in the bats' feces was independent of their relative abundances in intact and impacted sites when the data for all bats are considered; the only exception is *Pipistrellus rusticus*, which fed mainly on moths (sequential Bonferroni correction, $p$ tablewise = 0.05; Rice 1989). Most bats consumed beetles preferentially over other insects; these patterns are clear when the incidence of beetles and moths in bat feces by species was compared with their availability (Fig. 3).

**Table 4 The diets of the bats are shown as the percentages (±1 SD) of the different orders of insects that constituted at least 5% of fecal volume.**

| Species | Site status[a] | $n_b$[b] | $n_s$[c] | Orders[d] | Primary/Secondary/Next (>5%)[e] |
|---|---|---|---|---|---|
| **Species with sample sizes of >7 bats** | | | | | |
| Eptesicus capensis | IN | 29 | 115 | 6 | C65.3 ± 26.0/L21.6 ± 22.7/H5.5 ± 11.5 |
| Eptesicus capensis | IM | 21 | 88 | 6 | C72.6 ± 27.8/L24.9 ± 25.9/none |
| Nycticeius schlieffeni | + | 11 | 55 | 7 | C47.7 ± 27.6/L23.6 ± 13.0/D9.1 ± 15.6 |
| Scotophilus borbonicus | IN | 40 | 170 | 5 | C80.5 ± 22.5/L16.5 ± 21.7/none |
| Scotophilus borbonicus | IM | 32 | 130 | 4 | C76.6 ± 20.4/L12.5 ± 17.2/H6.8 ± 11.5 |
| Scotophilus "other" | IN | 14 | 52 | 6 | C80 ± 22.6/L7.0 ± 6.7/none |
| Scotophilus "other" | IM | 12 | 51 | 2 | C74.6 ± 26.6/L20.9 ± 27.6/none |
| **Species with smaller samples** | | | | | |
| Eptesicus zuluensis | IN | 1 | 5 | 1 | L100 |
| Eptesicus melckorum | IN | 1 | 5 | 4 | C35/H30/Di30/L5 |
| Scotophilus dingani | + | 3 | 15 | 2 | C88.3 ± 13.1/L17.5± |
| Pipistrellus rueppelli | IN | 1 | 5 | 1 | L100 |
| Pipistrellus rusticus | + | 7 | 31 | 2 | L53.6 ± 36.1/C46.4 ± 36.1 |
| Tadarida condylura | + | 5 | 25 | 4 | C74 ± 17/L21 ± 16.2/none |
| Tadarida pumila | + | 7 | 31 | 4 | C52.9 ± 28.3/L42.1 ± 28.3/none |
| Tadarida nigeriae | IN | 1 | 4 | 2 | C70/L30 |
| Tadarida nigeriae | IN | 1 | 5 | 2 | C95/L5 |

[a] Intact woodland, IN; impacted woodland, IM.
[b] Number of bats.
[c] Number of stools analyzed.
[d] Number of insect orders eaten.
[e] Insects include Coleoptera (C), Lepidoptera (L), Hymenoptera (H), Diptera (D), and Dictyoptera (Di).
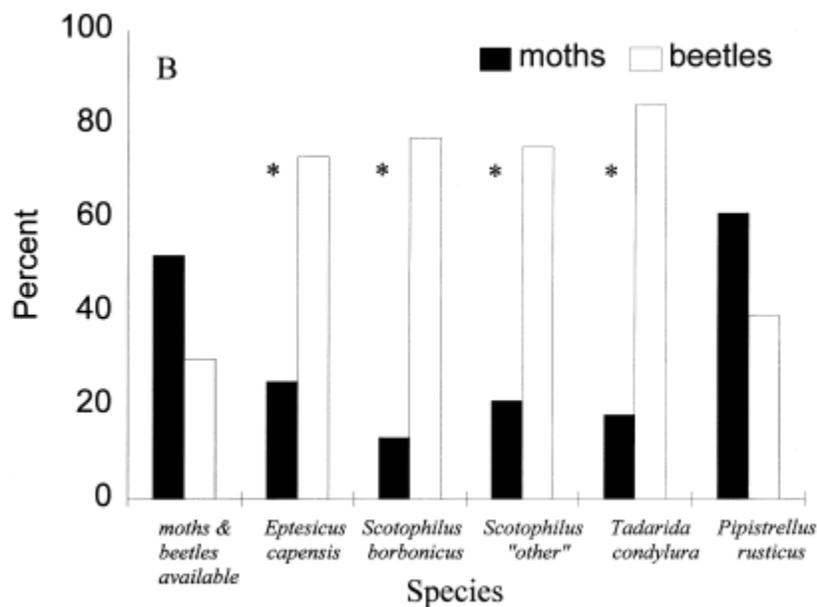


**Figure 3** The incidence of beetles and moths at lights at all of the intact (a) and impacted (b) woodlands compared with the incidence of beetles and moths in the feces of a selection of bats. The numbers of insects are shown in Table 3. An asterisk ( *) denotes differences that are significant. For Eptesicus capensis, the $\chi^2$ values for intact and impacted are 23.86 (df = 1, p < 0.001) and 42.39 (df = 1, p < 0.001), respectively; for Scotophilus borbonicus they are 40.75 (df = 1, p < 0.001) and 60.81 (df = 1, p < 0.001); for Scotophilus "other" they are 28.98 (df = 1, p < 0.001) and 76.47 (df = 1; p < 0.001); and for Pipistrellus rusticus, they are 0.1 (df = 1; p = 0.9394) and 7.56 (df = 1, p < 0.006). The $\chi^2$ value for Nycticeius schlieffeni is 27.69 (df = 1, p < 0.001), for Tadarida condylura 42.34 (df = 1; p < 0.001) and for Tadarida pumila 17.58 (df = 1, p < 0.001).

## *Discussion*

Our findings demonstrate the importance of woodlands to aerial-feeding bats, but they also show that these animals can live and reproduce in disturbed habitat. Although the species composition of the insectivorous bat fauna did not differ significantly between all intact and impacted sites, there were significant differences between the diversity, numbers, activity, and diets of bats at adjacent intact and impacted sites. At some sites, captures suggested that smaller species of bats (<10 g) were more affected by the loss of canopy trees than larger ones. The impact of disturbance on the biodiversity of bats differs markedly from that on birds, which were significantly less diverse at the impacted than at the intact sites we studied (Cumming et al. 1997). Furthermore, some species of birds are Miombo specialists (Benson & Irwin 1966;Cumming et al. 1997). In northern Botswana the impact of elephant damage to habitat on bird diversity was less clear in mopane and riverine woodland (Herremans 1995) than it was in our study area (Cumming et al. 1997).

Overall, our data are similar to those for bats from other dry woodlands (not Miombo) in Kruger National Park (Rautenbach et al. 1996), providing no evidence of bat species that are Miombo specialists. This contrasts with the situation of birds, among which some species are Miombo specialists (Benson & Irwin 1966). Using precisely the same netting procedures in dry woodlands in Kruger, Rautenbach et al. found an average of 21.1 bats per night of netting, compared to 22.9 in this study. Eleven species were shared between the Kruger sites and those in our study, and the same bats (*Scotophilus* spp., *Eptesicus capensis*, and *Nycticeius schlieffeni*) were most often captured. Seven species taken in the Kruger woodlands but not at our sites; there were three for whom the opposite was true. With the exception of *Tadarida nigeriae*, the species encountered in both studies occur in both countries (Smithers 1983). Levels of bat and insect activity also were comparable between the woodland sites we sampled and those in Kruger (Rautenbach et al. 1996), suggesting that our data are representative for bats in African woodlands. Bats in the families Nycteridae, Hipposideridae, and Rhinolophidae are absent from our samples and were not commonly netted in Kruger National Park (Rautenbach et al. 1996). Rhinolophids constituted 2.3% of the 568 bats netted in that study, and 10 of the 12 were caught in Riverine forest. Nycterids, which were not caught in our study, were netted in dry forest in Kruger National Park, but they represented only 1.1% of the bats sampled.

The timing of captures of *Scotophilus* species in the Mana area suggests that some of these bats roosted in intact areas and foraged in adjacent impacted ones. Elsewhere in southern Africa, radiotelemetry studies have demonstrated that individual *Scotophilus borbonicus* roost in hollows in trees and fly up to 7 km one way from roosting to foraging areas (Barclay 1985;Fenton & Rautenbach 1986). In other studies, captures of *Scotophilus* in the early part of the evening usually occur near their roost trees. Individual bats change roost trees almost nightly (Fenton & Rautenbach 1986), and the low density of trees in the impacted areas may indicate a shortage of roosts. This also is suggested by the distribution of small bats (<10 g) among areas because the smaller species may not fly as far to foraging areas. But indirect and direct evidence suggests that molossid bats found roosts in impacted woodland. The indirect evidence was the number of molossids we caught at impacted sites in the Matusadona area (Table 2). The direct evidence was a colony of 23 *Tadarida nigeriae* that roosted under the bark of a dead *Julbernardia globiflora* within 500 m of one of our sites.

Although a reduction in the density of canopy trees in the woodland creates fewer available roosts for bats, these changes do not appear to adversely affect the availability of flying insects. In southern Arizona, Hovorka (1996) found that although grazing by cattle had a significant impact on the vegetation, it did not adversely affect the incidence of flying insects and the abundance of insectivorous bats. Elsewhere, in the United Kingdom for example, human-generated habitat disturbances provide important foraging areas for the endangered *Rhinolophus ferrumequinum* (Jones et al. 1995), even though other bats were more active in more natural habitats (woodlands and those associated with water;Walsh et al. 1995). In northern Alberta, bats were more active in old mixed-wood forests than in younger forests, reflecting the proportional density of potential roosts in older stands (Crampton & Barclay 1996*a*, 1996*b*).

Other evidence suggests that prey availability for bats in our study area was not affected in impacted woodlands. The prevalence of beetles and moths in the diets of the bats we sampled generally reflects the findings of other workers (Black 1974;Freeman 1981). All of the bats we sampled in this study use echolocation calls dominated by sounds between 20 and 50 kHz (Fenton & Bell 1981; Fenton et al., unpublished observations), the bandwidths to which the ears of many African moths are most sensitive (Fullard & Thomas 1981). In this situation the prevalence of beetles in the bats' diets relative to their availability may reflect the lack of bat-detecting ears in most Coleoptera. The repeated occurrence of moths in the diet appears to be contrary to the predictions of work on the hearing-based defenses of moths against echolocating bats (Fullard & Thomas 1981;Jones 1992;Fullard 1994;Rydell et al. 1995), although bats catch and eat some moths with bat-detecting ears (Acharya 1995). In our study only *Pipistrellus rusticus* differed from the pattern of taking mainly beetles over moths. One species, *Eptesicus melckorum*, also fed on mantids, another group in which some species have bat-detecting ears (Yager 1990) and which occasionally are taken by bats (Cumming 1996).

The degradation and loss of habitat is a pervasive problem in conservation, and our study shows how habitat destruction can affect bats without reducing their biodiversity. The same picture does not apply to birds, emphasizing that not all organisms are equally affected by the reduction of canopy tree density in woodlands. The data also illustrate how the conservation of one species can negatively affect others. At our study sites, African elephants are a prime destructive force (Cumming et al. 1997), which raises the question of whether conservation efforts should be focused on species or habitats. Clearly, the perception of conservation problems varies both geographically and with the standpoint of the observer (Babbitt 1995;Crowe & Shryer 1995).

As small, flying, long-lived animals that fill a variety of trophic roles, bats can be good indicators of habitat quality, and some species are very sensitive to changes in habitat (e.g., phyllostomines;Fenton et al. 1992;Brosset et al. 1996). Our findings, however, demonstrate that in African savanna woodlands, the common vespertilionid and molossid bats, those feeding on airborne insects, are consistently present even in sites where the tree canopy has been virtually eliminated. This finding reveals that bats are not the first mammals to be affected by loss of tree canopy.

### *Bibliography*

Acharya, L. 1995. Sex-biased predation of moths by insectivorous bats. *Animal Behaviour* **49**:1461–1468.Anderson, G. D. & B. H. Walker. 1974. Vegetation composition and elephant damage in the Sengwa Wildlife Research Area, Rhodesia. *Journal of the Southern African Wildlife Management Association* **4**:1–14.Babbitt, B. 1995. Science: opening the next chapter of conservation history. *Science* **267**:1954–1955.Barclay, R. M. R. 1985. Foraging behavior of the African insectivorous bat, *Scotophilus leucogaster*. *Biotropica* **17**:65–70.Benson, C. W. & M. P. S. Irwin. 1966. The *Brachystegia* avifauna. *Ostrich Supplement* **6**:297–321.Black, H. L. 1974. A north temperate bat community: structure and prey populations. *Journal of Mammalogy* **55**:138–157.Brosset, A., P. Charles-Dominique, A. Cockle, J-F. Cosson>, and D. Masson. 1996. Bat communities and deforestation in French Guiana. *Canadian Journal of Zoology* **74**:1974–1982.Buchler, E. R. 1975. Food transit time in *Myotis lucifugus*. *Journal of Mammalogy* **56**:252–255.Crampton, L. H., and R. M. R. Barclay. 1996 *a*. Relationships between bats and stand age and structure in aspen mixedwood forests in Alberta. Pages 211–225 in B. Stelfox, editor. Relationships between stand age, stand structure, and biodiversity in aspen mixedwood forests in Alberta. Alberta Environment Centre, Edmonton, Canada.Crampton, L. H., and R. M. R. Barclay. 1996 *b*. Habitat selection by bats in fragmented and unfragmented aspen mixed wood stands of different ages. Pages 238–259 in R.M.R. Barclay and R.M. Brigham, editors. Bats and forests symposium. British Columbia Ministry of Forests, Victoria, Canada.Crowe, D.M. & J. Shryer. 1995. Eco-colonialism. *Wildlife Society Bulletin* **23**:26–30.Cumming, G. S. 1996. Mantid movements by night and the interactions of sympatric bats and mantids. *Canadian Journal of Zoology* **74**:1771–1774.Cumming, D. H. M. , et al. 1997. Elephants, woodlands and biodiversity in southern Africa. *South African Journal of Science* **93**:231–236.de la Cueva Salcedo, H., M. B. Fenton, M. B. C. Hickey, R. W. Blake. 1995. Energetic consequences of flight speeds of foraging red and hoary bats (*Lasiurus borealis* and *Lasiurus cinereus*; Chiroptera: Vespertilionidae). *Journal of Experimental Biology* **198**:2245–2251.Fenton, M. B. 1970. A technique for monitoring bat activity with results obtained from different environments in southern Ontario. *Canadian Journal of Zoology* **48**:847–851.Fenton, M. B. 1997. Science and the conservation of bats. *Journal of Mammalogy* **78**:1–14.Fenton, M. B. & G. P. Bell. 1981. Recognition of species of insectivorous bats by their echolocation calls. *Journal of Mammalogy* **62**:233–243.Fenton, M. B. & I. L. Rautenbach. 1986. A comparison of the roosting and foraging behaviour of three species of African insectivorous bats. *Canadian Journal of Zoology* **64**:2860–2867.Fenton, M. B., and I. L. Rautenbach. In press. The implications of ignorance, humans and elephants for the conservation of bats in African woodlands. In T. H. Kunz and P. A. Racey, editors. Bats: phylogeny, morphology, echolocation and conservation biology. Smithsonian Institution Press, Washington, D.C. Fenton, M. B., L. Acharya, D. Audet, M. B. C. Hickey, C. B. Merriman, M. K. Obrist, D. M. Syme, B. Adkins. 1992. Phyllostomid bats (Chiroptera: Phyllostomidae) as indicators of habitat disruption in the Neotropics. *Biotropica* **24**:440–

446.Freeman, P. W. 1981. The correspondence of food habits and morphology in insectivorous bats. *Journal of Mammalogy* **62**:166–173.Fullard, J. H. 1994. Auditory changes in noctuid moths endemic to a bat-free habitat. *Journal of Evolutionary Biology* **7**:435–445.Fullard, J. H. & D. W. Thomas. 1981. Detection of certain African insectivorous bats by sympatric, tympanate moths. *Journal of Comparative Phyisology* **A143**:363–368.Guy, P. R. 1981. Changes in the biomass and productivity of woodlands in the Sengwa Wildlife Research Area, Zimbabwe. *Journal of Applied Ecology* **5**:215–226.Hayman, R. E., and J. E. Hill. 1971. Order Chiroptera. Pages 1–73 in J. Meester and H. W. Setzer, editors. The mammals of Africa: an identification manual. Part 2. Smithsonian Institution Press, Washington, D.C. Herremans, M. 1995. Effects of woodland modification by African elephant *Loxodonta africana* on bird diversity in northern Botswana. *Ecography* **18**:440–454.Hovorka, M. D. 1996. The impacts of livestock grazing on Sonoran desertscrub vegetation, insect, and insectivorous bat communities. M.S. thesis. York University, Department of Biology, North York, Ontario. Huston, M. 1993. Biological diversity, soils, and economics. *Science* **262**:1676–1679.Huston, M. A. 1994. Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, Cambridge, United Kingdom. Jones, G. 1992. Bats vs moths: studies on the diets of rhinolophid and hipposiderid bats support theallotonic frequency hypothesis. Pages 87–92 in I. Horacek and V. Vohralik, editors. Prague studies in mammalogy. Charles University Press, Prague. Jones, G., P. L. Duvergé, and R. D. Ransome. 1995. Conservation biology of an endangered species: field studies of greater horseshoe bats. Pages 309–324 P. A. Racey and S. M. Swift, editors. Ecology, evolution and behaviour of bats. Symposia of the Zoological Society of London **67:**1–421.Lewis, D. L. 1991. Observations of tree growth, woodland structure and elephant damage on *Colophospermum mopane* in Luangwa Valley, Zambia. *African Journal of Ecology* **29**:207–221.McShane, T. O. 1987. Elephant-fire relationships in *Combretum/Terminalia* woodland in south-west Niger. *African Journal of Ecology* **25**:79–94.Petraitis, P. S., R. E. Latham, R. A. Niesenbaum. 1989. The maintenance of species diversity by disturbance. *Quarterly Review of Biology* **64**:393–418.Rautenbach, I. L. 1985. A new technique for the efficient use of macro mist nets. *Koedoe* **28**:81–86.Rautenbach, I. L., M. B. Fenton, M. Whiting. 1996. Bats in riverine forests and woodlands: a latitudinal transect in southern Africa. *Canadian Journal of Zoology* **74**:312–322.Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* **43**:223–225.Robinson, S. K., F. R. Thompson Iii, T. M. Donovan, D. R. Whitehead, J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* **267**:1987–1990.Rydell, J., G. Jones, D. Waters. 1995. Echolocating bats and hearing moths: who are the winners? *Oikos* **73**:419–424.Scholtz, C., and E. Holm. 1985. Insects of southern Africa. Butterworths, Durban, South Africa. Smithers, R. H. N. 1983. The mammals of the southern African subregion. University of Pretoria Press, Pretoria, South Africa. Swanepoel, C. M. 1993. Baobab damage in Mana Pools National Park, Zimbabwe. *African Journal of Ecology* **31**:220–225.Walsh, A. L., S. Harris, and A. M. Hutson. 1995. Abundance and habitat selection of foraging vespertilionid bats in Britain: a landscape-scale approach. Pages 325–344 in P. A. Racey and S. M. Swift, editors. Ecology, evolution and behaviour of bats. Symposia of the Zoological Society of London **67:**325–344.Whitaker, J. O., Jr. 1988. Food habits of insectivorous bats. Pages 171–189 in T.H. Kunz, editor. Ecological and behavioral methods for the study of bats. Smithsonian Institution Press, Washington, D.C. White, F. 1983. The vegetation of Africa. United Nations Educational, Scientific, and Cultural Organization. World Resources Institute. 1991. World resources 1990–1991. Report. Oxford University Press, Oxford, United Kingdom. Yager, D. D. 1990. Sexual dimorphism of auditory function and

structure in preying mantises (Mantodea: Dictyoptera). *Journal of Zoology, London* **221**:517–537.