

Reproductive ecology of Commerson's leaf-nosed bats *Hipposideros commersoni* (Chiroptera: Hipposideridae) in South-Central Africa: interactions between seasonality and large body size; and implications for conservation

F.P.D. Cotterill*

Principal Curator, Department of Mammalogy, Natural History Museum, P.O. Box 240, Bulawayo, Zimbabwe and Biodiversity Foundation for Africa, P.O. Box FM730, Famona, Bulawayo, Zimbabwe
woody@id.co.zw

R.A. Fergusson

Biodiversity Foundation for Africa, P.O. Box FM730, Famona, Bulawayo, Zimbabwe
woodyc@id.co.zw

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The annual cycle and reproductive ecology of a large population of Commerson's leaf-nosed bats, *Hipposideros commersoni*, was studied in central Zimbabwe. The influence of the extremely large body size of this microchiropteran, interrelating with a seasonal, tropical environment, was the central theme of this study. Adaptive responses to seasonal environmental changes differed between reproducing adults of the sexes. Reproductive females dispersed twice during the annual cycle, while in contrast adult males reduced activity during the cool, dry season. A polygynous mating system was characterised by breeding males defending demarcated territories within the daylight roost. Synchronized parturitions within maternity roosts (in late October) created a hot, humid microclimate which facilitated rapid post-natal development of neonates. The large body size of *H. commersoni* is suggested to have evolved in response to different selective agents, including: availability of large, hard shelled arthropods as prey; energetic constraints; and availability of fat reserves to 'ride out' inclement periods when food is limiting. Sexual selection may be the ultimate cause of a large body size. The conservation of *H. commersoni* is discussed given the history and pressures for guano exploitation of their breeding caves and the keystone role of these large bats in transferring nutrients and energy into the cavernicolous ecosystems where they roost and breed.

* Author to whom correspondence should be addressed at Biodiversity Foundation for Africa, P.O. Box FM730, Famona, Bulawayo, Zimbabwe.

The Hipposideridae, comprising over 61 species, are widely distributed across tropical Africa, Asia and Australia (Koopman 1993). *Hipposideros commersoni* (E. Geoffroy 1813) and *H. gigas* Wagner 1845 are two closely related Afrotropical species. Confined to equatorial Africa, *H. gigas* is the larger and is partly sympatric with *H. commersoni* (McWilliam 1982). The only other member of *Hipposideros* in southern Africa is *H. caffer* (7–11 g), occurring as far south as the Natal midlands, where female reproduction was investigated by Bernard & Meester (1982). Reproduction in *H. caffer* was also studied in Nigeria (Menzies 1973) and Gabon (Brosset & Saint-Girons 1980).

Alongside the Afrotropical *H. gigas*, *Saccolimus peli*, and the Australasian *Megaderma gigas*, *H. commersoni* is one of the largest extant Microchiroptera: body mass of a breeding male may exceed 200 g and forearm length varies between 112–120 mm (Kingdon 1974; Hill & Smith 1984). *H. commersoni* is represented by two subspecies: *H. c. niangarae* restricted to the equatorial regions of West Africa; and *H. c. marungensis* restricted to eastern and southern Africa (Hayman & Hill 1971) which reaches the southern limits of its distribution in Zimbabwe, Botswana and Mozambique (Meester, Rautenbach, Dippenaar & Baker 1986) and Pafuri, South Africa (Rautenbach, Schlitter & Braack 1984). Large caves are the typical roosts of *H. commersoni*, but solitary individuals may roost within tree canopies, and under the eaves of build-

ings (Vaughan 1977; Smithers 1983). Cave dwelling colonies of *H. commersoni* and *H. gigas* may be very large, with numbers exceeding 100 000 individuals. Reproduction has been studied in these large colonies of *Hipposideros* in Gabon (Brosset 1969; Brosset & Saint-Girons 1980), and coastal Kenya (McWilliam 1982).

Cranial and dental development of *H. commersoni* is exceptional, exemplified by the prominent sagittal crest (especially well developed in males), sturdy jaws and large canines (Freeman 1981, 1984; Smithers 1983). Freeman (1981) suggested these adaptations allow such bats to process prey items with hard exoskeletons, especially beetles. Limited observations on prey selection (Brosset 1969; Vaughan 1977; F.P.D. Cotterill unpublished data), suggests that *H. commersoni* specializes on large, hard shelled arthropods. Since *H. commersoni* is close to the maximum body size within the Microchiroptera (Kingdon 1974; Eisenberg 1981) its life history and autecology is of considerable interest. Furthermore, obtaining these data in a seasonal, tropical environment may help elucidate the evolution of microchiropteran life histories (see Bernard & Cumming 1997). This article describes the life history of *H. c. marungensis* in a seasonal tropical environment in Zimbabwe at 18°S, near the southern limit of the species' distribution.

Materials and methods

Study area

This study was conducted at a large dolomite cave (Mabura 1) in central Zimbabwe (Altitude 900 m) situated near the Ngo-doma and Munyati rivers, approximately 20 km north of Empress Mine (18° 18'S, 29° 25'E). Vegetation in the area is predominately mixed miombo woodland; dominant tree species include *Brachystegia boehmii* and *Kirkia acuminata*. A narrow fringe of riparian woodland lines the banks of both rivers. This more floristically diverse, denser woodland includes large trees such as baobabs (*Adansonia digitata*) and ebony (*Diospyros mespiliformis*). At lower altitudes miombo is replaced by monospecific stands of *Colophospermum mopane* (these vegetation types are described in detail by Irwin 1981). The climate, typical of miombo and mopane savanna, experiences three distinct seasons: cool-dry; hot-dry; and hot-wet through the year (Frost 1995). This region receives a mean annual rainfall of 607 mm, concentrated over the hot summer months of the year between November and April (Bernard, Cotterill & Fergusson 1996).

Mabura 1 Cave (Figure 1) has formed near the southern margin of the Lomagundi Series in the Mcheka Formation. The latter comprises siliceous dolomites of Proterozoic age (Sutton 1979). In addition to a smaller population of *Rhinolophus simulator* Anderson, 1904, Mabura 1 Cave supports a large colony of *Hipposideros commersoni*, but the two species roost separately in different chambers of the cave (Cotterill 1989, 1998). The largest (chamber 4) is over 100 m long by 30 m wide and the roof at least 13 m high, and is well ven-

tilated by the main entrance to Mabura 1 and a shaft in the centre of its ceiling. A smaller chamber, 3, joined cavern 4 and led to a narrow exit but was not used by roosting *H. commersoni*. Two networks of narrow passages, averaging 2 m in width, led beyond cavern 4 and extended at least 200 m in total extent. Of similar dimensions, another network, 1, opens at the main cave entrance and is at least 100 m in total extent. Chambers 2–4 of Mabura 1 have been surveyed (Truluck 1992, Figure 1).

Data collection

Following an exploratory visit in early December 1987, Mabura 1 Cave was visited on a monthly basis between June 1988 and August 1989, and four subsequent visits (in November and January of 1989 and 1990) were made to monitor parturition events. Activity of bats was monitored at the cave entrance from dusk until approximately 11 pm, and then intermittently until dawn. Behavioural observations of roosting bats were recorded with the artificial light of headlamps. This did not appear to disturb the bats, provided the observer maintained a distance of no closer than two metres from the subject. The entire cave network was searched to verify the presence or absence of females on three occasions during the course of this study.

Roosting bats were collected either by hand, or large hand nets to which extension poles were attached where necessary. Capture of bats commenced after behavioural observations were completed. Reproductive status of all individuals was assessed; incidence of pregnancy (detected by palpation) or

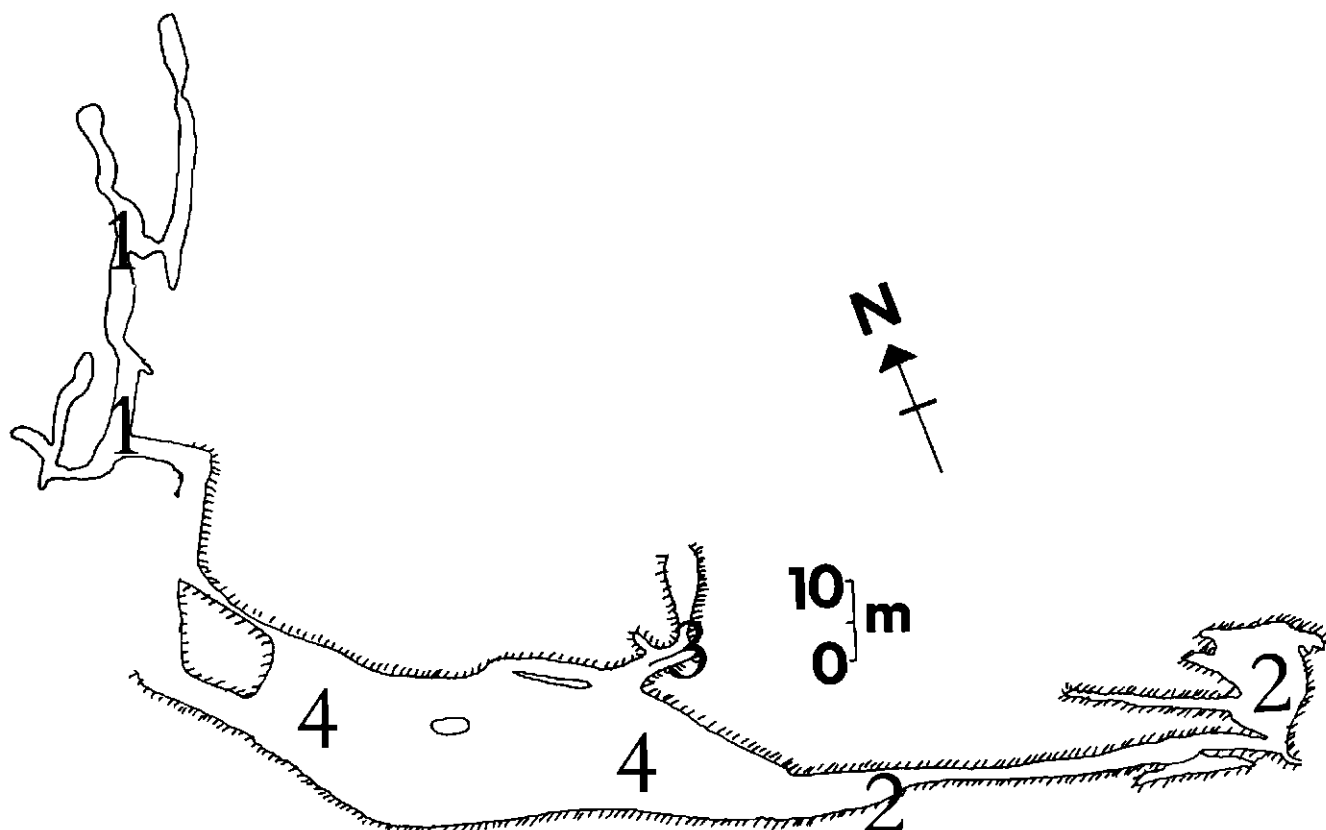


Figure 1 Map of Mabura 1 Cave modified after Truluck (1992). The configuration and extent of chamber 1 was not surveyed and is represented here in diagrammatic form. Numbered regions are referred to in the text

lactation being recorded in females. Juvenile bats were distinguished by incomplete ossification of the epiphyseal joints (Anthony 1988). For each individual, body mass was recorded on a Pesola balance and the length of the forearm was measured using vernier calipers. On each monthly collection, five adult animals of each sex were sacrificed in the field using ether, their reproductive tracts dissected out immediately and preserved for histological analysis. Only reproductively active males and parous females were sacrificed for histological samples and to assess fat levels (Cotterill 1989, F.P.D. Cotterill, unpublished data). Abdominal and subcutaneous fat deposits in these sacrificed animals was scored on a relative index of 1 (negligible or no fat deposits) to 5 (maximal fat deposits). The incidence of torpor was ascertained by the low body temperature when handling the bat. The majority of these specimens are deposited in the Mammal collection of the Natural History Museum, Bulawayo.

The following measurements were made on cleaned skulls of reproductive adults: Greatest Skull Length – least distance from anterior edge of canine teeth to posterior border of supraoccipitals; Zygomatic Breadth – greatest width across zygomatic arches perpendicular to longitudinal axis of cranium;

Greatest Height – least distance from top of sagittal crest and edge of glenoid fossae; Lower Jaw Height – least distance from base of dentary to edge of 3rd lower molar; Greatest Length of Lower Jaw – least distance between anterior edge of dentary and posterior edge of glenoid process; Lower Jaw Thickness – greatest width of dentary. Growth data were collected from neonates and juveniles after dusk, when their mothers were absent from the roost. The body mass and forearm length of ten animals of each sex were recorded. Curves were fitted to these mensural data using the curve-fitting algorithm in SigmaPlot 3.0 for Windows NT. Lines of best fit were calculated using the Logistic equation of the form:

$$y = K(1 - e^{-x})$$

Results

Age determination and sexual dimorphism

Over 1000 *Hipposideros commersoni* of both sexes (including juveniles) were examined and released. Sexual dimorphism in *H. commersoni* is distinctive, and males are significantly larger than females. Males have significantly longer forearms and wider, longer skulls, and the lower jaws of males are significantly longer and thicker (Table 1). This

Table 1 Comparison of forearm length (mm) and selected cranial measurements (mm) of reproductively active male and female *Hipposideros commersoni* to illustrate sexual selection. Mean values \pm 1SD are given; n = 20

Sex	Forearm length	Greatest skull length	Zygomatic breadth	Lower jaw height	Lower jaw thickness	Length of lower jaw
Male	102.5 \pm 2.5	36.0 \pm 0.9	20.1 \pm 0.6	16.0 \pm 0.7	5.35 \pm 0.5	24.0 \pm 0.7
Range	99.5–107.9	34.3–37.8	18.9–21.0	14.8–17.7	4.2–6.7	22.8–25.4
Female	95.9 \pm 2.3	32.0 \pm 0.6	17.23 \pm 0.5	12.4 \pm 0.7	3.1 \pm 0.3	22.1 \pm 0.4
Range	90.4–100.9	31.1–33.4	16.3–18.3	11.2–14.2	2.8–3.6	21.4–22.6
T test	t = 9.5	t = 15.4	t = 16.8	t = 19.4	t = 17.3	t = 12.0
	p < 0.0001	p < 0.00001	p < 0.00001	p < 0.00001	p < 0.00001	p < 0.00001

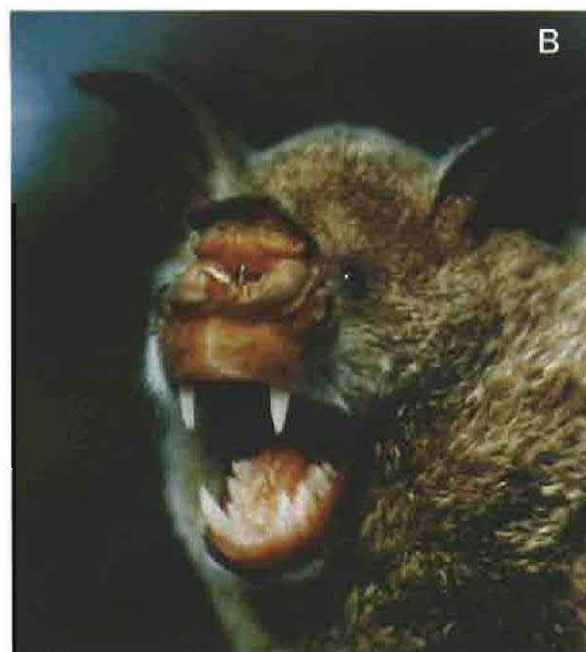


Figure 2a & b Comparison of adult *Hipposideros commersoni marungensis* from Mabura I Cave: a. An adult male showing the well-developed frontal gland above the noseleaf. b. An adult parous female showing rudimentary development of the frontal gland



Figure 2c Two reproductively active males of *Hipposideros commersoni* collected from Mabura I Cave on 5th January 1989. Lacerations and subcutaneous injuries to the upper body of both males are visible as well as large deposits of fat – illustrated in the dissected individual on the left

high degree of sexual dimorphism is also manifested in the highly developed frontal gland of reproductively active males, compared to adult females. Subadult males were distinguished by the rudimentary frontal gland, and comparatively thicker pelage (Figure 2). The rich reddish-brown pelage of parous females is longer and thicker compared to the grey fur of males. Parous female *H. commersoni* were distinguished from subadult and nulliparous individuals by their enlarged, deeply pigmented pelvic nipples. The degree of tooth wear (particularly of the canines) was a useful criterion for recognising parous females.

Male cycle

Male *Hipposideros commersoni* were present in Mabura I throughout the study, although their numbers fluctuated during the year. The annual cycle of adult male *H. commersoni* was characterised by large fluctuations in mean body mass and condition. The levels of fat and body mass declined over the cool, dry season (Figure 3). Body mass peaked between December and January, and males had accumulated large reserves of body fat by February (Figure 2c).

Roost selection

Some of the adult males demonstrated strong territoriality between February and June, when they roosted separately on the exposed walls and roofs of chambers 1 and 2. Aggressive encounters were observed between neighbours, particularly if a male attempted to alight near a roosting male. After roosting bats had been flushed (when animals were handnetted), these territories could easily be distinguished by the equidistant patches of urine (approximately 30 cm apart) on flat, near vertical sheets of dolomite. Some territory holders were reluctant to vacate their roosts even when disturbed and could be easily captured. Indirect evidence suggests that confronta-

tions between males had been violent, involving direct contact, with biting to the body. Many adult males examined in February exhibited open lacerations and wounds on the upper body and neck (Figure 2c). It is assumed that these resulted from competition between reproductively active males for territories. During this period, no subadult male was encountered roosting on exposed rock faces. They clustered into rock crevices, often alongside subadult and parous females. None of the bats in these crevices showed any evidence of the segregation characterising the roost selection of reproductively active males. Females and sub-adult males not only formed dense clusters, but appeared more catholic in their selection of roosts within the cave. Between August and March, concentrations of adult males (identified by their fully developed frontal glands) clustered into crevices in the roof of the main chamber (4, Figure 1). Physical examination of these males during mid-morning revealed them to be non-torpid.

Female cycle

Copulations were directly observed on two separate visits in June 1988, and early in July 1989. Copulation was a comparatively protracted affair, lasting approximately 30 minutes. Mating ensued when a female landed near a male on his territory. Conception proceeded immediately. Macroscopic evidence of pregnancy was observed in females dissected in July and August 1988 and August 1989, and was confirmed histologically (Cotterill 1989; unpublished data).

The numbers of female *H. commersoni* in Mabura I underwent marked changes during the study. Numerous parous females were seen in June, July and August 1988; and July and August 1989. No parous females were seen in September 1988 after the visit in late August. At the end of October 1988, large numbers of parous females had returned to give birth. No parous females were seen in Mabura I in March and April 1989.

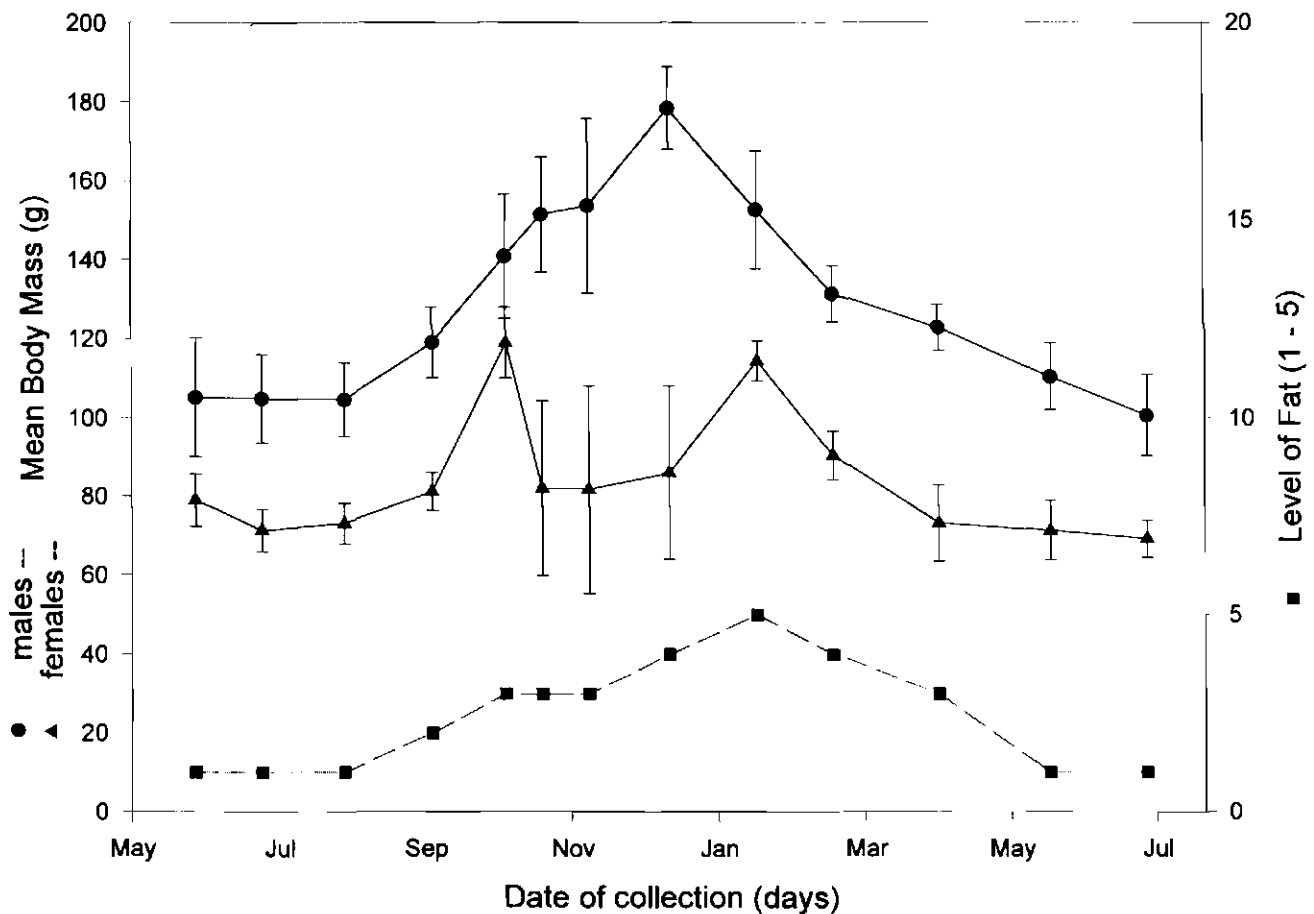


Figure 3 Changes in the body mass ($\bar{x} \pm 1$ SD) and levels of fat in reproductively active males and females between June 1988 to August 1989. Negligible differences in fat levels could be discerned between individuals of both sexes from each collection and an overall value is given

Levels of fat in females fluctuated in a similar manner to males (Figure 3). Maximum levels of fat were recorded in mid-February, towards the end of the hot-wet season. A continuous profile of these variables is not available, because parous females were absent for two separate periods during the year. Variation in body mass is further compounded by pregnancy: mass in pregnant females increased until parturition in October, when it declined sharply; and then increased to peak in February. Body mass and fat reserves then declined and were at their lowest during the cool-dry season. Most notably, parturient females who had returned to Mabura 1 in late October had laid down fat deposits despite carrying large foetuses (Figure 3).

On 1 November 1988, the majority of females were carrying new-born naked young, some with umbilical cords still attached. Numerous parturitions were observed directly on this visit. Similar evidence of recent parturitions was observed in early November of 1989 and 1990 – all adult females were carrying naked neonates. Neonates were only seen in the maternity chambers (1 and 2, Figure 1). Parturition was highly synchronised among breeding females, and visits to Mabura 1 in early December 1987 and mid November of 1989 and 1990 confirmed the occurrence of a birth peak – as an abundance of naked neonates were seen. The high temperature and humidity, and unpleasant levels of NH_4 and CO_2 in these maternity

chambers prevented a thorough search of the cave system on these occasions.

Daily and seasonal activity

Daily activity patterns differed markedly between seasons. Between August 1988 and April 1989, *H. commersoni* began to leave the roost at dusk, and numbers of exiting bats peaked approximately one hour after sunset. The total cross sectional area occupied by the stream of exiting bats was approximately 15m^2 . The intensity of activity at the cave exit at this time can be gauged by estimates of ten bats passing a fixed line perpendicular to the direction of exit at any time. No estimate of the total numbers of *H. commersoni* was attempted but it is conservatively estimated that Mabura 1 supported tens of thousands of individuals during this study, and the total population was tentatively estimated at over 100 000 when breeding females were in residence. Although quantitative data were not obtained, activity continued through the night, and bats were still returning to the cave at dawn. In marked contrast, activity was greatly reduced between May and August: searches of the cave system in the early evening revealed many adult males still within the roost. Nocturnal observations within the cave (after the major emergence at dusk has subsided) confirmed the high roost fidelity of adult males over the cool-dry season compared to females. Some of

these males were also observed defending their territories during these visits. A marked increase in male activity was observed in August of both 1988 and 1989. Compared to males, females demonstrated a more consistent emergence pattern over the annual cycle.

Post-natal development

After parturitions had occurred, females roosted throughout the passages of chambers 1 and 2 (Figure 1) where matings had occurred during the cool-dry season. Roost selection seemed indiscriminate, with these females roosting on dolomite sheets and within cranulated surfaces of the rock. Maternity roosts were located in the extensive side chambers (1 and 2). In early November, access into these chambers was very difficult due to the extremely unpleasant conditions therein. In addition to the very high temperatures, high levels of CO₂ and NH₄ caused hyperventilation and near loss of consciousness in human observers. Only closed breathing apparatus would have enabled unrestricted access into maternity roosts at this time and it was not possible to search chambers 2 beyond 20 m from their entrances.

Immediately after birth, the neonate was carried by its mother when flying within the roost: the neonate clung to its mother using the hind feet, and its mouth fastened to the pelvic nipples. Neonates were not carried when their mothers left the cave to forage. When approximately two weeks old, juveniles were already capable of short gliding flights within the

roost, but were still entirely dependent on their mothers' milk. Lactation continued for at least 13 weeks after birth – females examined in mid-February 1989 were still actively lactating. During daylight hours a large number of lactating females roosted in the main chamber (4, Figure 1) separately from their offspring. When separated from the mother, juveniles huddled in crevices and on the cave walls in dense clusters.

The forearm lengths of neonates almost doubled within 34 days (Figure 4). The logistic equation describing forearm growth for both sexes is given below. The lower asymptote for juvenile females reflects the sexual dimorphism in *Hipposideros commersoni* (females, mean forearm length = 94.3 + 1.38; males, mean forearm length = 103.7 + 1.71; n = 10).

$$\text{MALES: } y = 102.3(1 - 0.607e^{-0.045x})$$

$$\text{FEMALES: } y = 40.0(1 - 0.466e^{-0.067x})$$

The annual cycle of *H. commersoni marungensis* observed in Mabura I Cave is summarized in Figure 5, where important reproductive events can be compared.

Discussion

A primary objective of this study was to investigate the influence of a large body size on the reproductive tactics of *H. c. marungensis* in its savanna habitat. Body size holds a central role in interspecific life history variation within mammals (Stearns 1983, 1992; Read & Harvey 1989). The highly distinctive sexual dimorphism in *H. commersoni* was noted by

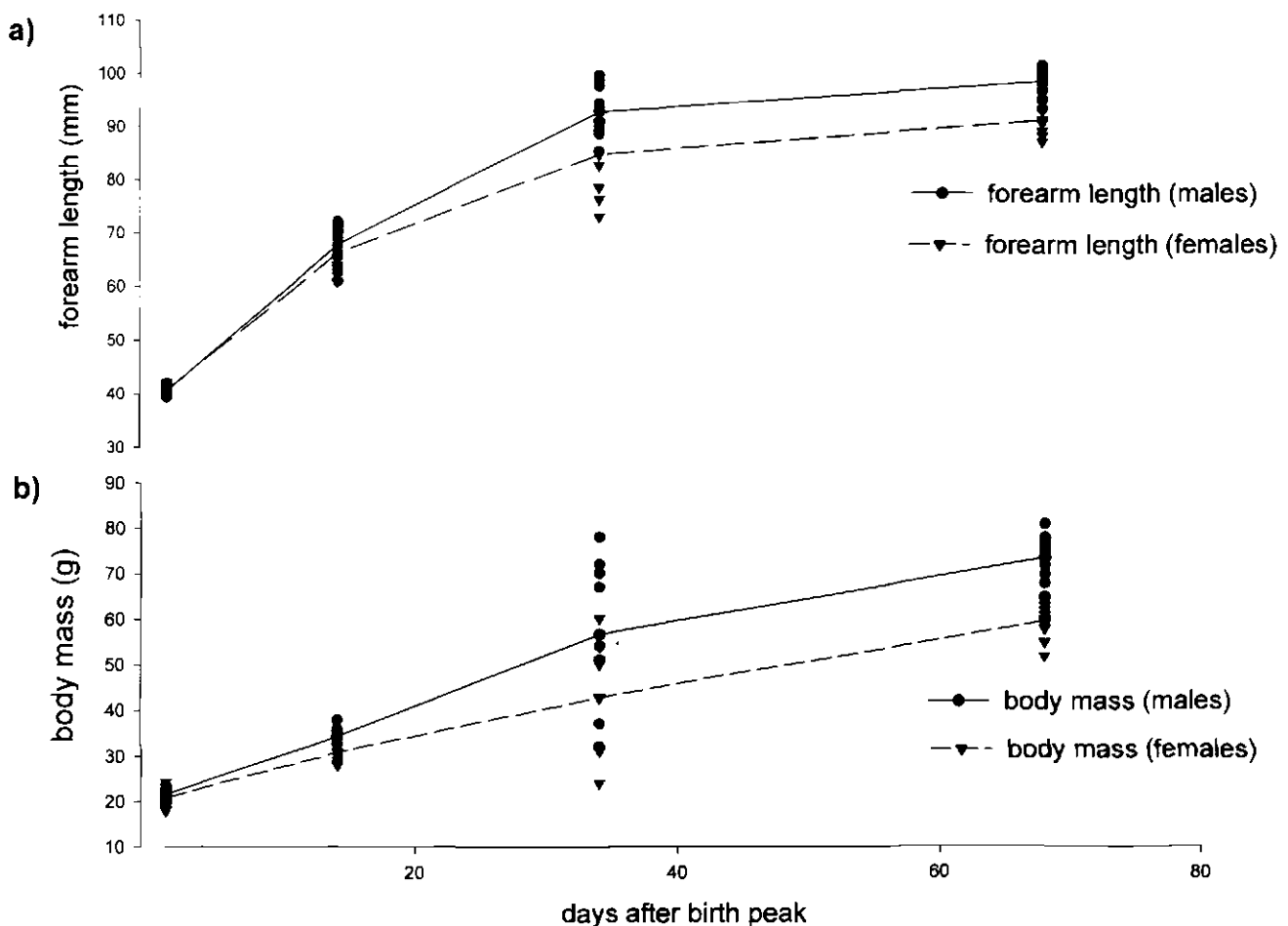


Figure 4 Changes in forearm length and body mass of juvenile male (n = 10) and female (n = 10) *Hipposideros commersoni* in Mabura I over the period 1st November 1988 to 6th January 1989. Logistic growth curves are shown for each data set

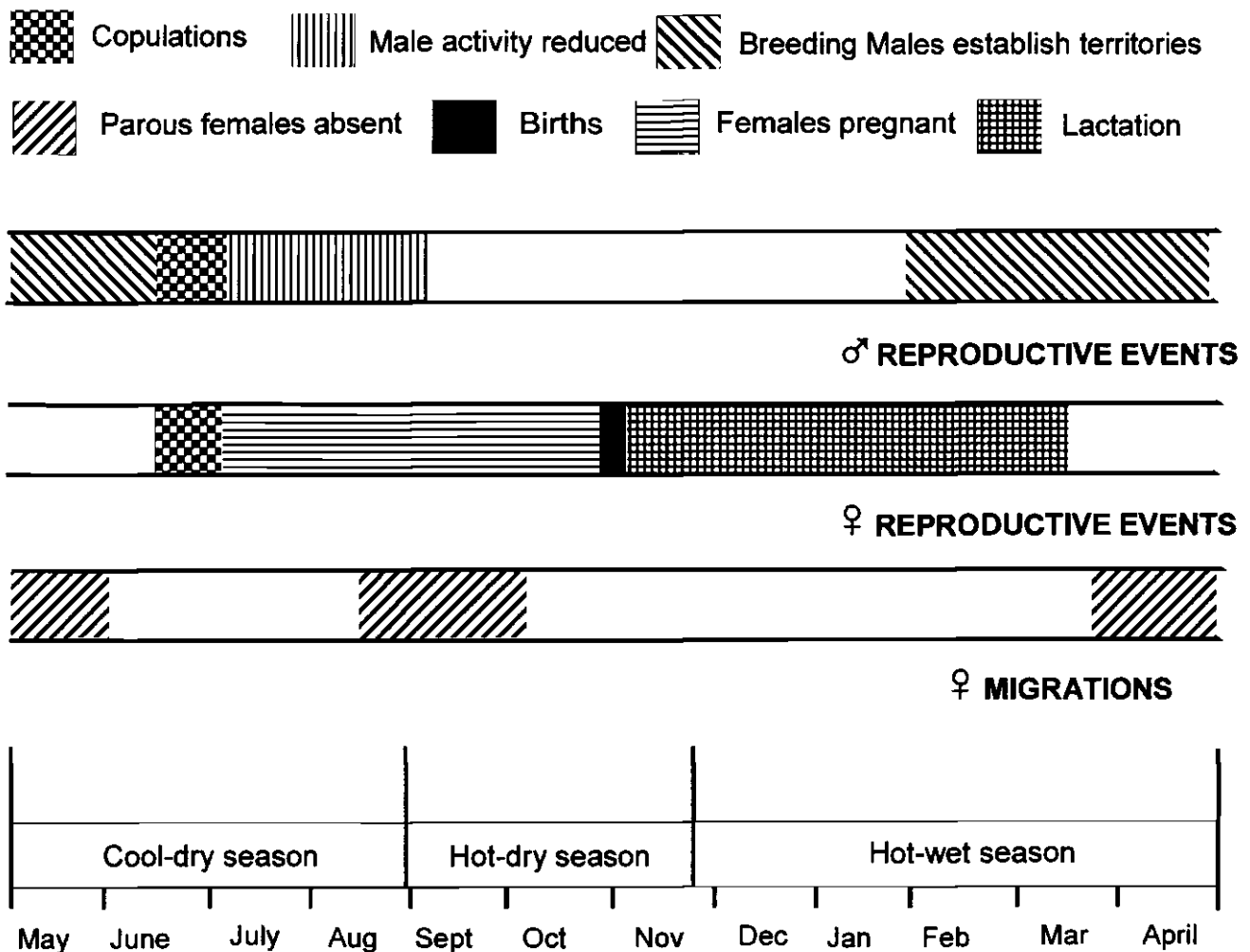


Figure 5 Schematic outline of seasonal reproductive events in *Hipposideros commersoni marungensis* in Mahura 1, observed between June 1988 and November 1990. Timing of copulations, territory establishment, and durations of prenatal development and lactation are shown. Periods of dispersal and inactivity in reproductively active females and males, respectively, are shown in the lower outline

Brosset (1966) and Ansell (1967) and characterises both *H. gigas* and *H. commersoni* in Kenya (McWilliam 1982).

Mating system

The mating system of *Hipposideros commersoni* can be described as a form of resource defence polygyny (Vehrencamp & Bradbury 1984) with breeding males defending territories on roosting space on cave walls. Although no direct census of breeding *versus* non-breeding males was undertaken, the operational sex ratio appears highly skewed in *H. commersoni*. Further evidence was apparent in the large numbers of non-reproductive males roosting in crevices and not on exposed walls. The high densities of females and competition for space in daylight roosts has likely facilitated the evolution of a polygynous mating system. Furthermore, intense male-male competition may also be associated with sperm competition, as uteri of recently mated females were distended by a large volume of ejaculate and their vaginas were occluded by a copulatory plug. The accessory reproductive organs of reproductive males are hypertrophied between February and June, and large ejaculates are released in copulations (McWilliam 1982; Cotterill 1989, unpublished data). This suggests that multiple matings occur. Prolonged copulations and the

large ejaculates in *H. commersoni* supports Fenton's (1984) hypothesis that these characters may indicate sperm competition – originally suggested for vespertilionids and rhinolophids.

Roost selection, reproduction and post-natal development

Although no microclimatic data were recorded, large concentrations of *H. commersoni* raised the temperature and humidity within chambers 1 and 2 (Figure 1) especially when large numbers of females gave birth synchronously. These conditions contribute to rapid postnatal development of offspring (Tuttle & Stevenson 1982), which decreases the time to weaning in insectivorous bats (McNab 1982). This would be advantageous for a large microchiropteran in a seasonal environment, since newly volant young would have to learn to forage effectively before resources become constrained in the cool-dry season. The selection of maternity roosts, with modification of their microclimates, reduces maintenance requirements of neonates who can allocate more energy to somatic growth (McNab 1982; Tuttle & Stevenson 1982). A faster growth rate would be adaptive for *H. commersoni* whose weaning period is longer than smaller Microchiroptera

(Eisenberg 1981; Peters 1983; Happold & Happold 1990; Bernard & Cumming 1997; Figures 4 & 5).

Brosset (1969) suggested a lactation period of five months for *H. gigas* in Gabon; much longer than the 14 week weaning period of the same species in Kenya (McWilliam 1982), and that observed in this study (at least 13 weeks). The daily milk requirements of *H. commersoni* offspring would be very high over this period of intensive skeletal growth. The roosting behaviour of lactating females (roosting separately from their progeny), may allow females to compensate for increased energy demands of lactation by entering torpor in this cooler microclimate. The ability of a lactating female bat to enter torpor, so lowering her metabolic rate, compensates and reduces her overall daily energy expenditure (Racey & Speakman 1987). This is similar to observations of compensation in lactating females, and rapid postnatal growth of offspring in temperate zone vespertilionids (Racey & Speakman 1987) and Afrotropical rhinolophids (Cotterill 1998).

Adaptive responses to seasonal constraints and energetic costs

An integrative theme interlinking these data on the ecology of *Hipposideros commersoni* is the strong correlation between biological phenomena and environmental seasonality. Although not directly investigated, it is assumed that prey availability is limiting to these bats in part of the annual cycle, especially during the cool-dry season, as has been demonstrated for *H. commersoni* in Kenya during dry seasons (McWilliam 1982) and is interpreted as a pervading energetic constraint on metabolic and reproductive processes in Afrotropical bats (Bernard & Cumming 1997; Cotterill 1998).

Responses to seasonality differ between reproductively active male and female *H. commersoni*. Between June and into August (the cool-dry season) adult males remained within Mabura I and reduced activity. They exhibited an unusual behaviour in not flying but were not torpid as is typical of smaller microchiropterans when inactive during the same season. This phenomenon in *H. commersoni* was recently observed by Churchill, Draper & Marais (1997) in Namibia. An extremely large body size may allow these volant insectivores 'to ride out' this predictable period of food scarcity each year, primarily by storing fat and reducing activity.

By contrast, females dispersed from Mabura I on two occasions: whilst in mid pregnancy; and after offspring had weaned. The destination(s) of these particular animals is unknown, but the possibility of great distances being travelled exists. In Kenya, pregnant female *H. commersoni* left their roosts in coastal caves after copulation and implantation, and only returned approximately eight weeks later to give birth. These females had migrated more than 300 km inland, where they roosted in caves in a region where the 'long rains' broke at least six weeks earlier than at the coast (McWilliam 1982).

Gravid female *H. commersoni* left the breeding roost at the end of the long dry season in Kenya, when insect availability was reduced (McWilliam 1982, *pers. comm.*). In both populations (Kenya and Zimbabwe), gravid females had increased fat deposits during the period when absent from the breeding roost (McWilliam 1982; this study, Figure 3). Migrations of female *H. gigas* and *H. commersoni* were also observed in Gabon (A.N. Brosset *pers. comm.*). In Drotsky's Cave, west-

ern Botswana, Smithers (1971) noted the complete absence of the *H. c. marungensis* colony in June, although they were present when the cave was visited in May and September, but no data on the sexual composition of this population was recorded. Migrations of female *H. commersoni* may be a ubiquitous adaptation of the species, particularly in populations where females are reproductively active during periods of reduced prey availability. Reproductively active females dispersing from Mabura I cave obtain sufficient food in mid-pregnancy to sequester fat deposits, which have increased when they return. To obtain sufficient insect prey, we hypothesize that they may forage in areas where the rains have already started – such as northern Zambia or central Angola approximately 700 to 900 km from Mabura caves – and prey populations are burgeoning during September and October.

Diet specialization and sexual dimorphism

The phenological discrepancy between fluctuations in body mass and fat levels in adult males is interesting and difficult to explain: body mass peaked in December while fat deposits were maximal in February. The large decrease in body mass of breeding males began in January and culminated in the cool-dry season. It is likely associated with high reproductive costs, seasonal periods of food scarcity, or both these factors. These costs likely arise from territory establishment, defense, and copulations. In particular, territorial defense is associated with intense male-male competition, particularly when oestrous females are in residence (McWilliam 1982). These large fluctuations in male body mass represent a complex response to the high energetic costs of breeding during the cool-dry season when the availability of insect prey is limiting. A similar pattern of annual cyclicality in male body masses was recorded in coastal Kenya for both *H. commersoni* and *H. gigas* (McWilliam 1982). Vaughan's (1977) observations over a Kenyan wet season demonstrated that female *H. commersoni* are specialized predators of large Coleoptera, particularly Scarabaeidae. The temporal pattern of abundance of these insects is highly seasonal (Vaughan 1977). Nevertheless, the highly seasonal pattern of scarab emergence and activity (Anderson & Coe 1974; Janzen 1983; Schlotz & Holm 1984; Doube, 1991; Gardiner, 1995), may constitute an important energetic constraint on *H. commersoni* for part of the year, especially during dry seasons. This 'energetic crunch' quite possibly accounts for the large fluctuations in body mass and condition observed in *H. commersoni* in seasonal environments (McWilliam, 1982; this study).

There is extreme divergence between the cranial and dental anatomy of the smaller *H. caffer* compared to both *H. commersoni* and *H. gigas* (Freeman 1981, 1984). Skull and dental morphology suggests *H. caffer* to be a moth specialist, as confirmed by field studies (Fenton 1985; Bell & Fenton 1984). The latter studies, and Vaughan's (1977) observations on female *H. commersoni* feeding on large, hard-shelled beetles, supports Freeman's hypothesis of the existence of beetle (with harder, thicker exoskeletons) and moth (with softer thinner exoskeletons) specialists in the Microchiroptera. *H. commersoni* (especially the adult males) has a large gape and powerful bite, aptly demonstrated by their ability to bite through thick leather gauntlets easily penetrating human flesh.

The dietary specialization of *H. commersoni* on this seasonally abundant resource of large arthropods would be highly cost effective as these bats can select large prey items; allometrically associated cranial and dentary adaptations permit efficient prey capture and ingestion (Freeman 1984). Thus, *H. commersoni* can specialize on large prey items unavailable to smaller animalivorous bats. A 'CF movement detector' sonar system (Schnitzler, Hackbath, Heilmann & Herbet 1985; Neuweiler & Fenton 1988; Neuweiler 1989) would allow these large *Hipposideros* to capture large insects from perches, which Vaughan (1977) suggested to be more energetically conservative compared with the hawking foraging strategies. Nonetheless, foraging bats are characterized by their flexibility in foraging behaviour and *H. commersoni* may alternate between hawking, hunting from perches and perhaps gleaning, and its sonar system is also suited to foraging along cluttered habitats in edge situations (see Fenton 1990).

Nonetheless, a dietary specialization on large, hard-shelled arthropods does not account for significant sexual dimorphism in *H. commersoni* – intense competition between breeding males for mates is the most likely explanation. This raises interesting questions about ultimate and proximate causation. What originally selected for a large body size in the ancestors of these *Hipposideros*? The ability to exploit large arthropods – a large body size and teeth, wide gape and strong jaws might constitute exaptations (*sensu* Gould & Vrba 1982) derived from traits originally evolved in direct response to sexual selection in an ancestral population roosting in large concentrations in cavernicolous roosts. Investigations of the ontogenetic expression of these traits, given their sexual dimorphism, would also be interesting.

Human impacts and conservation of *Hipposideros commersoni*

Large colonies of *H. commersoni* are known only from scattered localities in northern Zimbabwe – in the Chinoyi district, and the Munyati and Sanyati Basins – within dolomite formations in the Lomagundi Series (see Sutton 1979). The colony at Mabura I Cave is exceptional in its size and density of bats. Comparatively few, very large, colonies of *H. commersoni* are known (A.N. McWilliam, *pers. comm.*), including Drotsky's Cave, Botswana (Smithers 1971) and central Mozambique (D.G. Broadley, *pers. comm.*) and scattered localities in Zambia (Ansell 1978). These colonies represent the southern limit of breeding populations of *H. commersoni* near the southern edge of the species' overall range. The apparently widespread occurrence of this species across Zimbabwe is based largely on collections of single bats in mistnets or roosting singly in trees and on buildings (Smithers & Wilson 1979; F.P.D. Cotterill, *unpublished data*).

Guano was extracted from Mabura Caves in the early decades of this century (Flack 1921) and very little remains of the original deposit, which was originally estimated at over 6 m deep in places (Sutton 1979). Since 1981, Mabura Caves have received increasing attention as a guano resource, after mining had ceased in the mid 1960s (Ellert 1983). The site was declared a national monument in 1990 by the National Museums and Monuments of Zimbabwe, but soon after the Ministry of Mines in Zimbabwe declared guano a mineral.

The Mines and Minerals Act holds precedence over the National Museums and Monuments Act and The Parks and Wildlife Act. An all-weather gravel road had been constructed to Mabura I by mid 1990 to support sustained guano extraction. Guano was extracted from part of the cave system in 1991 by a commercial operation but was halted by authorities soon after its initiation. All these attempts have proceeded despite the lack of a detailed inventory of guano within Mabura I, which is popularly believed to extend over tens of kilometres, but is distinctly delimited (Figure 1).

By July 1992 and with this recent mining, the numbers of *H. commersoni* using the main amphitheatre of Mabura I as a winter roost had declined considerably. Very few breeding females were seen in chamber 2 in November 1996. (On the same visit, *Rhinolophus simulator* which is dependent on chamber 3 in Mabura I as a maternity roost [Cotterill 1998] was also not seen.) Coincidentally, both these parts of the cave were heavily impacted by guano extraction.

The findings presented in this article have a direct relevance to the conservation of *H. commersoni*. If guano extraction occurs in breeding roosts, it will disturb the bats (as has recently occurred in Mabura I Cave). Mining should not occur during the crucial periods of territory establishment, mating, and parturitions, and the ensuing post-natal development. In total, these phenomena occupy ten months of the year; and disturbance cannot be condoned when large concentrations of bats are in residence and reproductive activities are occurring.

Nevertheless, the reality of the situation is that Mabura I Cave is surrounded by a burgeoning population of humans, many in dire economic straits. Manual extraction of guano from Mabura I Cave during early September, when a highly organised extraction (minimising mechanical damage to the dolomite substrate and invertebrate fauna) might be possible, subject to further studies of impacts on invertebrate biodiversity. Furthermore, it may be possible for a sustainable extraction system to benefit local communities, following a conservation model which has become popular in Africa. Nevertheless, risks to human health requires evaluation as fungi (*Histoplasmosis* sp.) occur in the cave system.

Conservation plans for species such as *H. commersoni* must not only maintain key habitats but encompass the metapopulation (*sensu* Chesser, Rhodes & Smith 1996). Mating, conception and post-natal development are not the only population processes susceptible to disturbance in large colonies of *H. commersoni*. The migrations of reproductive females constitute potentially endangered biological phenomena (*sensu* Brower & Malcolm 1991). Considered within an ecological context, these large bats are the charismatic species in a cavernicolous ecosystem whose geographical extent has barely been mapped: its biodiversity – particularly invertebrates and especially microbial fauna – has yet to be studied. *H. commersoni* holds a keystone role in importing nutrients and energy into this subterranean portion of the landscape.

Conclusions

Mabura I Cave constitutes an important breeding roost for *Hipposideros commersoni* in Zimbabwe, where copulations occur in June/July, and single young are born in late October at the start of the hot-wet season. The mating system of

H. commersoni exhibits a form of resource defence polygyny, in which males defend demarcated territories located on the walls of the daylight roost. Sexual dimorphism is extreme and the large size of males is likely associated with sexual selection. It is, nonetheless, unclear whether intrasexual competition or feeding on large, hard-shelled arthropods ultimately selected for a large body size in the ancestors of *H. commersoni*.

This study demonstrated that reproductive females migrate twice during the annual cycle, and these may occur over a regional scale between southern Africa and habitats further north in central Africa. Migration characterises the female cycle of the Mabura I colony of *H. commersoni*, in common with populations elsewhere in Africa. Studies of the alternative resources exploited, especially when gravid and post lactating females are absent from breeding roosts, would provide valuable information towards conserving the metapopulation of *H. commersoni* in south-central Africa. Conservation of *H. commersoni* must address the entire metapopulation. The first step towards maintaining its integrity is to elucidate the status, structure and geographical locations of the subpopulations within the range of the species. Any exploitation of guano from roosts used by *H. commersoni* must be planned within the context of the seasonal cycles and ecology of the bats which maintain the resource.

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