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Cave utilisation by Namibian bats: population, microclimate and roost selection

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Ten caves in central Namibia were searched for cave bats during May and June 1996. Up to seven species were found sharing a single cave. Different species of bats were found to select roost sites with significantly different microclimates, based on temperature and relative humidity. Bats were using these caves as over-wintering sites and were selecting either cool microclimates in which to enter daily torpor or warm microclimates to enable them to remain active with minimal energy expenditure. *Hipposideros commersoni* was observed to remain inactive at the roost for days without entering torpor or leaving the cave to forage. This large bat appears to over-winter by relying on its considerable fat store at this southern limit of its distribution. Roost behaviour, colony size and roost location within the cave was examined for each of the nine bat species encountered.

Keywords: colony size, Namibia, roost behaviour, roost microclimate selection, tropical cave bat, *Hipposideros caffer, H. commersoni, Miniopterus schreibersii, M. inflatus, Nycteris thebaica, Rhinolophus clivosus, R. darlingi, R. denti, R. fumigatus*

Introduction

Most studies of Namibian bats have been aimed at establishing a faunistic inventory (Roer 1978), and much of the recorded behavioural and ecological information is based on random observations. Similarly, cave studies in Namibia have primarily produced baseline information about this habitat, with incidental notes on observed ecological phenomena.

Contemporary Southern African caves have developed since the late Tertiary. One Namibian cave has been dated at over 200 000 years bp (Brooke, Cowart & Marais in press), but most extant caves may be of a more recent origin. It is likely that cave habitats have been available to bats for most of the Quaternary. During this period the climatic conditions in Namibia were relatively stable. The behaviour of bats roosting in caves could therefore have evolved over a long period. The massive quantities of guano extracted as fertiliser from several Namibian caves suggests either a long history of bat use, or recent occupation by large populations.

Bats use caves for a variety of reasons but primarily because they provide stable microclimates for roost sites and protection from predators. Large complex caves such as those examined during this survey provide bats with a diversity of potential roost conditions. Cave microclimate (temperature and relative humidity) varies with distance from the cave entrance, height above the floor, depth below the surface, distance from the water table, presence of pools of water, amount of air movement, size and shape of cave passages or chambers, and the presence of other bats (Twente 1955; Dwyer & Harris 1972; Churchill 1991). Bats need a range of different microclimates during the year to suit their changing needs. For example, females and young during the summer months prefer warm and humid roosts to help the young maintain body temperature (Dwyer & Hamilton-Smith 1965; Bernard & Bester 1988). In winter many bats roost in cool conditions to help reduce their body temperature (to enter torpor or hibernation). This lowers their resting metabolic rate during this period of limited food resources (Nagal & Nagal 1991; Webb, Speakman & Racey 1996). Other species, that cannot enter torpor, will select roost microclimates that approximate their thermoneutral zone (Churchill 1991; Baudinette, Churchill, Christian, Nelson & Hudson in press).

This study was conducted during May and June (austral winter) in Namibia, near the Tropic of Capricorn. We were particularly interested to see what roost microclimates these tropical bats would use when not constrained by reproductive activities (pregnancy, lactation and mating).

Most published data on roost selection are concerned with microclimate of maternity roosts (Hall, Young & Spate 1975; Dwyer & Hamilton-Smith 1965; Dwyer & Harris 1972) or hibernacula of temperate species (Twente 1955; Raesley & Gates 1987; Gaisler 1970; Daan & Wichers 1967; Van der Merwe 1973). Published data on the microclimate of diurnal roost sites used by tropical cave bats are scarce (Churchill 1991; Bonaccorso, Arends, Genoud, Cantoni, & Morton 1992; Rodriguez-Duran 1995).

The aim of this study was to identify the species of bats using these caves, the roost microclimate selected by each species, colony sizes, spatial distribution and roost behaviour during the cooler months of May and June.

Study area and methods

This study was conducted in northern central Namibia. Ten caves that were known to contain bats were selected for investigation during May and June 1996.

Caves were explored during daylight hours, when bats were roosting, to determine roost site selection, spatial distribution and microclimate selection. Species encountered within the caves were captured with hand nets, identified, measured and released. Voucher specimens were deposited with the National Museum of Namibia in Windhoek. Population size estimates were made by either direct counts or extrapolation where concentrations were high.

Temperatures and humidities were measured with a wet/dry thermometer (Bacharach swing psychrometer) to within 0.5°C. Temperature readings were taken as close to the roosting bats as possible (usually within 10 cm). The distance from the cave entrance was measured in metres using a hip-chain. The presence of daylight and the air movement in the cave (felt as draughts) were recorded. The location of each bat colony was recorded at the time directly onto cave maps. Bat activity levels were defined as (i) *Torpid:* bats that remained at their roosts until at least 5 min after disturbance and felt cool to touch; (ii) *Alert*: bats that dispersed readily when disturbed and felt warm to touch; (iii) *Active:* bats flying within the cave.

Roost behaviour patterns were noted, and spatial separation distances recorded. We defined the bat's roosting postures as three main types. (i) *Free hanging:* bats that hang by their feet either from the ceiling or the wall. Although their wings may be in contact with the wall they are not using them for support (eg. rhinolophids and hipposiderids). (ii) *Propped:* bats that hang on walls by their feet but use their wings to hold themselves away from the wall. The thumb claws are used to help the bats grip the roost surface (eg. emballonurids and sometimes nycterids). (iii) *Clinging:* bats that grip the wall or ceiling with their feet and wings (thumb claws) and hold their bodies close to the rock surface. They are often found squeezed into small cracks and crevices (eg vespertilionids). These groups were further subdivided by spatial arrangement. (i) *Solitary:* individual bats roosting alone. (ii) *Spaced:* individual bats within a group but not in contact with any other bats or (iii) *Clustered:* bats hanging together close enough to touch each other and at times in such aggregations (in clinging bats) that they may be roosting several bats deep.

During the cave visits the cave floor was examined for bat skeletal remains. This provided information about cave usage as maternity sites and occupancy by other species at times other than the May to June cave visits.

The exact locations of caves visited during this study are omitted in the interests of conservation. Caves and bats are not accorded any protection under current Namibian legislation, and unfortunately, disclosure of cave sites has led to unreasonable damage. Researchers may, however, obtain precise information from the National Museum of Namibia.

Results

Roost Sites

Arnhem Cave

Arnhem cave is situated in the camelthorn savanna of Namibia (Giess 1971), which consists of open *Acacia* savanna on a sandy substrate. The mean annual rainfall in the surrounding area is 200 to 300 mm, with a rainfall variability (% of mean annual precipitation) of 30 to 40% (Van der Merwe 1983).

The cave entrance is located on top of a long hill, which is the bulge of an anticline rising from below the surrounding Kalahari sand. The cave developed within the anticline in stratified dolomitic rock of the Buschmannsklippe Formation under a cap of quartzite. This is the largest recorded cave in Namibia, with a composite length of over 4 500 m (Martini, Irish & Marais 1990). A major part of the cave consists of a series of very large collapse chambers, connected by spacious passages. The passage development shows significant altitudinal variation. Several pools are located where the cave intersects the water table, but these pools are often isolated by constrictions and do not seem to affect the cave climate. Large quantities of bat guano have been commercially extracted from the cave, particularly between 1932 and 1943.

This large and complex cave provides a broad range of microclimate conditions and was used by seven species of bats during the time of this study.

Twenty-eight torpid *Rhinolophus clivosus* were roosting free-hanging and widely spaced across the ceiling, in a cool draughty area of the cave at the end of the entrance chamber. They roosted in conditions of 23.5°C and 45% relative humidity (RH). Solitary individuals were seen scattered throughout the cave (25°C, 52%RH).

A colony of 160 *Rhinolophus darlingi* was found near the entrance chamber free-hanging from the sloping ceiling. The bats were spaced but in close proximity, within 5 cm of each other, in conditions of 24°C and 48%RH.

Four hundred and sixty *Rhinolophus denti* roosted over 500 m from the entrance above a small pool of water. The bats were free-hanging from the sloping ceiling in a cluster, with most bats in contact with several neighbours. They were roosting within 1.5 m of the water surface. Humidity at this site was very high (92%RH) with a temperature of 23°C.

Five *Hipposideros caffer* were found roosting in a small humid side passage (25°C and 79%RH) 250 m from the cave entrance. Many more were seen during the evening exodus.

Twenty *Hipposideros commersoni* roosted in a small group, free-hanging from the ceiling approximately 8 m above the floor (roost conditions were not measured). This is the most southerly record of this species. A colony of 50 *Miniopterus schreibersii* shared this site.

Miniopterus schreibersii were found in small tightly packed clusters of 3 to 80 bats clinging to the walls and ceiling. These clusters were scattered throughout the deeper sections of the cave, often associated with areas of mild temperatures (23 to 25°C) and high humidity (75 to 85%RH). All individuals examined ($n = 12$) were males.

A colony of approximately 1000 *Nycteris thebaica* was found roosting in a side passage about 10 m long and 2 m high. The bats were close to each other but not touching, they were free-hanging from the ceiling or propped against the walls. This side passage was 24.5°C and 54%RH.

Nooitgedacht Cave

This cave is surrounded by thornbush savanna (Giess 1971), comprising fairly dense stands of *Acacia* shrubs, predominantly *Acacia mellifera*, on gravel and calcrete substrates. The mean annual rainfall is 200 to 300 mm, with a variability of 50 to 60% (Van der Merwe 1983).

The cave developed in a light grey calcitic marble of the Khomas subgroup, and is the largest recorded Namibian marble cave (composite length 755 m). The cave is a typical phreatic maze, though with unexpected abrupt enlargements (Irish, Martini & Marais 1992). The bat guano from this cave has been mined commercially, and two shafts were sunk into different parts of the cave to ease extraction (Entrances 2 and 3).

A colony of 500 *Rhinolophus fumigatus* was roosting in the last chamber of the cave over 300 m from Entrance 1. They were free-hanging from the ceiling and spaced at least 15 cm apart. This area was considerably warmer and more humid than the rest of the cave with a temperature of 26.5 to 27°C and relative humidity of 55 to 70%.

A solitary *R. clivosus* was found torpid in a small avon (a conical depression in the ceiling that often traps warm air) 1 m above the floor and 115 m from Entrance 1. The microclimate was 24°C and 27%RH.

Five *R. denti* were seen flying out of a warm high side passage 30 m from Entrance 2. The microclimate 3 m below the ceiling was recorded as 26°C and 60%RH but actual roost conditions could not be measured.

Over 700 *Nycteris thebaica* shared the last chamber with *R. fumigatus*, roosting in groups of 10 to 30 in small roof avons and scattered over ceiling and walls. They were closely spaced but not touching. The bats were very alert and active. They were roosting in conditions of 26.5 to 27.5°C and 55 to 74%RH.

Several *M. schreibersii* and one *H. caffer* were caught flying in the cave but their roost sites were not found.

Mopane savanna caves

The following caves are all situated in the mopane savanna (Giess 1971). The vegetation is dominated by *Colophospermum mopane*, which forms a shrubby and fairly dense woodland. The mean annual rainfall is 300 to 400 mm, with a variability of 30 to 40% (Van der Merwe 1983).

Münsterland Cave

The cave is situated on the edge of a calcrete plateau next to the Ugab River. It is almost entirely excavated in late Tertiary alluvia, consisting of calcareous sandstone, under a cap of hardpan calcrete. Numerous collapse holes in the calcrete lead to the cave, which consists of semi-vadose passage systems leading to the Ugab ravine (Sefton, Martini & Ellis 1986).

A colony of 25 *R. fumigatus* was found in the main chamber of this cave. The bats were free-hanging from the ceiling and well spaced around the chamber. The colony had been severely reduced the previous week by boys with slingshots. Twenty-one bodies were found in this chamber but it is likely that many more died in other parts of the cave or while foraging, as we had captured several badly injured bats in a bat trap at the cave entrance. The roost conditions were 24°C and 28%RH. A further four *R. fumigatus* were found in 25°C and 59%RH

Although *N. thebaica, M.schreibersii* and *H. caffer* were captured at the cave entrance their roost sites were not found. One *M. schreibersii* carcass was found amongst the dead *R. fumigatus* in the main chamber.

Otgrot

Otgrot is a small cave developed in vertical dolomite beds of the Hüttenberg Formation (Tsumeb Subgroup). It consists of a smallish chamber in the western hand of a small doline (a large surface depression in limestone above a cave). Bat guano was extracted from this cave by local farmers for fertiliser during WW2.

Approximately 500 *R. fumigatus* were seen roosting in a high avon 20 m above the cave floor, roost microclimate could not be measured. This roost was shared by a cluster of 50 closely packed *M. inflatus* and over 200 *N. thebaica*. A secondary roost containing five *R. fumigatus* had a roost microclimate of 20°C and 86%RH. Approximately 50 *N. thebaica* were counted roosting on an old winch, 15 m from the entrance (25°C and 30%RH). These bats joined the individuals in the avon making population counts difficult.

Tsumasa

This small cave, within the fenced Halali Rest Camp area of Etosha National Park, developed in one of the several isolated dolomitic outcrops to the north of the main carbonate platform in northern Namibia (Marais & Irish in press).

This cave was only 1 m wide, 10 m deep and 4 m long and therefore provided less microclimate choice than any other cave examined during this study. It contained surprisingly large numbers of bats for such a small cave. Twenty-three *R. denti* were counted roosting amongst over 80 *H. caffer*. The bats were free-hanging from small ledges or against the walls each spaced at least 5 cm from its neighbours. Roost conditions were 28 to 28.5°C and 40%RH.

More than 150 *N. thebaica* were seen roosting at the lowest part of the cave completely covering a large area of wall space and clustering against each other. Temperature was 28.5°C and 38%RH. It was difficult to see the extent of this colony as the further reaches of the cave were inaccessible to humans. During the exodus count we counted 326 *N. thebaica*.

Ludwig

This cave has developed in the Maieberg Formation (Tsumeb Subgroup), and is situated on the side of a fairly bare dolomitic hill. Access to the cave is through a large, elongated solution cavity, from where two small tubular passages lead to a series of large passages (Martini & Marais unpublished).

A colony of 480 *R. denti* was roosting 3 to 5 m above the floor on a vertical wall over 158 m from the cave entrance. Bats were spaced 5 to 10 cm apart, they were torpid and cool to touch. Microclimate conditions were 25°C and 80%RH.

Two torpid *R. fumigatus* were found hanging separately 15 m from the cave entrance and 2 m above the floor. The bats were in deep torpor and cold to touch, they were not aroused by handling. The conditions were 25°C and 40%RH. A colony of 230 was found hanging in tight clusters amongst a group of large stalactites 145 m from the cave entrance. These bats were in torpor and cool to touch but became partially aroused by our presence. The microclimate was 25°C and 65%RH. A solitary individual was recorded free-hanging from the ceiling 94 m from the entrance. This bat was active and flew within seconds of our entering the chamber. The conditions at this site were 25°C and 82%RH.

No *H. caffer* were seen in this cave but 42 were counted during the exodus count.

A forearm of a *H. commersoni* was found amongst barn owl (*Tyto alba*) pellets 10 m from the entrance. Large numbers of *M. inflatus* skulls and skeletal material were found within the owl pellets, with every pellet examined (n = 27) containing between one and five *M. inflatus* skulls. Skull length measurements were taken of undamaged skulls to help with species identification (total length of skull; mean = 16.21, *SD* = 0.0949, range = 16.1–16.4, n = 14, confirming the identification). The large accumulation of dung and skeletal remains within the cave indicate that there are large numbers of *M. inflatus* using this cave at other times of the year.

Obab

Obab is located just outside the south eastern corner of Etosha National Park on a calcareous plain. The cave consists of a single large, banana-shaped cavity developed along the water table in the massive, sub-horizontal sheet of calcrete covering the Etosha Pan basin (Martini & Marais unpublished). The calcrete in the cave is presumably of Tertiary age, and is largely lithologically uniform.

Twelve *R. denti* were found roosting among a group of 80 *H. caffer* only 9 m from the entrance. The bats were widely spaced (at least 20 cm apart) and free-hanging from the ceiling or propped against the near vertical wall. All the bats were active and the conditions were 25.5°C and 98%RH. One *R. denti* was found roosting alone 65 m from the entrance in 27°C and 96%RH. Four *H. caffer* were found roosting solitarily within the cave in conditions of 27°C and 94% to 100% RH.

One active *R. fumigatus* was seen 107 m from the entrance in 26°C and 100%RH.

Five *N. thebaica* were found hanging from a tree root 75 m from the entrance. They were active and left the roost as the light was shone on them. The conditions were 27°C and 96%RH. The main roost site was not found. We counted 265 leaving the cave during the exodus counts.

Otavi mountainland caves

This last set of caves are all situated in an elevated carbonate platform, which mainly consists of dolomitic bedrock. This mountainous area of Namibia is also locally known as the Karstveld. The vegetation consists of dry mountain bushveld with a number of endemic tropical species. The unusually high rainfall for the area, with an annual mean of 600 to 700 mm and variability of 25 to 35% (Van der Merwe 1983) is probably due to the orogenic effect of the mountainous terrain.

Danté

This cave developed within the collapse breccia of an older sinkhole in the Abenab Subgroup. It consists of a shaft-like collapse chamber interconnected with other chambers, from which several typical phreatic passage systems extend (Irish & Marais unpublished information). The CO_2 content of the cave was previously quite high, probably because a landowner had closed the entrance with a concrete slab to prevent cattle or people from accidentally falling in. This has now been completely removed and the CO_2 levels are low.

A group of 62 *R. denti* was found torpid, free-hanging against a sloping ceiling 2.5 m above the cave floor and 55 m from the cave entrance. The roost temperature was 24°C and 96%RH. A single individual was found a further 32 m into the cave in a torpid condition in 23°C and 96%RH.

Two torpid *R. darlingi* were roosting separately (3 m apart) about 80 m from the cave entrance. Microclimate conditions at both sites were 24.5°C and 96%RH. Both bats were free-hanging from the ceiling in small passages less than 1 m in diameter.

One *R. fumigatus* was found in a torpid state free-hanging from a stalactite 67 m from the entrance in 25°C and 86%RH.

H. caffer were not found at their roost but 84 were counted during the exodus counts.

Seven *M. inflatus* were found scattered through the cave from 55 to 80 m from the entrance. All were torpid and roosting alone in conditions of 24 to 24.5°C and 90% to 93%RH.

Ghaub

This cave, which is a declared national monument, is one of the earliest caves to be investigated in Namibia. It is situated on an undulating plain in fairly thick shrub, where a small, inconspicuous doline leads to the cave. It has been suggested that the doline, which is the only access into the cave, only developed during this century (Schneiderhöhn 1920). The cave is a joint-controlled hyperphreatic maze, with a few collapse chambers. It developed at fairly regular elevation above the present water table in the Abenab Subgroup, with only a single passage leading to and intersecting the water table (Sefton *et al.* 1986).

A colony of 41 torpid *R. denti* were found 58 m from the cave entrance and 4 to 5 m above the floor. The bats were well spaced (5 to 20 cm apart) free-hanging from a steeply sloping wall in conditions of 24°C and 86%RH.

Approximately 30 *H. caffer* were found roosting from 225 to 270 m from the cave entrance at the eastern end of the cave. The bats had started exiting the cave by the time of our arrival at the roost site, so that colony size could not be determined. There is evidence (dung piles and skeletal remains) of large numbers of bats congregating at this site at other times of the year. That this site is used as a maternity site for *H. caffer* was evidenced by the numbers of juvenile skeletons found, some still attached to the dead mother. The conditions in this area were 25°C and 94%RH. *N. thebaica* also uses this roost at times as several skeletons of this species were found here. No live *N. thebaica* were seen in the cave but 56 were counted during the exodus counts.

Aigamas

Aigamas is essentially a large, fault-controlled, canyon passage in the Maieberg Formation, which reaches the surface in five places (Sefton *et al.* 1986). The passage slopes downwards to the water table. The cave pools are the only known population of an endemic catfish, *Clarias cavernicola* (Skelton 1990), which feed on bat guano.

This large cave was difficult to explore due to its vertical nature and large pools of water. Most bats were roosting in inaccessible areas of the cave ceiling up to 80 m above the floor. A large colony of 3000 *H. commersoni* were found roosting across a large area of cave wall over 100 m from the cave entrance. The bats were well spaced (at least 20 cm apart) and although quiet and inactive, were not in torpor. Two individuals, taken from the cave wall by hand while abseiling the vertical wall on which they roosted, were warm to touch and very aggressive, although they had made little

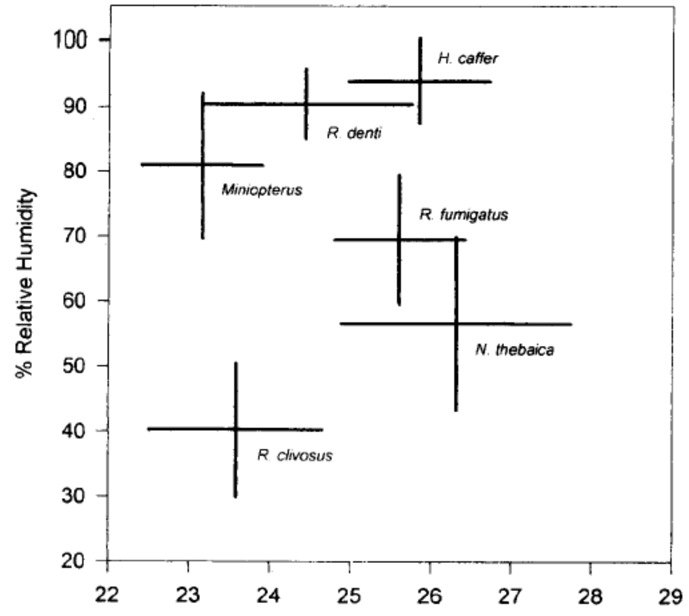

Figure 1 Mean temperature and relative humidity, with 95% confidence limits showing comparative roost microclimates of seven species of cave bats. (Data for the two species of *Miniopterus* are so similar they are combined and plotted together for clarity; *H. commersoni* and *R. darlingi* were not included owing to the low number of roost microclimates recorded.)

Table 1 Summary of roost microclimates (*S.D.* = 1 standard deviation, *C.V.* = coefficient of variation) (excluding data from Tsumasa Cave). Mean mass for each species (in grams)

Species	Variable	Mean	*S.D.*	*C.V.*	Min.	Max.	*n*	Mass
R. denti	°C	24.44	1.55	6.35	22	27	8	6.2
	% RH	90.38	6.37	7.05	79	98	8	
R. darlingi	°C	24.17	0.29	1.19	24	24.5	3	11.2
	% RH	60.67	31.01	51.11	38	96	3	
R. clivosus	°C	23.58	1.02	4.33	22	25	6	14.0
	% RH	40.17	9.75	24.26	27	52	6	
R. fumigatus	°C	25.61	1.05	4.12	24	27	9	22.4
	% RH	69.44	12.94	18.54	55	94	9	
H. caffer	°C	25.86	0.95	3.65	25	27	7	9.8
	% RH	93.86	6.89	7.34	79	100	7	
H. commersoni	°C	24	–	–	–	–	1	100.2
	% RH	44	–	–	–	–	1	
M. schreibersii	°C	23.2	0.76	3.27	22.5	24.5	5	11.1
	% RH	80.4	14.26	6.38	55	88	5	
M. inflatus	°C	23.13	1.32	5.69	22	24.5	4	12.4
	% RH	81.25	17.08	21.02	56	93	4	
N. thebaica	°C	26.32	2.12	8.07	21	28.5	11	11.5
	% RH	56.55	19.78	34.97	29	94	11	

effort to avoid capture. During three nights of exodus counts at this cave only one *H. commersoni* was seen leaving the cave. During a 3-h watch spent sitting quietly at the entrance to the roost chamber after sunset, the bats made no noise, no attempt to fly or any of the usual restless behaviour seen in bats preparing to leave the cave. They behaved as if torpid but were clearly awake and alert. Roost conditions were 24°C and 44%RH.

Two active *R. denti* were found roosting 2 m above the water surface and 60 m from the cave entrance on a vertical cave wall. Roost conditions were 23°C and 50%RH, water temperature was 26°C. One torpid *M. inflatus* was roosting 5 m above the water surface in the same area. Roost conditions were 22°C and 56%RH.

Roost microclimate

Figure 1 shows that each of the seven species of cave bat (*M. inflatus* and *M. schreibersii* are combined) has a characteristic combination of temperature and relative humidity at its roost. Stepwise discriminate function analysis (SAS Institute Inc. 1985) showed significant differences in species selection of roost microclimate according to relative humidity (partial $r^2 = 0.66$; order of entry = 1; Wilk's $\lambda = 0.34$; $p = 0.0001$; *d.f.* 5, 44) and temperature (partial $r^2 = 0.36$; order of entry = 2; Wilk's $\lambda = 0.22$; $p = 0.0012$, *d.f.* 5, 44).

Table 1 gives a summary of roost microclimates selected by each species as well as mean body mass.

Discussion

The caves selected for this study are extensive, complex and provide a broad range of temperature and humidity. Given a wide choice of available roost conditions, it is likely that bats select roost microclimates most suited to their thermoregulatory and water balance needs. The conditions preferred by each species can therefore be determined by an examination of their roosts. During this study we measured conditions ranging from 19°C and 22%RH to 28°C and 100%RH.

The thermoregulatory needs of bats vary with time of year, age, sex and reproductive condition and many species will change roosts or select different caves to suit these changing needs. This study was conducted during the early winter (May to June), when reproductive demands are minimal but insect food resources are limited. The bats' primary aim is to minimise energy expenditure. They do this by selecting suitable cave microclimates. The most important criteria for roost microclimate selection appear to be temperature and humidity (McNab 1982; Baudinette *et al.*, in press) for both temperate (Twente 1955; Davis 1970) and tropical species (Churchill 1991; Rodriguez-Duran 1995).

Hipposideros caffer selected the most humid and warm conditions available within the caves. Bats of the family Hipposideridae are primarily restricted to the tropics and most species are incapable of entering torpor. These roost microclimates provide the bats with conditions that approximate their thermoneutral zone, allowing them economically to maintain their body temperature. This species succumbed rapidly to hypothermia when inactive and outside the cave environment resulting in death within hours of capture in bat traps.

Rhinolophus denti also showed a strong preference for humid roosts. Although only half the weight of *H. caffer*, they were not as sensitive to bat trap death as they were capable of entering torpor. Their use of torpor meant that *R. denti* often selected cooler roosts than *H. caffer* to enable them to reduce their body temperature, thereby reducing metabolic rate and energy expenditure. The high humidity allows them to maintain water balance.

An exception to these trends was found in Tsumasa Cave where both *H. caffer* and *R. denti* roosted in unusual conditions of low relative humidity (40%RH) and high temperature (28.5°C, 1.5°C higher than at any other roost). This cave was small and very isolated and unlike the other caves examined, offered little choice of alternative roost microclimate. This site must have been energetically very expensive to these bats but perhaps the cost may have been offset by the presence of a large, permanent waterhole only 200 m away.

Rhinolophus clivosus was always found in the cool, less humid areas of the cave in 22 to 25°C. All bats were in torpor and roosting alone or very widely spaced. These temperatures are warmer than those recorded in South Africa by McDonald, Rautenbach & Nel (1990).

Rhinolophus darlingi was found in only three roosts, two solitary individuals and one clustered group. Their choice of roosts showed a broad tolerance of humidity (38 to 96%RH) but a narrow range of temperature (24 to 24.5°C).

Rhinolophus fumigatus was found to roost in areas of moderate temperature and humidity. The bats were generally torpid at these roosts. It is interesting that at Ludwig's Cave *R. fumigatus* was found at three roosts. These roosts were all 25°C but differed markedly in their relative humidity. Near the entrance the heavily torpid bats roosted in 40%RH; towards the end of the cave a large group were in a mild torpor and were partially aroused by our presence while roosting in 65%RH; and one alert and active individual was roosting in the most humid part of the cave in 82%RH. On the basis of these very limited observations it seems possible that levels of relative humidity may be important for determining the depth of torpor in this species.

Rhinolophus species were found to enter hibernation only in temperatures of less than 11°C in a review by Webb, Speakman & Racey (1996) of observed conditions in temperate hibernacula.

Temperatures in Namibian caves averaged 24.9°C (*SD* = 1.78; *n* = 52; range 21–28.5), too high to enable bats to reduce body temperatures to hibernation levels. However, reduction in temperature by even a few degrees provides significant savings in energy expenditure (Webb, Speakman & Racey 1993), and we obtained many records of daily torpor in Namibian cave bats.

This energy saving by daily torpor is considerably less than that of hibernation, and these bats must leave the cave most nights to forage, as they were observed to do during this study (with the exception of *H. commersoni*). The time spent away from the cave is metabolically expensive and must be justified by sufficient food intake. Cold winter nights cost energy and inhibit insect movement. Most bats spent as short a time as possible foraging and restricted this to the hours immediately after sunset (Churchill & Draper, in press) when the ambient temperature was still warm and flying insects most abundant.

Hipposideros commersoni was observed to remain quietly at its roost for days at a time without leaving the cave or entering torpor. This roosting behaviour is unusual and has not been reported elsewhere for this species. The two individuals examined during this study had large fat deposits around the pelvis, lower back, upper legs and tail. McNab (1969) reports a situation in Brosset (1962a,b) where species of *Hipposideros* in northern India store large amounts of fat during the autumn and use them during the winter. These bats are never found in deep torpor, but have '...cycles of extended rest during which they live on their biological reserves and do not hunt' Brosset (1962a). This same species in southern India does not store fat and McNab (1969) suggested that these differences may be expected so close to the boundary between tropical and temperate climates. The colonies of *H. commersoni* encountered during this study in Namibia are at the southern limit of distribution for this widespread tropical species. They appear to be using a similar stratagem to the Indian bats.

Miniopterus schreibersii and *M. inflatus* in Namibia, selected similar roost microclimates. Their preferred conditions were cooler than those selected by other species, 22.5 to 24.5°C, with high humidity, 55 to 85%RH. Most individuals were roosting in small clusters of 3–40 bats or solitarily through the cave.

Baudinette, *et al.* (in press) examined the influence of humidity on microclimate selection in *M. schreibersii* in northern Australia (latitude 13°S). The laboratory microclimate at which the ratio of metabolic water production to evaporative water loss (MWP/EWL) was balanced was the same as the microclimate selected by this species in the field. Of nine northern Australian species studied during May and June, *M.schreibersii* selected the coolest cave roosts, conditions were 25.4 to 27.5°C with 63 to 78%RH (Churchill 1991).

In South Africa (latitude 34°S) roost conditions in the field during May and June ranged from 9.9 to 19.3°C with 23 to 79%RH (Brown & Bernard 1994). However, in the laboratory, they found that euthermic *M. schreibersii* selected roost temperatures of between 23°C and 28°C in winter, whereas torpid bats preferred temperatures of 16 to 18°C in winter and 20 to 23°C in summer. Our Namibian findings (latitude 20°S, this study) are similar to Brown & Bernard's (1994) laboratory measurements for euthermic winter bats and for torpid summer bats.

It would appear that euthermic *M. schreibersii* selects similar roost microclimates throughout its broad distribution, with a temperature range of 22 to 28°C and humidity of 55 to 85%.

Nycteris thebaica in Namibia roosted in warm areas of the cave but exhibited a broader range of microclimate selection than any other cave bat. This is to be expected from a species that uses a wide variety of roost sites. They have been found roosting in tree hollows, road culverts, houses, rock fissures, and aardvark (*Orycteropus afer*) burrows (Skinner & Smithers 1990). The Nycteridae are primarily a tropical family and are not known to enter torpor.

Nine species of bats were identified as inhabiting the caves of northern central Namibia. *M. inflatus* is recorded from this locality for the first time. Colony size estimates at each cave were recorded. They showed characteristic roost behaviour in terms of defined criteria of posture and spatial separation. This study has demonstrated distinct differences in the selection of roost microclimate by these Namibian cave bats.

These differences reflect the different energy conservation requirements of these bats.

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