Metabolism and thermoregulation of individual and clustered long-fingered bats, *Miniopterus schreibersii*, and the implications for roosting

C.R. Brown

Department of Zoology and Entomology, Rhodes University, P.O. Box 94, Grahamstown, 6140 South Africa
C.Brown@ru.ac.za.

Oxygen consumption of individual long-fingered bats, *Miniopterus schreibersii*, was measured at air temperatures (T_a) between 2 and 42°C and that of clusters of four and six bats between 5 and 30°C. BMR of individuals was estimated to be 2.29 ml O_2 g^{-1} h^{-1} between 34 and about 38°C. *M. schreibersii* showed two different responses to T_a, either maintaining body temperature (T_b) by increasing metabolic rate, or allowing T_b to fall close to ambient temperature and conserving energy (torpor). Euthermic clusters of four and six bats had lower rates of mass-specific oxygen consumption and lower thermal conductances than individuals at equivalent temperatures and torpid clusters maintained a greater temperature differential between T_b and T_a. Lowest rates of metabolism were measured for euthermic bats at air temperatures higher than those available to them in their natural roost in summer, so typical roost temperatures result in metabolic rates that are about 2.4–3.1 times estimated BMR. Roost temperatures of *M. schreibersii* in South Africa are substantially higher in winter than are generally accepted as being suitable for hibernation but these do not substantially affect torpid metabolic rates, which are low and independent of ambient temperature below 22°C. Clearly at least some species of insectivorous bats are capable of hibernating at temperatures generally considered to be too warm for this activity.

The small size and highly vascularized wings of microchiropteran bats result in potentially high rates of heat loss. Furthermore, insectivorous species may also experience periods of food shortage in winter when thermoregulatory demands are elevated by low ambient temperatures (T_a). Although roosting in caves and other sites offering buffered microclimates may alleviate some thermal stress, high mass-specific metabolic rates, limited capacity for fat storage, and high cost of thermoregulation compel most species of bats either to migrate or to temporarily abandon homeothermy. Many microchiropteran bats consequently use either daily torpor and/or hibernate during periods of low T_a and food shortage (McNab 1969, 1982).

Although insectivorous bats are generally heterothermic, the precision with which they regulate body temperature (T_b) and the amount by which they allow T_b to fall is species specific (Lyman 1970). Many tropical species show only moderate hypothermia when exposed to low temperatures (Kulzer 1965; McNab 1969, 1989; Genoud, Bonaccorso & Arends 1990; Audet & Thomas 1997) whereas temperate species, especially of the families Vespertilionidae and Rhinolophidae, are deep hibernators and will often allow T_b to fall close to freezing (Kulzer 1965; Herreid & Schmidt-Nielsen 1966; Davis & Reite 1967; Lyman 1970). In general, lower T_as are associated with a lower T_b and lower rates of metabolism, and a longer time that the bat can survive on its fat stores during torpor or hibernation.

Temperatures in caves and other bat roosts in much of North America and Europe are generally cool (< 10°C) and provide suitable microclimates for hibernating bats. In southern Africa, however, roost temperatures are generally much warmer than in Europe, especially during winter (Brown & Bernard 1994; Churchill, Draper & Marais 1997), and may be substantially warmer than is regarded as suitable for hibernation by all but the smallest, solitary bats (Twente 1960; McNab 1974). Nevertheless, numerous species of bats are

found in southern Africa and many of these bats use torpor on a daily basis and hibernate during winter. One of these, Schreiber's long-fingered bat, *Miniopterus schreibersii*, is a small (9–13 g) cave-dwelling, insectivorous bat. It has a wide distribution, extending through much of Europe, eastwards through parts of the Middle East, southern India, Far East and Australia and is also widespread through Africa (Smithers 1983). In South Africa. *M. schreibersii* commonly roosts in clusters in caves and mine adits, sometimes forming colonies numbering in the thousands or tens of thousands (Van der Merwe 1975). The species usually migrates from summer roosts to hibernating roosts in winter (Van der Merwe 1975; Norton & Van der Merwe 1978; Sera-Cobo, Sanz-Trullén & Martinez-Rica 1998), although some colonies can be found in the same roosts in summer and winter (pers. obs.). I investigated the metabolic rates of individuals and clusters of *M. schreibersii* to assess their thermoregulatory capabilities, the effect of clustering on their thermoregulation, and the implications of roost microclimate for metabolism and hibernation in the species.

Materials and methods

Study animals

Bats were collected throughout the year from storm-water drains in Grahamstown, South Africa (33°38'S, 26°31'E), from a 3 m diameter stream tunnel under a freeway about 10 km outside the city, or from a narrow (1.0 × 1.5 m) water-pipe tunnel through a hill on a farm about 12 km outside the city. Bats were collected early in the morning and were transported to the laboratory in a cloth bag. In the laboratory bats were kept in holding boxes (30 × 12 × 12 cm) lined with plastic mesh from which they could hang. Bats were not fed during captivity and measurements were made on the day of capture or the following day, after which the bats were released.

Because numbers of bats at the roosts varied from hundreds to thousands, the chance of recapturing the same individuals were very low. Consequently, it is unlikely that any bat was used more than once in the course of the study and each datum thus represents a single measurement on an individual or cluster at a single T_a.

Experimental protocol

Oxygen consumption was measured between about 2 and 42°C using an open flow-through system. Bats were weighed to 0.01 g using an electronic balance and placed individually or in groups of four or six bats into a 0.9 l or 1.7 l mesh-lined perspex metabolic chamber in a darkened constant temperature cabinet. Dry, CO_2-free air was drawn through the chamber by a pump placed downstream. Air exiting the chamber was passed through a Carbosorb/silica gel tube to absorb carbon dioxide and water before entering an Applied Electrochemistry S-3A/1 oxygen analyser. The O_2 analyser was calibrated with dry, CO_2-free room air to 20.95% before and after each experimental run. Flow rate was measured immediately upstream of the chamber using a rotameter type flowmeter calibrated against a bubble flow meter and corrected to STPD (Levy 1964). Flow rates ranged from 125–200 ml min⁻¹ for individuals and up to 800 ml min⁻¹ for clusters, which ensured that oxygen concentration in the excurrent air remained above 20%.

After being placed in the chamber, bats were left for at least 15–30 min to settle and for the chamber air to equilibrate. Washout time for equilibration depended on the flow rate but at the lowest flow rate in the smaller chamber averaged 25.5 min to 95% of baseline, as determined from the washout time of an injected nitrogen bolus. It was assumed that conditions after this period were steady (for example that oxygen consumption was constant) and that T_b measured at the end of each experimental run consequently represented the T_b during the run (compare Hosken 1997; Hosken & Withers 1997, 1999). Readings of chamber temperature and $\%O_2$ in the expired air were subsequently recorded at 5 min intervals for 2–4 h. Body temperature (T_b) of the bats was measured immediately after each run (within 30–45 s) on a Sensortek model BAT-12 thermometer by inserting a 29 gauge needle thermocouple under the skin of the back just posterior to the scapulae. This has been shown to provide a good measure of deep body temperature (Brown & Bernard 1991).

Oxygen consumption (VO_2) was calculated from equation 4a of Withers (1977). For euthermic individual bats and clusters this was based on the lowest stable period of metabolism of at least 20 min during each experimental run. If bats entered torpor after being placed in the chamber it took an additional 70–120 min before stable conditions were reached and measurements began only after this with the VO_2 of torpid bats being taken from the last 20–30 min of measurements. For some of the later runs, DATACAN data acquisition and analysis software (Sable Systems Inc., Las Vegas) was used to record data directly onto a microcomputer. During data capture, the computer was programmed to record parameters every 20 sec for 2–4 h.

Statistical analysis

Mean values (± 1 SD) were compared using Student's t-tests,

Analysis of Variance (ANOVA) or, where assumptions of normal distribution and equal variance were not met, their non-parametric equivalents. Where differences between more than two groups were significant, multiple range tests (Newman-Keul's for parametric tests or Dunn's test for non-parametric tests) were used to determine between which groups the differences occurred. Regressions were compared using analysis of covariance (Zar 1974).

Results

M. schreibersii responded well to the experimental situation and when placed in the metabolic chamber quickly adopted a resting position hanging from the mesh sides or top of the chamber.

Body temperature

Individual bats

The highest T_bs of euthermic *M. schreibersii* were measured above 35°C and averaged 39.8 ± 1.24°C. Below 35°C. although the T_bs were very labile, there was no significant relationship between T_b and T_a ($r^2 = 0.006$, $P = 0.50$, $n - 74$), and body temperature averaged 36.6 ± 1.8°C (range = 31.1 – 39.4°C, Figure 1A). This was significantly lower than T_bs of bats above 35°C ($t = 5.22$, $P < 0.001$, $df = 81$). The T_b of torpid bats paralled T_a (Figure 1A), the relationship between T_b and T_a being described by the equation

$$T_b = 2.64 (\pm 0.30) + 0.962 (\pm 0.01)T_a \quad (r^2 = 0.98, n = 101, P < 0.001)$$

Clusters

T_bs of euthermic bats in clusters of four (35.3 ± 3.0°C, $n - 22$, Figure 1B) and clusters of six (36.2 ± 2.3°C, $n = 17$, Figure 1C) were not significantly different from each other or from that of individuals below 35°C ($H - 5.69$, $P > 0.50$) Overall mean body temperature of euthermic bats, whether measured as individuals or in clusters, was thus 36.3 ± 2.2°C.

As with individual bats, mean T_b of torpid bats in clusters was significantly correlated with T_a, the relationship being described by

$$T_b = 1.26 (\pm 1.03) + 1.06 (\pm 0.07)T_a \quad (r^2 = 0.96, n = 13, P < 0.001)$$

for clusters of four bats and

$$T_b = 4.11 (\pm 0.77) + 0.970 (\pm 0.04)T_a \quad (r^2 = 0.98, n = 15, P < 0.001)$$

for clusters of six bats (Figures 1B and 1C). The slopes of these relationships are not significantly different from each other or from that of individual bats ($F = 1.18$, $P > 0.25$), but their elevations are ($F = 9.13$, $P < 0.005$) with bats in clusters of six bats maintaining a greater differential between T_b and T_a than individuals and clusters of four bats.

Oxygen consumption

Individual bats

As ambient temperature decreased, *M. schreibersii* either remained euthermic by increasing heat production, or entered torpor and allowed body temperature and metabolism to decrease. Their response to temperature depended on season and whether they were fasted or not. In winter (May to August), when *M. schreibersii* normally hibernates, most bats
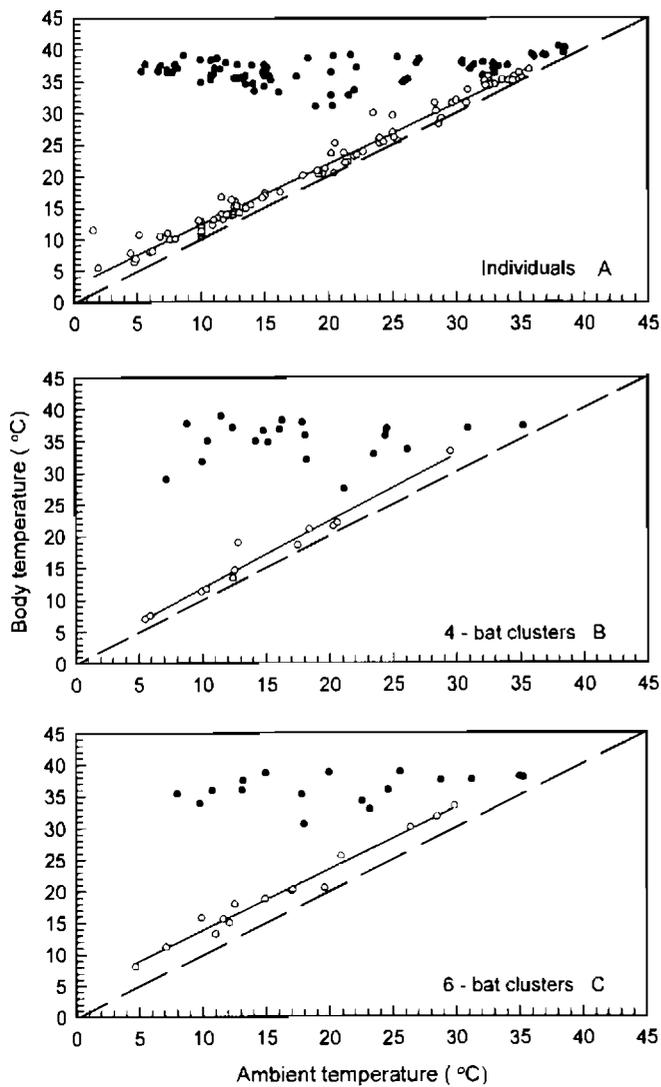
Figure 1 Body temperatures of euthermic (closed circles) and torpid (open circles) individuals (A) and clusters of four (B) and six (C) long-fingered bats (*Miniopterus schreibersii*) in relation to ambient temperature. Each point represents the mean temperature for the cluster. The dashed line represents equality between T_b and T_a

entered torpor on the day of capture and remained torpid unless disturbed. In summer (September to April), most individuals remained euthermic on the day of capture, even when exposed to low temperatures. After a night of fasting in the laboratory, however, bats frequently entered torpor. This is similar to the behaviour of brown long-eared bats (*Plecotus auritus*) in the laboratory (Speakman 1988). *M. schreibersii* that entered torpor had significantly lower body mass (10.23 ± 1.03 g, range 7.08–12.59 g, n = 86) than bats that remained euthermic (11.79 ± 1.20g, range 9.41–14.24g, n = 63; t = 8.51, P < 0.001, df = 147).

Visibly pregnant females did not differ in their metabolic responses to T_a compared to males and non-pregnant females. The regression relating VO_2 to T_a for pregnant females of mean mass 13.76 ± 1.42 g (n = 21) that remained euthermic was statistically indistinguishable from that of males and non-pregnant females in both slope (t = 1.106, P > 0.20, df = 81) and intercept (t = 0.960, P > 0.20). Similarly, pregnant

females readily entered torpor and their VO_2 was not significantly different from that of males and non-pregnant females (t = 1.796, P > 0.05, df = 64). Data from pregnant females were consequently pooled with those from other individual bats.

Although a lower critical temperature and thermal neutral zone could not clearly be distinguished, the lowest rates of oxygen consumption were measured between about 34 and 39°C and averaged 2.29 ± 0.38 ml O_2 g^{-1} h^{-1} for eight individuals of mean mass 11.10 ± 1.17 g. This is assumed to be the BMR for *M. schreibersii*. The VO_2 of euthermic bats increased approximately three-fold between T_as of 34–5°C (Figure 2A), the relationship between VO_2 (ml g^{-1} h^{-1}) and T_a (°C) within this temperature range being given by the expression

$$VO_2 = 10.55 (± 0.26) - 0.226 (± 0.01)T_a \quad (r^2 - 0.79, n - 77, P < 0.001)$$

A single individual measured at 42°C showed signs of heat stress, an elevated T_b of 42.7°C and an elevated VO_2 of 3.70 ml g^{-1} h^{-1}.

Below 24°C, the VO_2 of torpid bats was lowest and independent of T_a ($r^2 - 0.04$, P > 0.05, n = 76), averaging 0.31 ± 0.16 ml g^{-1} h^{-1}. Above 24°C, the VO_2 of torpid bats increased and approached that of euthermic individuals above about 34°C. Speakman (1988) considered little brown bats with T_bs <28°C to be torpid but individual *M. schreibersii* with T_bs above this clearly had VO_2s well below that of euthermic individuals (Figure 2A). Even at T_as above 34°C, two groups were distinguishable. Of 14 individuals measured between 34 and 39°C, six had relatively low VO_2s (1.61 ± 0.13 ml g^{-1} h^{-1}), low T_bs (35.8 ± 0.7°C) and, consequently, a smaller differential between T_b and T_a (1.0 ± 0.4°C) whereas eight had significantly higher VO_2s averaging 2.29 ml g^{-1} h^{-1} (BMR) (t = 4.13, P < 0.002), higher T_bs (39.2 ± 0.9, t - 7.83, P < 0.001) and larger temperature differentials (2.2 ± 0.7°C, t = 4.11, P < 0.002). Although they were probably capable of flight (Herreid 1963; Roverud & Chappell 1991), the former group were considered to be hypothermic and were, for convenience, included with the torpid bats and were excluded from calculation of BMR.

Clusters

The relationship between T_a and VO_2 of euthermic clusters of four bats is described by the equation

$$VO_2 - 8.57 (± 0.77) - 0.215 (± 0.04)T_a \quad (r^2 - 0.63, n - 21, P - 0.001, \text{Figure 2B})$$

and that of clusters of six bats by

$$VO_2 - 6.65 (± 0.50) - 0.144 (± 0.02)T_a \quad (r^2 = 0.86, n = 16, P < 0.001; \text{Figure 2C})$$

The slopes of these relationships and that for individuals are not significantly different (P - 0.50), but the intercepts are (F = 50.58, P < 0.001). Overall, the VO_2 at any particular T_a decreased with an increase in cluster size.

The VO_2 of torpid bats below 24°C was independent of T_a (four bats r^2 = 0.10, P > 0.10, n = 18; six bats r^2 = 0.13, P > 0.25, n = 10) and averaged 0.24 ± 0.12 and 0.35 ± 0.14 ml g^{-1} h^{-1} for clusters of fours and six bats, respectively. These were
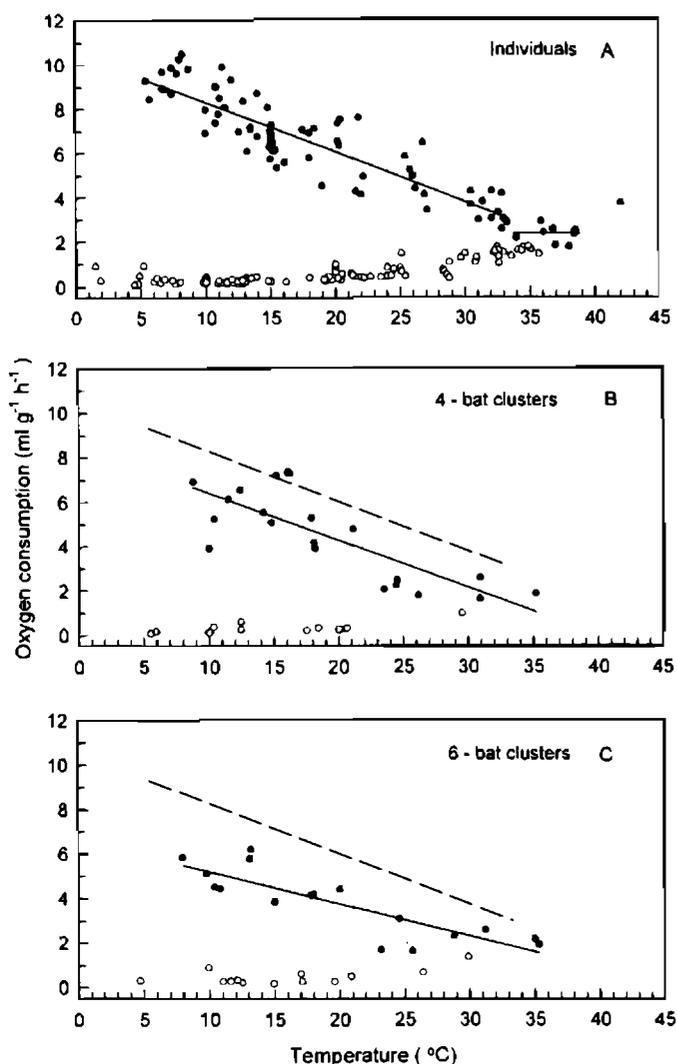
Figure 2 Relationship between FO_2 and temperature in euthermic (closed circles) and torpid (open circles) individuals (A) and clusters of four (B) and six (C) long-fingered bats (*Miniopterus schreibersii*). Each point represents a different individual or cluster. The dashed line in B and C is the regression for individuals for comparison. Equations for regression lines are given in the text.
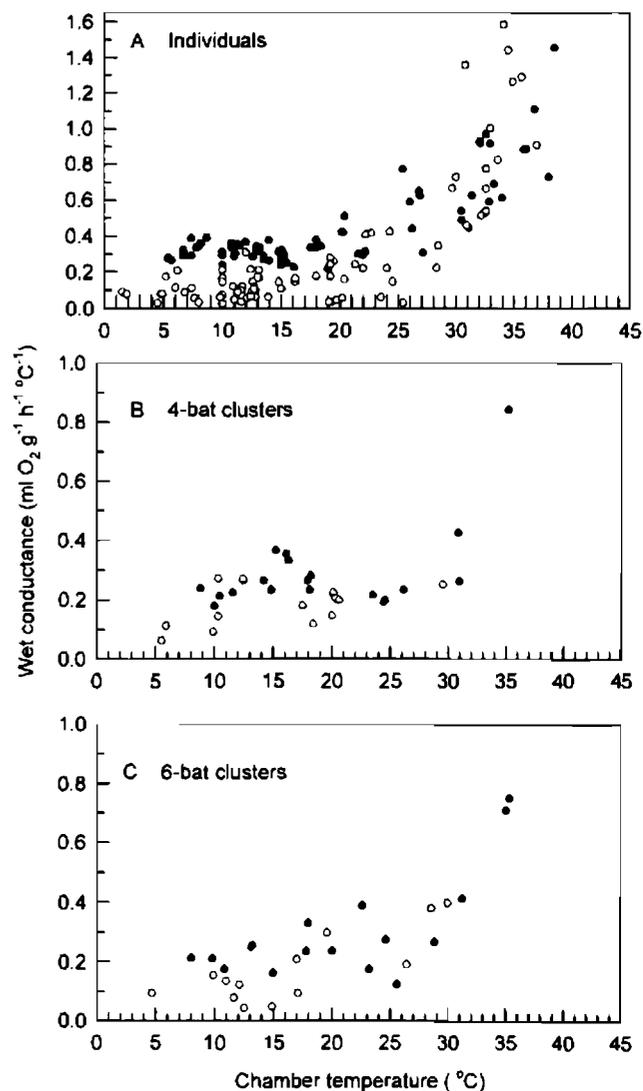

Figure 3 Relationship between wet thermal conductance and temperature in euthermic (closed circles) and torpid (open circles) individuals (A) and clusters of four (B) and six (C) long-fingered bats (*Miniopterus schreibersii*). Each point represents a different individual or cluster

not significantly different from each other or from that of individuals ($F = 1.95$, $P > 0.10$, $df = 103$).

Thermal conductance

Individual bats

Wet thermal conductance (C_{wet}) was calculated for each individual and each cluster as $C_{wet} = VO_2/T_b-T_a$ (McNab 1980). C_{wet} of euthermic individuals was relatively constant and independent of T_a below $22^{\circ}C$ ($r^2 = 0.019$, $P > 0.25$, $n = 55$ Figure 3A) and averaged 0.32 ± 0.05 ml O_2 g^{-1}h^{-1} $^{\circ}C^{-1}$. Above $22^{\circ}C$, C_{wet} increased to a maximum of 1.45 ml O_2 g^{-1}h^{-1} $^{\circ}C^{-1}$ at a T_a of $38.5^{\circ}C$. Mean C_{wet} of torpid individuals was very variable and often difficult to calculate because of the very small differences in T_b-T_a. Nevertheless, C_{wet} of torpid bats below $22^{\circ}C$ was lower than that of euthermic individuals, averaging 0.133 ± 0.10 ml O_2 g^{-1}h^{-1} $^{\circ}C^{-1}$ (U = 4628, P < 0.001, $df = 113$).

Clusters

Below $22^{\circ}C$, C_{wet} of euthermic clusters was reduced in comparison to individuals, averaging 0.27 ± 0.06 (n = 13 clusters) and 0.23 ± 0.05 (n = 9 clusters) ml O_2 g^{-1}h^{-1} $^{\circ}C^{-1}$ for clusters of four and six bats respectively (Figures 3B & 3C). The difference between individuals and clusters was significant (F = 13.2, P < 0.001), but the difference between clusters of four and six was not (P > 0.05). C_{wet} of torpid bats in clusters of four and six bats averaged 0.17 ± 0.07 (n = 12) and 0.13 ± 0.08 (n = 10) ml O_2 g^{-1}h^{-1} $^{\circ}C^{-1}$, respectively and were similar to that of torpid individuals (H = 3.12, P > 0.20).

Discussion

The estimated thermal neutral zone of *M. schreibersii* was similar to that of several other species of temperate insectivorous bats, which also have thermal neutral zones in the 30–

40°C range (McNab 1969; Hosken 1997; Hosken & Withers 1999). Lowest metabolic rate of *M. schreibersii* recorded within this range was 2.29 ml g⁻¹ h⁻¹ and is thus probably indicative of their BMR which is slightly greater (110%) than expected from Kleiber's (1961) equation relating BMR to body weight. In contrast, McNab (1969, 1982) found that insectivorous bats generally have BMRs between 53 and 93% of predicted, a characteristic he suggested to have evolved in response to an unpredictable food supply.

The heterothermic response of *M. schreibersii* to temperature is typical of many temperate microchiropterans (McNab 1969; Lyman 1970; Genoud, Bonaccorso & Arends 1990; Hosken 1997; Hosken & Withers 1997, 1999). Their response to temperature depended on both season and nutritional state (that is whether fasted), both factors previously reported to influence thermoregulation in microchiropterans (Stones & Weibers 1966; McNab 1982; Speakman 1988; Audet & Thomas 1997). The behaviour of *M. schreibersii* in the laboratory was typical of that observed at their roost sites. In summer they are normally euthermic and capable of immediate flight even on relatively cool days, suggesting a T_b above 30–35°C (Herreid 1963; Roverud & Chappell 1991), but they may use daily torpor during periods of inclement weather when, presumably, they are unable to feed (pers. obs.). The maintenance of a high T_b in summer has also been reported for other microchiropterans such as *Tadarida mexicanus* (Herreid 1963) and *Myotis lucifugus* (Kurta & Kunz 1988). In contrast, in winter *M. schreibersii* hibernate (Van der Merwe 1973; Hall 1982; Bernard & Bester 1988; pers. obs.) and even after being aroused by capture tended to enter torpor immediately in the laboratory, even at moderate to high temperatures.

In general, *M. schreibersii* is able to thermoregulate over a wide range of temperatures between about 5°C (the lowest measured for euthermic bats in the present study) and about 40°C. *M. schreibersii* readily enters torpor and can withstand T_bs of at least as low as 5.5°C and arouse spontaneously. Two out of six bats measured below 6°C, however, had slightly elevated T_bs and VO_2, suggesting that at least some individuals may regulate T_b when T_a decreases below this level. A similar pattern of some individuals maintaining slightly higher T_b at low T_a and others not has also been observed in other species (Hosken 1997; Hosken & Withers 1997, 1999). The mean torpid VO_2, calculated between approximately 5 and 15°C for comparison with other studies, averaged 0.24 ± 0.09 ml g⁻¹ h⁻¹, within the range of 0.15 and 0.30 ml g⁻¹ h⁻¹ reported for *Nyctophilus major* and *Chalinolobus gouldii* from Australia (Hosken 1997; Hosken & Withers 1997) and slightly higher than most measurements for northern hemisphere vespertillionids (e.g. Hock 1951; Thomas, Cloutier & Gagné 1990; Genoud 1993 cited in Hosken 1997).

Clustering behaviour

Clustering or huddling behaviour is known to reduce individual metabolism in many small mammals and birds (see, for example, Withers & Jarvis 1980; Chaplin 1982; Vogt & Lynch 1982; Brown & Foster 1992). In bats, clustering can affect thermoregulation in three ways; (1) it can increase T_a in the immediate vicinity of the cluster through collective heat production (e.g. Dwyer & Harris, 1964); (2) it reduces the cost of individual thermoregulation by collectively reducing

the ratio of surface area to volume; and (3) it can moderate the effects of variations in the external environment on individuals in the cluster.

Reductions in metabolism for clustered bats have been shown for several species (Herreid 1967; McNab 1969; Kurta & Kunz 1988; Roverud & Chappell 1991). Reductions are typically 20–40%, depending on T_a and the size of the cluster. In the present study, clusters of four and six *M. schreibersii* showed a 22% and 36% reduction in VO_2, respectively, compared to individuals at 10°C, approximately the lowest temperature recorded in their roost (Brown & Bernard 1994), and a 30% and 37% reduction, respectively, at average summer roost temperatures of 19.5°C. The extent to which larger cluster sizes are effective at reducing individual VO_2 is uncertain, but Herreid (1967) suggests that for *T. brasiliensis* the upper limit is about 16 bats and that a further reduction in individual metabolism does not occur in larger clusters. For cluster sizes up to 16 bats, Roverud & Chappell (1991), however, noted significant reductions in metabolism at 10 and 20°C only with cluster sizes of up to four bats and that increases in cluster size above four had little additional influence on the VO_2. Both Herreid (1967) and Roverud & Chappell (1991) also showed that, although reduction in metabolism of clusters was substantial at lower temperatures, there was little difference at moderate to high temperatures, suggesting that clustering might not be advantageous at higher temperatures. This probably accounts for the preference of *M. schreibersii* for looser clusters or individual roosting in summer when roost temperatures are warmer or even in winter in roosts where temperatures are warm, as has been observed for several species of bats, including *M. schreibersii*, in warm caves in Namibia (Churchill *et al.* 1997).

Although reducing metabolic costs of euthermy in *M. schreibersii*, clustering had no marked effect on metabolism of torpid bats. Clustering did, however, result in significant reductions in the thermal conductances when compared to individuals and allowed the maintenance of a greater temperature differential between T_b and T_a.

Metabolism and roost site selection

The choice of roost sites, especially those providing T_as suitable for winter hibernation, is limited by what is available in the environment and may not necessarily be optimum for this activity. Many bats change roost sites seasonally, occupying warmer caves (or regions of caves) compatible with euthermy in summer and cooler caves compatible with hibernation in winter (Lyman 1970). *M. schreibersii* shows seasonal movements that may be local or may involve relatively long migrations (Van der Merwe 1975; Bernard & Bester 1988; Sera-Cobo, Sanz-Trullén & Martínez-Rica 1998.). In South Africa, Bernard & Bester (1988) describe seasonal inter-cave movements of *M. schreibersii* between three mine adits less than one kilometre apart but which nevertheless have slightly different microclimates. Van der Merwe (1975) reports much farther movements of *M. schreibersii* over about 150 km between caves in the Transvaal bushveld and the highveld, and also between caves in the highveld about 60 km apart.

Given a choice of temperatures in a gradient, individual *M. schreibersii* in summer most frequently selected temperatures between 28 and 32°C and few (<8%) individuals selected

temperatures within their estimated thermal neutral zone (Brown & Bernard 1994). Even these selected temperatures are higher than those generally available in their natural roosts in South Africa. T_as in roost sites of *M. schreibersii* in summer are typically between 15 and 18°C (Van der Merwe 1973; Bernard & Bester 1988). Mean temperatures in the tunnel roost from which bats for the present study were usually obtained average 19.5°C in summer, although temperatures as high as 22°C may occasionally be encountered (Brown & Bernard 1994). The VO_2 of euthermic bats at typical roost temperatures (calculated from the regression of VO_2 on T_a) are thus between 6.2 and 7.2 ml g^{-1} h^{-1} or about 2.7–3.1 times estimated BMR in individuals. The VO_2 of euthermic clusters of four bats at typical roost temperatures are between 5.3 and 4.4 ml g^{-1} h^{-1} and for clusters of six bats are between 5.6 and 3.9 ml g^{-1} h^{-1}. These are between 2.4 and 3.1 times the lowest metabolic rate measured for clusters.

M. schreibersii in natural roosts in South Africa are occasionally found torpid during summer and more frequently in autumn (pers. obs.). In the laboratory a number of individuals were torpid with low levels of VO_2 and T_bs close to T_a at temperatures exceeding 30°C (see Figure 2A). These temperatures are substantially higher than those encountered in natural roosts in South Africa. At typical South African summer roost temperatures of 15–18°C torpid *Miniopterus* had rates of oxygen consumption of about 0.31 ml g^{-1} h^{-1} whereas that of euthermic individuals averaged about 6.9 ml g^{-1} h^{-1}. Daily torpor in summer consequently represents an energy saving of about 95% over remaining euthermic but is presumably only necessary when inclement weather prevents nightly foraging.

In winter, most temperate, insectivorous bats hibernate and allow their T_bs to drop close to T_a (provided it is above freezing) or regulate T_b at a substantially lower than normal temperature. Cooler temperatures are accepted as being better for hibernation because the lower the T_a selected the lower the T_b and metabolic rate and the greater the energy saving (see for example Davis 1970; McNab 1982; Nagel & Nagel 1991). The selection of suitable winter roosts may consequently have a significant effect on survival (Speakman & Racey 1989). Twente (1960) suggested that some species of bats cannot survive winter if roost temperatures exceed 12°C because energy reserves are exhausted before the end of winter. Similarly, McNab (1974) suggested that roost temperatures in Florida, North America, in winter (12–15°C) are too warm for all but the smallest, solitary bats to hibernate and that all but three of the 17 species of North American insectivorous bats overwinter farther north where temperatures are cooler. Winter temperatures of roosts in North America and Europe are generally <10°C (Twente 1955; Gaisler 1970; Harmata 1973). Although Webb, Speakman & Racey (1996) report temperatures at which bats have been found hibernating to range from −10 to 21°C, modal temperatures selected by vespertilionids and rhinolophids were 6 and 11°C, respectively. *M. schreibersii* in Europe appears to favour winter temperatures of 7–10°C (Gaisler 1970). These conditions are, however, seldom found in southern Africa. Nevertheless, *M. schreibersii* normally forms dense clusters and hibernates in winter at temperatures generally considered to be too high for this activity. Winter temperature in the roost used by bats in the present study averaged about 14°C with winter minima ranging from 9.9–15.4°C and winter maxima from 17.6–19°C (Brown & Bernard 1994). These temperatures are typical of winter roosts in South Africa (Van der Merwe 1973; Norton & Van der Merwe 1978). Most frequently selected temperatures of *M. schreibersii* that entered torpor in a thermal gradient in winter were 16–18°C, within the range of winter temperatures measured in their natural roost. Similarly, several species of *Rhinolophus* in South Africa hibernate in dense clusters at relatively high temperatures, often sharing roosts with *M. schreibersii* (pers. obs.). The VO_2 of torpid bats measured in the laboratory was not significantly related to T_a across the temperature range typical of winter roosts and averaged 0.35 ml g^{-1} h^{-1} for clusters of six bats. Assuming the VO_2 of torpid bats measured in the laboratory approximates that during longer hibernation bouts in winter roosts, hibernation by *M. schreibersii* in clusters at typical winter roost temperatures still offers a 91–93% saving in energy when compared with euthermy. Clearly at least some species of insectivorous bats are capable of hibernating at temperatures generally considered to be too warm for this activity, although Churchill *et al.* (1997) noted several species of *Rhinolophus* and *Miniopterus* in Namibia to be torpid (but not hibernating) in caves with autumn/winter temperatures ranging from 22–27°C. They suggested that these temperatures are too warm for effective hibernation and, although bats may be torpid during the day, they must arouse each night to forage (and probably drink).

Acknowledgments

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