

Survival tactics within thermally-challenging roosts: heat tolerance and cold sensitivity in the Angolan free-tailed bat, *Mops condylurus*

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Received 17 March 1998; accepted after revision 29 September 1998

We studied roost microclimates, thermal preferences and temperature-related variation in body temperatures and flight abilities of *M. condylurus* from three roosts in man-made structures in South Africa. Roosts were characterized by marked spatio-temporal variability in ambient temperature and relative humidity on a daily and seasonal basis. Microclimates were thermally challenging, being very hot ($>40^{\circ}\text{C}$) for several hours daily in summer and autumn, and cold ($<10^{\circ}\text{C}$) for much of the night in winter. Thermal preference tests revealed that the bats actively selected temperature zones ($35^{\circ}\text{--}42^{\circ}\text{C}$) in which basal metabolic rate could be maintained, and above the minimum necessary for sustained flight. This presumably allowed them to minimize energy costs of thermoregulation without compromising reproductive activity or their ability to avoid predators. Bats displayed pronounced heat tolerance and hyperthermia in response to prolonged experimental exposure to high temperatures (40°C). They also exhibited cold-sensitivity, characterized by hypothermia and entry into torpor, when exposed to ambient temperatures below the thermal neutral zone. This response to low ambient temperatures would conserve energy in cold periods when the high energetic costs of foraging may not be met owing to reduced insect availability. We hypothesize that this broad roosting tolerance has energetic, ecological and evolutionary benefits that outweigh attendant disadvantages, which are largely compensated for by an unusual physiology.

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Bats spend more than half of their lifetimes within roosts, and over 20% of their daily energy budgets may be associated with the roosting environment (Burnett & August 1981). The roost microclimate is thus an important selective force in the physiological adaptation of these animals (McNab 1982; Rodrigues-Durán 1995). Physical conditions within roosts directly affect resting metabolism, thermoregulatory strategies and water homeostatic mechanisms (McNab 1982; Studier, Wisniewski, Feldman, Dapson, Boyd & Wilson 1983) and consequently impact on virtually every aspect of bats biology, from foraging habits (Kunz 1974; McNab 1982) to ecological distributions (Geluso 1978; Brown & Bernard 1994), migration patterns (Herreid 1963), and reproductive strategies (Dwyer & Harris 1972; Bernard & Cumming 1997).

The most important microclimatic factors which influence bats within their roosts are temperature, relative humidity and spatio-temporal variation in these factors (Bakken & Kunz 1988). Microchiropteran bats employ both behavioural and physiological mechanisms to counteract potentially stressful roost conditions. Under moderate conditions, behavioural thermoregulatory mechanisms centred around site selection, intra-roost movements and huddling (Studier *et al.* 1983; Roverud & Chappell 1991) facilitate parsimonious energy

and water usage. More extreme roost microclimates, however, force bats to employ compensatory physiological mechanisms. These include active thermoregulation, adaptive hypothermia and daily torpor in response to cold (McNab 1982; Bell, Bartholomew & Nagy 1986; Speakman & Racey 1989; Hosken & Withers 1997), and thermolability, lowered conductance and tolerance of hyperthermia in the heat (Licht & Leitner 1967; Genoud, Bonaccorso & Arends 1990; Rodrigues-Durán 1995).

The ecophysiology of temperate zone bats inhabiting cool roosts, in which ambient temperatures are well below the thermal neutral zone and relative humidities are high, has been well studied (e.g. Stones & Wiebers 1965; McNab 1974; Bernard & Bester 1988). Considerably less attention has been paid to the impact of hot roost microclimates on the roosting physiology of microchiropterans, but there is mounting evidence that heat stress represents an important factor in the biology of these animals. Bats inhabiting caves and above-ground roosts (such as buildings and trees) in tropical areas often encounter high environmental temperatures (Twente 1956; Herreid 1963; Genoud 1993; Rodrigues-Durán 1995). Hot roosts are not, however, limited to tropical areas: even in poorly-ventilated temperate zone roosts, temperatures reach

35°–54°C for short periods during summer (Licht & Leitner 1967; Audet & Fenton 1988).

Given the paucity of information regarding the impact of hot roost microclimates on bats, their physiological and behavioural responses to high environmental temperatures warrant further study (Bonaccorso, Arends, Genoud, Cantoni & Morton 1992). Free-tailed bats (Molossidae) are ideal study subjects since they have the most adaptable thermoregulatory strategies, catholic roosting requirements and greatest heat tolerance among microchiropterans (Herreid 1963; Licht & Leitner 1967; Lyman 1970).

The Angolan free-tailed bat *Mops condylurus* (A. Smith, 1833) is widely distributed in sub-Saharan Africa by virtue of its broad habitat and roosting tolerances (Happold & Happold 1988; Koopman 1993). It is particularly abundant in the hot lowland savannas of south-eastern Africa, where individuals congregate in colonies numbering into the thousands, depending on available roosting space. Such colonies readily exploit man-made structures such as bridges, water towers and buildings (Fenton, Rautenbach, Smith, Swanepoel, Gossel & Van Jaarsveld 1994), and commonly roost under corrugated iron roofs where temperatures 'must at times rise very high' (Skinner & Smithers 1990). But, except for one observation that temperatures in such roosts may exceed 50°C (Mutere 1969, cited in Happold & Happold 1988), no published studies have detailed the complexities of the roost microclimate, or the thermal predilections of these bats. Such information, although lacking for most species, is essential for a proper understanding of chiropteran ecophysiology (Bakken & Kunz 1988). We therefore investigated roost conditions, temperature preferences and heat tolerance in several colonies of *M. condylurus* inhabiting buildings in the hot subtropical savanna of South Africa.

Materials and methods

Roosts studied

We studied three roosts on the southern border of the Kruger National Park, near Komatipoort (Mpumalanga Province) during the southern hemisphere summer-winter (February to June) seasons of 1996, and summer (January to March) of 1997. Physical descriptions of these roosts are as follows:

Ngwenya Lodge (25°21'S; 31°50'E). This roost was located in a 10 cm deep cavity between a pitched (13°) corrugated iron roof and the wooden ceiling of a game viewing deck at Ngwenya Lodge, on the banks of the Crocodile River. The game viewing deck is rectangular in shape (12 m × 11 m), with the axis of the building facing NW. During the day roosting activity in the ceiling was restricted to an L-shaped area (longest axes 4 m × 5 m), at the rear (south-western) side of the building, which received full afternoon sun. Towards dusk the bats also moved into a gap (5 m × 2 m × 5 cm deep) between wooden panelling and a facebrick supporting wall on the western side of the building, en route to two well-defined entrance/exit holes located under the gables of the roof. Based on visual emergence counts (Thomas & LaVal 1988) at these holes, the colony was estimated at 580–700 individuals.

Komatipoort Station (25°26'S; 31°57'E). Precise dimensions of this roost, which was located under a pitched clay-tile roof of a railway station, were not determined. Visual inspection, however, suggested that the bats roosted on top of the wooden

ceiling (approximately 8 m × 5 m), as well as in vertical ventilation chutes and double cavity walls. Emergence counts were complicated by the use of multiple entrances, and the egression of many individuals in rapid succession, but suggested that more than 1000 individuals were present.

Station Bat Hotel (25°25'S; 31°55'E). This roost was located in a structure erected by the South African Transport Services (Spoomet) in 1953 specifically to attract bats to the area, as part of a malaria-mosquito control programme (P. Greyvenstein, Komatipoort Tourism Association, *pers. comm.*). This bat hotel, which is approximately 3.5 m wide × 6 m long × 1.5 m tall and raised 5 m above ground level, consists of a wooden shell with four horizontal wooden platforms (covered with wire mesh) about 30 cm apart, and a pitched asbestos roof. Visual emergence counts were again hampered by the multitude of entrance/exit sites, and the quick succession in which many individuals emerged, but suggested that the colony comprised more than 2000 individuals.

Roost microclimates

Detailed monitoring of spatio-temporal variation in roost microclimate using continuous recording techniques was done only at Ngwenya Lodge during summer-winter 1996. Inter-roost comparisons in summer 1997 were limited to a single site within each of the three roosts, using remote data sensing probes.

Continuous data recording techniques (Ngwenya Lodge)

Macro-climatic conditions outside the roost were monitored using a complete weather station erected on the roof of the building adjoining the game deck. This weather station measured ambient dry bulb temperature, relative humidity, solar radiation levels and windspeed. Data were recorded at 15 min to 1 hr intervals using a MCS Model 120-02EX Datalogger System (Mike Cotton Systems, Cape Town, South Africa), downloaded at regular intervals to a Laptech 3300V micro-computer.

The thermal regime within the roost was measured at six sites chosen to circumscribe as much spatial variability as possible. Ambient temperatures were measured using bare, calibrated copper-constantan thermocouples, whereas operative temperatures (the thermal load a bat would experience owing to its size, shape, colour and conductance) were estimated using taxidermic mounts, following Bakken & Kunz (1988). Taxidermic mounts were constructed from study skins of adult *M. condylurus* provided by the Transvaal Museum (Pretoria). Dry taxidermic mounts, to measure operative temperatures associated with dry conductivity, were made by inserting a copper-constantan thermocouple into the cotton wool stuffing of these specimens. Wet taxidermic mounts were prepared by replacing the cotton wool stuffing with condoms filled to original body mass with a water-based coolant gel, and a central thermocouple. Thermocouples were connected to an Omega OM-5000 data logger, which recorded temperatures at 15 min to 1 hr intervals.

Remote sensing techniques

Ambient temperatures and relative humidities within three roosts were monitored simultaneously during summer (February) 1997 using HOBO relative humidity and temperature

data logger probes (Onset Computer Corporation, Pocasset, Massachusetts USA). These were inserted at least 10 cm below the roof at a single, arbitrarily-chosen site in each roost.

Thermal preferences

As the roof design did not allow us to directly visualize bat movements, their location(s) in the roost was determined indirectly using a stethoscope placed against the wooden paneling. Thermal preferences *in-situ* were determined by recording the presence/absence of bats in relation to temperatures at each of the six sites in the roost, at two-hourly intervals over one day in summer 1996.

Temperature preferences of *M. condylurus* were also determined experimentally, using a horizontally-oriented thermal gradient chamber. This consisted of a 75 cm × 23 cm perspex cylinder, equipped with a wooden floor and an inner wire mesh casing, and an extractor fan for ventilation. The cylinder was divided into 10 equal size thermal 'compartments', each equipped with two copper-constantan thermocouples (located midway at the top and bottom of each cell), which were connected to a Physitemp Model BAT-12 temperature recorder. A gradient approximating the spectrum of temperatures (20°–56°C) encountered within the Ngwenya Lodge roost was established in the chamber by heating one end with a commercial fan heater, and cooling the other with commercial ice-bricks.

Groups of 12 bats, caught at the roost entrance the previous evening and kept captive overnight, were used for trials under conditions which simulated post-absorptive resting states within the day roost. The bats were placed in the chamber and allowed to acclimatize for two hours, during which a stable thermal gradient was established. The number of bats located in each thermal compartment was then recorded at 30 min intervals for two to three hours, in diffuse low light conditions (to avoid artefacts resulting from stress and possible light avoidance).

Minimal flight temperature (MFT)

The minimum body temperature required for flight was determined following Roverud & Chappell (1991), during the active period (dusk) at the game viewing deck below the Ngwenya Lodge roost. Body temperature (T_b) was measured rectally using a copper-constantan thermocouple connected to a Physitemp Model BAT-12 temperature recorder. Each bat was then suspended approximately 2 m over a soft foam-rubber pillow, and gently dropped. If the bat was able to recover from the fall, gain altitude and fly off, it was deemed to have flown successfully; if it landed on the pillow the flight attempt was deemed unsuccessful. If the bat recovered from the fall, but landed on the ground within three metres of the launch site, the flight attempt was recorded as marginally successful.

Heat tolerance

Heat tolerance of *M. condylurus* was investigated by placing 10 post-absorptive adults in a 1.5 l glass container, in a well-ventilated oven at 40°C. Ambient and body temperatures were measured every two hours for 12 hrs, and behaviour of the bats within the flask was assessed visually at regular intervals.

Circadian rhythms in body temperature

Bats captured emerging from the Ngwenya Lodge roost were individually marked for easy identification, and maintained for 26 hrs in quiet, darkened rooms under three ambient temperature regimes, at $T_a = 19.2 \pm 2.3^\circ\text{C}$, $T_a = 25.5 \pm 1.7^\circ\text{C}$ and $T_a = 27.7 \pm 2.4^\circ\text{C}$, respectively. The bats were housed in groups of 10 to allow clustering, as may occur within the natural roost, and to minimize potential isolation stress that may result if individuals of a highly-social species are kept singly. Body temperatures were measured every two hours, and measurement times were kept as short as possible (usually < 10 min per session) to minimize handling stress.

Statistical analyses

Assumptions of normality and homoscedasticity were tested prior to parametric analyses using the Kolmogorov-Smirnov D-statistic, and Hartley's F_{\max} test, respectively. When these criteria were upheld, the significance of differences in the spatio-temporal profiles of roosts was tested using either Analysis of Covariance (ANCOVA) with time of day or site as covariates, and/or nested Analysis of Variance (ANOVA) designs. Kruskal-Wallis ANOVA was used to test for statistical differences when significant deviations from normality, or heteroscedasticity were observed. Statistical significance was assumed at $p < 0.05$.

Results

Roost microclimates

Spatio-temporal variability: Ngwenya Lodge

The summer of 1996/97 at Komatipoort was wetter and slightly cooler than the long-term average: whereas the 50-year mean precipitation values during December–February are 324 mm, 378 mm was recorded during this period in 1996. The long-term average daily maximum temperature for this period is 32.6°–33.9°C, but did not exceed 32.5°C during the 1996/7 summer season (M. Jacobs, South African Weather Bureau, Pretoria, *pers. comm.*)

During the nine-day study period (9–18 February 1996), winds were gentle, seldom exceeding 5 m.s⁻¹ (Figure 1). During the peak of the day (10:00–14:00), external solar radiation levels were highly variable owing to fluctuating cloud cover, with maxima of $502.6 \pm 229.8 \text{ W/m}^2$. External ambient temperatures were mild by both night ($23.5 \pm 2.7^\circ\text{C}$) and day ($29.2 \pm 5.8^\circ\text{C}$), and seldom exceeded 40°C. Relative humidities were generally high and variable owing to occasional rainshowers, usually in excess of 90% at night, with a decrease to around 60% during the heat of the day.

As a result of the relatively high solar radiant loads on the corrugated iron roof, ambient temperatures within the roost were significantly higher than outside (ANOVA $F_{22,153} = 4.04$; $p < 0.01$), but generally followed external trends ($r = 0.43$; $p < 0.05$) with a two-three hour lag period. Owing to higher temperatures in the roof, mean relative humidities within the roost were generally lower than outside, averaging between 65–75% at night, with a decline to $57.6 \pm 8.9\%$ during the heat of the day.

Ambient temperatures within the roost (measured using bare thermocouples) did not differ significantly from operative temperatures measured using dry/wet taxidermic mounts

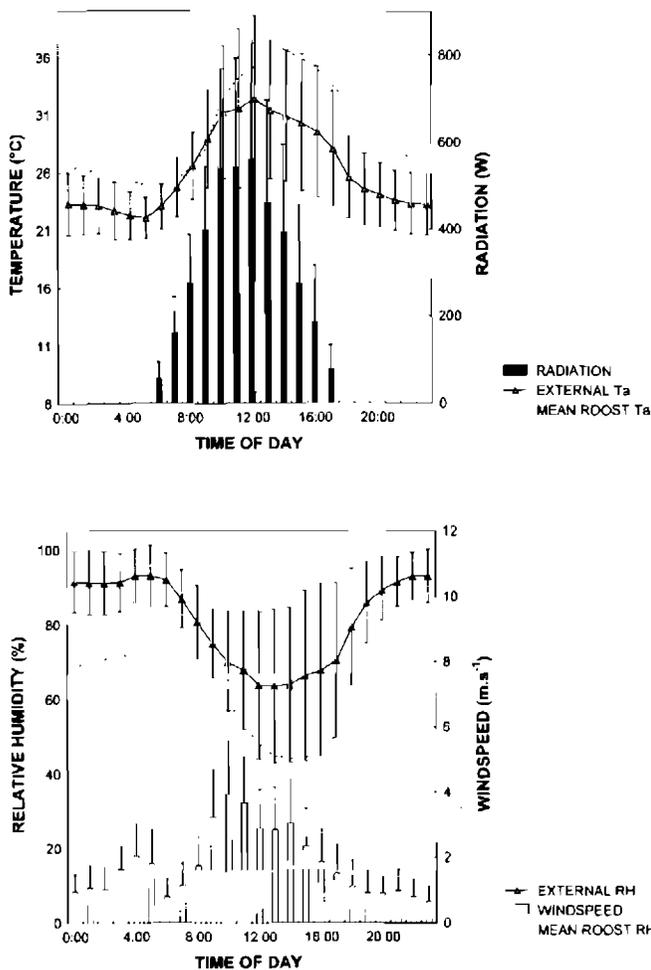


Figure 1 Diel variation (hourly means \pm 1sd) in external climatic conditions at Ngwenya Lodge, in relation to mean temperature and relative humidity within the roost, during 9–18 February 1996

(ANCOVA $F_{3,3162} = 0.219$; $p > 0.05$), reflecting the low thermal inertia of these small mammals. These data sets were therefore pooled in further analyses.

Spatial variation in roost temperatures over a single summer day (Figure 2) was negligible at night, but highly significant during the daylight hours (ANCOVA $F_{1,386} = 35.2$; $p < 0.001$). During the hottest hours of the day, when solar radia-

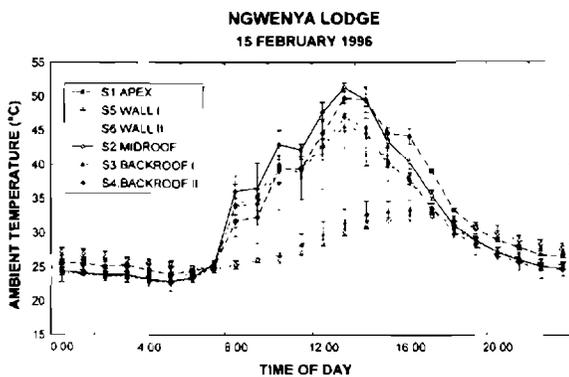


Figure 2 Spatio-temporal variation in ambient temperatures (hourly means \pm 1sd) at six sites in the Ngwenya Lodge roost over a single day during summer 1996

tion was highest, a temperature gradient of about 25°C existed between the two coolest sites (S5–6), located in the wall cavity, and the four hottest sites (S1–4) situated directly below the corrugated iron roof. Mean temperatures at the four sites under the roof exceeded 40°C for over six hours (10:00–16:00). The midroof site (S2), which received full afternoon sun, was the hottest by day, and the coldest at night. Relative to the roof sites, the wall sites were thermally buffered, with significantly lower diurnal and somewhat warmer nocturnal temperatures.

The same pattern of spatio-temporal variation was evident in a temperature profile for eight days in summer 1996 (Figure 3): at the hottest time of the day (14:00), a temperature gradient of 35°C existed between the coolest site (S5) located in the wall cavity, and the hottest site (S2), in the midroof region. The absolute maximum temperature in the roof

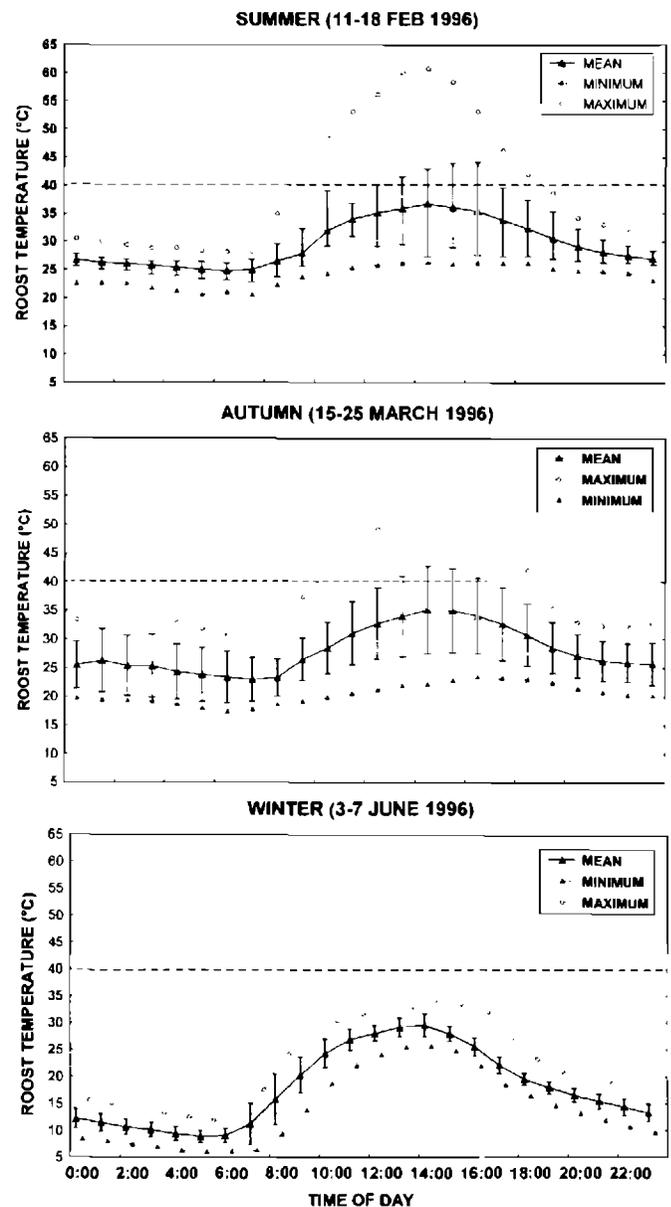


Figure 3 Seasonal variation in the roost microclimate at Ngwenya Lodge, as indicated by mean ambient temperatures (\pm 1sd), and absolute maxima and minima, across the six sites in the roost that were monitored

exceeded 40°C for more than 10 hours daily, with maxima above 60°C for up to two hours, but were relatively mild and stable ($28.5 \pm 2.2^\circ\text{C}$) at night. Temperatures at the cool, thermally buffered wall sites fluctuated between only 20°–25°C, even during the heat of the day.

Conditions within the roost remained warm during autumn 1996 (Figure 3), with the hottest sites experiencing temperatures in excess of 40°C for up to nine hours daily. The amplitude of spatial variation in temperature during the heat of the day was, however, reduced to about 30°C, and maxima never exceeded 53°C. Temperatures within the roost at night were more variable than in summer, largely due to higher absolute maximum temperatures (possibly related to reduced rainfall), but never dropped below 19°C.

In winter 1996, ambient temperatures within the roost were markedly lower than in summer or autumn, and spatio-temporal variability was greatly attenuated, with a differential of about 10°C between absolute maximum and minimum temperatures by both day and night (Figure 3). During the hottest part of the day(s), mean temperatures approached 30°C, but maxima never exceeded 35°C. The roof sites, which were hottest by day, were the coolest by night, with minimum temperatures that dropped as low as 6°C during the early hours of the morning. Even in the thermally buffered wall cavity, minimum temperatures at night declined to less than 15°C.

Inter-roost comparisons: summer 1997

Temperature and relative humidity profiles for the three roosts studied in late summer 1997 are shown in Figure 4. Diel variability in roost ambient temperature was greatest at Ngwenya Lodge, and lowest at the Station Bat Hotel. During the heat of the day, mean ambient temperatures at Ngwenya Lodge ($37.9 \pm 6.3^\circ\text{C}$) were significantly higher (Kruskal-Wallis ANOVA: $H = 25.9$; $p < 0.01$) than at the other roosts (Komatipoort Station = $35.0 \pm 4.9^\circ\text{C}$; Station Bat Hotel = $35.3 \pm 4.2^\circ\text{C}$). At all three roosts, maximum diurnal temperatures exceeded 40°C for at least six hours daily.

Nocturnal temperatures seldom fell below 20°C, but differed significantly among the three roosts (ANCOVA $F_{2,1382} = 37.93$; $p < 0.001$), being appreciably lower at Ngwenya Lodge ($24.9 \pm 2.8^\circ\text{C}$) and the Station Bat Hotel ($25.3 \pm 2.8^\circ\text{C}$) than at Komatipoort Station ($27.1 \pm 2.8^\circ\text{C}$).

Relative humidity profiles within the three roosts predictably showed an inverse diel pattern relative to ambient temperature, and fluctuated between 30–95%. Variability was greatest at the Station Bat Hotel, where relative humidities were significantly higher (ANCOVA $F_{2,1252} = 96.00$; $p < 0.01$) at night, but significantly lower during the day (Kruskal-Wallis ANOVA: $H = 149.6$; $P < 0.001$), than at either of the other two roosts. While diurnal temperatures at the Ngwenya Lodge roost were significantly higher than at the other roosts, maximum humidities over the study period were more stable, implying that factors other than temperature influenced relative humidity. These could include differences in roost design and ventilation, orientation with respect to wind direction, and especially location relative to open water sources. (The Ngwenya Lodge roost is located on the banks of a river, whereas the other two roosts are situated approximately 1 km away from open water.)

Thermal preferences

In-situ observations

The dispersion of bats among the six sites monitored within the Ngwenya Lodge roost was not even, implying that some form of active site selection occurred. During the heat of the day, the bats roosted mainly at two or three sites (S2-4) located in the midroof and backroof (Figure 5a), where ambient temperatures were high ($>35^\circ\text{C}$) and relative humidities low ($<40\%$), rather than in the buffered wall cavity, as might be expected. Bats were found at the cooler sites, located in the roof apex (S1) and back roof (S3), only at dusk as they moved towards the two entrance\exit holes in preparation for nocturnal foraging activity.

Temperature gradient experiments

The overall distribution of bats among thermal compartments in a gradient chamber was not random ($\chi^2 = 134.3$; $df = 11$; $p < 0.001$; $n = 291$), and deviated significantly from normality (Kolmogorov-Smirnov $D = 0.09$; $p < 0.05$), with slight positive skewness ($g1 = 0.127 \pm 0.143$) and moderate platykurtosis ($g2 = -0.678 \pm 0.285$). This distribution had a wide plateau ranging from 27.5–42.5°C (Figure 5b), indicating a broad temperature tolerance but clear avoidance of the cooler thermal compartments ($T_a < 25^\circ\text{C}$). There was no clear effect of exposure time on preferred roosting temperature(s). Even after more than two hours of experimental exposure (four hours including acclimation), several individuals selected temperatures above 45°C, but no bats were observed in the 20°–25°C region of the chamber at any stage during the experiments. The modal temperature selected during the experiments was 37.5°C, and more than 65% of observations were at temperatures exceeding 35°C.

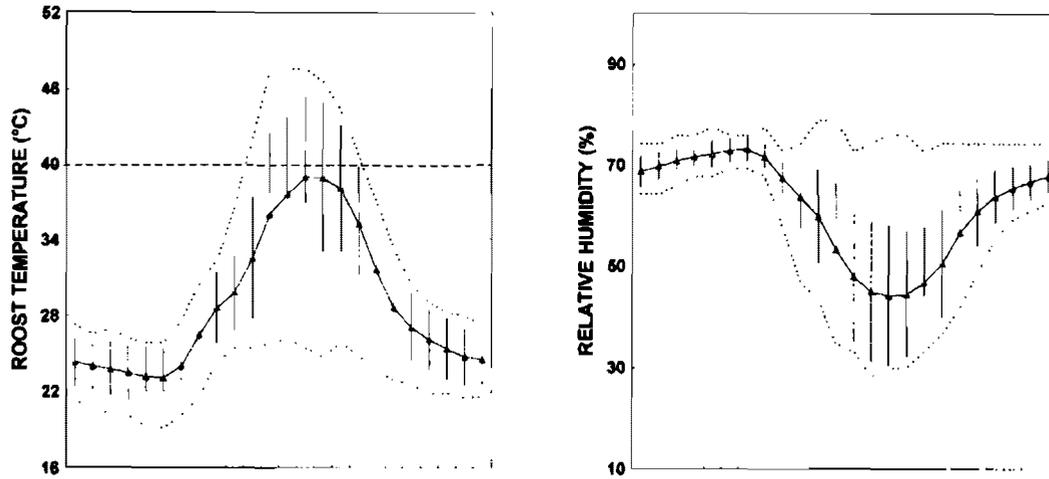
Minimum flight temperatures

The MFT during this study was approximately 35°C, although there was some overlap of body temperatures of bats allocated to the three flight categories. All of the bats which flew successfully had body temperatures above 35°C (mean $T_b = 38.6 \pm 1.5^\circ\text{C}$; $n = 40$), and only four individuals capable of marginal flight (mean $T_b = 35.2 \pm 1.7^\circ\text{C}$; $n = 10$) had a body temperature below this limit. Bats with body temperatures below 31.5°C (mean $T_b = 31.8 \pm 3.1^\circ\text{C}$; $n = 24$) were unable to fly at all. Mean body temperature of free-ranging bats emerging from the roost ($40.5 \pm 1.1^\circ\text{C}$; $n = 228$) was significantly higher ($F_{1,263} = 146.9$; $p < 0.001$) than in those returning after foraging ($38.2 \pm 0.9^\circ\text{C}$; $n = 38$).

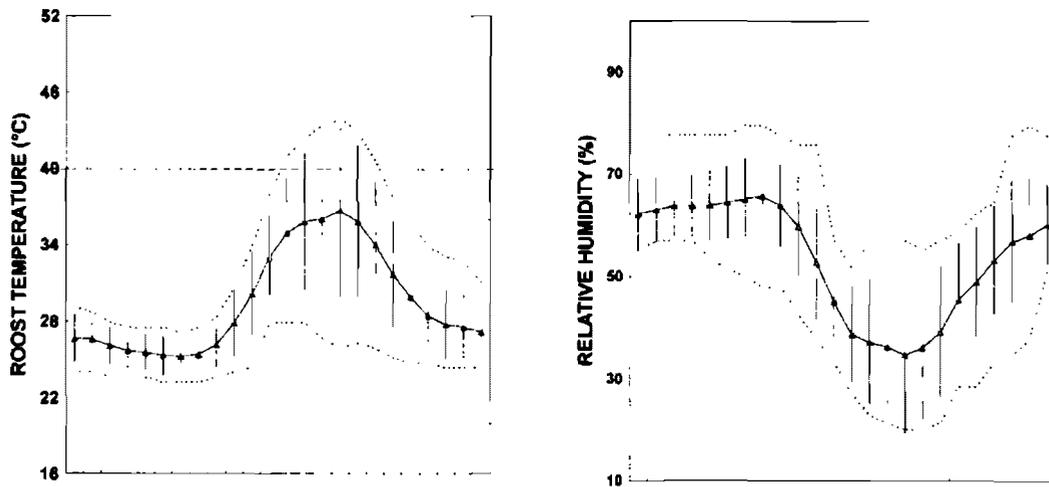
Heat tolerance

Thermal tolerance tests showed that *M. condylurus* was able to survive temperatures of 40°C for 11 hours. During the first nine hours of exposure, body temperatures generally increased (Figure 6), and exceeded 42°C in some individuals. However, body temperature and exposure time were only weakly correlated ($r = 0.45$; $p < 0.001$), owing both to marked individual variability in T_b at all times, and a slight reduction in T_b after 11 hours of exposure. Variability in body temperatures, as indicated by the coefficient of variation, was strongly correlated with exposure time ($r = 0.86$; $p < 0.05$), and markedly elevated after seven hours of exposure. Passive heat

NGWENYA LODGE



KOMATIPOORT STATION



STATION BAT HOTEL

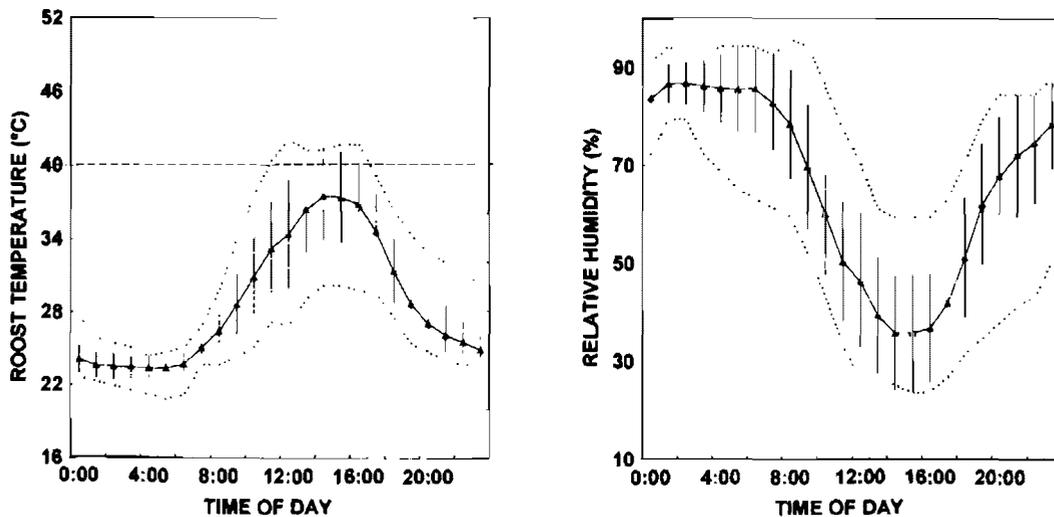


Figure 4 Diel variability in microclimates of three roosts during summer 1997, as indicated by mean ambient temperatures and relative humidities (hourly means \pm 1sd), and absolute maxima and minima (dotted lines)

storage was therefore complemented by active physiological compensation in some individuals as exposure to high ambient temperature progressed. No wing fanning was observed during the exposure period, but several bats panted and sweated in the inter-scapular region, suggesting that evaporative cooling was invoked to survive prolonged thermal stress.

Circadian rhythms

A circadian rhythm in body temperature was evident over all three ambient temperature ranges (Figure 7), and both resting body temperature and the extent to which it was endogenously elevated in the late afternoon were Ta-dependent (Kruskal-Wallis ANOVA: $H_{2,411} = 137.40$; $p < 0.001$). Animals housed at the two warmer temperature regimes showed

a progressive decline in body temperature during the night, with a nadir (09:00–13:00) the following day. During this period mean body temperature was two to four degrees below that at capture, and a temperature differential of seven to eight degrees was maintained relative to ambient. The body temperatures of seven individuals (35%) fell below 30°C for at least two hours, indicating that they had entered a shallow torpor. All of the individuals raised their body temperature endogenously in the late afternoon, to levels (at dusk) that approximated minimum flight temperature (35°C).

Individuals housed at the colder ambient temperature showed a more marked decline in body temperature during the night, with a nadir (09:00–13:00) during which mean body temperature was about 28°C (approximately 9°C above ambient). Body temperatures dropped below 30°C in three individuals, and below 25°C in a further five animals. Although a slight endogenous increase in body temperature was evident at dusk, this was not sustained, and only two bats achieved the minimal temperature necessary for flight.

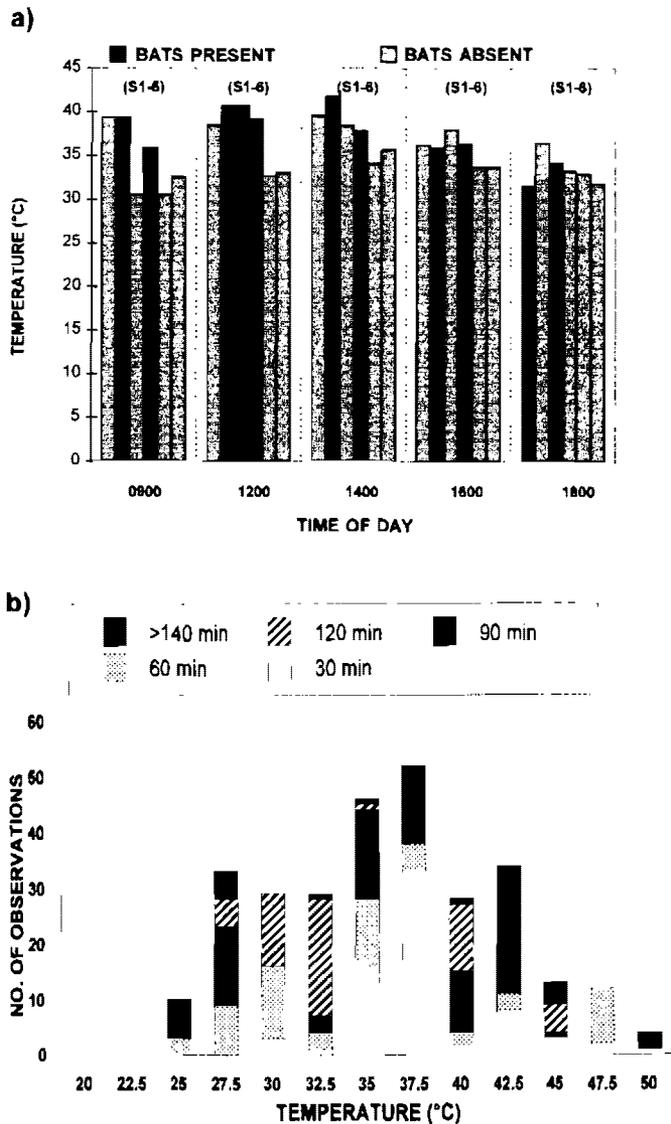


Figure 5 Thermal preferences of *M. condylurus*, as indicated by: (a) sites occupied in relation to ambient temperatures and relative humidities over a nine hour period in the Ngwenya Lodge roost on 6 February 1996; and (b) the number of observations per thermal compartment in relation to exposure time during six temperature gradient experiments

Discussion

Our results confirm that thermal conditions within the roosts of *M. condylurus* are highly variable and potentially challenging, but suggest that the bats avoid the full impact of temperature stress through behavioural means. Selection of appropriate microhabitats within the roost presumably allows these bats to minimize thermoregulatory energy expenditure without compromising alertness, predator avoidance capacity or reproductive activity.

The three roosts studied showed marked diel and seasonal variability in ambient temperature. Maximum temperatures (in summer and autumn) were above the limits of the heat tolerance of most small mammals (Cossins & Bowler 1987), and minimum (nocturnal) temperatures in winter were sufficiently low to induce hypothermia in this species (Kulzer 1965). Intense solar radiation on sunny days in summer and autumn generated steep spatial gradients in ambient temperature and relative humidity within the roosts, particularly at Ngwenya Lodge where temperatures exceeded 45°C for several hours at most sites in the roof. Given that a 10°C+ differential

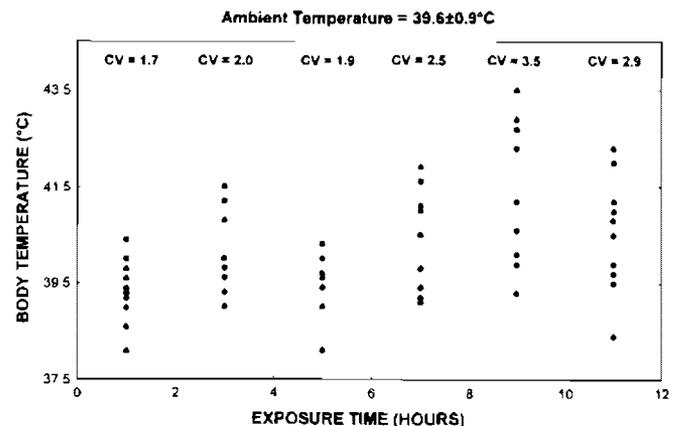


Figure 6 Variability in body temperatures of 10 *M. condylurus* exposed to high temperatures (40°C) in an oven for 12 hours. CV = coefficient of variation

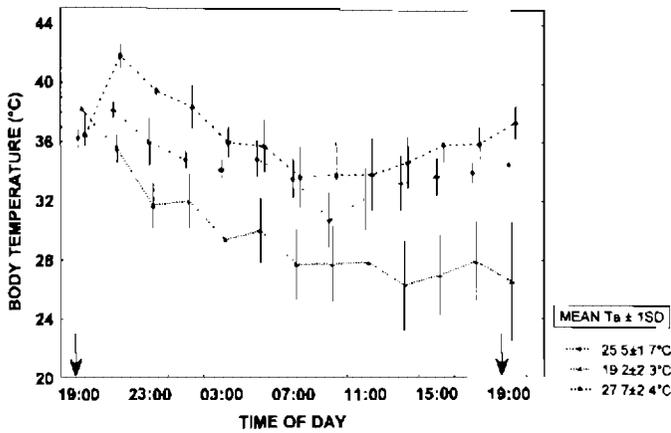


Figure 7 Daily circadian profile in body temperatures (bihourly means \pm 1sd) of groups of 10 *M. condylurus* housed at three different ambient temperature regimes over a 25 hour period during autumn 1996. Arrows indicate the time of emergence of bats from the roost at Ngwenya Lodge

existed between temperatures outside and inside this roost, the bats are exposed to potentially challenging thermal conditions when external ambient temperatures reach 30°C. Long-term weather averages indicate that external ambient temperatures exceed 30°C on 167 days annually in the Komatipoort area, implying that *M. condylurus* colonies probably encounter high temperatures within roosts on a frequent and sustained basis.

The range of ambient temperatures recorded during summer and autumn are similar to those reported for neotropical molossid inhabiting caves (8°–43°C; Herreid 1963; Rodrigues-Durán 1995) and temperate zone buildings (28°–49°C; Licht & Leitner 1967). However, maximum temperatures at Ngwenya Lodge consistently surpassed the highest temperatures (54°–55°C) documented for roosting bats (Chew 1965; Henshaw & Folk 1966). During winter temperature variability was less pronounced and approximated the conditions found in temperate caves (Brown & Bernard 1994; Bernard & Bester 1988).

Pronounced spatio-temporal variation in thermal characteristics may be a critical factor influencing roost selection by *M. condylurus*, since it provides the opportunity for behavioural thermoregulation with minimal energy expenditure. Our observations on thermal proclivities of the colony at Ngwenya Lodge suggest that the bats selected sites with daily temperatures between 35°–42°C and relative humidities of 30–40% (Figure 5a). While these data are equivocal, since factors other than temperature may have influenced site selection within the roost, the same thermal range was actively selected in temperature gradient experiments (Figure 5b). This range of ambient temperatures also coincided with the body temperatures of bats caught at the roost entrance, as well as with those of animals that were able to fly successfully. The apparent thermal preferendum furthermore corresponded with the range of ambient temperatures in which the metabolic rate of this species is basal (Maloney, Bronner & Buffenstein in press).

Mops condylurus therefore appears to select temperature zones that allow it to minimize metabolic energy expenditure without resorting to torpor, and in which neither alertness nor the ability to detect and flee from predators is compromised. Predator avoidance is undoubtedly an important demographic strategy, since predation rates on molossids are high (Fenton *et al.* 1994), and terrestrial predators (such as the Eastern Tiger Snake *Telescopus semiannulatus semiannulatus*, which we observed in a colony on three different occasions) may also enter the roosts to feed.

The thermal preferendum of the *M. condylurus* colony studied is considerably higher than those reported for most other species inhabiting temperate caves or buildings (Kunz 1974; Audet & Fenton 1988; Brown & Bernard 1994). In particular, the range of temperatures preferred by *M. condylurus* is even higher than in the arid-adapted and heat-tolerant molossid *Tadarida brasiliensis mexicana*, which prefers temperatures between 25°–38°C in its natural roosts, and only initiates behavioural avoidance when ambient temperatures within horizontal gradient chambers rise above 35°C (Licht & Leitner 1967; Herreid 1963).

Behavioural mechanisms, whilst undoubtedly important in the thermoregulatory repertoire of bats, may not always be sufficient to avoid thermal stress in roosts characterized by extreme temperatures. Our results show that behavioural thermoregulation by *M. condylurus* is complemented by tolerance of high ambient temperatures, during which heat storage is employed to some extent, probably to reduce the thermal gradient for conductive and convective heat gain. But, being of small mass, body temperatures of the animals fast approached 41°C, whereafter the bats thermoregulated physiologically, most noticeably by evaporative cooling.

Pronounced heat and dehydration tolerance would obviously be advantageous to such bats confronted by a roost milieu that is too hot for compensation by purely behavioural means. Adaptive hyperthermia may suffice if hot conditions do not prevail for long, and excess heat can be offloaded at night from the extended wing membranes, which serve as excellent convectors during flight (Morris, Curtin & Thompson 1994). If extreme conditions prevail for longer periods, however, the bats may be forced to compensate by evaporative cooling, with consequential depletion of body water pools. That free-ranging *M. condylurus* rely on both of these tactics is confirmed further by significantly higher body temperatures and pronounced haemoconcentration in bats emerging from the diurnal roost, relative to those returning after foraging (Buffenstein, Maloney & Bronner, 1999).

While it is clear that *M. condylurus* is heat tolerant, it is also evident that this species is cold-sensitive. Circadian rhythms in body temperature indicated facultative hypothermia and reliance on torpor (*sensu* Altringham 1998) that was Ta-dependent at ambient temperatures below the lower critical limit (29°C; Maloney *et al.* in press). As in many temperate insectivorous bats, the employment of energy-conserving torpor by *M. condylurus* during cold periods is probably an adaptive strategy related to rapid rates of heat exchange resulting from small body size, and a reduction in insect prey availability to the extent that the high energetic costs of flight are not met by foraging (Racey & Swift 1981; McNab 1982; Kurta 1991; Altringham 1998).

Alternatively, the torpor we observed may have been nutritionally induced, since the bats studied had not fed since at least the dawn before capture. Poor nutritional status is a strong cue to abandon homeothermy at ambient temperatures below the thermal neutral zone, thereby minimizing thermoregulatory energy costs and extending the lifespan of energy reserves until environmental conditions more favourable for foraging return (Lyman 1978; Buffenstein 1985). Differences in nutritional status could explain the quite marked individual variability in body temperature observed under all three ambient regimes used. Any such effects were, however, probably eclipsed by ambient temperature during this study, since individuals caught at the same time as those used in circadian trails entered facultative hypothermia when exposed to 15°C during thermoregulatory experiments (Maloney *et al.* in press), but were able to endogenously raise their body temperatures to levels necessary for sustained flight upon subsequent exposure to normal air temperature ($\pm 25^\circ\text{C}$). Regardless, the endothermic elevation of body temperatures at dusk in our circadian studies clearly indicates that this species adaptively enters torpor when exposed to cold roost conditions and/or concomitant nutritional stresses. Daily employment of torpor by this species is, however, unlikely since roost temperatures generally fall within the thermal neutral zone.

Given that *M. condylurus* is heat-tolerant and cold-sensitive, its preference for hot roosts becomes clear. But, why does this species choose roosts that are thermally so hot and variable, instead of more stable, clement microhabitats typically used by other microchiropterans? And what selective force led to the evolution of such pronounced heat tolerance? We hypothesize that the benefits associated with this strategy more than compensate for any attendant disadvantages. By selecting hot, but thermally-variable roosts, this species is able to select appropriate microhabitats where it can minimize roosting energy expenditure without compromising its ability to avoid predators, and yet also promote foetal development and post-partum maturation rates, thereby maximizing reproductive potential through seasonal polyoestry (Bernard & Cumming 1997). These demographic advantages could outweigh the disadvantages of occasional periods of thermal stress, which may be ameliorated to a large degree by the employment of heterothermy and other physiological mechanisms (see Maloney *et al.* in press). The catholic roosting requirements and pronounced heat tolerance of this species may also allow it to successfully outcompete other species with more specialized roosting requirements, especially in areas where more clement roosting opportunities are limited, with obvious ecological and evolutionary advantages.

Acknowledgements

This work was approved by the Animal Ethics Committee of the University of the Witwatersrand (AESC#96/29/2a). Funding was provided by the Foundation for Research Development, Potchefstroom University Subsidized Research Fund, and Transvaal Museum (Pretoria). SKM was a University of the Witwatersrand Post-Doctoral Fellow. We are grateful to Mr John Hume and Dr Brian Whiting (Winchester Marketing) for subsidizing our accommodation and logistical support, and the staff of Ngwenya Lodge for their hospitality and

enthusiastic co-operation. Helen Driver, Debbie Bellars, Andrew Robinson, Jackson Kone and Ryan Woodley kindly assisted with fieldwork.

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