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Role of light and temperature in the roosting ecology of tropical microchiropteran bats

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Abstract. Tropical microchiropteran bats need to seek out environments of thermoneutrality which in the tropics, of course, may mean selecting 'cooler' places for the diurnal roosts. Thus the roosting sites of all the species studied, *Rhinopoma hardwickei*, *Taphozous melanopogon*, *Hipposideros speoris*, *Hipposideros bicolor* and *Megaderma lyra* inhabiting caves, caverns, interiors of temples and a cellar were cooler by several degrees and showed a relatively constant temperature than outside in the open. Such a lower and relatively constant temperature found in the roosts apparently aid in lowering the metabolic rate and cost and may be vital in these tropical species that do not hibernate and some of which may be (such as *Hipposideros speoris*) continuous breeders. This paper presents the temperature and light intensity profiles of bat roosts over 24 h periods for the course of an entire year. It is found that physical protection from predators, relative constancy of temperatures, lower levels of illumination and high humidity seem to determine the choice for roosts in these species of bats.

Keywords. Roosting ecology; behavioural thermoregulation; bats.

1. Introduction

It is well known that the microchiropteran bats are eclectic in their choice of diurnal roosting sites (Brosset 1962). Roosting preferences may involve several factors such as conditioning, habituation and social influence (Klopfer and Hailman 1965). Further, roost preference may not be exercised by merely a visual response to the topology of the substratum but may also involve some secondary, perhaps microclimatic variables such as temperature, light, humidity, protective cover and shade superimposed on these structures (Schoener 1971). Since the rate of energy expenditure (metabolic rate) is affected by such external factors (Stones and Wiebers 1965) the selection of the appropriate habitat is ecophysiologically important (McNab 1982). This may indicate that microchiropteran bats, owing to the high energy demands, their mode of locomotion and small body-size impose on them, must conserve energy and efficiently cut down on loss of heat to the outer environment.

Tropical microchiropteran bats are successful in solving this ecophysiological problem (Davis 1970). This evolutionary success is reflected in the fact that they roost during the day in many secluded situations from total darkness to broad day light (Greenhall and Paradiso 1968), avoiding high temperatures in the roosts by moving away to cooler parts (Wilson 1971; Wilson and Laval 1974; Vaughan and Vaughan 1986).

If such 'inherent' thermal preferenda exist their role in the habitat selection of the species under natural conditions must be considered. This requires examination of various parameters of roosts. An attempt has been made to study the roosting sites of *Rhinopoma hardwickei*, *Hipposideros speoris*, *H. bicolor*, *Taphozous* *melanopogon* and *Megaderma lyra*. A population of the species *R. hardwickei* that inhabits an environment in which thermo-regulatory responses are of particular interest was studied in great detail. Special emphasis was placed on light intensity and temperature vagaries of roosting sites as possible determinative factors in roost selection.

2. Materials and methods

Studies were conducted in various bat roosts from April 1978 through April 1979 in Madurai District (9° 58′ N, 78° 10′ E). Colony morphology and composition are given in table 1.

The climate is that prevailing in tropical plains, consisting of a long, hot and dry summer. Temperature of 37–40°C may prevail for several days. Precipitation occurs primarily during September through December. The most striking feature is that these months may pass with little or no rain (Meher–Homji 1978). Temperature and humidity in the roosts were recorded with automatic Lambrecht KG, Goettingen Type 252 UA, thermohygrographs. Special temperature probes were used as necessary.

Light intensity profiles in the roosting areas were measured using an AEG lux meter and a UDT (40 lux) optometer. Light intensity profiles were obtained from dawn to dusk as measured in the region of the caves where the first cluster of bats are found. Their general behaviour were studied using a noctovision sniperscope (home made). Meteorological data (wind speed, wind direction, precipitation, ambient temperature and humidity) were obtained from the Meteorological station of the Department of Animal behaviour, School of Biological Sciences, Madurai Kamaraj University, Madurai.

3. Results

The mean ambient air temperature and humidity outside the roosts fluctuated widely from 20·6–36·4°C and 25–95% respectively during the study period (figure 1A), while the roosts showed relatively constant temperature. The patterns of temperature change in the roosting sites of study subjects are given in figures 1 and 2.

The constancy of temperature was well pronounced in those caves inhabited by *H. speoris* and *H. bicolor*, at KKK (figures 1B and 2), where the absolute temperature is much lower and more constant than the ambient temperature. Over an year the mean recorded temperature in those roosts was 27°C. However, at KKB and KHC where *H. speoris* roosts, the temperature was higher at a relative constancy of 30°C (figure 2).

Caves occupied by *M. lyra* showed temperature variations of 1·5–2°C at SLP and PM whereas the range of variations exceeded approximately to 7°C at KKK (figures 1 and 2). Of particular interest was the maximal temperature fluctuations of the diurnal roost of *M. lyra* which occurred during the months of April and November. Typically on 16 April 1978 the highest temperature recorded was 30·5°C at mid-day at SLP and the lowest temperature for the rest of the day was 30°C.

In crevices inhabited by *T. melanopogon* the temperature variations were moderate, ranging from 5–6°C during the months of March through December in contrast to the much more marked variations of the ambient temperature outside

Table 1. Population size (approximate) of the various species and a brief description of their roosting sites.

Location	Species	Population		Nature of roosting site
Keela Kuyil Kudi (KKK)	*Hipposideros speoris*	ca. 500–600	Cave	Dark: temperature and humidity constant
–"–	*Hipposideros bicolor*	ca. 150	Cave	–"–
–"–	*Hipposideros speoris*	ca. 50	Cave	–"–
–"–	*Megaderma lyra*	ca. 20–30	Cave	Well lit and temperature constant
–"–	*Taphozous melanopogon*	ca. 70	Creek	–"–
Kanavai Katha Bootham (KKB)	*Rhinopoma hardwickei*	ca. 1500	Cavern	–"–
–"–	*Hipposideros speoris*	ca. 1000	Cave	Dark: polluted by NH_3, temperature constant
Pulian Kulam (PKM)	–"–	ca. 100	Crevice	Well lit and temperature constant
Kennet Hospital Cellar (KHC)	–"–	ca. 30	Cellar	Dimly lit and temperature constant
Pannian Malai (PM)	*Megaderma lyra*	ca. 200	Cave	Dark and temperature constant
	Hipposideros speoris	ca. 400		
	Rhinopoma hardwickei	ca. 400		
Seelayampatti (SLP)	*Megaderma lyra*	ca. 20	Temple roost	Well lit and temperature constant

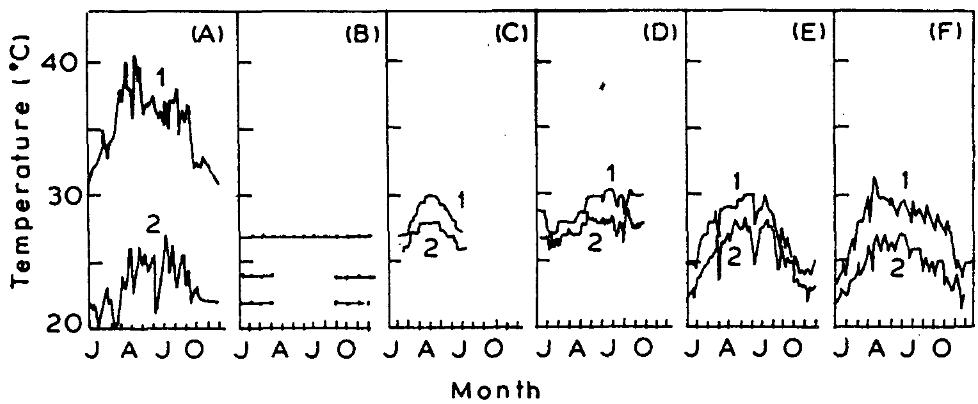

Figure 1. Patterns of ambient temperature recorded at the meteorological station with a thermograph and at various roosting sites inhabited by different species of bats for a period of one year (1978–1979). Maximum and minimum temperatures are shown as continuous and broken lines respectively. **A.** Maximum and minimum temperatures of the outside environment. Temperatures at the roosting sites inhabited by; **B.** *H. speoris* at KKK (●) and *M. lyra* at PM (-●-); **C.** *H. speoris* at KHC; **D.** *R. hardwickei* at KKB; **E.** *M. lyra* at KKK; **F.** *T. melanopogon* at KKK.

approximately upto 13°C. Over a 24 h period the temperature within the crevice showed only minor variations which ranged from 2–3°C.

R. hardwickei preferred a different type of roost. Even during the hot summer days, the mean temperature variation was only 2·5°C at the roost. These animals moved daily deeper inside the cave or crevice from the original roosting sites and selected areas where temperature fluctuations were insignificant. For example on 21 March 1979 the temperature at the mouth of the crevice ranged from 26–32°C (figure 3) but the magnitude of temperature variation was less at a place 5·5 m interior. The temperature at the deepest part of the crevice, which is approximately 14·5 m from the entrance where the bats were found most of the day, was between 27 and 29°C. The bats progressively moved to cooler places, thus covering various areas in the crevice in the course of the day (figure 3).

Light intensity profiles are shown in figure 4 for all the roosting areas. The caves occupied by *T. melanopogon*, *R. hardwickei* and *M. lyra* are well lit during the day light hours, the intensity of light varying between 0·1 and 115 lux, 0·3 and 24 lux and 0·05 and 0·6 lux respectively. A cave that is occupied by *H. speoris* at KKK characterized absolute darkness (1000 s exposure of the photo element registered no light at all). However, caves such as the PKM occupied by the same species is well lit throughout the day. The variations recorded from dawn to dusk ranged between 1·3 and 18 lux.

4. Discussion

The study reveals that most species of bats occupy regions of the roosts, where temperature fluctuation is relatively insignificant (figures 1–3). Similar temperature preference by pallid bats is known to some extent (Vaughan and O'Shea 1976). Vaughan and O'Shea (1976) recorded the temperature in a grotto which varied by

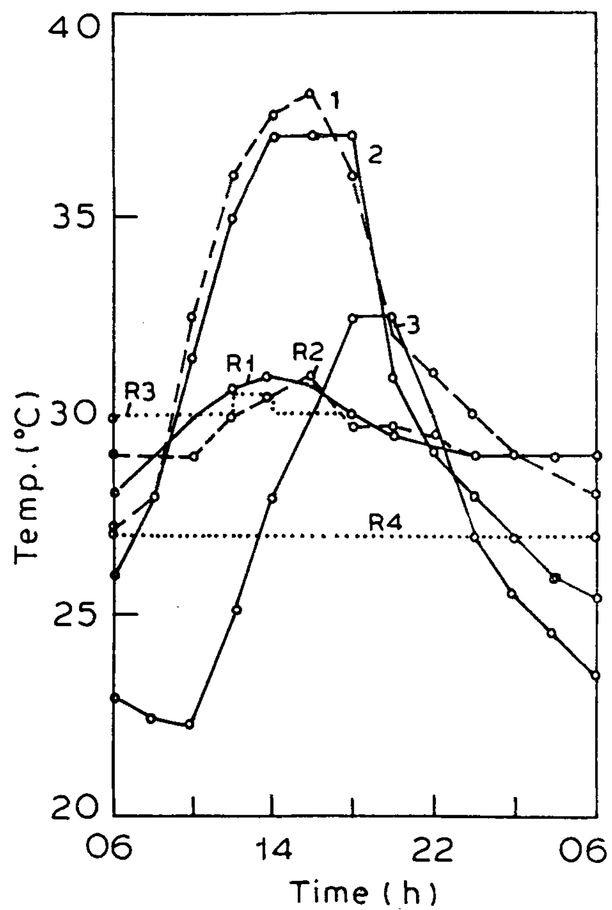

Figure 2. Patterns of ambient temperature recorded with a thermograph at the meteorological station on February 28(3), April 15(2) and April 16(1). R_1-daily profile of temperature of the cave inhabited by *H. speoris* at PKM; R_2-daily profile of temperature of the roosting site inhabited by *H. speoris* at KKB; R_3-daily profile of temperature of the roosting site inhabited by *M. lyra* at SLP; R_4-daily profile of temperature of the cave inhabited by *H. bicolor* at KKK.

only 0·8°C over a 24 h cycle. In addition to this favourable stable temperature pallid bats cluster and as a result decrease the total surface area exposed per bat (Vaughan and O'Shea 1976). The metabolic cost is greatly reduced by formation of large colonies and clustering behaviour and choice of roost configuration that maximise retention of dissipated heat (Tuttle 1975). Such clustering was not noticed among the bats studied by me. If the roosting microclimate is affected, only the alternate roosting sites can afford better protection as reported for *Myotis sodalis* by Humphrey *et al* (1977) and the African yellow winged bat *Lavia frons* (Vaughan and Vaughan 1986). For instance the relative scarcity of free-tailed bats *Tadarida* species (Davis *et al* 1962) where the temperature is above 30°C suggest the occurrence of some temperature selection. Similar roosting site preference as per the environmental factors is reported in Jamaican bats also (Goodwin 1970). Even though the different roosting areas of *H. speoris* have different roost temperature,

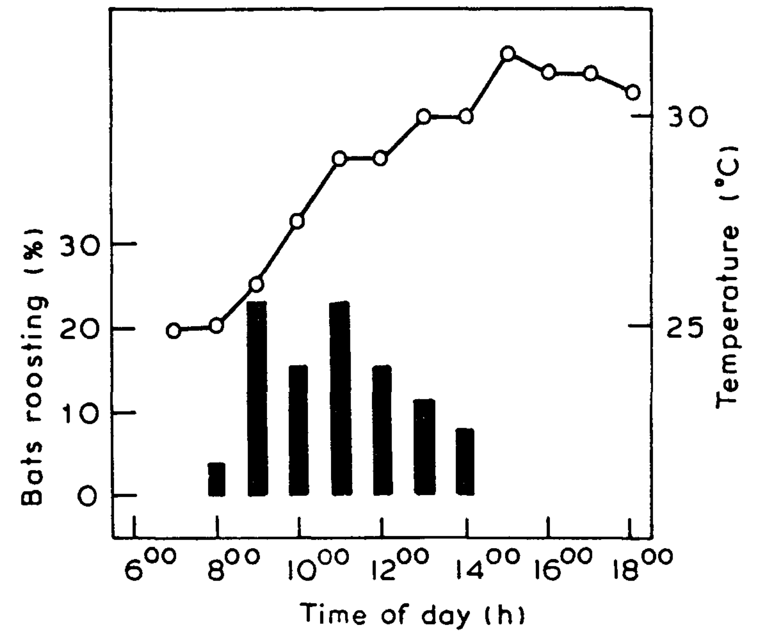

Figure 3. The line shows increase in the temperature 2 meters into the cave during daylight hours. The histogram denotes the number of bats roosting around the spot where the thermograph was placed. Note that temperature increased from 25–32°C and movement of bats to deeper parts of the caves is reflected in declining numbers where the thermograph was located.

the relative constancy of temperature is significant. This condition of thermal neutrality promotes the maintenance of homeothermy and rapid growth in the young (Kunz 1973). The thermal neutrality is particularly important for some of the tropical bats are continuous breeders.

Marked temperature fluctuations are not suitable for the roosts (O'Farrell and Bradley 1970). In some instances temperatures within the caves may vary greatly over the seasons and depending upon the patterns of air circulation within the caves. In such a situation, bats possibly move to cooler sites in the roosts at times of 'heat stress'. In roost flying also increases the surface area for heat loss and the bats seem to be able to reduce their body temperature (Herreid 1963). Bats prefer a constant temperature surrounding even at the expense of their metabolic energy. So it is not surprising to find that cave bats select temperature constancy even within the cave system. Some bats in the day roosts, for e.g. *T. melanopogon* and more particularly *R. hardwickei* are able to reduce the environmental stress by behavioural means like selecting the areas of the caves where the temperature does not fluctuate significantly.

Such diurnal thermo-regulatory movements have also been described in some insectivorous bats (Licht and Leitner 1967). These intra-roost migrations form a compromise between avoidance of fluctuating temperature and protected roosts. Downward movement from the roof of the cave and progress into the interior recesses of the cave when the sun is in its zenith are common and regular occurrence among the bats studied. They remained as one group and 'cooling off'

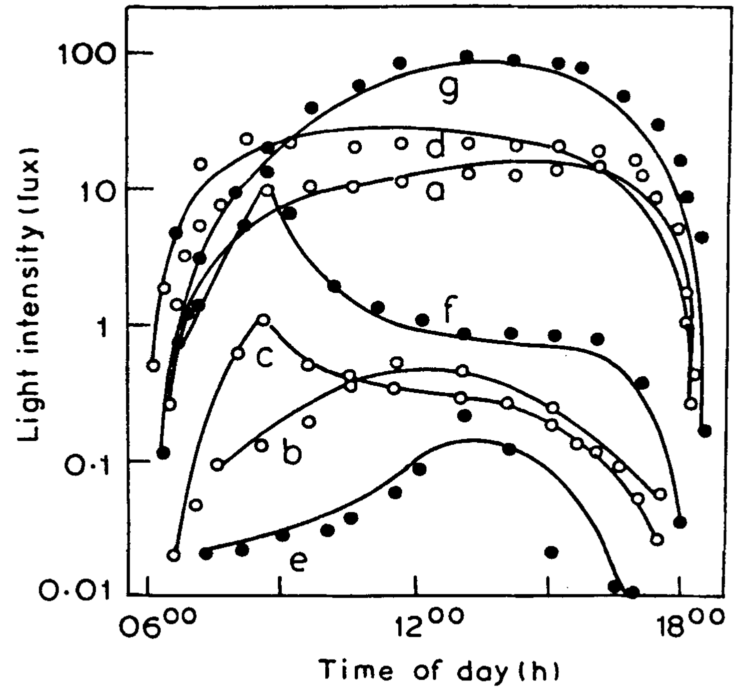

Figure 4. Variations in the light intensity of various roosting sites. **a.** *R. hardwickei* at KKB; **b.** *H. speoris* at KKB; **c.** *H. speoris* at KHC; **d.** *H. speoris* at PKM; **e.** *H. speoris*; **f.** *M. lyra* at KKK; **g.** *T. melanopogon* at KKK.

flights were very meagre. This is in full agreement with the view of Studier and O'Farrell (1972) that behavioural thermoregulation by 'in-roost movements' is as important as physiological thermoregulation in providing these bats a survival value. Such downward movement to the floor and breaking of tight clusters are reported in *Myotis nigricans* (Wilson 1971; Wilson and Laval 1974).

A high degree of humidity is required by tropical bats (Brosset 1962) but not essential for specialised functions as hibernation (Fenton 1970). Temperature seems to be a prime factor in the roosting ecology of bats since *R. hardwickei* and *T. melanopogon* live under relatively less humid regions. These bats can also be observed in well lit places, while *H. speoris* are found in total darkness in diurnal haunts (figure 4). Darkness is no doubt a favourable factor because of the protection from predation. Kunz (1973) even reported that at Wilmore, bats occupied dimly lighted areas and the darkest areas were not occupied. Tropical bats, however, do roost in the darkest places of the caves provided they have access to relative temperature constancy.

Both rapid dissipation of body heat in the morning prior to torpor through most of the day and passive warming in the evening prior to taking to flight depend upon the ability of the bats to position themselves appropriately in the thermal gradient in roosts (Studier and O'Farrell 1972). This is also the case of tropical bats where warming up prior to flight is achieved by moving to the proximity of the cave mouth. It serves dual purpose of warming up the body and 'light sampling' (Twente 1955) without departing from the roosts (Kunz 1974). Interestingly *H. speoris* which have colonized in Madurai cave environments where the temperature is virtually invariant also do not move about in the cave. In fact, these bats show a remarkable sense of 'personal space' and site fidelity and roost in them day after day (Selvanayagam and Marimuthu 1984). *R. hardwickei* as noted earlier resorts to behavioural thermoregulation to some degree and as a consequence denies itself a right to place fidelity and personal space.

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References

Brosset A 1962 The bats of central and western India part I; *J. Bombay Nat. Hist. Soc.* **59** 1–57

Davis W H 1970 Hibernation: ecology and physiological ecology; In Biology of Bats (ed.) W A Wimsatt (New York: Academic Press) **1** 265–300

Davis R B, Herreid C F and Short H L 1962 Mexican free-tailed bats in Texas; *Ecol. Monogr.* **32** 311–346

Fenton M B 1970 Population studies of *Myotis lucifugus* (Chiroptera: Vespertilionidae) in Ontario; *Life Sci. Contr. R. Ont. Mus.* **77** 1–34

Goodwin R E 1970 The ecology of Jamaican bats; *J. Mammal.* **51** 571–579

Greenhall A M and Paradiso J L 1968 Bats and bat banding; *Bur. Sport Fish. Wildl. (US) Res. Rep.* **72** 1–46

Herreid C F 1963 Survival of migratory bat at different temperatures; *J. Mammal.* **44** 431–433

Humphrey S R, Richter A R and Cope J B 1977 Summer habitat and ecology of the endangered Indiana bat *Myotis sodalis*; *J. Mammal.* **58** 334–346

Klopfer P H and Hailman J P 1965 Habitat selection in birds. In *Advances in the study of behaviour* (eds) D S Lehrman, R A Hinde and E Shaw (New York: Academic Press) **1** 279–303

Kunz T H 1973 Population studies of the cave bat (*Myotis velifer*): reproduction, growth and development; *Mus. Nat. Hist. Univ. Kans.* **15** 1–43

Kunz T H 1974 Feeding ecology of a temperate insectivorous bat (*Myotis velifer*); *Ecology* **55** 693–711

Licht P and Leitner P 1967 Behavioural responses to high temperatures in three species of Californian bats; *J. Mammal.* **48** 52–61

McNab B K 1982 Evolutionary alternatives in the physiological ecology of bats. in *Ecology of bats* (ed.) T H Kunz (New York, London: Plenum Press) pp 151–200

Meher-Homji V M 1978 Ecological climatography and vegetation cartography; *Proc. School Plant Ecol.* 26–42

O'Farrell M J and Bradley W G 1970 Activity patterns of bats over a desert spring; *J. Mammal.* **51** 18–26

Schoener T W 1971 Theory of feeding strategies; *Annu. Rev. Ecol. Syst.* **2** 369–404

Selvanayagam P F L and Marimuthu G 1984 Spatial organization of roosting in the insectivorous tropical bat *Hipposideros speoris*; *Behav. Processes* **9** 113–121

Stones R C and Wiebers J E 1965 A review of temperature regulation in bats (Chiroptera); *Am. Midl. Nat.* **74** 155–167

Studier E H and O'Farrell M J 1972 Biology of *Myotis thysanodes* and *M. lucifugus* (Chiroptera: Vespertilionidae) I. Thermo-regulation; *Comp. Biochem. Physiol.* **A41** 567–595

Tuttle M D 1975 Population ecology of the gray bat (*Myotis grisescens*): Factors influencing early growth and development; *Occas. Pap. Mus. Nat. Hist. Univ. Kans.* **36** 1–24

Twente J W 1955 Some aspects of habitat selection and other behaviour of cavern-dwelling bats; *Ecology* **36** 706–732

Vaughan T A and O'Shea T J 1976 Roosting ecology of the pallid bat *Antrozous pallidus*; *J. Mammal.* **57** 19–42

Vaughan T A and Vaughan R P 1986 Seasonality and the behaviour of the African yellow-winged bat; *J. Mammal.* **67** 91–102

Wilson D E 1971 Ecology of *Myotis nigricans* (Mammalia: Chiroptera) on Barro Colorado Island, Panama Canal Zone; *J. Zool. Proc. Zool. Soc. London* **163** 1–13

Wilson D E and Laval R K 1974 *Myotis nigricans*; *Mamm. Species* **39** 1–3