# TEMPERATURE REGULATION AND CAVE-DWELLING
# IN BATS : AN EVOLUTIONARY PERSPECTIVE

by

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Dans cette étude les chauves-souris sont réparties en trois groupes : celles qui sont incapables de maintenir leur température interne au-dessus de la température ambiante pendant une période d'inactivité, celles qui peuvent tomber en léthargie mais sont capables également d'une certaine homéothermie, et les homéothermes parfaits. Une répartition de ces différents groupes en fonction de l'habitat et du climat est envisagée. L'auteur avance également des hypothèses sur l'évolution de la thermorégulation chez les chauves-souris et sur leur adaptation à la vie cavernicole qui ne semble pas avoir joué de rôle significatif dans cette évolution. La faculté de tomber en léthargie serait plus marquée chez les chauves-souris les plus évoluées, les homéothermes parfaits appartenant à des groupes plus « conservateurs ».

While agreeing with Birch and Ehrlich (1967) that « we cannot know the past » I am of that class of biologists who are chronically afflicted by a desire to pattern observations in time. The observations for evolutionary interpretation in this paper relate to bats. This large order of mammals exhibits an extraordinary range of dietary preferences, of foraging and roosting habits, and of reproductive and thermoregulatory patterns ; it includes migratory and non-migratory species and embraces several distinctive forms of social organization (Allen 1939, Bradshaw 1962, Dwyer 1970, Griffin 1958, Stones and Wiebers 1965, Wickler and Uhrig 1969). These adaptive modes have emerged and been refined in the course of more than 60 millons years. They have not left a significant record of their past. Any attempt to give them an evolutionary basis must, therefore, take cognisance of several points. (1) Morphological evidence has not yielded a clear picture of the phylogenetic relationships of chiropteran families. Hence a conventional yardstick against which a particular class of adaptive strategies may be ranked is largely unavailable (c.f. Cade 1964). (2) When a major energetic parameter of an organism has had a long history and has emerged via a temporally diverse sequence of selective forces it may show little impress of its more distant past. I find myself si-

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multaneously in accord with McNab (1969) when he writes that « energetics is closely attuned to conditions in the environnement » and with Irving (1969) when he writes that populations « must always adapt to specific natures that are derived from their past » and I find the conjunction of these statements of especial relevance in attempting to understand the evolution of bats.

Here I am primarily concerned with thermoregulatory patterns and the habit of cave-dwelling in bats. Twente and Twente (1964) and McNab (1969) have discussed these in an evolutionary context but I find myself in substantial disagreement with their conclusions. Briefly, Twente and Twente argue that « heterothermy » in bats arose from a condition of homeothermy and as an adaptation to roosting in cool microenvironments, especially of caves, while McNab argues that « torpor » evolved in the tropics as an adaptation by small insectivorous bats to periods of food scarcity ; he implies that « torpor » is derived from a homeothermic state. An alternate view, that « torpor » (or « heterothermy ») is a « primitive » characteristic of bats has been proposed by several authors (e.g. Eisentraut 1960, Hock 1951, Kulzer *et al.* 1970) but has not been elaborated and has failed to satisfactorily account for the rather specialized concomitants of torpor (e.g. spontaneous arousal, endocrine changes in relation to hibernation, etc.) in this group. McNab's (*op. cit.*) thesis embodies greater sophistication than any others dealing with these questions and in large part the present paper is in reply to his views. In developing my own interpretation I shall indicate relevant points of disagreement with previous writers. The alternative approach of directing counter-arguments at specific areas is largely unavailable for where there are few historic facts there is no opportunity for disproof. The strength of an evolutionary explanation lies in its capacity to accommodate information (Hull 1967) and it is often only in these terms that an interpretation of historic events may be assessed or that disagreement with earlier hypotheses may be judged.

I first consider some essentially ecological relationships between thermoregulatory patterns and the habit of cave-dwelling in bats. Subsequently I hypothesize the evolutionary background to each of these. In large part the former section provides the comparative base for the latter section. Some cautionary remarks are necessary from the outset. I have deliberately employed an oversimplified view of the cave environment and I have consciously imposed a classificatory rigidity that does not exist upon thermoregulatory patterns. By doing this I have found it easier to emphasize primary adaptive strategies and historic themes. My aim at this time is to arrive at an overview. But I have attempted to achieve « openness »

of explanation in the sense that where the need for modification, or refinement, arises in consequence of my conscious simplification then the direction of this is implicit in the explanation I propose. Table 1 lists taxa cited in the text and indicates their thermoregulatory mode.

TABLE 1

Taxa cited in text with indication of thermoregulatory
mode where this is known

| | | |
|---|---|---|
| *Superfamily Pteropopoidea* | | |
| Family Pteropodidae | *Pteropus poliocephalus* | Group 3 |
| | *Rousettus* | Group 3 |
| | *Dobsonia* | |
| | *Eonycteris* | |
| | *Notopteris* | |
| *Superfamily Rhinopomatoidea* | | |
| Family Rhinopomatidae | | Group 3 |
| Family Emballonuridae | *Taphozous melanopogon* | Group 3 |
| Family Noctilionidae | *Noctilio labialis* | Group 3 |
| | *Noctilio leporinus* | Group 3 |
| *Superfamily Rhinolophoidea* | | |
| Family Megadermatidae | *Macroderma gigas* | Group 3 |
| Family Nycteridae | | |
| Family Rhinolophidae | *Rhinolophus ferrum-equinum* | Group 2 |
| | *Rhinolophus hipposideros* | Group 2 |
| | *Rhinolophus megaphyllus* | Group 2 |
| Family Hipposideridae | | Group 2 |
| *Superfamily Phyllostomoidea* | | |
| Family Phyllostomatidae | *Carollia perspicillata* | Group 2 |
| | *Tonatia bidens* | Group 3 |
| | *Leptonycteris sanborni* | Group 3 |
| Family Mormoopidae | | Group 2 |
| *Superfamily Vespertilionoidea* | | |
| Family Vespertilionidae | | |
| Subfamily Vespertilioninae | *Myotis lucifugus* | Group 1 |
| | *Myotis myotis* | Group 2 |
| | *Myotis emarginatus* | Group 1 |
| | *Eptesicus fuscus* | Group 2 |
| | *Eptesicus pumilus* | Group 1 |
| | *Histiotus* | Group 2 |
| | *Chalinolobus* | Group 1 |
| | *Lasiurus* | Group 1 |
| Subfamily Miniopterinae | *Miniopterus schreibersii* | Group 2 |
| | *Miniopterus australis* | Group 2 |
| Family Mystacinidae | | |
| Family Molossidae | *Eumops perotis* | Group 2 |
| | *Tadarida brasiliensis mexicana* | Group 2 |

## WHAT CAVES MEAN TO BATS

### PREAMBLE

Cave temperatures, especially of the deep interior, approximate the mean annual temperature (MAT) of the region in which the cave is found. Towards the entrance (or entrances) of a cave the temperature becomes increasingly variable showing seasonal fluctuations that follow those of the surface but which are buffered from surface extremes. The magnitude of these fluctuations will vary with the size of the cave, with depth into the cave, with the size and number of entrances, with the presence of streams or rivers running through the cave, etc. Caves with a single entrance that slopes steeply downward may be consistently cooler than MAT. Cave-dwelling bats are most abundantly represented in the variable temperature zone of caves beyond the twilight areas. A given species may, however, select a narrow range of temperatures within this zone.

Bats exhibit a wide range of thermoregulatory patterns. Current understanding of the body temperature processes of bats, especially as regards their propensity for torpor, suggests three primary groupings.

(1) Species that enter torpor readily at low ambient temperatures $(T_a)$ and, in general, appear to be incapable of sustaining a body temperature $(T_b)$ much in excess of ambient if they are inactive for a prolonged period of time. This group may be characterized by *Myotis lucifugus* (Henshaw and Folk 1966, Hock 1951).

(2) Species that are able to voluntarily enter torpor but are also able to maintain high $T_b$ when inactive at quite low $T_a$. This group is characterized by *Miniopterus schreibersii* which may regulate $T_b$ at 30°C for $T_a$'s as low as 10°C (Morrison 1959, Shimoizumi 1959a) ; this temperature is some 10°C lower than $T_b$ during flight. At temperate latitudes this is the usual behaviour of the species in summer (Dwyer 1964, Shimoizumi 1959a). The winter torpor of *M. schreibersii* at temperate latitudes is more intermittent than that shown by bats of Group 1.

(3) Species that do not voluntarily enter torpor and may, in fact, regulate $T_b$ precisely at high levels over a range of activity states. This group is chracterized by *Pteropus poliocephalus* and *Macroderma gigas* (Bartholomew *et al.* 1964 ; Leitner and Nelson 1967). *P. poliocephalus* has some ability to maintain $T_b$ below $T_a$ at extreme levels of $T_a$; in *M. gigas* this ability is less evident.

It is apparent from some recent studies that a range of condi-

TABLE 2. — The occurrence of bats in caves by latitude
according to thermoregulatory mode (MAT equals mean annual temperature)

| Cave type: | Thermoregulatory pattern | | |
|---|---|---|---|
| | Group 1 | Group 2 | Group 3 |
| | (1) Obligate heterotherm<br>(2) Inactive; $T_b \simeq T_a$<br>(3) Insectivorous | (1) Voluntarily enter torpor<br>(2) Inactive; $\Delta T$ may be large<br>(3) Insectivorous | (1) Obligate homeotherm<br>(2) Inactive; $T_b$ generally independent of $T_a$<br>(3) Varied diet |
| Very high latitudes<br>MAT < 2°C | Too cold in winter<br>Too cold in summer<br>Very few bats present | Too cold in winter<br>Too cold in summer | Diet prevents representation of Group 3 Bats at high latitudes. High cost of thermoregulation would render caves unsatisfactory as roosting places. |
| High latitudes<br>MAT 2-12°C | Good for hibernation<br>Too cold in summer<br>Group 1 bats dominant in caves at these latitudes | Increasing cost of thermo-regulation in summer with decreasing MAT limits occurrence of Group 2 bats in high latitude caves. | |
| Middle latitudes<br>MAT 12-22°C | Generally too warm in winter<br>Generally too cool in summer<br>Group 1 bats increasingly represented as MAT increases; avoid caves in times of food scarcity. Unlikely to be abundant. Preference for entrance regions likely. | Group 2 bats dominant at these latitudes; behavioural patterns compensate for "unfavourable" environment. | Group 3 bats poorly represented. Primary restriction on occurrence is diet rather than thermoregulatory mode. |
| Low latitudes<br>MAT >22°C | | Group 2 bats well represented at these latitudes; little necessity for behavioural adaptations. | Group 3 bats well represented at these latitudes; cave environment does not dictate presence or absence. |

tions may occur between Group 1 bats and Group 3 bats;this being expressed in terms of the magnitude of $\Delta T$ ($T_b$ — $T_a$) for particular values of $T_a$ (see Kulzer *et al.* 1970, McNab 1969). For example, several species (e.g. *Carollia perspicillata*) show highly variable responses to a declining $T_a$, some individuals maintaining a high and regulated $T_b$ and others maintaining a small $\Delta T$ as $T_a$ decreases (Studier and Wilson 1970); such species are classed in Group 2. *Eumops perotis* in California behaves as a Group 2 bat but when regulating $T_b$ while inactive it does so at higher levels than are evident for *M. schreibersii* (Leitner 1966). Certain species that show « relaxation » of $T_b$ at intermediate levels of $T_a$ but which return to high $T_b$ as $T_a$ falls rather than enter torpor (e.g. *Tonatia bidens,* McNab 1969) are classed here as Group 3 bats.

At high latitudes bats are faced by two problems that do not exist to the same degree in the tropics. Firstly, all bats at high latitudes are aerial insectivores and a winter food source is virtually non-existent. (In New Zealand *Mystacina* may be in part arboreal, or terrestrial, and may have other winter sources of food available Dwyer 1962). Hibernation or migration are strategies adopted to meet this problem. For most hibernating bats temperatures at hibernacula are in the range 2° to 12°C (Griffin 1958). Secondly, the diurnal metabolic requirements (e.g. digestion, mating and especially nursing of young) of high latitude species in summer and of low latitude species throughout the year call for at least moderately high $T_b$ (about 30°C or higher) (Menaker 1962) ; the actual temperature required probably varies between species. Small bats of Group 1 must, therefore, select sites offering appropriately high $T_a$ and, in general, it may be assumed that such sites will be less abundant at high latitudes than at low latitudes. In this regard the literature has tended to overemphasize the daily rhythm of torpor in temperate latitude Group 1 species ; their usual behaviour in summer is to avoid torpor by selecting high $T_a$ (Menaker *op. cit.*)

On the basis of the above points it is possible to predict relationships between mode of thermoregulation and the occurence of bats in caves according to latitude. The explanation developed below assumes firstly that cave temperatures approximate MAT of the region concerned and secondly that cave-dwelling bats thermoregulate in one of the three ways described above. Table 2 summarizes the major themes of my explanation.

### PREDICTION

*Group 1 bats.*

At very high latitudes (MAT <2°C) caves will be completely

inappropriate to the summer requirements of these bats and, with the exception of rare microsituations, will be too cold to serve as safe hibernacula. Bats of this group should, therefore, be rare in caves at very high latitudes and, in winter, would either select suitable hibernating quarters outside caves, move to cave hibernacula at somewhat lower latitudes, or migrate to feeding areas at even lower latitudes. At high latitudes (MAT 2-12°C) caves provide appropriate hibernating quarters for bats of this group but are extremely unlikely to provide suitable summer quarters. At these latitudes a long term process of trial and error could lead to the repetitive use of a few « safe » hibernacula by a high proportion of the population in any given area with the consequence that a pattern of winter aggregation and summer dispersion could emerge (see Davis and Hitchcok, 1965, for *M. lucifugus*). In the middle latitudes (MAT 12-22°C) caves may be best described as too hot in winter and too cold in summer for bats of this group. In this latitude range, however, caves with several large entrances may offer a greater range of temperatures than enclosed caves and it may be expected, therefore, that sufficient microsituations will be available to accommodate numbers of at least some species. At lower MAT there would be a higher probability that appropriate hibernating quarters might exist while at higher MAT there would be a higher probability that appropriate summer quarters would exist. At low latitudes (MAT > 22°C) the status of Group 1 bats with regard to cave-dwelling is not immediately obvious. In general bats of this group are small (< 20g) and insectivorous. A low $T_b$ could be advantageous to them in times of food scarcity (McNab 1969) and it is probable that both cooler and warmer situations exist outside caves than exist inside. Cave temperatures would prohibit low $T_b$ and hence the cave environment might impose a serious metabolic drain in periods of food scarcity ; nor would cave temperatures, in general, be high enough to satisfy diurnal metabolic needs of Group 1 bats during periods of food abundance. (Note that at low latitudes seasonal variation in temperature is markedly less than at higher latitudes ; this will have the effect that the range of cave temperatures, especially near entrances, available to low latitude bats will be substantially reduced.) On these bases I would predict an increase in the tendency for Group 1 bats to be cave-dwelling at low latitudes but would not expect cave-dwelling to emerge as a dominant pattern.

*Group 2 bats.*

While bats of this group are able to maintain a high $\Delta T$ at low $T_a$ it is clear that the cost of thermoregulation will increase as

$T_a$ decreases and, hence, that while Group 2 bats may use caves as summer roosting places at latitudes where Group 1 bats are excluded in this season, caves will become increasingly inappropriate as summer roosting places as latitude increases. At very high latitudes cave temperatures will again be too low to allow hibernation. At high latitudes hibernation in caves would be possible but inasmuch as the winter torpor of Group 2 species is necessarily intermittent (cf. *M. schreibersii*) then they may be excluded from high latitude caves in winter because very little food is available. During the winter, therefore, caves at high latitudes may be more appropriate to Group 1 bats than to Group 2 bats. It is in the middle latitudes that this relationship should reverse. This would apply particularly in the summer ; caves at these latitudes are too cold for Group 1 bats in summer but may not impose too serious a burden on Group 2 bats. There will, however, be some energy cost for Group 2 bats ; this will depend in part upon the size of the species concerned and in part upon the magnitude of $\Delta T$. We may expect firstly that larger species of this group will extend into higher latitudes than smaller species and secondly that species of this group might minimize thermoregulatory cost by selecting sites such that $\Delta T$ was reduced. This could be achieved in several ways ; selection of the warmest caves available within the region concerned and the warmest sites within these caves, by clustering for insulation, and by direct modification of $T_a$. In New South Wales (lat. 28-32°S) *M. schreibersii* behaves in all these ways in summer. Direct modification of $T_a$ is achieved by clustering in ceiling depressions or domes ; the air in these sites is warmed as a result of heat loss from the bats, the interval between $T_a$ and $T_b$ is thereby reduced and the cost of thermoregulation reduced. On two counts the situation described here may be insufficient to the requirements of rearing young. Firstly, the new-born young of small bats approach the minimum weight at which a homeotherm can regulate $T_b$ (see Lasiewski 1963, Pearson 1948) and, secondly, it is apparent from several studies and from many field observations that late pregnant and lactating female bats must maintain high body temperatures (Kolb 1950, Stones and Wiebers 1967, Wimsatt 1969). If Group 2 bats are to remain in caves at middle latitudes for these phases of reproductive activity they must ensure that their young are born and nursed in appropriate situations. Selection of especially warm sites or gross modification of $T_a$ would be called for. In *M. schreibersii* in south-eastern Australia gross modification of $T_a$ is accomplished by establishing very large nursery colonies in caves of such a structure that they serve to trap the heat generated by thousands of individuals (Dwyer and Hamil-

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ton-Smith 1965). In the same way that Group 1 bats, at high latitudes, might become dependent upon relatively few hibernacula we can predict that Group 2 bats, at middle and high latitudes, might become dependent upon relatively few nursery caves and might exhibit a pattern of summer aggregation and winter dispersion. In the middle latitudes Group 2 bats may solve the problems imposed by winter in one of two ways ; they may migrate to lower latitudes where a regular food supply is available or they may combine rigorous selection of the coolest situations available with intermittent feeding in favourable conditions. *M. schreibersii* has adopted the latter solution with the addition that fat reserves are laid down before winter. More fat is accumulated by populations living in colder regions than by those living in warmer regions (Dwyer 1964, 1966a ; Shimoizumi 1959b). At low latitudes Group 2 bats would be faced with fewer problems in choosing sites of appropriate temperature than exist in the middle latitudes. The higher temperatures of caves at these latitudes. would mean that $\Delta T$ was relativly small for Group 2 bats and that caves would be appropriate roosting places provided food was abundant. It would only be in periods of prolonged food scarcity that cave-dwelling bats of this group might have to vacate caves for cooler situations that allowed deeper torpor.

*Group 3 bats.*

Bats of this group should decline in abundance in the cave environment as latitude (and $\Delta T$), and hence the cost of thermoregulation, increases. The extent to which Group 3 bats penetrate high latitudes will be matched by greater exposure to an inadequate winter supply of food. This group includes species of diverse food habits ; frugivorous, nectarivorous, carnivorous, insectivorous. Since torpor does not occur in Group 3 bats their presence or absence at a given latitude range will depend importantly upon diet. Frugivorous and nectarivorous species will in general be restricted to relatively low latitudes unless they practice seasonal migration. Insectivorous species will be immediately excluded from areas of unreliable winter food unless migration occurs or fat is accumulated before predictable periods of food scarcity. Larger insectivores of this group could penetrate into higher latitudes than smaller species. Carnivores should theoretically be able to penetrate into higher latitudes than insectivores but since these species (Megadermatidae and a few Phyllostomatidae) are, in fact, largely insectivorous and since their carnivorous tendencies appear to be often directed at small insectivorous bats (Douglas 1967, Wal-

ker 1968) it is likely that their latitudinal range is ultimately determined by the availability of insects through the winter. For Group 3 bats, therefore, caves at low latitudes should provide appropriate roosting sites. At higher latitudes bats of this group will seldom occur in caves but this will stem more from the fact that they are excluded from the latitude range in question by reasons of diet than from the fact that the cost of thermoregulation in caves has increased. At low latitudes where Group 3 bats may be expected to be abundantly represented in caves there is no thermoregulatory basis for predicting a « seasonal » pattern of aggregation and dispersion.

## Water regulation.

Heat regulation and water regulation are correlated phenomena in vertebrates. In bats little attention has been directed to questions of water loss. Studies by Herreid and Schmidt-Nielsen (1966) and Carpenter (1969) have not revealed any special capacity to conserve water in desert-living bats. Herreid and Schmidt-Nielsen (1966) have demonstrated that torpid bats (*Tadarida mexicana* and *Eptesicus fuscus* ; Group 2) lost one third to one half as much water by evaporation as did active bats at $T_a$ below 30°C and, further, that the rate of water loss of *E. fuscus* in dry air would not allow a torpid individual to survive more than a few days. Their study permits two predictions of relevance to the present discussion. Firstly the hibernating quarters of Group 1 or Group 2 species must be humid and hence these bats will be exclused from especially dry caves at high latitudes and secondly cave-dwelling bats of Group 2 will be restricted to humid caves. In bats problems of water loss may, to a large extent, be offset by their ability to fly (Carpenter 1969). It is possible, however, that if a Group 2 species regularly occurs in dry caves, or if a small Group 3 species occupies dry caves at relatively high latitudes, special mechanisms for water retention may be found.

### VERIFICATION

It is not possible in the context of the present paper to provide a detailed demonstration of the extent to which the preceeding explanation is satisfied by current knowledge of bats. Number of species and number of cave-dwelling species increases toward the equator in both hemispheres (e.g. Hamilton-Smith 1966, Rosevear 1965, Ryberg 1947). This accords with expectation based on a the section in which the two portions of the figure overlap the data

is similar. In areas of low MAT (< 12°C) Group 1 bats predominate in caves ; they occur in humid caves through the winter and generally abandon them in summer (Bels 1952, and cf. Fenton 1970). In Holland summer colonies of *Myotis myotis* and *M. emarginatus* have been reported from caves (Bels 1952). *M. myotis* is, however, known to behave as a Group 2 bats (Hanus 1959) while *M. emarginatus* was found in direct (i.e. contact) association with a Group 2 species, *Rhinolophus ferrum-equinum* (Bels 1952). Commensalistic behaviour of this kind could obviate the necessity for a Group 1 species to abandon cold caves in summer ; the habit could emerge where Group 1 species and Group 2 species shared the same hibernating quarters. I have described other forms of apparent thermocommensalism in *Miniopterus* in New south Wales ; *M. schreibersii* will sometimes deposit its newborn young within a cluster of older young of *Rhinolophus megaphyllus* (Dwyer and Hamilton-Smith 1965) while at its southern limit of distribution *M. australis* appears to be dependent upon *M. schreibersii* to provide appropriate conditions for rearing young (Dwyer 1968). In areas of intermediate MAT (12-22°C) Group 2 bats (*Rhinolophus, Miniopterus*) predominate in caves, at least numerically, and utilize them in both the summer and the winter. In Australia the distribution of these species is clearly associated with humidity although *R. megaphyllus* appears to be more tolerant of dry caves and extends further into semi-arid areas (Halmiton-Smith 1966). Neither of these genera is migratory. The wintering behaviour of *Miniopterus* has been discussed above. In the middle latitudes *Rhinolophus* shows little prewinter increase in weight and feeds quite regularly through the winter (Dwyer 1966 *b*, Ransome 1968, Saint Girons *et al.* 1969). *Rhinolophus* may forage upon non-flying insects (Blackmore 1964) and it is likely, therefore, that a winter food source is more abundant than would be the case for a strictly aerial insectivore like *Miniopterus*. The American bat *Tadarida brasiliensis* is a Group 2 species that occurs in humid caves in the middle latitudes through the summer, that artificially warms nursery sites, and that avoids food scarcity through the winter by migrating to lower latitudes (Henshaw 1960, Herreid 1963*a, b*, 1967, Herreid and Schmidt-Nielsen 1966, Villa and Cockrum 1962). Through the middle latitudes there appears to be a change in the behaviour of those Group 1 bats that are cave-dwelling such that they cease to use caves as significant hibernacula and, instead, are found to be aggregated in caves through the summer and scattered inside and outside of caves through the winter. In eastern Australia *Eptesicus pumilus* is found outside caves through the entire latitudinal knowledge of species diversity for vertebrate groups generally

but, in terms of our present understanding of the ecology of bats, lies beyond explanation (cf. Tamsitt 1967). In northern Scandanavia the proportion of cave-dwelling species to the total bat fauna is low (i.e. 2 : 13 ; see Ryberg 1947) but further south (Holland and southern Scandanavia) the proportion rises dramatically (i.e. 9 : 15 ; Bels 1952, Ryberg 1947) without a substantive increase in number of species. This would be expected in terms of the foregoing discussion. In Australia there are no cave-dwelling species at latitudes higher than 40°S (i.e. in Tasmania). The high latitude pattern of winter aggregation in caves and summer dispersion outside caves is not found in Group 1 bats in eastern Australia. This is because few caves are available that provide consistently low temperatures and these are highly localized in their distribution. A bat will not simply occupy a cave because it provides an appropriate temperature environment ; the habit of cave-dwelling is part of the genetic endowment of a species and is unlikely to develop unless there are sufficient suitable caves available in a sufficiently large region.

Figure 1 compares data for selected regions in Europe and Africa with data for latitudes of comparable MAT in eastern Australia. The cave-bats of the areas considered are included in the following familial or subfamilial taxa : Pteropodidae, Rhinopomatidae. Emballonuridae, Nycteridae, Megadermatidae, Rhinolophidae, Hipposideridae, Miniopterinae, Vespertilioninae, and Molossidae. Not all species concerned have been investigated for their thermoregulatory behaviour but the following classification is suggested from knowledge currently available ([1]) : Species of Pteropodidae, Rhinopomatidae, Emballonuridae and Megadermatidae behave as Group 3 bats ; (some neotropical emballonurids seem not to behave in this way ; McNab 1969, Studier and Wilson 1970). Species of Rhinolophidae, Hipposideridae, Miniopterinae and Molossidae behave as Group 2 bats while it is only the Vespertilioninae (with some known exceptions) that may be classed as Group 1. Torpor has not been observed in the Nycteridae but no detailed information is available ; it is unlikely that they are Group 1 bats (McNab 1969) and in the analysis they have been placed between Group 2 and Group 3 species. The figure shows the proportion of cave-dwelling species belonging to each of the groups defined above. For range but becomes a common cave-dwelling species once the MAT approaches or exceeds 18.5°C. Aggregation is pronounced in the

(1) This summary is based on the observations and conclusions of many authors (e. g. Bartholomew et al. 1964 ; Brosset 1961 ; Eisentraut 1960 ; Hanuš 1959 ; Kulzer 1963, 1965 ; Kulzer et al. 1970 ; Leitner and Nelson 1967 ; Morrison 1959 ; Saint Girons et al. 1969 ; Shimoizumi 1959 a).
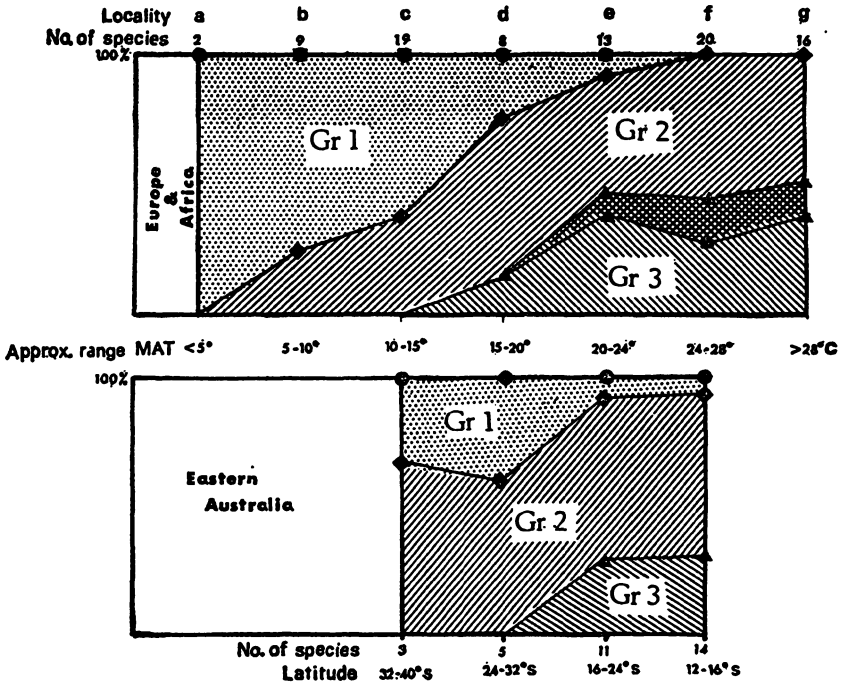
MAMMALIA



Fig. 1. — Percentage of Group 1, 2 and 3 bats in the cave-dwelling fauna of
eastern continental Australia and regions of comparable mean annual tem-
perature (MAT) in Europe and Africa. For Europe and Africa localities, and
sources, are as follows : (a) northern Scandanavia, Ryberg (1947) ; (b)
Holland, Bels (1952) ; (c) Italy, Toschi and Lanza (1959) ; (d) Lebanon,
Lewis and Harrison (1962) ; (e) Egypt, Hoogstraal (1962) ; (f) west Africa,
Rosevear (1965) ; (g) Kenya and Tanganyika, Kulzer (1959). The data for
Kenya and Tanganyika is based on a sample of species only. Primary
sources for Australian data are Hamilton-Smith (1966), Lavery and Johnson
(1968) and McKean and Price (1967). See text for explanation.

summer and situations near cave entrances are selected as nur-
sery sites. Within Australia generally the genus *Chalinolobus*
shows some predilection toward cave-dwelling (and summer aggre-
gation) at MAT's between 15.5° and 18.5°C (Dwyer 1966c, Hamil-
ton-Smith 1966). This genus does not appear to behave other than
as Group 1 (Kulzer *et al.* 1970) ; nor does it practice gross modifi-
cation of $T_a$ (Dwyer, unpublished). Apparently this genus differs
from most microchiropteran bats in not requiring high tempera-
tures for the birth and development of young and, hence, can use
cooler caves as summer quarters. Finally, in areas of high MAT
(> 22°C) Group 3 bats are well represented in caves while Group
1 bats are proportionally poorly represented. All cave-dwelling

species at these latitudes appear to use caves throughout the year but there is evidence to suggest that many of them may make use of a range of roosting sites in addition to caves. In eastern Australia this is so for *Miniopterus, Rhinolophus* and probably *Macroderma* (Dwyer unpublished, Harrison 1962).

McNab (1969) has observed that for bats having a common food habit the smallest weight class is more prominent in the tropical lowlands than in subtropical or temperate regions. In the earlier discussion it was predicted that with increasing latitude the cave environment would become increasingly inappropriate to smaller bats of Group 2. Figure 2 suggests that this prediction holds good.
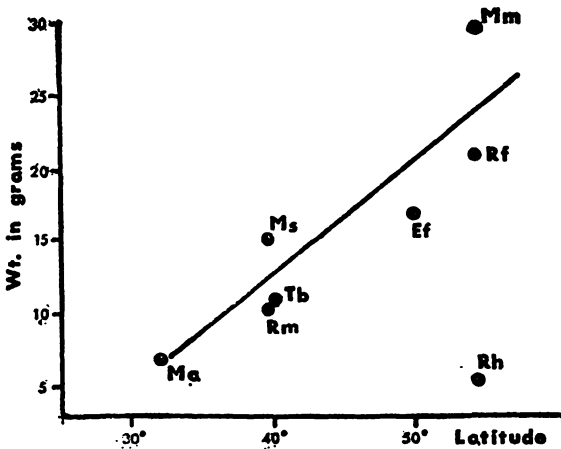


Fig. 2. — Weights of cave-dwelling bats of Group 2 plotted against approximate limit of range (north or south respectively). Species are : *Rhinolophus megaphyllus* (Rm), *R. ferrum-equinum* (Rf), *R. hipposideros* (Rh), *Myotis myotis* (Mm), *Eptesicus fuscus* (Ef), *Miniopterus australis* (Ma), *M. schreibersii* (Ms), *Tadarida brasiliensis* (Tb). *R. hipposideros* does not fit the trend apparent for other species. It does not remain in high latitude caves through summer.

The primary themes of the prediction are upheld by the examples discussed above ; Group 1 bats are not significantly represented in caves except at high latitudes where they use them as hibernacula, Group 2 bats are the predominant cave-dwelling forms of the middle latitudes, and Group 3 bats are well represented at low latitudes but, primarily for reasons of food supply, are excluded from caves at other latitudes. It may be noted that some Group 3 bats are found throughout the latitudinal range of eastern continental Australia, at least in summer, but these are lar-

ge megachiropterans that do not echolocate (Nelson 1965). A few microchiropterans of Group 3 are, similarly, found at temperate latiudes of North America (e.g. *Leptonycteris sanborni*, Carpenter and Graham 1967) but these are migratory species and are not cave-dwelling. Several important exceptions have also been indicated ; e.g. the failure of Group 1 bats to make significant use of caves as hibernacula in eastern Australia, the possibility that thermo-commensalism may allow some Group 1 species to occupy high or middle latitude caves in summer, and the possibility that middle latitude caves would become available as summer quarters for Group 1 bats that can rear young at moderate temperatures. The present analysis has not treated altitudinal effects upon cave temperature. In large regions that include many caves at a variety of altitudes some modification of my primary explanation would be necessary ; the direction of modification is, however, implicit in the explanation. The data for the northern hemisphere with Group 1 bats well represented in caves at middle latitudes (see Italy, Fig. 1) probably reflects an effect of the above kind.

## THE ORIGIN AND EARLY EVOLUTION OF BATS

The earliest bat known is early Eocene (Jepson 1966). By the Oligocene a radiation of great magnitude had occurred and most modern families and several modern genera (e.g. *Rhinolophus, Myotis*) were in existence (Simpson 1945). Bats probably evolved in the tropics from small, arboreal and nocturnal insectivores (Allen 1939, Griffin 1958, McNab 1969, Twente and Twente 1964). The daytime retreats of prebats and early bats were probably associated with trees. It is likely that the early phases of evolution were characterized by strong selection for improved flight and aerial foraging ; less adequate flight or arboreal foraging would imply competition with strictly arboreal insectivores. Hence the origin of bats may be viewed as tachytelic in the sense of Simpson (1944). Once flight developed bats must have found themselves in a virtual ecological vacuum ; only a few nocturnal birds (e.g. Caprimulgidae) would have been potential competitors. In this situation, therefore, bats had almost unlimited scope for perfection of flight and aerial foraging and for radiation. The preexistence of a diurnal avifauna of aerial insectivores probably told against emergence of a diurnal bat fauna (Griffin 1958).

Nocturnal habits and the perfection of flight and aerial foraging on insects would, in concert, operate as intense selective agents upon any tendency towards echolocation. It is in this con-

text that I see the development of echolocation in microchiropteran bats ; from its earliest appearance echolocation would be selected for its dual roles of obstacle avoidance and insect capture. (This interpretation implies early divergence of, or separate origins for, megachiropteran and microchiropteran bats.) I cannot agree with Twente and Twente (1964) that echolocation in microchiropteran bats evolved as a mechanism for survival in a cave environment ; this would imply that the role of echolocation in insect capture was secondary and that bats were cave-dwellers before they were tree-dwellers. Presumably Twente and Twente could argue that non-echolocating forms occupied the twilight zone of caves and that the advent of echolocation was advantageous in allowing deeper penetration of caves and thereby providing more, and safer, roosting sites. (This could be the basis for the development of echolocation in the megachiropteran *Rousettus* ; the mechanism differs from that in the microchiropterans and is not employed in foraging (Kulzer 1960)). But Twente and Twente would still have to explain how and why prebat or early bat moved from arboreal to cavernous daytime retreats. Even apart from the considerations I raise below it would seem that Twente and Twente's scheme entails a chain of events that would occupy an enormous time scale. My interpretation allows for simultaneous change in a concert of correlated structures and accords better with the one clear palaeontological clue available — « whatever did happen, it happened fast ».

## THE EVOLUTION OF THERMOREGULATION IN BATS

Homeothermy presumably evolved from poïkilothermy. The development of increasing levels of endothermism was probably initially correlated with muscular activity such that an animal showed some homeothermic ability when active but reverted to poïkilothermy when inactive (Heath 1968). As the capacity for endothermism increased, mechanisms for regulating heat loss would emerge with the consequence that, at least during activity, the organism could behave homeothermically over a wide range of $T_a$. Up to this point I follow Cade (1964) and it is this last thermoregulatory condition with two additions, that I envisage for the progenitor of bats. Prebat was a small nocturnal insectivore behaving as a moderately good homeotherm when active but reverting to poïkilothermy when inactive. (I shall use the term « heterotherm » to designate this state ; see Hock, 1951). As a heterotherm prebat would have been tolerant of low body temperatures but as

a tropical heterotherm this tolerance would not have embraced extremely low $T_a$ (Eisentraut 1960, Kulzer 1965). My additions to this are, firstly, that prebat would have incorporated a « clock » attuned to its day-night cycle of inactivity and activity and appropriate to switching the organism from ectothermism to endothermism (cf. Heath 1968) and, secondly, that as an organism reproducing in some fundamentally mammalian way prebat would at times need to select sites providing high $T_a$ as daytime retreats. Inherent in this second characteristic is the immediate likelihood of selection in the direction of « complete » homeothermism (i.e. of homeothermism over a range of activity states), for this would obviate possible disadvantages imposed by the need to temperature select during inactivity. This shift was, however, countered by the fact that reduction in $T_b$, arising in an obligatory way but controlled to some extent by site selection, was advantageous during periods of food scarcity. McNab (1969) points out that populations of insects in the tropics show appreciable seasonal variation in abundance and argues that « a reduced rate of metabolism with the subsequent relaxation of a rigid homeothermy » carries especial advantages for small insectivores that are faced with food shortage ; for strictly aerial insectivores or for small insectivores restricted to a specific foraging schedule the advantages would be enhanced.

Twente and Twente (1964) state and McNab (1969) implies that the torpor characteristic of some tropical bats evolved from « complete » homeothermism. These authors are unwilling to accept the opinion that torpor is a « primitive » characteristic of bats (e.g. Eisentraut 1960, Hock 1951, Kayser 1965) ; they are impressed by the ecological efficacy of torpor and McNab rightly points to confusion as to what is meant by « primitive » in this context. But if the propensity for torpor in small, tropical, insectivorous (and modern) bats carries the advantages which McNab suggests, and with which I agree, one is forced to wonder how prebat or early bat, as a small insectivore behaving as a « complete » homeotherm, managed in an equivalent environment. I do not intend to designate torpor, as it is manifest in modern representatives of Group 1, as « primitive » — it is certainly not that — but I do consider that it carries more than just a little impress of its distant past. By this I mean that modern tropical representatives of Group 1 have never passed through a phase of « complete »homeothermism. The ecological advantages of a capacity to behave « poikilothermically » at certain times have denied these bats access to « complete » homeothermism. It is largely because Group 1 bats have the ability to a-

rouse spontaneously, either in response to dangerously low $T_a$ or in response to day-night cycle or both, that several authors have argued against the view that torpor in bats is a « primitive » characteristic ; while agreeing that it is not « primitive »I do not see that it then becomes necessary to argue that torpor is derived from « complete » homeothermism. The ability to arouse spontaneously may be incorporated into the thermoregulatory repertoire that I have described above for pre-and early bat. Indeed it seems to me that this is the simplest interpretation available. The heterothermic behaviour I suggest for pre- and early bat is primarily obligatory ; the incorporation of spontaneous arousal amounts to the addition of a facultative aspect (cf. McNab 1969) with obvious survival value. The question of the origin of spontaneous arousal cannot be answered, we know too little of the mechanism(s) involved, but there is certainly no *a priori* basis for claiming that spontaneous arousal from torpor must have been derived from « complete » homeothermism (see Menaker, 1961, 1962, for discussion of relationships between thermoregulation and circadian rhythms in bats).

It is important to stress that tropical bats of Group 1 will still be intolerant of extremely low $T_a$. Their extremely infrequent exposure to very cold temperatures would not have conditioned development of such tolerance ; hypothermic reactions or « alarm » reactions (i.e. increased metabolic rate) occur instead (Kulzer 1965).

Resident within the characteristics I have now defined for Group 1 bats lies the potential for polyphyletic development of Group 2 and Group 3 bats. Group 1 bats still retain an obligatory aspect to their torpor (when inactive their $T_b$ falls to $T_a$) but since they can arouse spontaneously and can increase metabolic rate if $T_a$ is too low then their torpor is a regulated condition. Group 2 bats have moved further towards a wholly facultative expression of torpor. When inactive over a given range of $T_a$ they may either permit $T_b$ to approximate and follow $T_a$ (retaining the ability to arouse spontaneously) or they may allow $T_b$ to drop only to a level such that spontaneous flight is not impossible. For most Group 2 bats a $T_b$ of around 30°C seems to be appropriate. By behaving in this way Group 2 species avoid the necessity to always select sites that lie within a narrow range of $T_a$ and to have available a variety of sites that satisfy needs that may change, sometimes abruptly, in time but they have retained the advantages bestowed upon small insectivores by a capacity for torpor. A Group 2 bat may conserve or utilize energy at will without changing its roosting site ; the metabolic rate of an inactive Group 1 bat is ulti-

mately dictated by $T_a$ and it must always select a $T_a$ appropriate to the needs of the moment. The necessity to partition roosting sites as bat diversity increased could have provided the initial impetus to shift in the direction of Group 2. But perhaps, more importantly, the competitive partitioning of food resources may have, at first in part and finally in total, released may tropical bats from the need for torpor. Amongst insectivorous species the capacity to forage upon non-flying insects would mean that food was less likely to be temporally unstable (McNab, 1969, makes essentially the same point when contrasting birds and bats) while utilization of larger insects would be matched by an increase in size and, hence, by a larger energy reserve. In both cases there would be decreased reliance upon periods of torpor. A shift to carnivorous habits would exaggerate this. Inasmuch as a bat was released from reliance on torpor there would be the likelihood of a shift towards « complete » homeothermism. As the limits of $T_b$ became narrowed independent of activity state and over an ever-widening range of $T_a$ there would be a concomitant loss of tolerance to deep hypothermia (Cade 1964). In other words as « complete » homeothermism emerged the propensity for torpor would be lost and we would have arrived at the thermoregulatory state of a Group 3 bat.

A shift from insectivorous to frugivorous habits would also promote a shift towards « complete » homeothermism. This would stem in part from an increase in food particle size correlated with an increase in weight and basal metabolic rate (McNab 1969). It could also arise if the availability of food was guaranteed through time. The reciprocal dependency of certain flowering trees and Old World nectarivorous bats (Pijl 1961) provides the most striking instance of this. The more general suggestion that year-round flowering in tropical forests has evolved in parallel with the emergence of an obligatory frugivorous and nectarivorous fauna (Janzen 1967) is also relevant.


## LOW LATITUDES AND HIGH LATITUDES

The above discussion relates to tropical environments. It assumes that the primary radiation of bats occurred in the Old World Tropics and that, from here, bats invaded higher latitudes to the north and south and, via the Nearctic, finally colonized the Neotropics. In this last region a major radiation (Phyllostomatoidea) occurred. Variants upon the thermoregulatory patterns described above, that are currently represented at high latitudes, probably have a Pleistocene or post-Pleistocene origin.

Group 3 bats are largely excluded from higher latitudes. The few that penetrate beyond the subtropics are seasonal migrants (some frugivores and nectarivores). Some insectivorous members of this group reach the limit of the subtropics (e.g. *Taphozous mela-nopogon*) ; they appear to rely upon accumulated fat deposits during periods of food scarcity (Brosset 1961). Only bats of Group 1 and Group 2 are significantly represented at higher latitudes. Some of them migrate to low latitudes for the winter (e.g. *Lasiurus* ; Findley and Jones 1964) ; others hibernate or exhibit extended periods of light torpor (Beer and Richards 1956, Leitner 1966). It is in this latter class of bats that we discover variants upon the thermoregulatory patterns previously discussed. These include (A) an increased tolerance to low $T_a$ (Eisentraut 1960, Kulzer 1965), (B) behaviour appropriate to selecting or modifying $T_a$, (C) a seasonal change in the expression of torpor, (D) the prewinter storage of fat and (E) a repertoire of physiological and neural mechanisms appropriate to hibernation and not different in expression to those shown by other hibernating mammals (Kayser 1965). Different species rely upon these variants to differing degrees and in different combinations. Within a species it is likely that the expression of wintering adaptations may vary with latitude (e.g. compare *R. ferrum-equinum* in England and France ; Ransome 1968, Saint-Girons *et al.* 1969). In general Group 2 species rely upon B, C and D while Group 1 species rely upon D and E ; an increased tolerance to low $T_a$ is relevant for both groups. In Group 2 species behaviour appropriate to modifying $T_a$ may make a significant contribution to the economics of thermoregulation in summer.

Implicit in this overview is the opinion that the propensity for torpor as expressed in tropical Group 1 or Group 2 species has been preadaptive to the environments of higher latitudes. This accords with the view of most workers (e.g. McNab 1969, Kulzer *et al.* 1970). Inasmuch as a bat has moved in the direction of « complete » homeothermy so the potential to evolve mechanisms appropriate to hibernation has been decreased. The reliance of Group 2 species upon B, C and D rather than E accords with this. A taxon that had already moved to Group 3 would require more time to evolve the relevant mechanisms, and develop the concomitant tolerance of low $T_b$, than a Group 1 bat. To date there does not seem to have been enough time.

At high latitudes the winter and summer temperature environments of non-migratory Group 1 bats are extremely different. It is likely that a period of acclimatization would be relevant before hibernation occurred (Henshaw and Folk 1966) or before females

moved to nursing colonies (Dwyer and Harris, MS in prep.) and it is possible that this might have the concurrent result of increasing (pre-winter) or decreasing (pre-summer) tolerance to low $T_a$. This could explain Menaker's (1962) observation that *Myotis lucifugus* collected in summer were unable to arouse from very low $T_a$ although individuals collected in winter could arouse from the same temperature (5°C). Menaker concluded that his results implied a fundamental difference in the summer and winter physiological states of Group 1 species. My explanation would seem simpler and would allow for individual exceptions to the general pattern (see, for example, Stones and Oldenburg 1968).

At this point it is necessary to examine in detail certain matters raised by McNab (1969, p. 264). McNab does not find in torpor a reflection of « primitive organization ». He argues forcefully that the energetics of bats are « closely attuned to conditions in the environment » and is of the opinion that torpor « evolved in the tropics because of the ecologically imposed inability of certain species to expend energy at the rates required for precise temperature regulation ». But McNab then suggests that it is difficult to understand why « tropical members of Rhinolophidae and Vespertilionidae, like their temperate relatives, show little temperature regulation » whereas « strictly tropical, insectivorous families » show considerable temperature regulation. Here he seems to be saying that the latter (e.g. Molossidae, Rhinopomatidae) are more attuned to the conditions in a tropical environment and therein seems to refute his own opinion regarding the advantages of torpor to small tropical insectivorous bats. He continues by pointing out that certain Neotropical and Palaeotropical vespertilionids (*Histiotus* and *Miniopterus*) show more « temperature independence of $T_a$ than is typical of the cosmopolitan members of Vespertilioninae ». He implies that the former have had a longer history in the tropics than many of the latter and then suggests « that an appropriate modification in energetics (and thermoregulation) occurs in *tropical bats of a temperate origin* where there has been sufficient time (and opportunity) to do so ... » (my italics). Are we to understand by this that tropical Rhinolophidae and tropical Old World vespertilionines have a temperate origin ? This is unacceptable. McNab's explanation would also seem to imply that the appearance of thermoregulatory modes has taken an inordinantly long time (*Rhinolophus* and *Myotis* are known from the Oligocene) and this too would seem to counter his own view that energetics is closely attuned to the environment. Finally McNab appears to have misunderstood the thermoregulatory characteristics of

rhinolophid bats ; he aligns them with the majority of the vesper-
tilionines but they should clearly be placed in Group 2 with *Miniop-
terus, Histiotus* and the Molossidae. McNab has found it diffi-
cult to embrace certain species within his general explanation
of the economics of temperature regulation in bats and the parti-
cular explanation he devises for these is contrary to his primary
thesis. In this regard therefore, my interpretation is more accom-
modating of the available information.

When McNab refers to « tropical bats of a temperate origin »
he is especially concerned with Neotropical forms. I have sugges-
ted that a propensity for torpor was not only appropriate to, but
preadapted bats to, dispersal from low to high latitudes. It is per-
tinent to ask, however, whether movement in the opposite direc-
tion would call for changes of any kind. Could refinements of tor-
por developed at high latitudes restrict access to low latitudes ?
For McNab the answer seems to be « no » ; the bats may colonize
tropical latitudes and change may occur with time at these lati-
tudes. I suspect that for temperate latitude Group 1 bats, at least,
this answer is unsatisfactory. Group 1 species present at high lati-
tudes would presumably have a relatively sophisticated comple-
ment of adaptations appropriate to wintering ; in particular they
would bear an obligatory aspect to their torpor, compensating for
this, as need be, by selecting $T_a$. As they colonized lower latitudes
they would have less need of torpor. In this context the most sim-
ple adaptive response appropriate to a movement into the tropics
would be a shift in the direction of Group 2. In other words I am
claiming that if the Neotropical bat *Histiotus* has, in fact, had a
Nearctic origin then it is a Group 2 species not simply because it has
had a long history in the tropics but primarily because it could not
otherwise have entered the tropics. More generally, we may expect,
on zoogeographic grounds, that Group 1 thermoregulatory charac-
teristics will be less in evidence among Neotropical vespertilionines
than among Palaeotropical forms.


## THE PREADAPTATION OF BATS TO CAVE-DWELLING

Bats are the only group of vertebrates that are well represen-
ted in caves. A few species of birds use caves in a comparable man-
ner but these are confined to tropical latitudes. Cave-dwelling in
bats has an almost cosmopolitan air. A necessary correlate of un-
derground life for a flying vertebrate is a means of orientation that
is independent of vision. In bats, in cave-swiftlets (*Collocalia*) and
in oil birds (*Steatornis*) this has been achieved by echolocation (Grif-

fin 1958) and for microchiropteran bats, at least, it may be assumed that the origin of echolocation preceded, and preadapted bats to, cave-dwelling (see above). Thus it is of note that most megachiropterans do not echolocate and are not found in caves. *Rousettus, Dobsonia, Eonycteris* and *Notopteris* are exceptions and of these the first has evolved an independent mode of echolocation while the second and third are confined to the twilight zone. It is only for *Notopteris* that the matter is confused. This bat is reported to live in « complete » darkness but does not appear to echolocate ; it could be, however, that the species penetrates caves to a zone that lies beyond the range of human visual perception while not yet exceeding its own (Hamilton-Smith, pers. comm.).

At tropical latitudes torpor is not associated with the habit of cave-dwelling (see Fig. 1). Rather there would seem to be an inverse relationship between cave-dwelling and the propensity or need for torpor. Again, therefore, I disagree with Twente and Twente (1964) who suggest that torpor originated in the tropics as an adaptation to the cool microenvironments of roosting sites, especially caves. If this were so we would expect Group 1 bats to be well represented in tropical caves. In addition, their hypothesis is too simplistic for it does not take into account or explain the fact that Group 1 bats will need to have available a variety of roosting sites that offer a range of $T_a$. In the tropics torpor is not an adaptation to living in cool situations, it is an adaptation to food shortage but, to have relevance, it necessitates selection of cool situations.

The relevance of a capacity for torpor to cave-dwelling is not evidenced until we reach the middle latitudes (Group 2 bats) or high latitudes (Group 1 bats). At these latitudes the significance of torpor is again related to food scarcity. When food is abundant and the bats are feeding regularly torpor must, in general, be avoided either by maintaining a relatively high and regulated $T_b$ (Group 2 bats) or by selecting sites of high $T_a$ (Group 1 bats). Group 2 bats can accomplish this in caves (especially if they select warm sites or modify $T_a$) ; Group 1 bats can seldom satisfy their summer metabolic requirements in caves. When food is in short supply or is absent then middle latitude caves may be appropriate to Group 2 bats inasmuch as they allow a satisfactory balance between energy conservation and the availability of food through the winter. At high latitudes torpor has provided a basis for the emergence of hibernation and caves may frequently provide appropriate quarters for this.

the use that a bat can make of a cave at any given latitude is, therefore, largely dictated by its thermoregulatory characteristics.

A bat does not simply « decide » to be cave-dwelling and mould its thermoregulatory characteristics within the context of the cave environment. In general, cave-dwelling can only emerge if a bat is preadapted to the particular characteristics of the cave environment at any given latitude range. For most Group 1 bats cave-dwelling was only possible once the capacity to hibernate had developed ; for most Group 2 bats cave-dwelling was possible in the tropics and could be carried into temperate latitudes only inasmuch as thermoregulatory characteristics could be modified in an appropriate direction. But the cave environment has not served as a background for selection ; from an evolutionary perspective bats have not adapted to caves, they have exploited them. In an important sense this is reflected by a subtle « intolerance » to the cave environment. Thus, for example, there is an air of precision to the way in which *Rhinolophus ferrum-equinum* selects temperatures through the winter and moves from site to site or cave to cave according to its needs of the moment (Ransome 1968, Saint Girons *et al.* 1969). If the thermoregulatory characteristics of bats had evolved within the context of the cave environment we might expect greater tolerance to changes in $T_a$ than actually exist. It is because caves are buffered to a great extent from daily and seasonal fluctuations in temperature that they provide some sort of guarantee that a site selected for its $T_a$ today will provide approximately the same $T_a$ tomorrow and a year hence. For Group 1 and Group 2 bats in particular, and especially at higher latitudes, it is precisely this guarantee that has fostered cave exploitation and the emergence of a « professionally » cave-dwelling bat fauna.

I do not consider therefore that the cave environment has played a significant role in the evolution of thermoregulation in bats. In the tropics a shift from Group 2 to Group 3 would not be denied by cave-dwelling but would not arise as a consequence of cave-dwelling. At higher latitudes the emergence of sophisticated behaviours appropriate to temperature selection would tend to stabilize the thermoregulatory mode of a Group 1 or Group 2 bat. There is, however, one evident exception to this. Where Group 1 and Group 2 species shared the same hibernacula there would be the potential for the appearance of thermocommensalism in Group 1 bats ; in this way a Group 1 bat might be able to remain as a cave-dwelling species through the summer. This, in itself, could lead to selection in the direction of Group 2 thermoregulation.

## THE PHYLOGENY OF THERMOREGULATION IN BATS

The 18 families of bats may be grouped as five superfamilies each of which appears to represent a phylogenetic unit (Simpson

1945). These superfamilies may be ranked in terms of increasing
specialization of the shoulder joint for flight (e.g. Miller 1907) ;
i.e. Pteropopoidea, Rhinopomatoidea, Rhinolophoidea and Phyllos-
tomatoidea, and Vespertilionoidea. The Old World Rhinolophoidea
and the New World Phyllostomatoidea (excluding Mormoopidae)
have shoulder joints of comparable structure. Most workers would
favour the view that for microchiropteran bats this arrangement
has a phyletic base in the sense that Rhinopomatoidea are struc-
turally nearer to, and the Vespertilionoidea are structurally more
distant from, pre- and early bat. The Mormoopidae may be vie-
wed as Neotropical counterparts of the Vespertilionoidea (Vaughan
and Bateman 1970). The position of the Pteropopoidea would be
in question though I have argued for early or separate divergence.
This sequence therefore is near to the antithesis of the evolutio-
nary sequence I have proposed for thermoregulation in bats (cf.
Table 1). In bats torpor is manifest most clearly in the phyloge-
netically advanced groups and « complete » homeothermy is most
evident in the phylogenetically more conservative groups ; this
is the reverse of Cade's (1964) interpretation for rodents and, at
first sight, would seem anomalous.

Microchiropteran bats evolved as small aerial insectivores.
Thereafter the mainstream of evolutionary change was towards
perfection of flight and aerial foraging upon small insects.The
Vespertilionoidea (especially the Vespertilionidae) may be regar-
ded as the final expression of these evolutionary themes. The form
of the shoulder joint found in Rhinopomatoidea and Rhinolophoi-
dea (with Phyllostomatoidea) reflect, in part, stages in the evolu-
tion of vespertilionoid flight. Perfection of flight would at each sta-
ge give considerable advantage in aerial foraging to the structu-
rally advanced forms. The structurally conservative forms would,
in general, survive only if they shifted, or had shifted, to a diffe-
rent foraging mode. This, in fact, appears to have happened.

Most insectivorous Rhinopomatoidea show an increase in food
particle size as reflected by their relatively large size (Rhinopo-
matidae, most Old World Emballonuridae, and *Noctilio labialis* ;
*N. leporinus* is piscivorous). The insectivorous Rhinolophoidea
(especially Rhinolophidae and Hipposideridae) appear to be adap-
ted to foraging directly from vegetation and in this sense may have
largely relinquished « genuine » aerial foraging ; there appears to
have been some increase in food particle size in the sense that a
rhinolophoid of size *n* grams takes larger items than a vespertilio-
noid of the same size. This is correlated with a tendency to « hang-
up » whilst actually feeding (cf. Phyllostomatidae ; Vaughan and

Bateman, 1970). The Rhinolophoidea have also shifted to carnivorous habits (Megadermatidae). Amongst the Phyllostomatoidea many food habits are represented ; insectivorous, carnivorous, frugivorous, nectarivorous and sanguivorous. The phyllostomatoid radiation appears to have paralleled that of all Old World bats. In my view it would have been derived from small aerial insectivores and the mainstream would have been in the direction of perfecting flight and aerial foraging upon insects (represented by modern Mormoopidae ; see Vaughan and Bateman, 1970). But the subsequent advent of vespertilionoids in the Neotropics may well have led to partial replacement of a comparable phyllostomatoid fauna of strictly aerial insectivores. These paradoxically would have been structurally advanced forms. Finally, within the Vespertilionoidea, the Molossidae stand out as a distinct family in terms of their thermoregulatory characteristics. But molossids too have undergone a significant shift in foraging habits ; they compare with the swifts in that they forage high and over large areas and have achieved a mode of flight that is energetically less demanding than that seen elsewhere amongst bats (Vaughan 1959).

At tropical latitudes torpor would only seem advantageous to small aerial insectivores that were likely to be subjected to periods of food scarcity. The propensity for torpor would not, therefore, have ever been lost from the mainstream of microchiropteran evolution. But all the shifts away from this mainstream that are outlined above would release bats, in part or whole, from the need for torpor and would promote a shift from Group 1 to Group 2 or Group 3 status. In these terms, therefore, it is possible to appreciate why the structurally more conservative bats should be the very ones to have moved furthest in the direction of « complete » homeothermy.

There is a special class of exceptions that are allowed for in this explanation which would prove of considerable interest should they exist. The high species diversity of the tropics has been compatible with the persistence of particular « relict » forms. It is not impossible, therefore, that at tropical latitudes small aerial insectivores that retain a propensity for torpor are represented among the structurally more conservative bats (Rhinopomatoidea). It is likely in this case that such species would be structurally conservative members of the taxon to which they belonged. If such species do exist it would be of great interest to examine their thermoregulatory behaviour in detail for there is the possibility that the expression of torpor might be substantially different from that currently recognised in Group 1 vespertilionines. The Emballonuridae

seem most worth investigating in this regard. There is the suggestion that some Neotropical emballonurids may enter torpor (McNab 1969) while in the Palaeotropics the genus *Emballonura* includes some exceptionally small insectivorous species. To date there does not appear to be any knowledge of the thermoregulatory behaviour of this genus.

## THE « MYTH » OF GROUP 1

The concept of bats as heterothermic mammals proposed by Hock (1951) has been clung to somewhat tenaciously. Yet the history of discovery in this area has been one of abandoning this concept as being broadly applicable to bats (see, for example, Bartholomew et al. 1964, Burbank and young 1934, Leitner 1966, Leitner and Nelson 1967, Morrison 1959). There has been some variance of opinion as to whether Group 1 status (as defined in this paper) should be accorded to temperate zone species alone or should be assigned, irrespective of latitude, on some taxonomic basis (compare, for example, Arata and Jones 1967, Carpenter and Graham 1967, McNab 1969, Studier and Wilson 1970). More recent studies on temperate zone species imply that some apparently Group 1 species may behave differently according to season or reproductive state (e.g. Bradley and O'Farrell 1969, O'Farrell and Studier 1970, Stones and Wiebers 1967) while Saint Girons et al. (1969) go as far as designating the Rhinolophidae and Vespertilionidae as « optional homeotherms ». McNab (1969) has given emphasis to the possibility that poor nutrition may influence thermoregulatory capability ; certain species that behave as Group 1 bats in laboratory studies may do so, in part, simply because of deficient nutritional status. In this paper I have exploited a long adhered to concept that may prove to lack the generality that has been assigned to it. This does not destroy the essence of my explanation. Species that I have classed as Group 1 may exhibit a range of thermoregulatory modes, exploiting their capacity for torpor in different ways dependent upon the environmental context within which they exist They will represent, as it were, twigs at some distance from one trunk. I have been concerned to discover the direction of that trunk. For example, in the evolution of microchiropteran bats, it is likely that those taxa which opted for small size would be exposed to intense selection in all areas relating to thermal economics. The suborder Microchiroptera includes some of the smallest mammals and it seems improbable that pre- or early bat was of this size order. The relevance of torpor in the energetics of very small bats could

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well mean that its expression here differs substantially from its expression in early Group 1 species. To a lesser degree the same might apply to some small, nectarivorous, Pteropodidae.

## SUMMARY

1. Bats are placed in three groupings on the basis of their thermoregulatory mode. Group 1 includes species that enter torpor readily at low ambient temperatures and, in general, appear to be incapable of sustaining a body temperature much in excess of ambient if they are inactive for a prolonged period of time. Group 2 includes species that are able to voluntarily enter torpor but are also able to maintain high body temperature when inactive at quite low ambient temperature. Group 3 includes species that do not voluntarily enter torpor and may, in fact, regulate body temperature precisely over a range of activity states. It is recognised that this classification is not rigorous.

2. It is predicted that Group 1 bats will not be significantly represented in caves except at high latitudes where they will use them as hibernacula, that Group 2 bats will be the predominant cave-dwelling forms of the middle latitudes and that Group 3 bats will be well represented in low latitude caves but, primarily for reasons of food supply, will be excluded from caves at other latitudes. These predictions are, in general, satisfied by present knowledge of distribution patterns.

3. An hypothesis is proposed in which the evolution of thermoregulation in bats passed through the stages Group 1 to Group 3. Torpor, as it is manifest in modern representative of Group 1, is not seen as a « primitive » attribute of bats but nor is it considered that Group 1 bats ever passed through a phase of « complete » homeothermism. It is suggested that the necessity to partition roosting sites and, more importantly, the competitive partitioning of food resources as bat diversity increased may have, at first in part and finally in total, released many tropical bats from the need for torpor. NcNab's view of torpor as adaptive to periods of food scarcity is accepted in this paper.

4. The capacity for torpor as expressed in tropical Group 1 or Group 2 species is seen as having been preadaptive to the environments of higher latitudes. Variants upon thermoregulatory modes have appeared in temperate latitude species, including increased tolerance of low ambient temperature, a seasonal change in the expression of torpor, and, particularly, a repertoire of physiological and neural mechanisms appropriate to hibernation.

5. The relevance of a capacity for torpor to cave-dwelling is not evidenced until the middle or high latitudes. Given that the species can echolocate, cave-dwelling can only emerge if the bat is preadapted in its thermoregulatory mode to the particular characteristics of the cave environment at any given latitude range. The cave environment has not played a significant role in the evolution of thermoregulation in bats.

6. In bats torpor is manifest most clearly in the phyllogenetically advanced groups and « complete » homeothermy is most evidenced in the phyllogenetically more conservative groups. It is suggested that the mainstream of

microchiropteran evolution was in the direction of perfection of flight and foraging upon insects, that the propensity for torpor was never lost from this mainstream, but that all the shifts away from this mainstream were such as to release bats, in part or whole, from the need for torpor and hence promoted a shift to Group 2 or Group 3 status.

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