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# Social Entrainment of the Circadian Rhythm in the Flight Activity of the Microchiropteran Bat *Hipposideros speoris* *

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**Summary.** 1. We investigated the problem of how members of the microchiropteran bat species *Hipposideros speoris* that live in a true cave clock their flight activity rhythms in the absence of time cues.

2. The bats become restless well in advance of sunset and then fly towards the cavemouth to sample light.

3. We investigated whether each bat roosting 40 m from the cave entrance must sample outside light levels for itself in order to emerge at the appropriate time. Three captive bats were tested and each began activity when the conspecifics left the cave in the evenings.

4. In another series of experiments a solitary bat was held captive in a solitary cave for 50 days and its circadian rhythm was recorded. In the absence of other conspecifics the circadian rhythm 'free ran' with a period shorter than 24 h.

5. We concluded from the results of our studies that there exists a clear-cut case for social synchronization of the circadian rhythms of this cave-dwelling bat.

## Introduction

When organisms are placed in constant light or darkness and invariant temperature, they do not become 'disoriented' as regards time (Buenning 1973). Implicating an endogenous origin, the rhythms 'free run' over the days, losing or gaining time, relative to the exact 24-h geophysical day; hence the concept of "subjective circadian time' (Pittendrigh and Minis 1964). Laboratory conditions that induce free runs in circadian systems hold no time cues about the 24-h day. There are, however, natural environments, such as the deep sea, outer space and caves, that also seem to lack time cues.

Natural, true caves also seem to lack any apparent environmental variable that can synchronize the rhythms of animals dwelling in them. The temperature and humidity are absolutely invariant and the darkness complete during day and night in some of these caves. Yet organisms inhabiting them, such as microchiropteran bats, fly out at the same time day after day (Subbaraj and Chandrashekaran 1977; Erkert 1978) indicating entrainment of their activity rhythms. Social and mutual tuning of the circadian rhythms by conspecifics can be an effective way of telling time (Gwinner 1966; Bovet and Oertli 1974; Crowley and Bovet 1980). We have examined this question by studying a colony of the microchiropteran bat *Hipposideros speoris* with 400–500 members living in a cave in Madurai. In this paper we amplify on our suggestion (Marimuthu et al. 1978) that there may be a 'social synchronization of the circadian rhythm' of these bats and present new supporting data. There is further evidence implicating a species specificity in such social Zeitgeber functions.

## Materials and Methods

*Study Site.* The site where the observations and experiments were carried out is a 'true cave' (cave 1), i.e. a cave with just one opening (Twente 1955), situated in a rock complex close to the Madurai Kamaraj University Campus (lat. 9°58′ N, long. 78°10′ E). The cave has several labyrinthine ramifications 15–50 m from the cave mouth, which opens on the northern flank of the rock complex. The bats use several of these pockets as their day-time roosting place. We chose a site, ca. 40 m inside the cave, that showed great constancy of temperature (27° C ± 0.5°) and relative humidity of 95% (Lambrecht-Goettingen thermohygrographs) and was absolutely dark (no light measurable over periods of 1,000 s even on the energy scala log scale of a United Detector Technology Optometer). A second cave (cave 2) was situated in the same rock complex but with the cave mouth on the southern side. The conditions obtained in cave 2 were very similar to the conditions in

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* Dedicated to Professor Erwin Buenning on the occasion of his 75th birthday

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cave 1; temperature was constant at 30° C, relative humidity was 85% and darkness complete. Since the depth of cave 2 was only approximately 5 m an artificial mud wall had to be constructed and a black cloth curtain erected to ensure absolute darkness.

*Recording Techniques.* Our behavioural observations and feeding of captive experimental bats were made using a noctovision apparatus with a far-red source of light projection and a viewing scope-screen. The bats did not respond to the switching on of the noctovision by either turning their heads towards the light source or flying away. We also used battery-powered torch lights with a combination of filters transmitting red light of >610 nm, which seemed not to disturb the animals as much as white light.

Bats were captured on their return flight to the cave in the early hours of the morning before sunrise and placed in light aluminium-framed activity cages wrapped on all sides with synthetic gauze material. The dimension of the cubical cages (30 × 30 × 30 cm) permitted flapping flight. Bouts of flight jiggled the cages, which were suspended from the arms of a metal column held by retort stands. The movements of the cages were transferred directly to mechanically wound thermohygrograph drums with the aid of bamboo strip stylets fitted with felt writing tips. Observations and experiments were made with a minimum of disturbance to the bat population within this rather restrictive cave, in which the ceiling in its roomiest region was 1–1.5 m from the floor. The captive bats were hand-fed at irregular hours of day and night with minced cockroaches.

## Results

The conditions in cave 1 appeared to be as conducive for the free run of circadian rhythms as any that can be contrived in a laboratory. Yet the onset of the evening foraging flight is very regular in these bats, occurring 10–15 min after sunset (Marimuthu, unpublished data). It is clear that the animals are aware of the time of sunset and act accordingly. The sequence of events culminating in such regular out flights can be summarized as follows:

The bats awaken well before sunset. They then stretch, preen themselves and undertake short flights within the dark recesses. The bats fly into an outer chamber that opens to the outside world through a small window-like cave mouth used by the bats for exit and entry at night. The bats fly around in this chamber 'sampling light' as other bats have been reported to do (Twente 1955; Voûte et al. 1974). When it gets sufficiently dark outside after sunset they begin flying out to forage.

Figure 1 sets out the results of an experiment that lasted for 50 days. The results show that even captive bats held in activity cages and thus denied access to the 'light-sampling' chamber still know the time and begin their flight activity precisely when the conspecifics living in the same cave begin their flight activity.

We undertook another series of experiments to test further the hypothesis of social entrainment. We recorded the daily flight activity of a *solitary bat* in a *solitary cave*. Cave 2 was originally inhabited by three male *Hipposideros bicolor*, which were captured and killed. The solitary *Hipposideros speoris* was placed in a flight cage and its activity was measured for 50 days. Figure 2 shows an impressive 'free run'

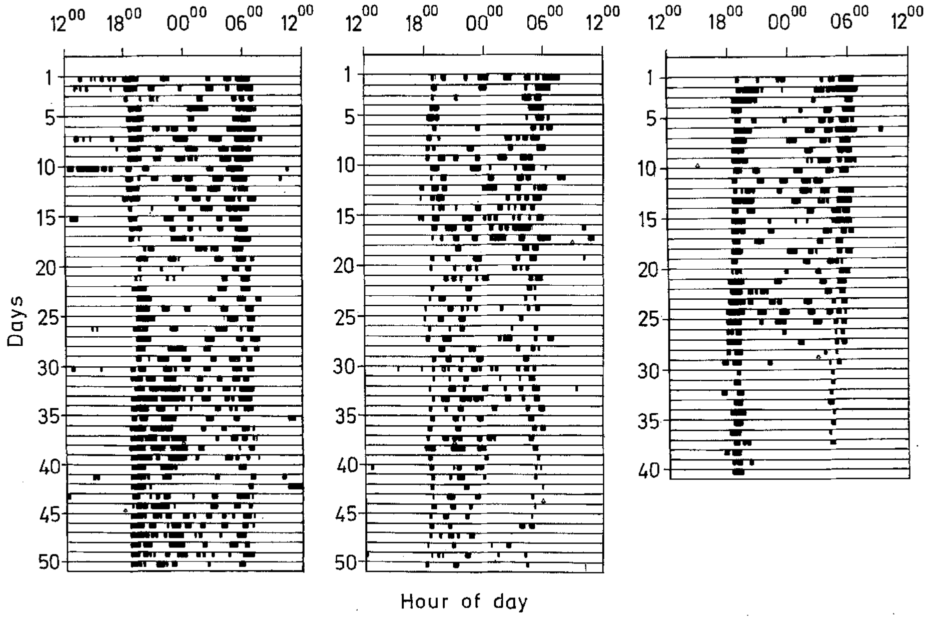

**Fig. 1.** The flight activity patterns of three captive bats for 40 days in one case and 50 days in the other two cases recorded 40 m inside a narrow 'true cave' in Madurai. The bats could fly within the flight activity cages and the movements of the cages were directly recorded. Activity bouts are indicated by vertical patches and the horizontal lines indicate rest. The activity/rest data are schematized from original data and presented one below the other for successive days

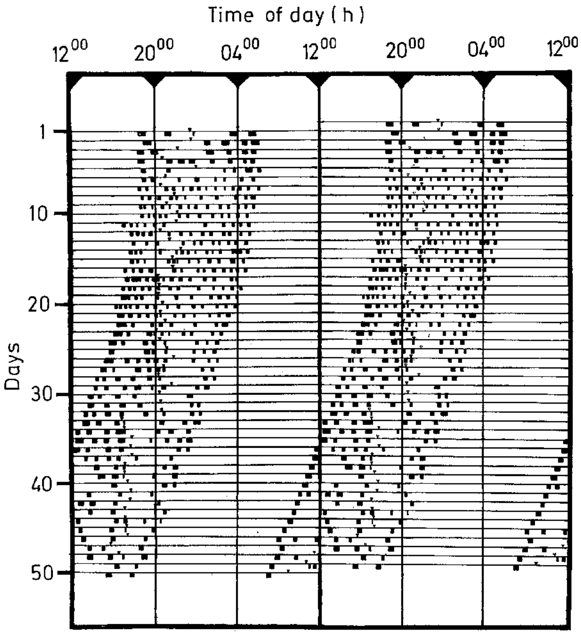

**Fig. 2.** A double plot of activity/rest pattern of a solitary male *Hipposideros speoris* recorded in a cave without any conspecifics over a period of 50 days. Triangles indicate feeding time. The details are schematized from original felt pen tracings. Other details as in Fig. 1

of the circadian activity rhythm in this bat in the *absence* of free-flying conspecifics, under natural cave conditions.

## Discussion

The entrainment of the activity rhythm of all three captive bats is absolute and is as stable as any entrainment we have achieved with two other species of microchiropteran bats (Subbaraj and Chandrashekaran 1978; Sripathi, unpublished data) and a palm squirrel using light-darkness cycles of 12:12 h in the laboratory (Uma, unpublished data). This phenomenon could be explained by social entrainment of the circadian rhythm in *Hipposideros speoris*. This social synchronization might result through (i) flight noise of conspecifics, (ii) acoustical and (iii) pheromonal cues. Pheromonal cues are present more or less constantly even though they can certainly steeply intensify during the onset of colony activity. Some flight noise is encountered throughout the day. For these reasons the acoustical cue is more likely to play the role of Zeitgeber by literally 'telling' the news of darkness setting in outside. If the cues are indeed acoustical then they are ultrasonic and in the range of 135 kHz (measurements of Dr. G. Schuller). These bats are 'silent' to humans.

Apparently the 'social cues' of our experiments (whatever they might eventually turn out to be) act as a Zeitgeber as effectively as light and darkness. The bimodality of the activity pattern of these captive bats further reinforces out conclusion that the activity is being socially synchronized by conspecifics. It must be emphasized here that such a clear-cut bimodality does not occur in free-running activity rhythms of this bat under *laboratory* conditions. The early bouts of activity signal the onset of foraging flight activity in the colony and the secondary bouts of activity signal solitary and group bat returns. We cannot, however, be certain at this stage that bimodality is *not* an inherent feature of the endogenous characteristics of circadian systems.

The issue of social synchronization is further reinforced by the data obtained in cave 2 without free-flying conspecifics and hence no 'social informers' (Fig. 2). Another aspect of this free run under natural cave conditions is that while in the cave, this solitary bat *did* have access to non-specific Zeitgeber influences from the outside world giving information about day and night. Thus, we could often hear crows and the Indian myna birds at a nearby waterhole during the day and the chirping of crickets during the night. Apparently such non-specific cues do not entrain the circadian rhythm of this bat even though *Hipposideros speoris* does indeed hear noises in this sound frequency range (measurements of G. Schuller). There may even be a *species specificity* in social synchronization of circadian rhythms in bats. It may, however, turn out that those species of bats that share roosting sites may entrain each others' circadian clocks. Our findings are contrary to the findings of Lohmann and Enright (1967) on birds and Wever (1979) on humans; bird and human circadian rhythms entrained also by non-specific cues.

It would be interesting to know how the biological clocks of these bats would respond if they were exposed to conflicting Zeitgeber influences such as social cues plus LD (light/darkness) and LL (continuous light) conditions. The results of experiments in progress in our caves and in our laboratory should help to understand these processes better.

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