

Seasonal changes in the precision of the circadian clock of a tropical bat under natural photoperiod

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Summary. The emergence and returning activity patterns of a colony of microchiropteran bats *Hipposideros speoris*, under natural light-dark cycles keep pace with the timings of sunset and sunrise respectively. The onset of emergence flight occurred at different environmental twilight intensities which vary over the seasons. The seasonal changes of phase relationship between the onset and end of flight activity to sunset and sunrise respectively are discussed. As a result ψ -onset, ψ -end, and ψ -midpoint all undergo marked seasonal variations and the values obtained are well in accordance with the seasonal rule of Aschoff. The changes in the timings of onset and end of activity reflect the changes in the duration of activity time of the colony. The activity time is positively correlated with the duration of night time. The possible involvement of the 'non-parametric' action on the entrainment of this colony is briefly discussed.

Introduction

Many bodily functions of organisms oscillate rhythmically and keep pace with the geophysical temporal order (Buening 1973, 1982). In higher vertebrates, the main entraining agent or 'zeitgeber' is the natural light-dark cycle (Aschoff 1960, 1964, 1969, 1981; Aschoff et al. 1982; Bruce 1960; Pittendrigh 1960). In animals, recording the locomotor activity both in laboratory as well as in natural conditions is among the easiest method to demonstrate the seasonal changes in phase relationship between activity cycles and environmental cycles. The timings of onset and end of activity can be easily used as reference points for the computation of several parameters of their rhythms (Chandrashekar et al. 1983).

In recent years many investigators have made systematic field studies on seasonal trends in the timings of activity in birds and mammals (Aschoff et al. 1970; Aschoff et al. 1972; Erkinaro 1972a, b; 1973; Daan and Aschoff 1975; Kenagy 1976; Pohl and West 1976). Among mammals bats are strongly nocturnal, but generally depend upon auditory rather than visual stimuli (Griffin 1958). They are of particular interest for investigating the effectiveness of the daily light cycle as an activity synchronizer. Endogenous rhythms in bats were first described by Griffin and Welsh (1937). In temperate regions, a few authors have shown interest on seasonal changes in timing of daily activity in bats with respect to the natural light-dark cycle under both field and

laboratory conditions (DeCoursey and DeCoursey 1964; Voûte 1972; Laufens 1973; Kunz 1974; Voûte et al. 1974; Erkert 1978; Swift 1980). However, these studies had to be carried out mostly during summer when the animals were out of hibernation.

In contrast the activity patterns of bats can be studied throughout the year in tropical bats. Yet very few studies on the daily onset and end of activity of bats under natural LD cycles have been carried out in the tropics (Subbaraj and Chandrashekar 1977; Usman 1981). It is often thought that the day length is practically invariant in the regions close to the equator. In the course of the seasons, significant variations occur even in Madurai (9° 58' N, 78° 10' E) both in the proportions of the LD cycles and in day length.

In the present study, it was observed that the onset and end of activity in a colony of ca. 500 hipposiderid bats *Hipposideros speoris* showed remarkable correspondence with the timings of sunset and sunrise over the seasons. The colony exhibited spectacular changes in the phase angle difference (ψ) and duration of activity (α) in relation to the environmental parameters.

Material and methods

The study area, Samanar hill complex of massive granite rock with an east-west axis, lies close to the village Keela Kuyil Kudi – about 8 km south-east of the Madurai Kamaraj University precincts. The area predominantly includes ponds and agricultural fields. A number of natural caves, caverns and crevices are located in the study area. The cave, with which this study was carried out, is perched on the northern slope of the hill at an elevation of about 108 meters from the ground level. It is typical having only one entrance which faces north-west. A colony of about 500 individuals of the bat, *Hipposideros speoris* of both sexes inhabits this cave. The cave has several labyrinthine ramifications 15–50 meters from the cave mouth. Some nooks of the cave are inaccessible to humans. The bats use several of these pockets as their roosting sites. A homeostatic environment exists in the cave. The temperature and humidity were recorded (Lambrecht-Goettingen thermohygrographs) continuously for fourteen months (December, 1977 to January 1979) at the deeper recesses of the cave. The values for temperature and relative humidity are remarkably constant at 27° C and 95% respectively, over the seasons (Fig. 1 A, B).

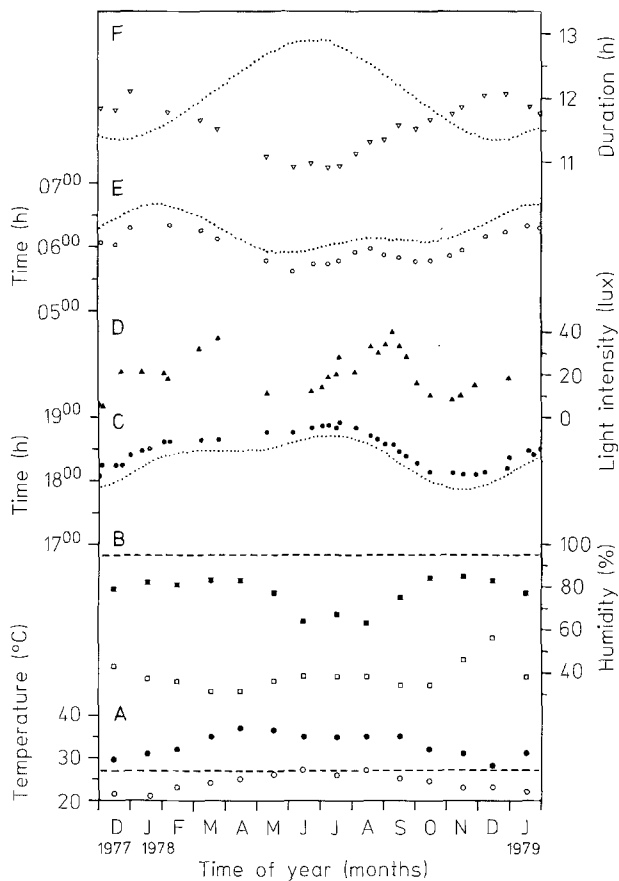


Fig. 1A–F. Summary of the nocturnal activity of the colony and the environmental parameters. **A** the temperature variations at the study area. Solid circles indicate the maximum ambient temperature, hollow circles indicate the minimum ambient temperature and the interrupted line indicates the constancy of temperature (27°C) inside the cave, over the seasons. **B** the variations in the values of relative humidity; solid squares indicate the maximum ambient, hollow squares indicate the minimum ambient and the interrupted line indicates the constancy of humidity (95%) inside the cave over the seasons. **C** the timings of the sunset (dotted line) and the onset of the exodus flight (solid circles). **D** the values of the environmental light intensity at the time of the onset of activity of the colony. **E** the timings of sunrise (dotted line) and the end of activity of the colony (hollow circles). **F** the relationship between the day length (dotted line) and the activity time (triangles) of the colony

Visual observations on the timings of emergence and returning activity at the mouth of the cave were made from December 1977 to January 1979. Additional data were also gathered from March–July 1980 and August–October 1981. At the cave entrance, it was possible to visually count departures and returns of the bats silhouetted emerging through the mouth of the cave against the sky. The time of emergence of the first bat was recorded and thereafter the number of bats emerging every minute was counted as long as the prevailing twilight permitted counting. The counts were then continued with the aid of dim red light (>610 nm) near the entrance of the cave, till the departure apparently ceased. The number of individuals returning to the cave was counted for successive 15 min intervals throughout night. Light intensity was measured during evening flights at the mouth of the cave with an AEG lux meter with the photosensor directed towards the zenith.

The lower level that could be directly and reliably measured was 0.5 lux.

Sunset and sunrise times were obtained from the tables of the Indian Ephemeris Nautical Almanac published by the Director of Observatories, Calcutta and were adjusted for longitude, latitude and Indian Standard Time (IST). Recordings of ambient temperature, relative humidity and precipitation, for the whole region were collected from a meteorological station situated within the University precincts. Timings of onset and end of activity were compared with the timings of sunset and sunrise respectively over the seasons. Seasonal variations of timings of onset and end of activity were used to calculate the phase angle differences and activity time following the method of Daan and Aschoff (1975) and Kenagy (1976).

Results

Pre-emergence activity

Since these bats emit no audible vocalizations silence prevailed during most of the day hours. During rainy seasons the interior regions of the cave are partially flooded and only the gurgling water breaks the silence. Prior to emergence approximately an hour before sunset, bats become 'restless' and exhibit head and ear movements, wing flapping, extensive autogrooming, swinging forward-backward motions and make short flights. The bats from the deeper recesses of the cave, move towards the entrance where they can perceive the environmental light. Prior to the normal exodus flights from the cave they begin to make circling flights in and around the entrance chamber. The commotion inside the cave increases in intensity just before sunset. When the twilight illumination drops, bats fly farther and farther towards the entrance before they emerge. About ten to twenty minutes after sunset (over the seasons) always a solitary bat darts out of the entrance and immediately returns to the cave. Usually this is the signal for the beginning of exodus from the cave, as groups of individuals break off tangentially from the mill in the entrance chamber and burst out of the cave. This predusk activity has been considered as a 'light sampling behaviour' (Twente 1955; Marimuthu et al. 1978, 1981) in order to judge the light situation outside.

Emergence activity

The time of departure of the first bat is considered as the index of onset of activity for the colony as whole only if it is followed by another within 5 min. In early periods, emergence of bats occurred singly or in small groups. About 10 min after the initial emergence groups were evident which varied in size between 5 and 15 individuals. At peak periods of emergence, the flight was a chain of separate groups following one another at short intervals. The intensified emergence consistently occurred over a period of about 60–90 min (Fig. 2). Thereafter the number of individuals flying out fell and only a few solitary individuals emerged sporadically for the rest of the night. However, on any given night, about 5–10% of the colony remained inside the cave.

Light intensity and onset of activity

Evening departure of bats usually occurred at low twilight intensities which ranged over the seasons from 4.5 to 40 lux.

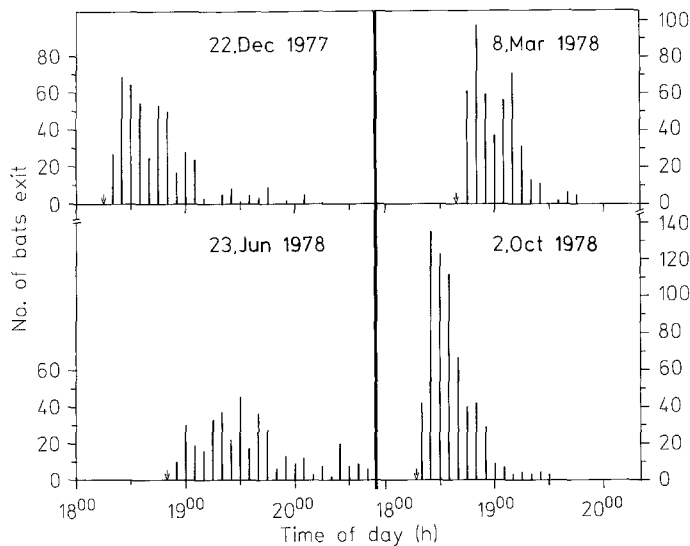


Fig. 2. Representative examples of the pattern of emergence flight for four different months. The bat-counts were made for every minute and added up to every five minutes. The arrow in each column indicates the time of the onset of the exodus flight

On a few occasions bats emerged out of the cave at higher light intensities, but they never flew away directly to the feeding areas. Instead they stayed at the 'secondary roosting site', a small creek situated close to the cave or they resorted to inward and outward flights between the cave mouth and the 'secondary roosting site'. When the light intensity dropped further to an optimum level they left for foraging and the light intensity then was noted. The variations of light intensities at the time when the first bat left the cave for foraging, over the seasons are shown in Fig. 1D. The onset of activity occurred at relatively higher light intensities during the months of neutral day lengths (March and September) and lower intensities during the months of longer (June) and shorter (December) day lengths.

Returning activity

It was not possible to decide the time of the precise onset of returning flight, because bats exhibited both inward and outward flights sporadically during most of the night. However, by around 03.00 h the flight was essentially back to the cave. Approximately two hours before sunrise, the bats exhibit numerous circling flights near the mouth of the cave at an altitude of one or two meters. Their activity near the cave mouth steadily increased. Returning flights are characterized by sporadic appearance of solitary bats then a build up gradually to small groups which reached their peak at predawn (Fig. 3).

The time at which the last bat returned to the cave was considered to denote the end of activity of the colony as a whole and this was about 10–25 min before sunrise over the seasons. Figure 1E illustrates the timings of end of activity which precisely preceded and paralleled the timings of sunrise over the seasons.

Activity time

The duration of the activity period of the colony was measured as the time elapsed between the emergence of the

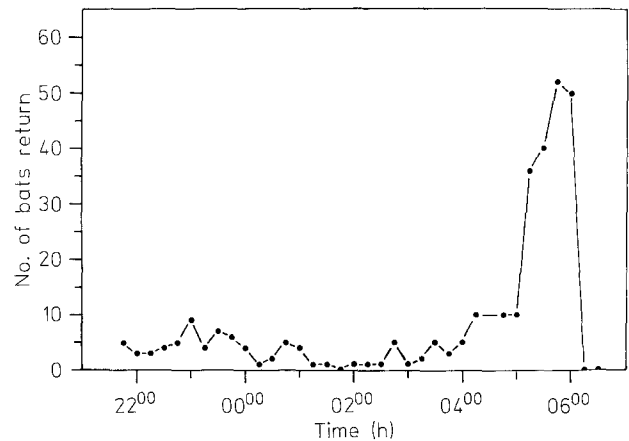


Fig. 3. Representative example for the returning activity of the colony. Bat counts were made for every 15 min interval for the whole night

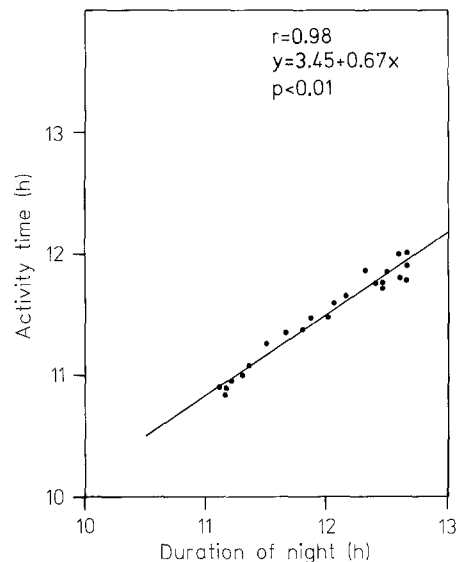


Fig. 4. Duration of activity period of the colony is plotted against the duration of night time

first bat and the return of the last bat. The seasonal course of the onset and end of daily activity showed that the activity time (α) followed the seasonal changes in duration of day length (or duration of night time). Consequently the duration of the activity time was longer during shorter day lengths and shorter during longer day lengths (Fig. 1F).

Regressions were calculated for the activity time in relation to the duration of night time (Fig. 4). The slope did not differ significantly from zero ($r = 0.98$; $P < 0.01$) indicating a positively correlated relationship between the activity and the night time.

Precision in the range of timings of onset and end of activity and their phase angle properties over the seasons

The timings of onset and end of activity systematically changed and paralleled the timings of sunset and sunrise

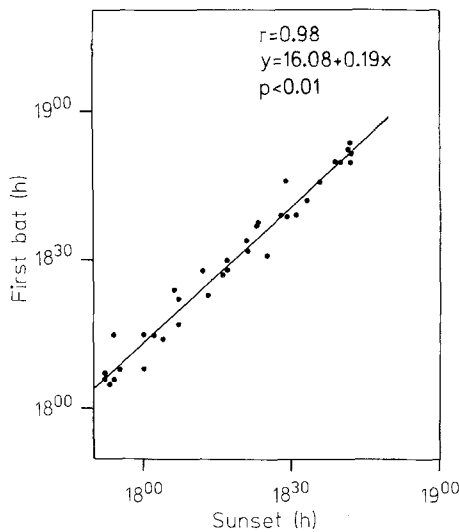


Fig. 5. Linear regression of time of emergence of the first bat in relation to the time of sunset

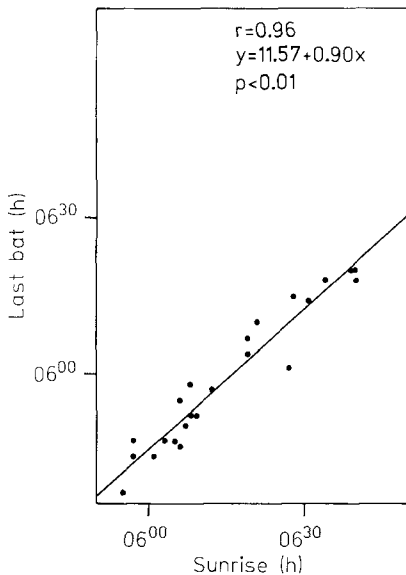


Fig. 6. Linear regression of the time of return of the last bat in relation to the time of sunrise

respectively. Figures 5 and 6 represent the regression analyses of the timings of sunset and emergence of the first bat, and the timings of sunrise and return of the last bat respectively over the seasons. These slopes do not differ significantly from zero indicating a precise relationship between onset of activity and sunset on the one hand and end of activity and sunrise on the other.

Figure 1C illustrates the timings of sunset over the seasons which varied over a range of 50 min (between 17.52 h and 18.42 h) and corresponding onset of activity which displayed a range of 49 min (between 18.05 h and 18.45 h). Similar kind of relationship was found between the termination of activity and sunrise (Fig. 1E). Time of sunrise during the year varied over a range of 45 min (between 05.55 h and 06.40 h) and termination of activity 43 min (between 05.37 h and 06.20 h).

The phase relationship between the biological and environmental cycles can be expressed by phase angle difference

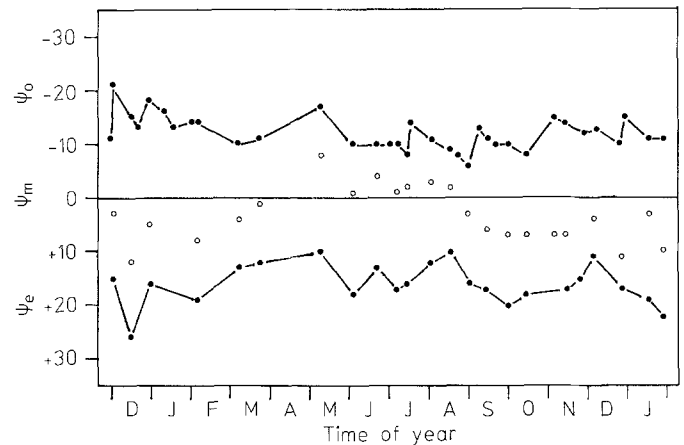


Fig. 7. Seasonal changes in the phase angle differences (min) for onset (ψ_o -upper part), end (ψ_e -lower part) and midpoint (ψ_m -unconnected hollow circles) of activity of the colony over the seasons

(PAD or ψ) of the onset (ψ_o) and end (ψ_e) of activity (see Daan and Aschoff 1975). Figure 7 shows that the ψ_o varied from -6 min to -21 min and ψ_e varied from $+10$ to $+26$ min. The bats had their largest (most positive or less negative) ψ_o and smallest (less positive or more negative) ψ_e in longer photoperiods; smallest ψ_o and largest ψ_e in shorter photoperiods. Consequently the seasonal variations in ψ_o and ψ_e roughly mirror image.

According to Aschoff (1965, 1969), a third measure of the phase angle difference between the activity rhythm and the entraining light-dark cycles is ψ -midpoint (ψ_m) i.e. the time interval between the midpoint of activity and midpoint of dark time. The seasonal course of ψ_m (Fig. 7) showed relatively lesser variations compared to ψ_o and ψ_e . Summer increase in photoperiod resulted in more negative or less positive ψ_m values.

Discussion

The hypothesis that the daily activity of an animal depends upon an endogenous timer and re-setting environmental cues is not peculiar to bats and my findings merely broaden the comparative base of a well-grounded theory formulated by several authors (Bruce 1960; DeCoursey 1960; Pittendrigh 1960; Aschoff 1963). The timings of daily onset and end of activity have been reported by many authors in several bat species. The actual onset of exodus flight in *H. speoris* was preceded by an arousal activity during the pre-dusk hours. In such cases, the endogenous regulator may act as a 'wake-up timer' (DeCoursey and DeCoursey 1964) to insure the arousal of the bats and 'turning on' the nervous system to regain the full sensory capacities before trying to perceive the external environment. A similar behaviour exhibited by *H. speoris* in the entrance chamber of the cave, the 'light sampling' was first reported by Twente (1955) and further discussed by Gaisler (1963), Herreid and Davis (1966), Kunz (1974) and Voûte et al. (1974). This may facilitate the members of the colony to check their endogenous clock against the light-dark cycles as they pass the cave exit and assess the outside light. Repetitive passages towards the cave entrance also allow them to assess the proper time for emergence.

The onset of emergence activity in *H. speoris* occurred within a certain range of environmental light intensity and it varied over the seasons. This variations implicate the absence of a 'fixed' lower threshold of intensity which triggers the emergence flight. Similar light intensity variations during the beginning of nocturnal activity was reported in Kangaroo rats (Kenagy 1976). Furthermore, it was indicated that absolute light intensity may not be a cue for the initiation of activity (Laufens 1969, 1973; Erkert 1974; Daan and Aschoff 1975; O'Farrell and Studier 1975; Subbaraj and Chandrashekar 1977; Pandian and Chandrashekar 1980) but rather the rate of change of light intensity appears to be the primary environmental cue for the beginning and end of activity.

The pattern of emergence observed in my bat species confirms the observations on other species of bats such as *Tadarida brasiliensis* (Davis et al. 1962), *Rousettus aegyptiacus leachi* (Jacobson and DuPlessis 1976) and *Pipistrellus pipistrellus* (Swift 1980). The emergence by *coup* (Novick 1977), when these bats emerge in large numbers, may be to divert the attention of predators, which often wait near the cave entrance every day. The observation that I made during one evening when an owl pounced on a single bat soon after it emerged from the cave further corroborates Novick's statement.

The comparison of activity time (α) as a linear function of day length (Fig. 1 F) or the duration of night time (Fig. 4) shows that α follows the seasonal variation rather closely (Kenagy 1976; Pohl and West 1976; Erkert 1978; Georgii 1981). In the Arctic cricle α follows the seasonal variations of day length only to a limited extent. For example in day active birds an S-curved relationship was reported (Aschoff 1969; Aschoff et al. 1970; Daan and Aschoff 1975). At days shorter than about 5 h and at days longer than 19 h the activity time is apparently independent of day length. My results obtained at Madurai (9° 58' N; 78° 10' E) where the day length does not vary much (0.26 min/day) over the seasons and perhaps for this reason cannot be related with the S-curves obtained by those authors.

It is a useful practice in circadian literature to relate onset and end of activity to corresponding phase points of the daily light-dark cycle, e.g. sunrise and sunset. The theory of oscillation suggests that day active animals have largest ψ -onset and smallest ψ -end in mid winter; smallest ψ -onset and largest ψ -end in mid summer. The opposite should be true for night-active animals (Aschoff 1969; Aschoff and Wever 1965). The phase relationship of *H. speoris* obeys this rule and concurs with several other similar reports (Daan and Aschoff 1975; Kenagy 1976; Pohl and West 1976; Subbaraj 1979; Usman 1981). Another interesting feature is that the seasonal variations of ψ -onset and ψ -end roughly mirror image each other (Fig. 7). This phenomenon of mirror imaging might have arisen through the events of light intensity variations at onset and end of activity over the seasons (Daan and Aschoff 1975). Such systematic seasonal shifts of the daily onset and end of activity relative to the light intensities are the reflection of the internally defined phases of the driving oscillation rather than externally evoked responses (Aschoff and Wever 1962).

Another important measure of the phase angle difference between the biological cycle and the environmental cycle is ψ -midpoint (Aschoff 1965, 1969; Wever 1967). ψ -midpoint is a complex function bearing little resemblance to either ψ -onset or ψ -end. Smaller seasonal variations in

ψ -midpoint as observed in *H. speoris* were also reported both for day active birds and night active mammals (Aschoff et al. 1972; Erkinaro 1972a; Voûte 1972; Kenagy 1976; Pohl and West 1976). From the laboratory experiments conducted in continuous illumination (LL), it was apparent that day active birds have a negative and night active mammals a positive dependence of period length (τ) on the light intensity (Aschoff 1960). Based on this seasonal rule or 'Jahreszeitenregel' was formulated by Aschoff (1964) which states that the summer increase in photoperiod should result in an increased phase angle difference (ψ_m) in day active animals and a decreased ψ_m in night active animals. The present results are in accordance with this rule (Fig. 7).

The phase angle difference between activity rhythms and zeitgebers can convey information about the mechanism of entrainment (Aschoff 1960; Bruce 1960; Pittendrigh 1960; Wever 1960) through which parametric and non-parametric action of a zeitgeber was distinguished. The term 'parametric' implies a continuous action of the zeitgeber on the biological oscillation. For example, the influence of different levels of illumination intensity on the free running period would be through a continuous (parametric) action. Such effect is per definition 'parametric'. Similarly under LD intensity ratio can also act parametrically and thus modify the phase angle properties. Since the habitat of *H. speoris* is the darkest recesses of the cave, it is unlikely that proportional (parametric) effects of light are involved in the natural entrainment.

Non-parametric entrainment is based on rather abrupt phase shifts of the endogenous oscillation. Such phase shifts are the result of traditional (differential) stimuli of the zeitgeber (Subbaraj and Chandrashekar 1981). Since the activity patterns precisely follow the timings of sunset and sunrise, transition from light to dark and vice versa is an important signal from the LD zeitgeber. Thus it is probable that the natural entrainment mechanism involved in this species is fundamentally non-parametric. Pittendrigh and Daan (1976) suggested that such a non-parametric action of LD cycles is functionally preferable for entrainment of biological clocks since this action does not entail the continuous estimation of lapse of time intervals.

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