

days. The reproducibility of this complex event during an experiment varies within a series of stimulations (Fig. 1 b).

A singing movement was counted as part of courtship behavior if it was frequently accompanied by subunits S1 or S2 or elements of these. In no experiment on any male isolated from a female was it possible to elicit, from the very onset of stimulation, the entire courtship unit with all subunits in correct sequence. But during a fairly long stimulation session, by suitable adjustment of the stimulus parameters (for example, frequency above 70 Hz and pulse amplitude at least 2.8 μ A in the third hour of the experiment with Site 3), all elements of the repertoire of movements comprising a courtship unit could be elicited at Sites 3, 4 and 5 (Fig. 1 a). On the other hand, at Site 6 the only courtship movement in addition to singing was head-shaking (S1), and at Site 7 the approach jump and movements of S2 (in this case singing sometimes appeared only as an after effect). With stimulation at Sites 4 and 5 the singing movement of S3 was preceded by activity closely resembling approach behavior. Singing was elicited most reliably, most reproducibly, and with the shortest latency by stimulation at Site 3; it began only a few seconds after stimulus onset, while the trunk of the male was still resting on the substrate and the antennae were lowered. Initially the S3 song passages were remarkably long and unaccompanied by other movement; this response was followed by the sporadic, increasingly frequent occurrence of head-shaking (S1) and jerking of antennae and hindlegs (S2), though all these movements were reduced in duration and amplitude as compared with the normal behavior (Fig. 1 e). This progressively developing "courtship" continued for at most one courtship unit after stimulation was stopped, when the male was alone in the arena. In the presence of a female the response could be maintained for a longer time following the end of stimulation. The remarkable effectiveness of stimulation at this site was further illustrated in an experiment in which this courtship behavior was elicited (though with a high threshold) during and after copulation.

Singing can thus be elicited in grasshoppers which stridulate with their hindlegs by stimulating the brain at the same sites that elicit cricket song, produced by rubbing the hindwings together [8]. The differences in effectiveness of various stimulus sites in eliciting the different subunits indi-

cate that neurons in the region of the mushroom body take part in the coordination of the behavioral elements of a courtship unit.

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Daily Activity Pattern of Fruit Bats under Natural Light Conditions

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Field studies of fruit bats, *Pteropus*, [7, 9] have shown that the bats begin to leave their nesting sites for feeding around dusk and return shortly before dawn. Little can be said, however, about the bats' activity patterns during the period as they were not observed. In isolation individuals of *Rousettus aegyptiacus* and *Eidolon helvum* [6] continuous light revealed a free-running circadian rhythm of activity. Our study was designed to investigate the daily activity pattern of groups of animals to ascertain the effects of varying day lengths and group interactions on the presumed circadian system.

Three adult *Pteropus giganteus* (two females; one male) and one male juvenile (8 months old) were housed in a 2 \times 2.5 \times 2.5 m naturally illuminated aviary. No artificial lighting was used. The temperature was held constant at 22 \pm 2 $^{\circ}$ C. On the ceiling of the aviary, above the food dishes, were eight rods for climbing. Six of them had microswitches connected to a recorder via a 1-s time-delay circuit so that only sustained movements would be recorded. The total activity of the colony was recorded rather than separate records for each animal. In addition, the animals were regularly observed

and behavioral notes routinely made. The bats were also participants in a learning experiment during the day and were regularly fed at 1000 local time (C.E.T.). The activity records were mounted one day under another and the onset and offset of activity periods determined by visual inspection.

The presumed circadian system of activity is capable of following the seasonal changes in the light-dark (LD) cycle despite the fact that in the bats' natural habitat (India) there is little seasonal change in the LD ratio (Fig. 1 a). This is similar to the finding of Erkert [6] using artificial light cycles. She also found that the animals' activity pattern was unimodal and when the dark period was greatly lengthened (up to 20 h) the duration of the activity period did not expand to fill the entire dark period; activity began considerably after sunset and ended considerably before sunrise. Activity onset throughout the year in *Pteropus* is usually before sunset (Fig. 1 b) and not always clearly demarcated, while activity offset is quite clear and coincides with sunrise (cf. [3] for a contradictory prediction). We found that *Pteropus* consistently showed bimodal activity peaks during the dark period (cf. [5]) and the duration of the actual active time varied considerably less than the variation in the duration of the night, i.e., the pause during the activity period varies positively with night duration. Thus, in at least three species of fruit bat, *Rousettus*, *Eidolon*, and *Pteropus*, there appears to be an upper limit on the

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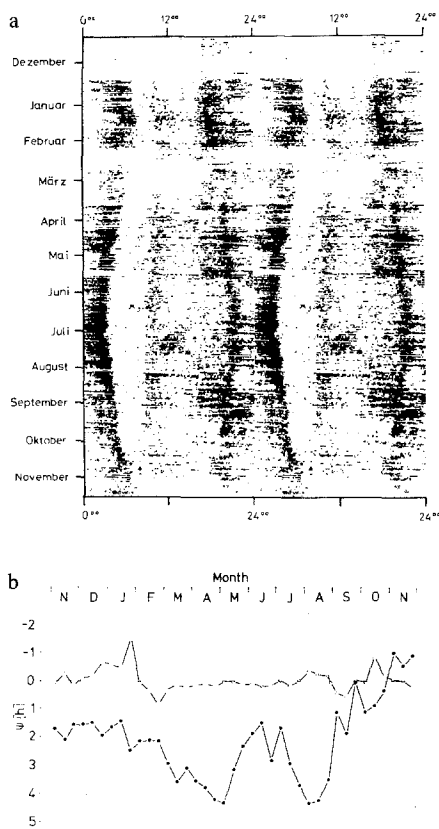


Fig. 1. (a) Activity record of fruit-bat colony under natural light conditions. The record for November to December is faint due to reproduction difficulties; the faintness in February is due to a failure in the recording circuitry. Time scale is in C.E.T. (b) Seasonal changes in phase-angle differences (ψ). Positive values represent hours before LD transition. Activity onset (●) occurs around sunset; activity offset (○) occurs around sunrise. Each point represents the mean of data for approximately 1/3 month

duration of the active time displayed within a single 24-h period.

The total duration of the activity period is greater during winter than during summer (December 17.6 h; June 9.9 h). Even so, during the short summer nights there was still evidence of a pause in activity in the middle of the darkness. This strengthens the argument that the bimodality seen under these conditions is a normal feature of the circadian system of activity (cf. [1, 10]).

It is also quite interesting to note that there was a regular increase in activity just before the 1000 C.E.T. daily feeding. Despite this potential Zeitgeber, and the evidence that the animal was perceiving it, there is no indication that it had any effect on the circadian locomotory behavior of the animal (cf. [4, 11]).

An interesting phenomenon is the dramatic change in phase angle of activity onset in early May and August (Fig. 1 b). Activity then begins about 4 h before sunset rather than the usual 2 h, while activity offset still occurs around sunrise. Thus, the fruit bats are active 2 h longer than would have been predicted. (A similar increase in activity onset, although occurring only once a year, has been observed in chaffinches [2, 3].)

Two possible explanations are suggested. First, this may represent a phase locking of the circadian system of locomotion to an evolutionarily selected optimal value for the natural habitat of *Pteropus*, India. In India the lengths of the light and dark periods per day are about equal for the entire year. This situation occurs twice a year at the latitude of our observations

(47° 58' N), mid-March and mid-September; close to the times of the observed phase-angle changes.

Another possible explanation is that the phase-angle shift is the result of a circannual rhythm related to reproductive behavior. Spring is the season when the bats normally give birth and Autumn when copulation usually occurs [7–9]. Thus, even though overt behavioral signs of reproductive activities may be lacking, the phase-angle shift in locomotory behavior may well represent the activity of a circannual system related to reproductive behavior, perhaps based on changes in the circulating titers of the sex hormones.

At the present time there are insufficient data to decide between these two possible explanations and further research must be performed.

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Buchbesprechungen

Microorganisms and Minerals. Ed. by E.D. Weinberg (Microbiology Series, Vol. 3). New York-Basel: Dekker 1977. 492 pp., SFr. 144,—.

Research concerning the relationships between minerals and the nutrition, development, metabolism and ecology of microorganisms has become increasingly popular. The role of iron, magnesium, zinc, manganese, calcium, molybdenum and copper as essential enzyme components, the bio-

transformation of inorganic substances by soil and aquatic microorganisms, and the relationship between inorganic pollutants and microbial populations are current fields of research. The appearance of this book exemplifies this growing interest. It deals mainly with one aspect of the microorganism relationship, namely, cation transport. Accordingly, a title like "Divalent Cation Transport in Microorganisms" would have done more justice

to the book. Transport of magnesium, calcium, manganese, zinc and iron is described and discussed in detail, and the literature on these topics is updated and comprehensive. Unfortunately, the roles of these metals in enzymatic reactions and in other biological phenomena is underemphasized. Subject balance suffers from the fact that the interesting chapters on mineral control of secondary metabolism, metal transformations, and the interaction