[*Experimental work on biological rhythms has centred mostly around the ubiquitous role of light darkness cycles (in nature as well as in the laboratory) in the entrainment or synchronization of biological clocks (circadian rhythms) for well over 100 years now. Work carried out in the past decades on circadian rhythms of higher vertebrates, especially those in birds, mammals and humans, has uncovered instances and possibilities of entrainment by unorthodox time cues (zeitgebers) such as 'social cues' and 'food cycles'. Work on the circadian rhythm in the flight activity of a species of microchiropteran bats implies social synchronization of the biological clocks of the individuals of a colony. Intensified and critical research on 'social cues and circadian rhythms' and more experimental, analytical and quantitative data would soon make the results of great importance in psychiatry, social medicine, preventive care, shift-work planning and possibly to aernauts and astronauts. A new branch of chronobiology called "social chronobiology" may well be launched in the not too distant future.*]

SOCIAL CUES AND CIRCADIAN RHYTHMS

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INTRODUCTION

THE light/darkness cycles generated by sunrise/sunset are nearly universally the synchronizing agents (also called Zeitgebers—a term anglicized from its German root) for circadian rhythms[1]. Circadian rhythms are endogenous rhythms which possess and express under appropriate conditions of constancy of light and temperature, periods close to but, rarely ever exactly, the 24 hr of the geophysical day. Hence circadian[2] from the Latin circa = about; dies = day. Examples are legion. The rhythms manifest themselves in the physiological processes of even algae and fungi right upto humans[3,4,5]. Well over 100 human body functions oscillate on a 24 hr basis and presumably would turn circadian if studied under social isolation[6]. The term 'circadian' is nowadays unfortunately used indiscriminately and uncritically[7]. In 1960 when the word was accepted in the first Cold Spring Harbor Symposium on Biological Clocks, it was done so on the understanding that it would be a substitute for the expression "endodiurnal" used by Pfeffer[8] and Buenning[9]. Although it might be too late to stem the tide, I might plead just once more that only such of those rhythms that display the following 4 diagnostic characteristics be designated circadian:

1. Persistence in LL or DD and constant temperature.
2. In so persisting expression of periods close to but never exactly 24 hr (circa) (free run).
3. Compensation of the period for temperature *i.e.* showing Q_{10} values close to unity.
4. Resettability of the rhythm by light and/or temperature perturbations.

All circadian rhythms are diurnal rhythms but not all diurnal rhythms are circadian. The

Abbreviations used: LD, light/darkness cycle. LL, constant light. DD, constant darkness. τ, period length.

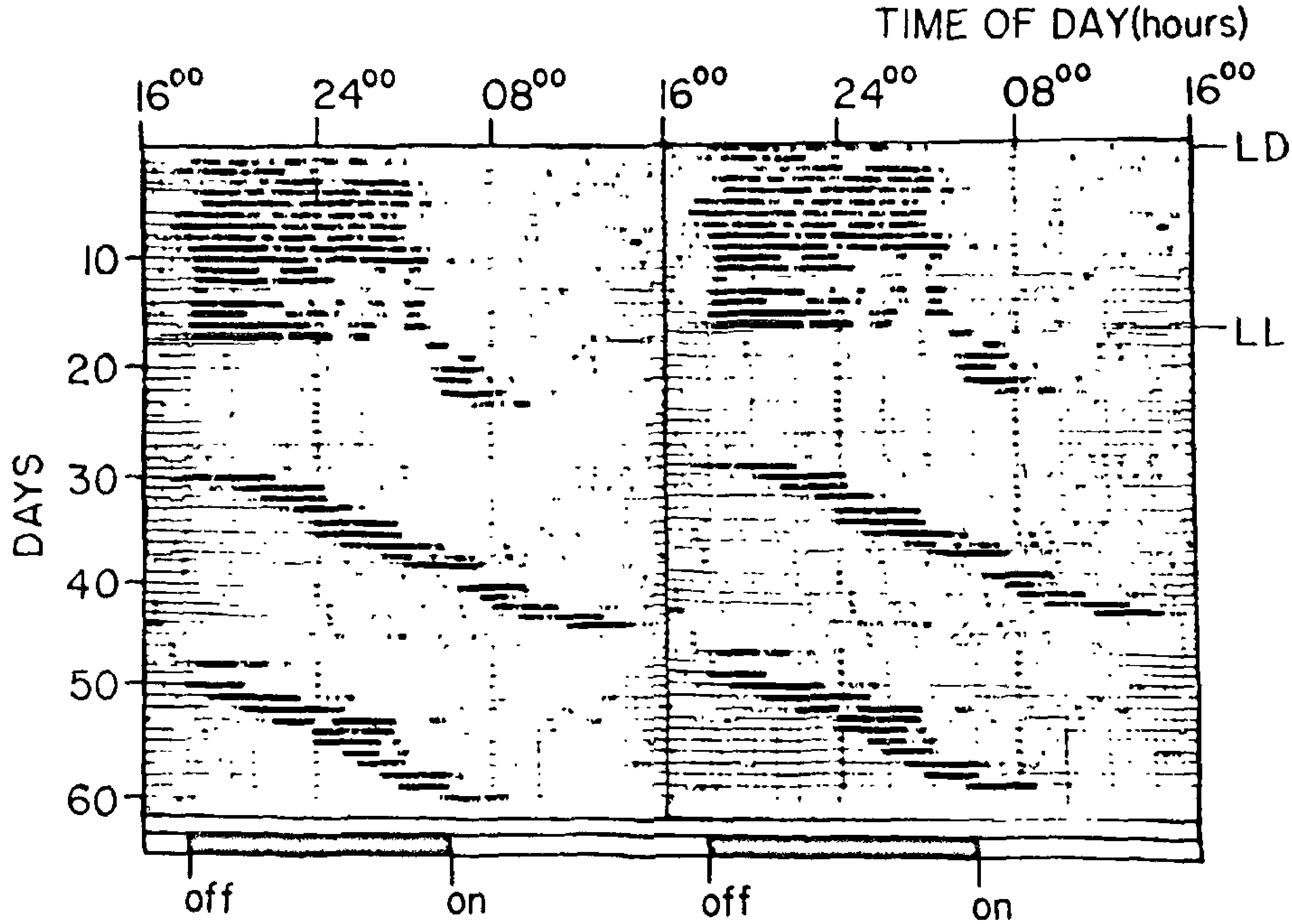

Figure 1. Entrainment and free run of a genuine circadian rhythm in the flight activity of a microchiropteran male bat of the species *Taphozous nudiventris kachhensis*. Days 1-18, the rhythm is entrained to LD cycles of 12:12 hr after which the rhythm free runs with $\tau > 24$ hr upto day 60. The figure is a double-plot with the right hand panel moved relative to the left by one day upwards.

burden of proof must rest with the claimant.

Figure 1 demonstrates the phenomena of entrainment and free run of a genuine circadian rhythm in the flight activity of a microchiropteran bat.

The role of social interaction in synchronizing activity/rest patterns of several species of birds and mammals seems only all too clear from the great synchrony with which flocks of animals leave their roosting sites to forage and return later to roost[10]. In literature such social interactions in the context of the activity rhythms have been accorded only cursory attention. This is surprising in view of the fact that such social cues that help to entrain the individual clocks or animals and bring about a synchrony during, for instance, the beginning of activity of the colony, are of vital importance to the very survival of the species[11]. Novick[12] called the synchronized emergence of bats from their caves "emergence by coup" and considers such behaviour as aiding in confounding predators. Moreover where many species of birds or mammals co-exist in a niche, the spatial overlaps and its constraints may be offset by a temporal partitioning in food-resource exploitation. This is much in evidence among a few species of insectivorous microchiropteran bats in Madurai (G. Marimuthu, K. Usman, J. Habersetzer, unpublished). From our experiments conducted at Madurai with bats both in the field and in the laboratory, we have evidence that the onset, end and amount of activity and rest are all under control of the circadian clock[13,14]. Apart from some of the papers cited in this brief review, experimental proof of the value of social cues in tuning circadian clocks in the individuals of a colony and/or species have been few and far in between[15].

EARLY REPORTS ON SOCIAL CUES AND CIRCADIAN RHYTHMS

One of the earliest reports to impute social synchronization among conspecifics was that of Johnson[16] for the mice of the genus *Peromyscus*. Subsequent reports described similar effects for blinded mice, *Mus musculus*[17], male chevrotain antelopes[18], wolf-coyote hybrids[19], beaver colonies of *Castor canadensis*[20], macaque monkeys[21], sexual cyclicity of female mammals[22] and so on. Several other reports seeking to causally connect social cues with circadian rhythms are anecdotal (however see refs. 10 and 23).

THE EXPERIMENTAL TRADITION AND SOCIAL CHRONOBIOLOGY

The experiments of Halberg *et al*[17] which claimed that blinded mice, *Mus musculus* were synchronized to LD cycles only if normal mice were housed in the same room, are among the earliest to be carried out in the modern experimental tradition. The authors postulated auditory and olfactory mechanisms to mediate social synchronization in this mice.

In 1966 one of the early studies[24] attempting to socially entrain (tune) the biological clock in the common sparrow, *Passer domesticus*, made use of the songs of conspecifics. The locomotor rhythm of the sparrow was successfully driven by playing back the bird song for four-and-a-half hours each day. Similar results came in for two other species of birds the same year and the findings generated much scientific enthusiasm since it all appeared to be in the fitness of things. However, a year later it was found[25], somewhat, unromantically, that cycles of mechanical noise administered by a loud buzzer entrained activity rhythms of three species of passerine birds!

SYNCHRONIZATION BY ULTRASONICS

Laboratory studies have their limitations, especially when they pertain to behaviour. This possibility of laboratory 'artifacts' is a real deterrent in behaviour research. Domesticity and rearing of animals under laboratory conditions may have profound effects on their behaviour. Wherever feasible behaviour seen and recorded in the laboratory must be counter-checked under field/natural/semi-natural conditions. The methods of the ethologist rather than those of the neurophysiologist or the experimental chronobiologist promise to yield richer dividends in the area of social chronobiology. In Madurai (9°58'N lat 78° 10'E long) the conditions are ideally suited for such ethological studies and eventual time structure and integrated analyses of behaviour of animals. Field ethological studies on the behaviour and biological clocks of microchiropteran bats have been carried out in Madurai inside natural caves.

A colony of about 400 to 500 insectivorous bats of the species *Hipposideros speoris* inhabit a 'true cave' (that is, a cave with just one opening) close to the Madurai University campus. The cave has several labyrinthine ramifications 15 to 50 m deep, that is, from its mouth. The bats use several of these pockets as their daytime roosting place. Most roosting spots show great constancy of temperature (27°C) and humidity (95%) and the darkness is absolute, day and night. Within the cave, there is hardly any clue to the passing of time. Yet foraging flight occurs regularly 10 to 15 minutes after sunset. It is clear that the animals are aware of the sunset.

The sequence of events culminating in such regular outflights are as follows. The bats awaken well before sunset. They then stretch, preen themselves and undertake short flights within the dark recesses. They fly into an outer chamber that opens to the world outside through a small window-like mouth; in this chamber they "sample-light"[26]. When it gets sufficiently dark outside they fly out.

The first question that arose was: should each bat sample light for itself or would conspecifics relay the information to those in the interior region? The only way to find this out was to keep a few bats prisoners in their own cave 40 m deep and record their flight activity. Flight cages with writing stylets and mechanically wound thermohygrograph drums were used in the study (figure 2). The activity data of the experiment which lasted 50 days (the blotches in figure 3) show that even the captive bats recognized the time. Evening after evening the captive bats started their activity when the free-living conspecifics inside the cave flew out. Interestingly they also responded to the several bat returns. There can be little doubt that the captive

Figure 2. Flight cages with writing stylets and mechanically wound thermohygrograph drums 40 m deep inside a natural cave.

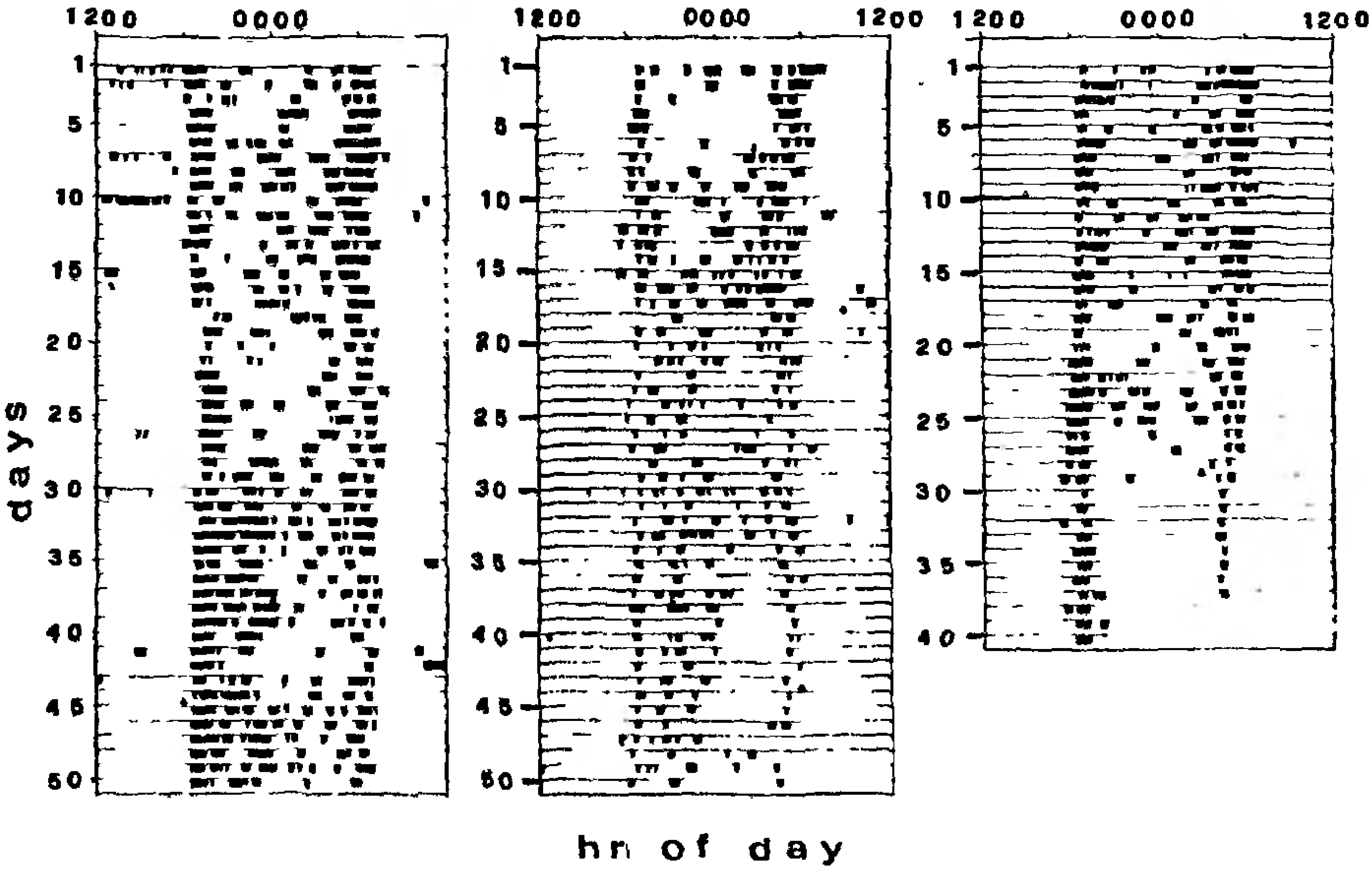

Figure 3. The flight activity patterns of three captive bats for durations of 40 days in one case and 50 days in the other two cases recorded 40 metres inside a narrow 'true cave'. The bats could fly within the flight activity cages and the movements of the cages were directly recorded. Activity bouts are indicated by vertical patches and the horizontal lines indicate rest. The activity/rest data are schematised from original data and presented one below the other for successive days. (After Marimuthu *et al.*, 1981[27].)

bats are responding to social cues. That means the free-flying conspecifics apparently transmit the news of the sunset[27].

A second experiment further probed the hypothesis of social synchronization of biological rhythms in this bat. If free-flying members of the bat colony transmitted the message of time, shouldn't a solitary bat in a solitary cave be helpless? This experiment was carried out in a different cave where there were virtually no bats living. (The word virtually was used since 3 bats of the species *Hipposideros speoris* did live there and these 3 animals had to be exterminated since it is nearly impossible to make these animals abandon their day time roosts; they would always return on the rebound with the aid of their "spatial memory"[28]). A solitary male *Hipposideros speoris* bat was held in this cave, devoid of any other bat and his activity was recorded over a period of 50 days. The solitary bat is indeed helpless as regards time (figure 4). Its rhythm "free runs" and gains about 20 minutes every day.

The following factors might mediate in the synchronizing process: (1) flight noise of free-flying members (2) some unknown pheromonal or chemical message emitted by the flying bats and (3) ultrasound that these bats emit.

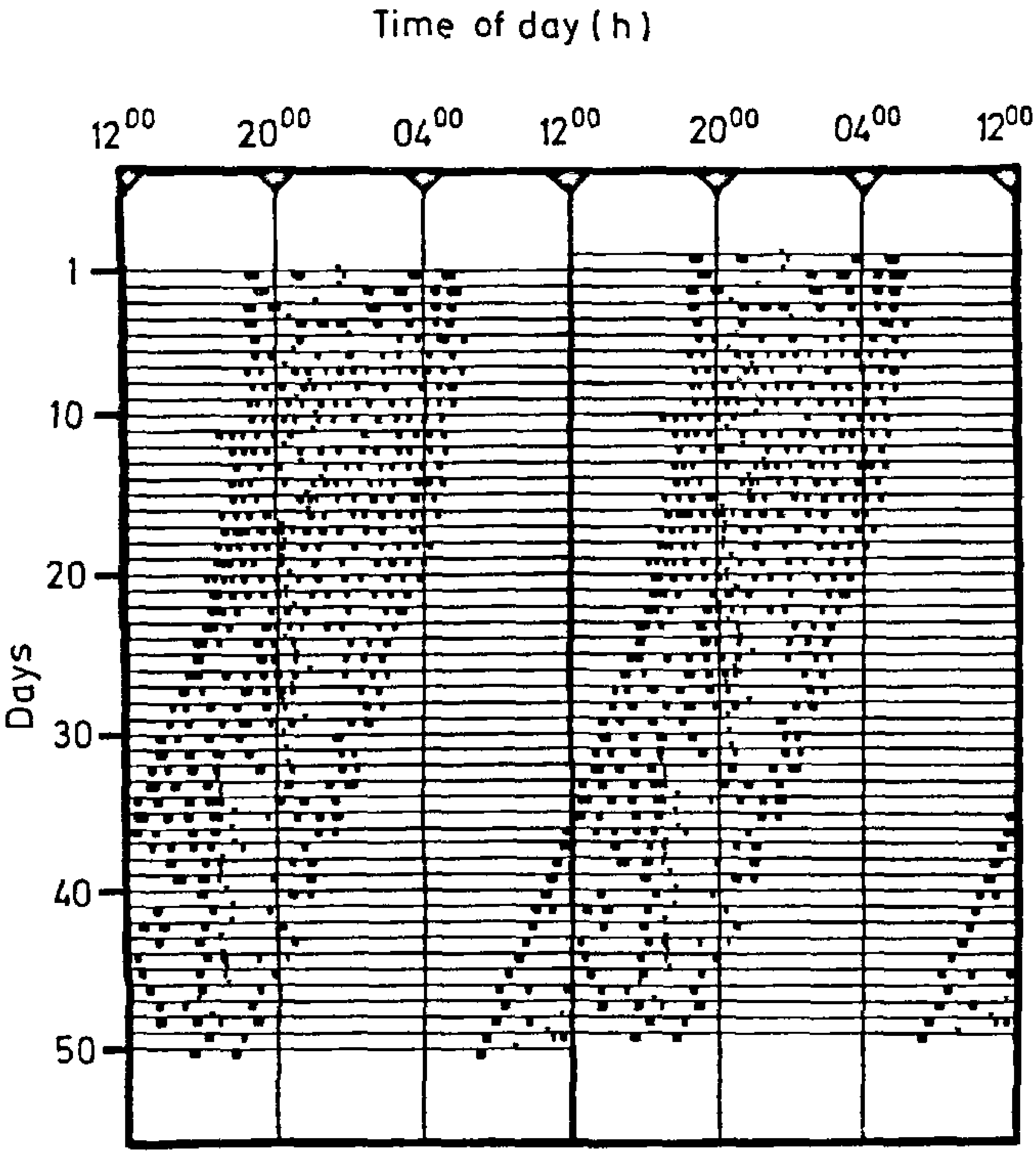

Figure 4. A double plot of activity/rest pattern of a solitary male *Hipposideros speoris* bat recorded in a cave without any conspecifics over a period of 50 days. Black dots indicate feeding time. The details are schematised from original felt pen tracings. Other details as in the previous figure. (After Marimuthu *et al.*, 1981[27].)

An interesting feature of this experiment must be pointed out. The solitary cave without any bats happened to be close to a water-hole where crows and mynas flocked during day time to drink. The investigators could hear them during the day and the stridulation of crickets and the croaking of frogs during the night. To that extent the cave was not entirely without social time cues, only the cues came from other species of animals.

The finding that non-specific social cues did not entrain the circadian rhythmicity in *Hipposideros speoris* egged us on to perform another experiment inside the *Hipposideros speoris* cave. In this experiment we held a non-hipposiderid bat, another insectivorous microchiropteran, *Taphozous nudiventris kachhensis*, captive 40 m deep in the cave and measured his daily flight activity. It turned out very surprisingly that the rhythm of the alien individual bat, free ran (figure 5). The captive and single *Taphozous* bat rhythm was not entrained by the bustle and wing-beats of some 400–500 *Hipposideros speoris* bats, which flew out evening after evening around 7 p.m. The possibility that even the wingbeat noise of these 2 species of bats might vary cannot be overlooked; even pheromones, if any involved, are known to be species specific. As regards the ultrasonic components *Taphozous nudiventris kachhensis* emits in the region of 80 kHz (and *H. speoris* emits in the region of 135

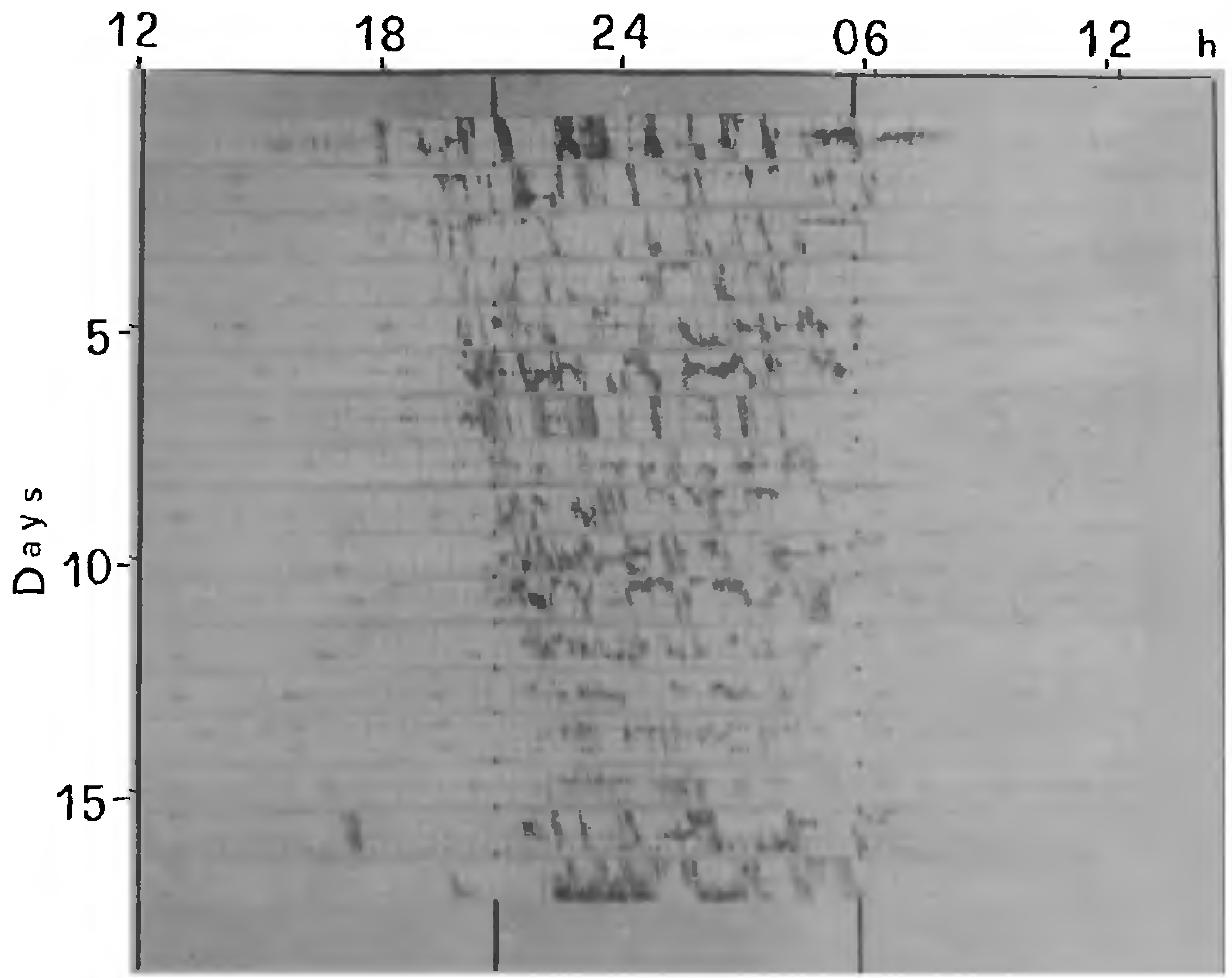

Figure 5. The flight activity rhythm of an alien bat (*Taphozous nudiventris kachhensis*) inside the darkness of a cave inhabited by 400-500 members of a colony of *Hipposideros speoris* bats for a period of 17 days. The bat could not "tell time" and the rhythm free ran.

kHz).

The first two factors are present continuously inside the caves; however, they could steeply intensify. While not ruling this out completely, we find the ultrasonics factor as the most interesting Zeitgeber.

H. speoris is silent to humans, whereas *Taphozous* can emit audible vocalization also. Ultrasound has been demonstrably used by bats only to catch prey, avoid obstacles and in such other immediate behavioural contexts. If we can establish the Zeitgeber role of ultrasonics in bats we would be giving it a new and social dimension. Experiments to unravel the phenomenon (with tape-recorded ultrasound, sound-proof experimental cubicles, etc.) are underway in Madurai[29].

SOCIAL CUES AND HUMAN CLOCKS

The experiments of E. Poppel[30] are to the point. When humans are kept in isolation in a bunker and denied knowledge of all time cues, their circadian rhythm in body temperature runs slower losing about one hour for every 24 hr. Their day thus tends to be 25 hr long (τ = 25hr) (figure 6) There are, however, interindividual variations in τ, which decrease if several human subjects are allowed to stay in the bunker. They then usually show the same circadian period which, nevertheless, is greater than 24 hr. Interestingly a 'compromise' on period length appears to be easier with two subjects than with four.

Experiments in the celebrated bunker[31] of the Max-Planck-Institut at Erling, FRG, revealed that LD cycles did not entrain any of the several circadian rhythms demonstrated in human subjects. The studies were carried out in hermetic isolation using eight human subjects. In contrast to this finding, 16 subjects living under the influence of LD cycles with supplementary sounds of a gong offered at regular intervals synchronized their circadian rhythms to the LD cycles (figure 7)[32]. Apparently artificial LD cycles are a very weak Zeitgeber but become effective when complimented by regular acoustic signals. Wever[32] concluded that the subjects perceived the gong beats as "social contacts" and that in man "social" Zeitgebers are more effective than "physical" synchronizers.

Aschoff and his colleagues performed another experiment[33] in the same bunker to further investigate the question of

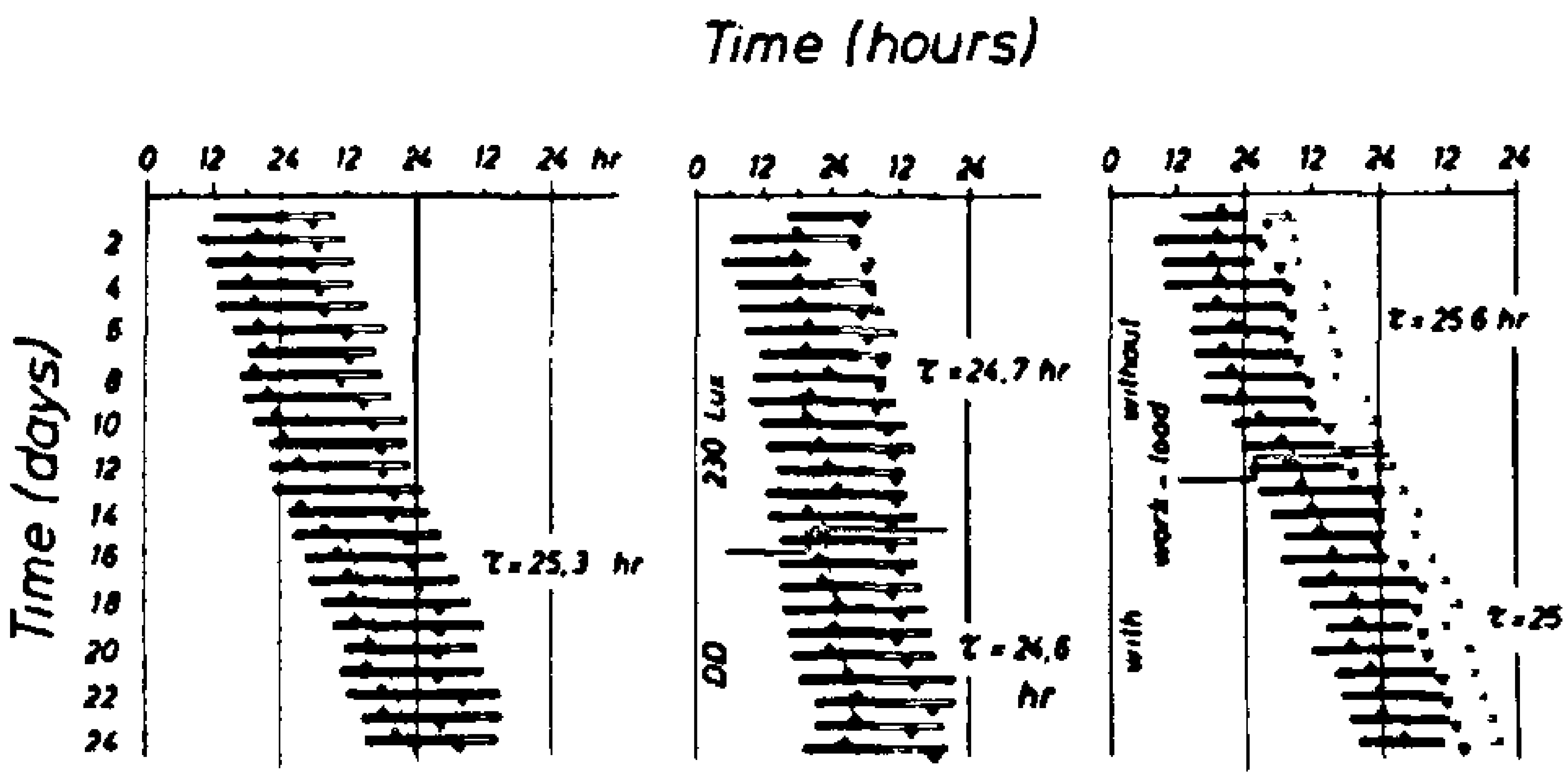

Figure 6. Circadian rhythms of wakefulness and sleep (black and white bars) and of rectal temperature (triangles above bars for maxima, below bars for minima), recorded in three subjects each of whom lived alone in an isolation unit; (*Left*) constant conditions; (*middle*) change from continuous illumination to darkness (DD); (*right*) change from a leisurely routine to work 7 times daily on a bicycle ergometer τ: circadian period. (From Aschoff, 1981a.)

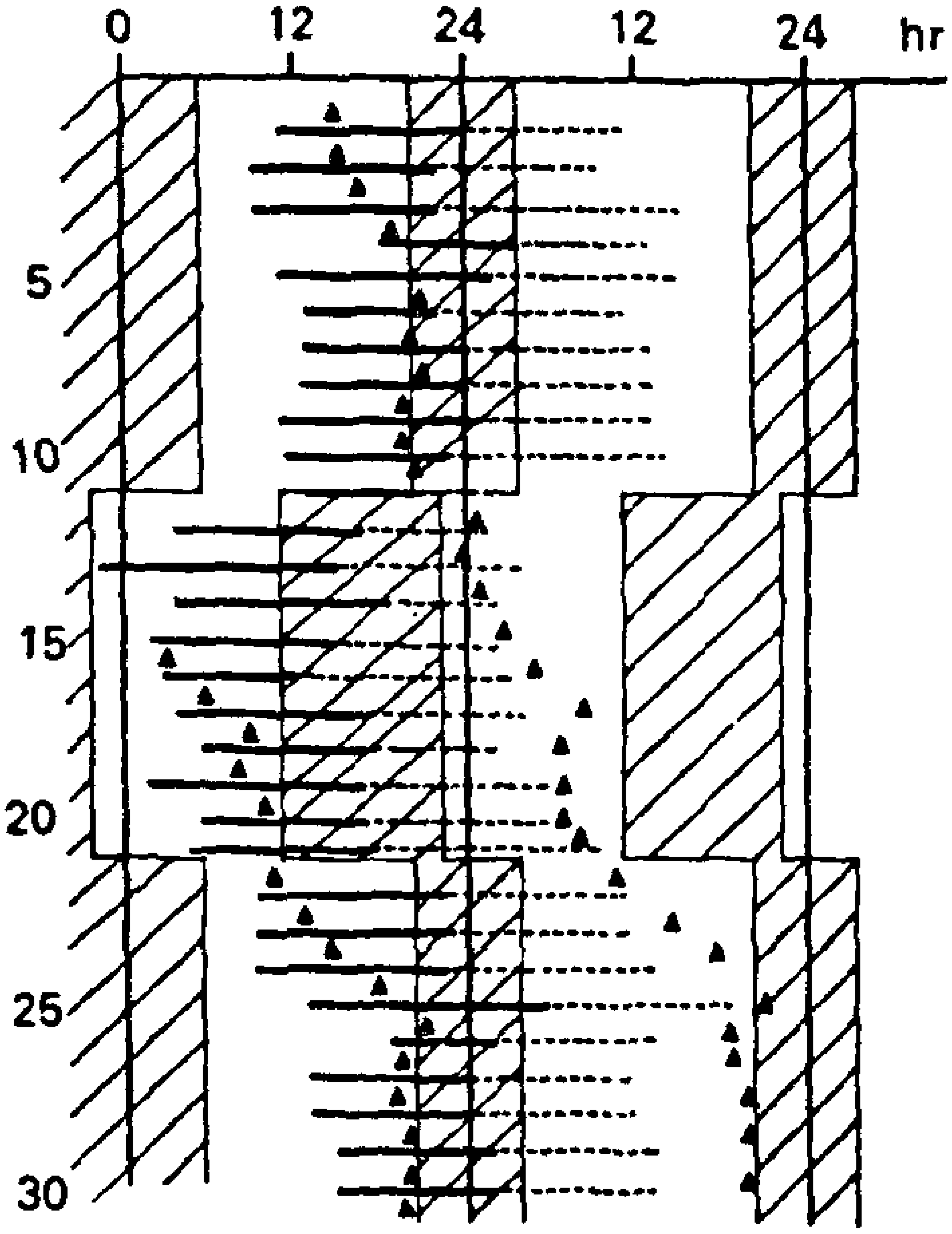

Figure 7. Circadian rhythm in a human subject under light/darkness cycles supplemented with gong beats at frequent intervals. The *Zeitgeber,* LD and gong beats were abruptly shifted (advanced and delayed) twice (days 11 and 21).

entrainment by means of social cues. Three groups of two subjects each were kept in under ground chambers, first for four days, in complete darkness. They lived on a rigorous time schedule. The rhythms measured in physiological and psychological functions at three hour intervals looked alike in the results obtained from the two segments of the experiment. Social cues, knowledge of time of day and living routine might have entrained the circadian rhythms of the subjects to a strict 24-hour societal day. The social cues apparently were sufficient to entrain human circadian rhythms and the absence of light did not change the mean phase and range of the socially entrained circadian system during four days.

Recent studies on adjustment to time zone changes in humans indicate that less disorientation takes place when subjects travel in groups and participate in testing programmes in a group setting[34]. Social psychologists have pointed out that the individual shows increased motivation when performance tests are taken in groups rather than in isolation, and in general social influences seem important in adjusting to circadian rhythms[23].

Deviations of the circadian rhythms in individuals interestingly appear to lead to symptoms of stress and distress. In a psychologically normal man who suffered from a severe cyclic sleep-wake disorder, investigations showed circadian rhythms in body temperature, alertness, performance, cortisol secretion and urinary electrolyte excretion were desynchronized from the 24-hour societal schedule. The rhythms all had periods which were indistinguishable from the period of the lunar day (24.9 hr)[35].

SOCIAL CHRONOBIOLOGY—THE FUTURE

Experimental work on biological rhythms has been so pre-occupied with the effect of LD cycles as Zeitgebers that it did seem for nearly a 100 years now[36] as if the field were a sub-discipline of photobiology. It is only work with higher animals and man carried out in the past few decades that has uncovered the effectiveness of other unconventional Zeitgebers such as "social cues" in synchronizing circadian rhythms. Food/starvation cycles, within the limits of entrainment of 19–27 hr seem also to entrain the circadian rhythms of rats[37]. Food availability restricted to 4 hr in 24 hr cycles entrains the circadian rhythm of locomotion in our common Indian palm squirrel, *Funambulus palmarum* (figure 8) (Uma Raju and S.K. Valli, unpublished).

Social chronobiology is really in its infancy. Research in this area is still in its anecdotal and phenomenological phase. More critical and quantitative work should be forthcoming if the results are to be used in the applied sciences of psychiatry, social

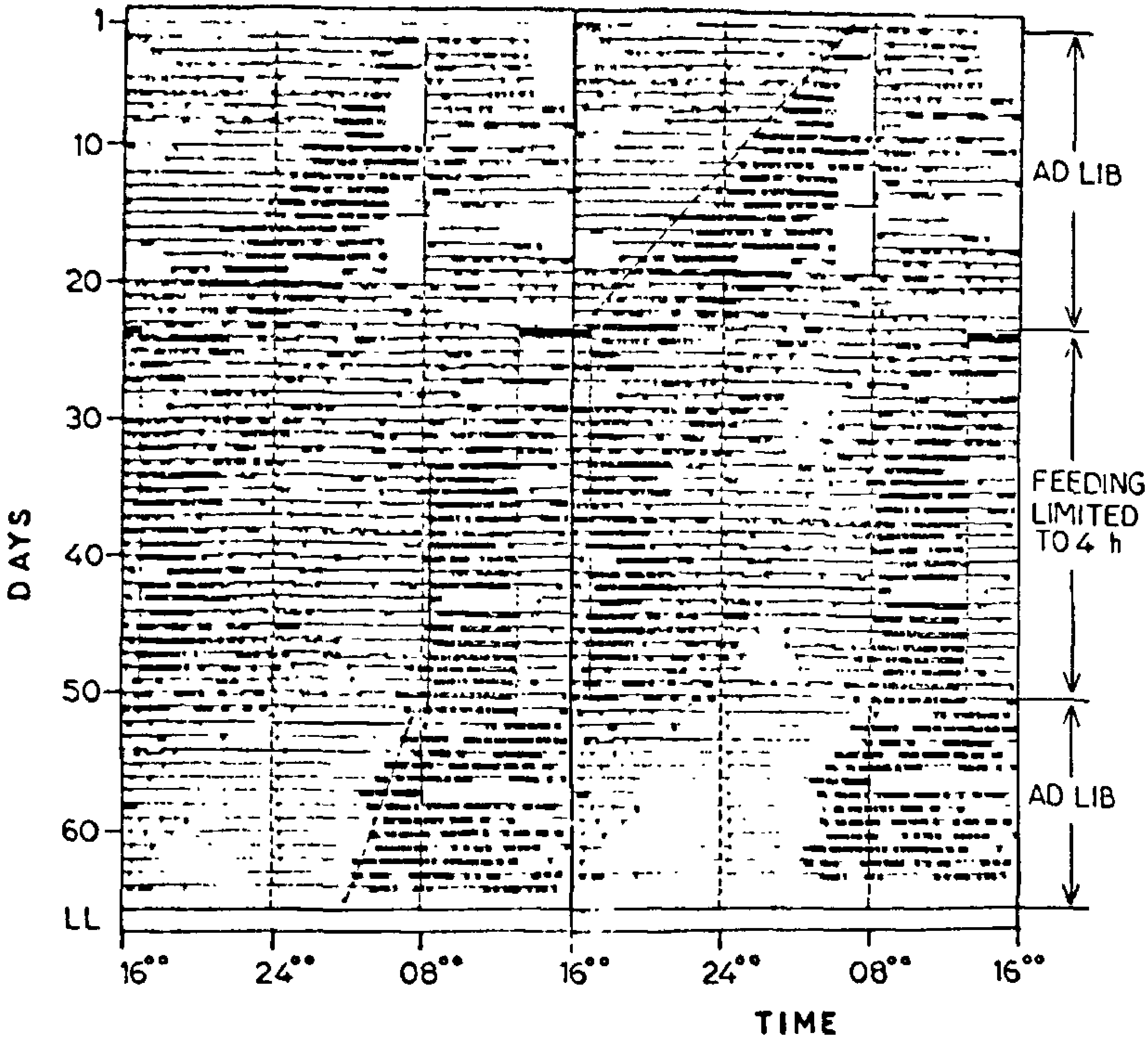

Figure 8. Entrainment of the circadian locomotor activity rhythm of the common squirrel, *Funambulus palmarum* to the feeding-starvation cycles (4:20 hr) in continuous LL of 4 lx. Black bars and the boxes between days 23-50 indicate time of food availability. The rhythm clearly entrains to the food cycles between days 30-50.

medicine and preventive care. Results of critically planned and carefully executed experiments in the field of social chronobiology should be of great interest to the ethologists, psychiatrists, researchers of aviation physiology and astronautics and students of behavioural physiology in general. Social synchronization of circadian rhythms is the topic of an important project underway in our Unit of Animal Behaviour at the School of Biological Sciences, Madurai Kamaraj University, supported by funds from the Department of Science and Technology, Government of India.

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