LD Ratios and the Entrainment of Circadian Activity in a Nocturnal and a Diurnal Rodent*

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Summary. The activity rhythms of 5 flying squirrels, *Glaucomys volans*, and 7 chipmunks, *Tamias striatus*, were examined under controlled conditions in the laboratory. Free-running, circadian rhythms were demonstrated using a total of 25 LL or DD experiments. With 46 LD schedules the limits of entrainment in a 24-hour day were determined, and the phase angle difference for each schedule measured. *Glaucomys* was able to synchronize to schedules ranging from 1 second of light per 24-hour day to at least 18 hours light per day with little or no change in the phase angle. *Tamias* showed an oscillatory type of entrainment when the photoperiod was less than 3 hours per 24-hour day or greater than 23 hours, but in the intervening region was capable of stable entrainment. A tendency was evident for the phase angle difference to become less positive as the LD ratio increased. In *Glaucomys* single, isolated light pulses of either one second or 24 hours duration were able to bring about relatively large shifts in the phase of the activity rhythm.

Precise endogenous timing of a very wide range of daily physiological functions has been recognized in a large number of plant and animal species. The most common evidence for such circadian clock phenomena has been the demonstration of a free-running rhythm under constant conditions which has a period close to, but not exactly 24 hours; these rhythms can be synchronized by means of specific cyclic factors of the environment called synchronizers, Zeitgeber or entraining agents (Aschoff, 1963). The widespread occurrence of circadian clocks and their importance in the ecology of animals has engendered much interest in recent years in the synchronization or entrainment mechanisms. For comprehensive coverage see the symposia volumes: Biological Clocks (Chauvnick, 1960); Circadian Clocks (Aschoff, 1965c); and Biochronometry (Menaker, 1971).

The concept that circadian entrainment must involve both frequency control of a non-24-hour function, as well as phase control, has stimulated several fruitful approaches towards understanding entrainment phenomena. Much investigation has been carried out with rodents because of the particularly clear expression of clock-controlled, locomotor activity in this group, and the consequent ease and precision with which measure-

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* Dedicated to Professor Jürgen Aschoff on the occasion of his 60th birthday.

ments can be made. Particularly productive in the rodent group has been the study of phase response systems, in which the effect of a single light signal on free-running rhythms has been systematically determined throughout the entire circadian cycle of an organism (summaries in Aschoff, 1965b; Pittendrigh, 1960, 1965). The method has been successful for several nocturnal rodents, including *Peromyscus* (Rawson, 1956), *Glaucomys* (DeCoursey, 1961), *Mesocricetus* (DeCoursey, 1964). These response systems can be used to explain in a qualitative way entrainment for the species measured, as well as for other nocturnal rodents in which entrainment is very similar, such as *Glis* (DeCoursey, unpublished), *Dipodomys* and *Neotoma* (Justice, 1960), and *Perognathus* (Stewart and Reeder, 1968). The first direct determinations of phase response systems in diurnal rodents proved rather difficult and unrewarding (DeCoursey, unpublished experiments; Swade, 1964), and entrainment in this group remained poorly understood. Very recently Kramm (1971) has made great strides in quantifying the phase response systems and entrainment patterns in the diurnal antelope squirrel, *Ammospermophilus leucurus*.

In an attempt to compare circadian entrainment of diurnal and nocturnal rodents, two less common techniques were used in this study. The limits of entrainment of the activity rhythms for a wide spectrum of LD ratios in a 24-hour-day schedule were first ascertained. Secondly, the phase angle differences of the entrained rhythms in these LD schedules were analyzed. Data are presented for one nocturnal rodent, the eastern flying squirrel *Glaucomys volans*, and one closely related diurnal species, the eastern chipmunk *Tamias striatus*.

Materials and Methods

Field observations of wild populations of flying squirrels and chipmunks were made on the University of Wisconsin Campus at Madison to supplement the laboratory experiments. For the laboratory experiments, seven *Tamias striatus* were live-trapped at Madison, Wisconsin; all animals used the wheels immediately, and all showed clear, rhythmic activity. Twelve ranch-raised, juvenile *Glaucomys volans* were used, but proved difficult to work with; therefore, supplementary data from previous experiments were incorporated into this paper.

All animals were housed singly for the experiments in a recording wheel cage, each in a light-proof chamber with individual lighting and ventilation systems. Light was supplied in the photoperiods and constant light periods for the flying squirrels by tubular incandescent fixtures. Light intensities for LL experiments were controlled by means of a variable resistor. All LD schedules for *Glaucomys* provided 0.5 f.c. during L, and 0.00 f.c. (no detectable light) during D, with a step transition from L to D. For LL intensity control in the *Tamias* experiments, the number of fluorescent lights was varied, and for very low intensities translucent white paper, or white cardboard sheets were inserted as neutral density filters under the glass shield of the lamp housing. Light intensity for the LD experiments was constant for a specific experiment, but varied in the different isolation chambers from 23–36 f.c., in all but a single 9L: 15D schedule for 1 chipmunk, where it equalled

57 f.c. Light intensity at the level of the nest chamber was measured with a McBeth Illuminometer. The temperature of the laboratory was maintained at $20°C \pm 1°C$; isolation cabinets were ventilated at the rate of $5 \text{ft}^3/\text{min}$, insuring that slight temperature changes within the cabinets, if present, were correlated with the specific light schedule of that cabinet. No attempt was made to sound-proof the cabinets, or eliminate building noises, but the ventilator fans effectively masked much of the background sounds. Food and water were available, *ad libitum*. The animals were checked, and food replenished at approximately weekly intervals, without change in the experimental light conditions, usually during the active time of each animal.

A preliminary series of constant light or LD experiments with the chipmunks was designed to check the general characteristics of their activity cycles and the validity of the measurement techniques. The results are described briefly in the observation section, and in DeCoursey (1972a) in greater detail. Comparable material is available for the flying squirrel in DeCoursey (1961). In the second series of experiments, the basic plan involved systematic variation of the LD ratio in 24-hour schedules for *Glaucomys* and *Tamias*. Animals were maintained on a specific schedule for several weeks until a stable phase relationship between activity onset and the light cycle had been established; then a new light schedule was initiated. LD schedules were selected to span the 24-hour day schedule, emphasizing the limits of entrainment. In a third series of experiments the effects of single, 1-second pulses of light at onset time, and of single 24-hour light periods were measured for *Glaucomys*.

Activity was recorded by means of a 20-channel Esterline-Angus Operations Recorder. The data of each individual were processed to graphically portray a chronological sequence of 24-hour activity scans (see DeCoursey, 1961 for details of method). Nomenclature follows the Circadian Vocabulary (Aschoff, Klotter and Wever, 1965).

Observations

Preliminary Considerations

Field observations of the two species were used in determining normal activity patterns. Observations of wild populations in Madison indicated that the chipmunks were active intermittently from dawn until dusk, and were rarely seen outside their shelters after dark, while the flying squirrels were highly nocturnal, initiating activity shortly after sunset and terminating activity before dawn.

Under laboratory conditions both species readily used the running wheels, and continued to show regular, rhythmic patterns of activity under a variety of environmental lighting conditions. Endogenous, free-running rhythms of activity were present in both *Tamias* and *Glaucomys* under constant lighting condition (Fig. 1); a summary of all constant lighting experiments further illustrates the circadian nature of the underlying clock function (Fig. 2). Fig. 1 contrasts a typical nocturnal entrainment response for *Glaucomys* in an LD schedule with the strongly diurnal pattern in *Tamias*.

The clear onset of activity for *Glaucomys* (DeCoursey, 1961) and for most *Tamias* made onset a convenient reference point for measuring the free-running periods, and also for determining the limits of entrain-
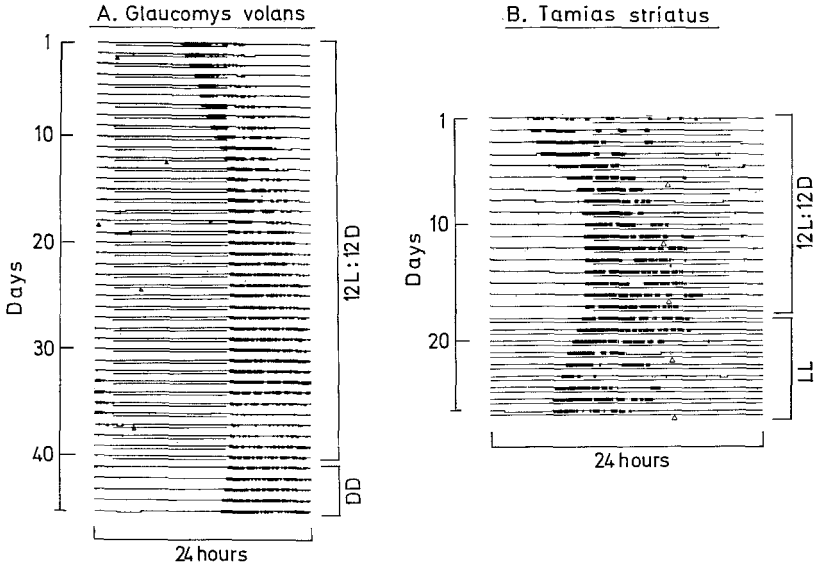
Fig. 1 A and B. Original records illustrating entrainment to 12L:12D schedules and subsequent free-running rhythms under constant conditions for nocturnal *Glaucomys volans* (A), and diurnal *Tamias striatus* (B). Consecutive 24-hour activity scans are arranged vertically, with deflections from the recorder baseline indicating activity in the running wheel; underlining designates light period of the LD schedule, and △ feeding in the light time. For further explanation see text
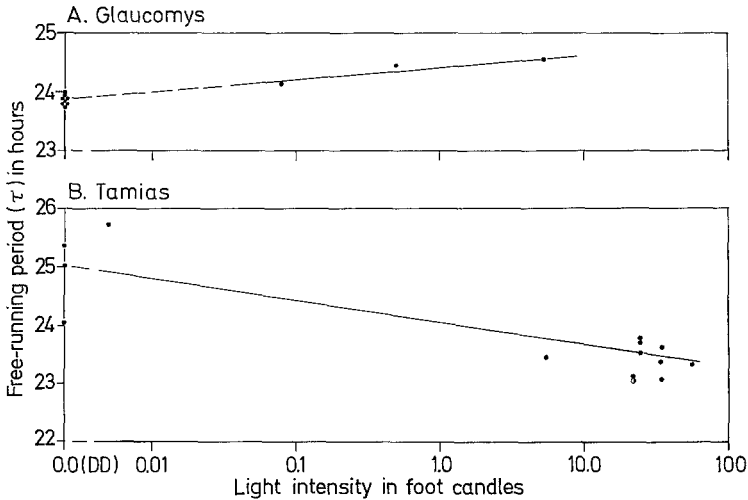

Fig. 2 A and B. Summary of free-running rhythms in *Glaucomys* (A) and *Tamias* (B). Circles indicate conditions: ● DD or LL; ◑ LD; curves are eye-fitted
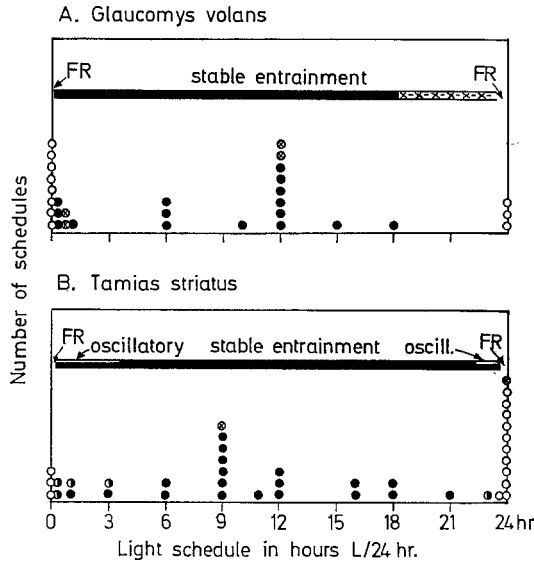
Fig. 3 A and B. Limits of LD entrainment for *Glaucomys* (A) and *Tamias* (B). Each circle represents the value in one test period for a single animal: ○ free-running rhythm, ◑ oscillatory phase angle during entrainment, ● stable phase angle, ⊗ masking or damping of activity, or results too erratic to analyze by onset method. The schematic line and symbols above the points summarizes entrainment limits: ■ stable entrainment, ▬ oscillatory entrainment, ☐ free-running rhythm, ⊠-×-⊠ no data available because of measurement difficulties, *FR* free-running rhythm. For further explanation see text

ment and phase angle differences. In contrast, the end of activity was almost always very irregular in both species (Fig. 1).

The effects of feeding, light, or social disturbances on the activity rhythms were carefully considered. The *Tamias* were particularly sus-ceptible to noise disturbance. Disturbance at any time in the hours prior to onset time very frequently initiated the activity period for that day, thus masking true onset time. No permanent phase shifts or frequency changes due to feeding or noise were noted, such as Eskin (1969) reported for the English sparrow. Therefore, by restricting maintenance disturb-ances to the active period of an animal, without change in the lighting conditions, most masking effects could be avoided.

In order to briefly evaluate the stability and reproducibility of LD synchronization data in a single individual, two *Tamias* were placed in a 9L:15D schedule and allowed to entrain for several weeks, then placed in LL, and finally allowed to resynchronize again in a 9L:15D schedule (Table 1). Results indicate a high degree of reproducibility under these
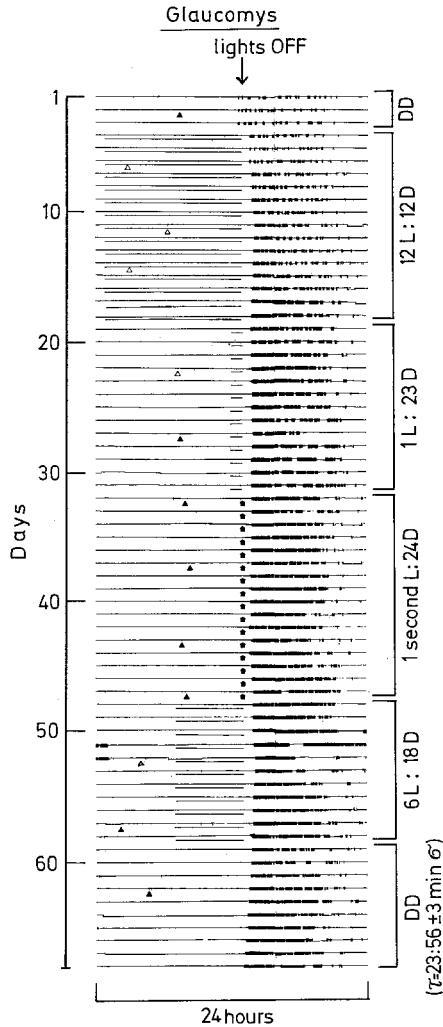
Fig. 4. Original activity records for *Glaucomys* in LD and DD schedules. Recording as in Fig. 1 with additional symbols: ▲ feeding in dark, ↑ impulse synchronizer of 1-second duration. For further explanation see text

circumstances, but do not permit any conclusions about *Tamias* in other schedules, or even about stability of an individual over longer periods of time with various intervening schedules. Variation between individuals is also briefly assessed for 4 animals on a 9L:15D schedule in Table 1. Mean values for phase angle differences range from + 34 to + 163 min,

Table 1. Variability in response of *Tamias* to a 9L:15D schedule with phase angle difference calculated as average minutes of activity onset before start of the light schedule

Animal	Light regime					
	First 9L:15D schedule			Second 9L:15D schedule		
	Mean in min	St. Dev.	Days	Mean in min	St. Dev.	Days
1401	163	±14	15	—	—	—
1402	62	±16	13	—	—	—
1405	34	±10	15	37	±15	16
1407	44	±12	17	42	± 9	17

suggesting considerable difference in response between individuals on identical LD schedules. Thus, the characteristics of activity rhythms of *Glaucomys* and *Tamias* in the preliminary experiments made it feasible to undertake systematic LD ratio experiments.

LD Ratio Experiments

In the second series of experiments, a systematic survey of the limits of entrainment was carried out for *Glaucomys* and *Tamias*. On each schedule the animal was allowed to achieve and maintain a stable phase for a minimum of 15 days (*Tamias*) or 10 days (*Glaucomys*). After testing in 0L:24D (DD) and 0D:24L (LL) the photofraction for *Glaucomys* was varied from 1 sec L:24 hours D to 18L:6D (Fig. 3). Photoperiods for *Tamias* ranged from $\frac{1}{4}$L:$23\frac{3}{4}$D to $23\frac{3}{4}$L:$\frac{1}{4}$D (Fig. 3). In order to avoid the extremely long runs often necessary for resynchronization and elimination of transients to occur, free-runs between LD schedules were usually omitted. In the majority of experiments the chief reference point at the start of a new schedule remained fixed: lights ON for the diurnal *Tamias*, and lights OFF for the nocturnal *Glaucomys* (Fig. 4, 5). However, in critical instances, to establish unequivocally that light was not exerting a masking effect and to demonstrate that the synchronization of a non-24-hour rhythm was occurring, the LD schedules were interspersed with several weeks of LL or DD (Fig. 6). To supplement the *Glaucomys* data, 11 schedules from earlier experiments (all schedules with 15 or more days of stable entrainment) were included.

Under these conditions it is apparent that both species are able to synchronize over a wide range of LD ratios (Fig. 3). *Glaucomys* was able to entrain to all schedules from 1 second of light per day to 18 hours of
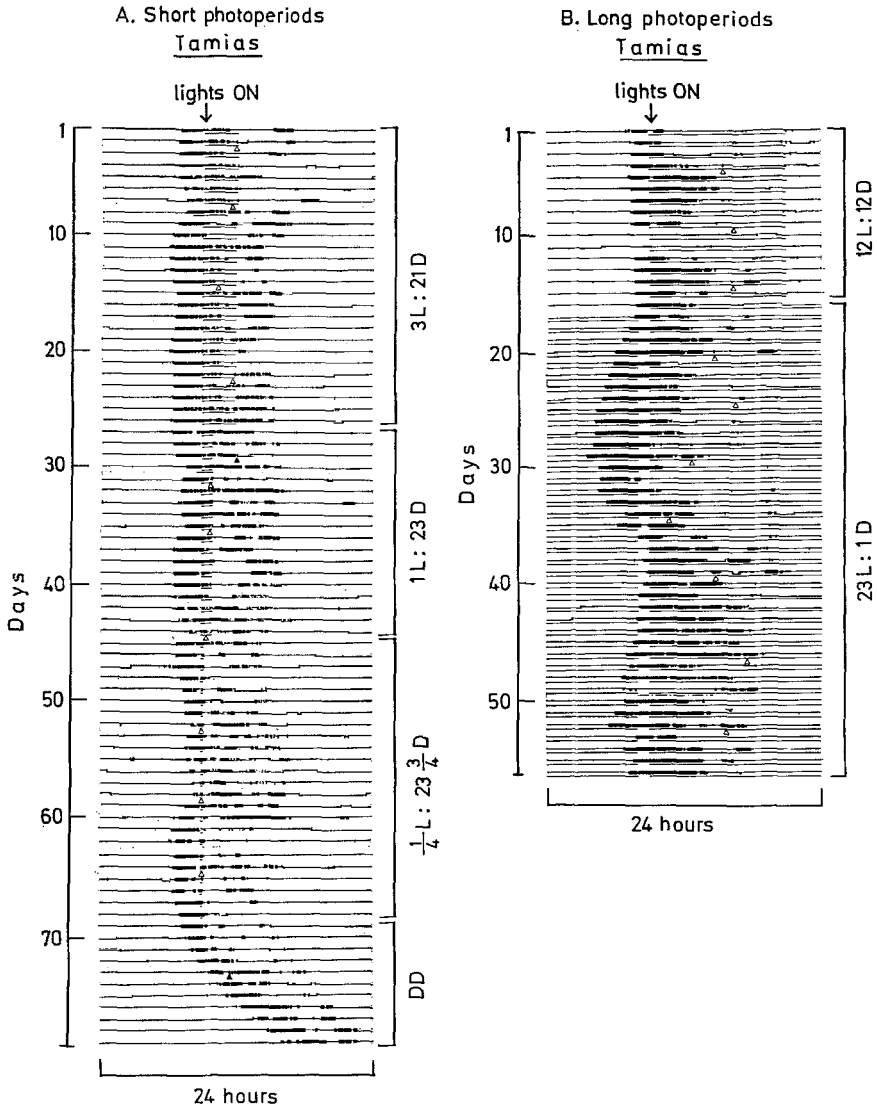
A. Short photoperiods
Tamias

B. Long photoperiods
Tamias

Fig. 5 A and B

Fig. 5 A–C. LD ratio experiments for limits of entrainment in *Tamias* in short photoperiods (A), and in long photoperiods (B and C). Symbols and recording as in Fig. 1 and 4 with additional symbol —·—·— for equipment failure. For further explanation see text

light per day with very little change in phase angle. Of particular interest in these experiments is the ability of *Glaucomys* to synchronize to an impulse signal of 1 second duration each day (Fig. 4, 6).
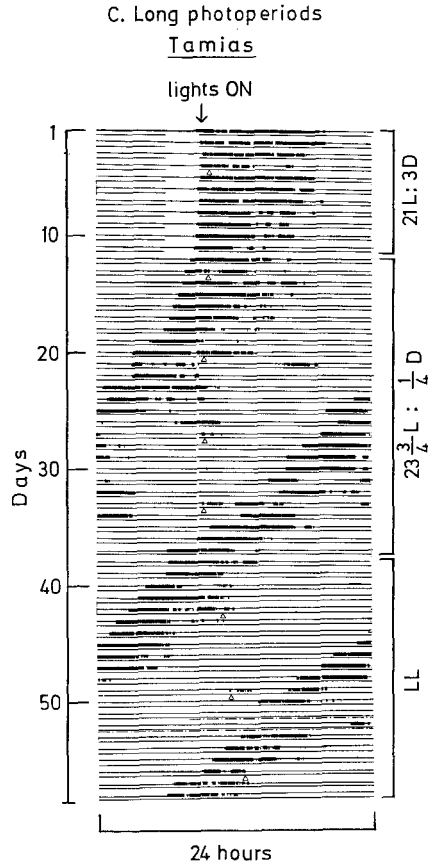
C. Long photoperiods
Tamias

lights ON
↓

Fig. 5 C

Tamias, similarly, was able to synchronize to a wide range of LD
ratios. Stable entrainment occurred for all animals tested between
6L:18D and 21L:3D. Complete failure to entrain was seen at
$23\frac{3}{4}$L:$\frac{1}{4}$D; with this schedule the free-running rhythm is evident,
scanning the 24-hour day in the course of 26 days. The period of the
activity rhythm continued unchanged in the subsequent LL (Fig. 5C:
τ in the LD $= 23:06 \pm 61$ min Std. Dev., while τ in LL of the same
intensity $= 23:05 \pm 66$ min). At either end of the LD ratio scale, between
the free-run and the stable entrainment regions, was a zone of oscillatory
entrainment. While many examples of transients were seen in *Glaucomys*
and *Tamias* entrainment, such "overshoots" usually subsided quickly.
In contrast, the oscillatory phenomena appeared to persist as long as
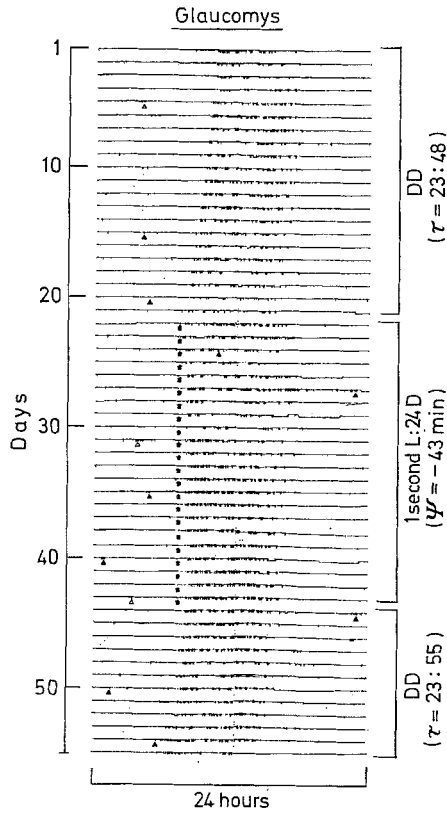
P. J. DeCoursey:

Glaucomys

Fig. 6. Impulse synchronization in *Glaucomys* by a 1 second pulse of light (0.5 f.c.).
Symbols and recordings as in Fig. 1 and 4, with additional symbol ψ for phase
angle difference, and τ for period

the schedule was continued with little or no change in amplitude,
suggesting perhaps the beginning of synchronization breakdown.

The consideration of phase angle differences for the LD schedules
gives further insight into the mechanism of entrainment. In the nocturnal
Glaucomys, the phase angle difference, calculated as onset of activity to
start of darkness, was negative for all LD ratios tested, and little, if any,
change was detectable from 1 second of light per day to 18 hours L per
day (Fig. 7A). The *Tamias* were not exclusively day-active, for with very
short photoperiods the activity extended well into the dark periods
(Fig. 5A). In spite of this "partial nocturnality", the phase angle dif-
ference values show a definite relationship between lights ON and onset
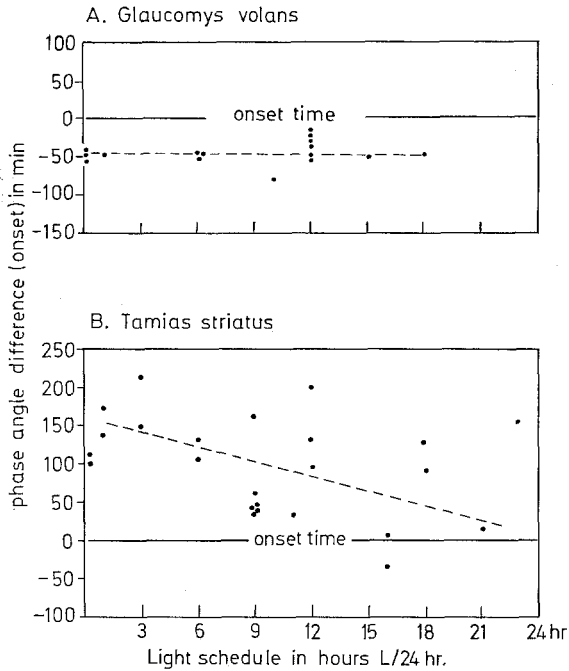of activity. A great deal more variability in the measurements is seen,

Fig. 7 A and B. Phase angle difference in relation to LD ratio in 24-hour light schedules, calculated for the nocturnal *Glaucomys* as onset of activity in minutes after (—) lights OFF, and for the day-active *Tamias* as onset in minutes before (+) or after (—) lights ON. Each point represents the average in 1 test schedule for a single animal. Regression line, calculated for stable entrainment schedules ---. For further explanation see text

probably reflecting large individual differences, as well as the greater lack of precision of the chipmunk in general. The data indicate a tendency for the phase angle to become less positive as the LD ratio increased, i.e. with longer daylight time the chipmunks started activity closer to the time of lights ON (Fig. 7 B).

To measure the ability of isolated pulses to shift the phase of the rhythm, several experiments were carried out. For one flying squirrel which had been synchronized to the impulse synchronization schedule (Fig. 4), the free-running rhythm was measured in DD ($\tau = 23:57$). Then a 1-second flash of light was tested at onset time. The resultant delays for two replicate tests, each 28 minutes, were adequate to correct the free-running rhythm to match the 24-hour period of the LD schedules. In similar fashion, replicate tests for a 24-hour light signal were made, yielding values of 38 minutes delay and 56 minutes delay, respectively.

Discussion

The observations of *Glaucomys* under natural field conditions (De Coursey, 1961), in cages under natural photoperiods (DeCoursey, 1960, Graefe, 1961) and in artificial LD schedules indicate a highly nocturnal habit. With *Tamias* the picture is almost a mirror image, for the observations of this study and of Graefe (1961) confirm its diurnal habits. Recent experiments with circadian rhythms have clarified such activity regulation processes. The complex interrelationships of animal rhythm to environmental parameters have been ably discussed in several works (Aschoff, 1965a, 1969; Aschoff and Wever, 1962b). After considering theoretical and practical factors, the experiments reported here were designed with step transitions between L and D, usually without intervening constant conditions and with relatively short entrainment runs. Certain limitations of such conditions should be kept clearly in mind. Gradual, long-term changes of free-running period have been reported with several species (Eskin, 1969; Kramm, 1971). Constant environment schedules in the present experiments were used primarily to illustrate the endogenous component, but complications could arise due to dependence of ψ on τ (Aschoff and Wever, 1962c; Hoffmann, 1963). Eskin (1969) and Kamm (1971) have also pointed out long persisting transients, and possible long-term changes in phase of animals. This difficulty was minimized for *Glaucomys* and *Tamias* by eliminating free-runs between schedules. It is possible, however, that the so-called oscillatory entrainment merely reflects such long-lasting transients.

The question that this work asks is whether the transition effects of light schedules are adequate to explain synchronization in *Glaucomys* and *Tamias*, or whether duration of photoperiod is responsible. The rationale behind the experiments is as follows. If a phase response system is demonstrated by means of light pulses, then an impulse synchronizing agent should be able to entrain the free-running rhythm (Aschoff, 1960; DeCoursey, 1961). Furthermore, a wide-range of LD ratios should be able to entrain without marked phase changes. Finally, single, isolated light signals should be able to correct the free-running rhythm to the period of the light cycle. These hypotheses seem to be upheld by the *Glaucomys* data, but it is well to remember that alternate explanations are possible using other models of entrainment (Achoff, 1965a; DeCoursey, 1972b).

If, on the other hand, the LD entraining schedule has a proportional effect on the underlying timer, then a smaller range of LD ratios might be expected to entrain, and a significant change in the phase angle difference would be expected. This seems to be the case with the day-active *Tamias*.

While it is known that many animals are able to use LD schedules for entrainment, relatively few workers have tested LD ratio limits or impulse synchronizers. Erkert (1970) tested the range between 4L:20D,

and 22L:2D for two species of fruit eating bats, and found that both species readily entrained. Eskin (1969) using the house sparrow, found entrainment from 0.5L:23.5D to 15L:9D, with an oscillatory type of entrainment at the short end of the spectrum. Similarly, Minis (1965) used 6L:18D to 18L:6D with the pink boll worm, and found all schedules effective. Using *Drosophila* eclosion, Pittendrigh (1960) assayed light periods in a 24-hour schedule ranging from 10 minutes to 23 hr:35 min. Even less is known of minimum duration of signals required for entrainment. In a few cases, impulse schedules have been effective, as in the 10 minute signals for *Drosophila* (Pittendrigh, 1960), but in birds the reduction of two skeleton photoperiods of an hour's duration each, to $1/_2$ hour each caused the birds to free-run (Enright, 1965), and a 15 minute signal for a bird in dim light resulted in relative coordination (Aschoff, 1965b).

The exact relationship between LD ratio and phase has been examined by Aschoff (1965a, 1969), Aschoff and Wever (1962a), and Enright (1966). Other fairly complete assays of this relationship are found in Pittendrigh (1960) for *Drosophila* and in Eskin (1969) for *Passer domesticus*.

The natural environment with all its multiple latent synchronizers, its greater amplitude of LD, its complex twilight transitions and weather, its yearly variations, as well as possible endogenous seasonal changes of the animal make the question of control in nature vastly more complex than in the simple LD regimes of these experiments with *Glaucomys* and *Tamias*. A number of papers have considered factors of the natural environment other than the LD ratio of step transition schedules. Swade and Pittendrigh (1967) studied circadian rhythms of rodents during the summer months in the Arctic. Even though the sun did not set, the animals still exhibited daily rhythmic activity. Furthermore, both Artic and temperate zone species were able to entrain in the laboratory to low amplitude sinusoidal light cycles in which the maximum-minimum ratio was as small as 2.5. Aschoff *et al.* (1970) have shown some of the complexities of synchronization of tree-shrews, hamsters and finches at high latitudes; Erkinaro (1970) has studied entrainment of the rodent *Apodemus* at the Arctic Circle. Several papers have stressed the importance of twilight in phase control (Aschoff and Wever, 1965; Wever, 1967).

In summary, laboratory experiments suggest that in the nocturnal *Glaucomys* the transitions of an LD schedule can be very effective in the entraining process, while *Tamias* is much more dependent on the LD ratio.

Conclusions

The flying squirrel, *Glaucomys volans*, is highly nocturnal, both in natural habitat and in a variety of artificial LD schedules in the laboratory, while the eastern chipmunk, *Tamias striatus*, is strongly diurnal.

Comparison of the ability of the two species to entrain to various LD ratios in a 24-hour day, and of the phase angle differences of the two species in these schedules showed marked differences. A stable phase angle was found in *Glaucomys* from 1 second of light per day to 18 hours per day, with little detectable change in the phase angle difference. Some *Tamias* were able to entrain over the entire range $\frac{1}{4}$L:$23\frac{3}{4}$D to 23L:1D but at the extreme ends of these schedules an oscillatory type of synchronization occurred which may indicate either long-lasting transients, or the beginning of synchronization failure.

Single pulse signals were shown in *Glaucomys* to shift the phase of the free-running rhythm enough to account for correction of the free-running rhythm to a 24-hour frequency.

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