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COMPARISON OF SEASONAL RHYTHMS OF ACTIVITY OF GREY SQUIRRELS
(*SCIURUS CAROLINENSIS*, RODENTIA) IN CAPTIVITY AND IN THE WILD

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Abstract. Seasonal changes in the activity rhythm in captive grey squirrels (*Sciurus carolinensis*) were recorded by a photocell system at the Cedar Creek Natural History Area, Minnesota. Photocell recordings from grey squirrels near the Arctic Circle at Kuusamo, Finland and at Andechs, West Germany were analyzed and compared with those from Cedar Creek. Activity rhythms of wild squirrels, and also of the captives, were monitored by radio telemetry at Cedar Creek.

The duration of activity time (α) in both captive and wild squirrels did not follow the duration of the photoperiod throughout the year. The very short α in late winter might be under the control of exogenous factors other than light, especially in wild squirrels. The marked increase in length of activity in September in wild squirrels was probably related to mast harvesting behavior. Seasonal differences in phase angle and duration of activity indicate larger variations in wild than in captive squirrels. Secondly, our data on grey squirrels suggest that day-active mammals exhibit larger variations in phase angle differences and duration of activity than day-active birds.

INTRODUCTION

Entrainment of circadian systems of vertebrates to a Zeitgeber has been studied primarily in birds and mammals in captivity, usually indoors, but sometimes under natural photoperiod and weather conditions. Aschoff (1969) and Daan and Aschoff (1975) summarized data on birds and mammals to explain this mechanism in different latitudes and seasons. Their interpretations are based on data from numerous day-active birds and a few night-active mammals. Only one day-active mammal, *Tupaia belangeri*, was studied.

Differences in the circadian clock in birds and mammals have been observed and reported by many authors (Aschoff 1965, Hoffmann 1969, Pittendrigh 1972, Gwinner 1973, Eskin 1971, Menaker 1971 and others). The entrainment of the circadian system to light cycles in some species of diurnal mammals shows much variability (Kenagy 1978, Halberg et al. 1982). Pohl (1982) investigated variability in entrainment of circadian rhythms and concluded: "... organisms show a high degree of variability probably related to special ecological requirements... It remains a matter of further study to analyze the specific adjustments of entrainment mechanisms in closely related species experiencing different light condition in their natural habitats."

Information on locomotor activity of wild or wild animals compared to captive animals of the same species is needed to understand entrainment

phenomena. Telemetry or radio-tracking with automatic recording of movement and activity, as reported by Mech et al. 1966, Rongstad and Tester 1977, Tester 1978 and Figala et al. 1984, provides an excellent opportunity to obtain such data on wild animals. Grey squirrels were chosen for this study because radio transmitters did not appear to influence their behavior or psychology (Bland 1977) and they were easy to maintain in captivity for long periods.

Simultaneous collection of data on wild and captive squirrels by use of telemetry and photocell-activated strip chart recorders made it possible to determine effects of captivity. Thus, behavior in response to natural day-night rhythms and weather conditions could be evaluated under both wild and captive conditions.

This paper reports on seasonal changes of activity rhythms and attempts to explain deviations from predicted patterns of entrainment in terms of behavioral and ecological factors influencing the squirrels. In addition, effects of captivity on activity rhythms are evaluated.

METHODS

Data on captive and wild squirrels were collected at the Cedar Creek Natural History Area in east-central Minnesota (45°24'N, 93°12'W) from 1 January 1976 to 31 December 1976. Four animals (1 adult male, 1 adult female, 1 juvenile male and 1 juvenile female) were held in 1 × 1 × 1 m wire cages positioned 1.1 m above the ground in mature deciduous forest. Nest boxes (40 × 40 × 40 cm) with bedding of dry oak leaves were attached outside each cage. Corn, sunflower seeds and acorns (in season) were provided ad libitum in food boxes attached outside each cage. Two other adults, a male and female, were kept in a large pen (2 × 4 × 1.5 m) with one nest box and one feeding box.

All squirrels were captured within 1.0 km of the pen in November 1975. They were placed in the experimental pens and allowed to acclimate to captivity until the experiment began.

In winter the roofs of the cages were covered with canvas to protect the animals against the snow. On 22 April the plywood bottoms on the nest boxes were replaced with wire to provide for air circulation. On 21 September the plywood bottoms were replaced on the nest boxes.

All animals were weighed 7 times during the year as a means of monitoring physical condition. Individual weights ranged from 550 to 800 grams, and all squirrels appeared to be in good physical condition. One juvenile male increased in weight from 450 g in December 1975 to 860 g in November 1976.

Locomotor and feeding activity were measured by photocells on the boxes and recorded on an Esterline strip-chart recorder. Kodak filter paper (Types 87 and 89B) was used to keep the intensity of the photocell bulbs as low as possible.

All caged squirrels were fitted with a radio transmitter in the 53 MHz range. The transmitters were designed as collars with the broadcasting antenna forming the collar loop. Weight of the transmitter was 35 gr, life was 180 days and range was about 1.7 km. Every 2 or 3 months the squirrels were trapped and the batteries in the transmitters were replaced.

Signals from all caged squirrels were monitored with a stationary antenna and continually recorded on microfilm. When the squirrel was motionless the signal appeared as a continuous black line on the microfilm records, whereas when the squirrel moved, the signal appeared as a broken interrupted line. These breaks were caused by modulation of the radio signal due to a change in circuit capacitance as the collar changed position on the neck of the squirrel.

The combination of photocells and telemetry produced 3 unique measures of activity. Transmitter activity (TA) is defined as any movement in the nest box detected by the radio transmitter. Nest activity (NA) is defined as the time the squirrel first left the nest box in the morning or last entered the box in the evening

as measured by the photocell. Feeding activity (FA) is defined as those periods when the photocell beam on the food box was interrupted.

The time an individual first left the nest box and the time of first feeding in the morning or vice versa in the evening were determined from the Esterline records. Since all movements of these squirrels were also recorded on microfilm, we transcribed movement data for 1 hour preceding the time the animal left the nest box and for one hour after the animal left the cage and entered the nest box to determine when "true" activity began and ended. The speed of the microfilm recorder made it possible to "read" movement shorter than one second, which made it difficult to establish the real time of awakening in the nest box or the time of last movement before beginning "real" sleep. Therefore, continuous movement of longer than 1 minute has been considered as "activity".

We could not use data from the Esterline record to determine which squirrel left the nest box first in the morning (or entered last in the evening) in the large pen containing 2 animals. Therefore, film records were analyzed for 60 min preceding and 30 min following the morning and evening initiation and cessation of activity as indicated by the nest box photocell.

During the research period we utilized the Cedar Creek automatic radio tracking system (Cochran et al. 1965) to determine activity (WA) of 9 wild squirrels. Individual squirrels were monitored for periods ranging from 1 to 8 months, with the average being 3.7 months (Figure 1). Signals from each animal were recorded on microfilm every 45 seconds.

Cessation or end of activity in wild squirrels was determined as that time when more than 4 minutes of uninterrupted bars were recorded on the microfilm. This 4 minute period was chosen based on information on the beginning and ending of activity in captive squirrels, as described above. If there was no exact evidence of the time of beginning or ending of activity, we did not calculate values for that day.

The times of sunrises and sunsets were determined from U. S. Naval Observatory Chart No. 1155 for Minneapolis. Weather data were recorded at the U. S. Weather Bureau Station at the Cedar Creek Natural History Area.

Comparable data on nest activity of captive grey squirrels in Andechs, West Germany and in Kuusamo, Finland were kindly provided by J. Aschoff, Max. Planck Institute für Verhaltensphysiologie. At Andechs (47°58'N, 11°30'E) nest activity measured by a photo cell was recorded nearly continuously for a single captive grey squirrel from January 1967 to December 1970. At Kuusamo (66°27'N, 29°21'E), near the Arctic Circle, a single captive grey squirrel was similarly monitored from September 1967 through December 1968.

The combined data from the 3 locations resulted in 17,000 records of onsets and ends of activity. Measurements from Cedar Creek were grouped into 24 1/2-month averages and measurements from Andechs and Kuusamo were grouped into 36 1/2-month averages.

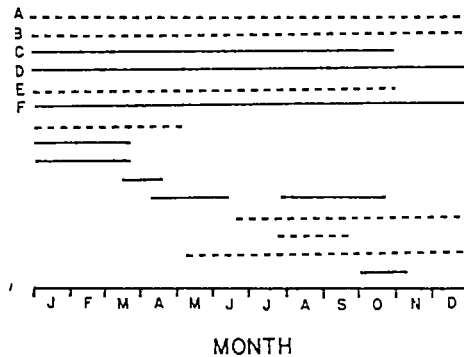


Fig. 1. Dates when radio-marked male (solid line) and female (dashed line) grey squirrels were monitored at Cedar Creek in east-central Minnesota. Letters indicate squirrels held in outdoor pens.

RESULTS

During 1976 six squirrels were monitored in captivity and nine in the wild. The time period that each squirrel carried an effective radio transmitter varied (Figure 1).

Onset and cessation of activity

Onset and cessation of daily activity are usually related to sunrise and sunset or to a specified level of light intensity. The time difference, measured in hours, between sunrise and the onset of activity is referred to as Ψ onset. Similarly, Ψ end is the time between cessation of activity and sunset for day-active animals. Positive values indicate that activity began or ended earlier than the time of the Zeitgeber. This results in a positive phase-angle difference. Negative values indicate that activity onset or end occurred later than the Zeitgeber, resulting in negative phase-angle differences. Daan and Aschoff (1975) unified both values and, categorizing them as "large" or "small", found the following pattern of Ψ : at high latitudes day-active animals have their largest Ψ onset and smallest Ψ end in mid-winter and the smallest Ψ onset

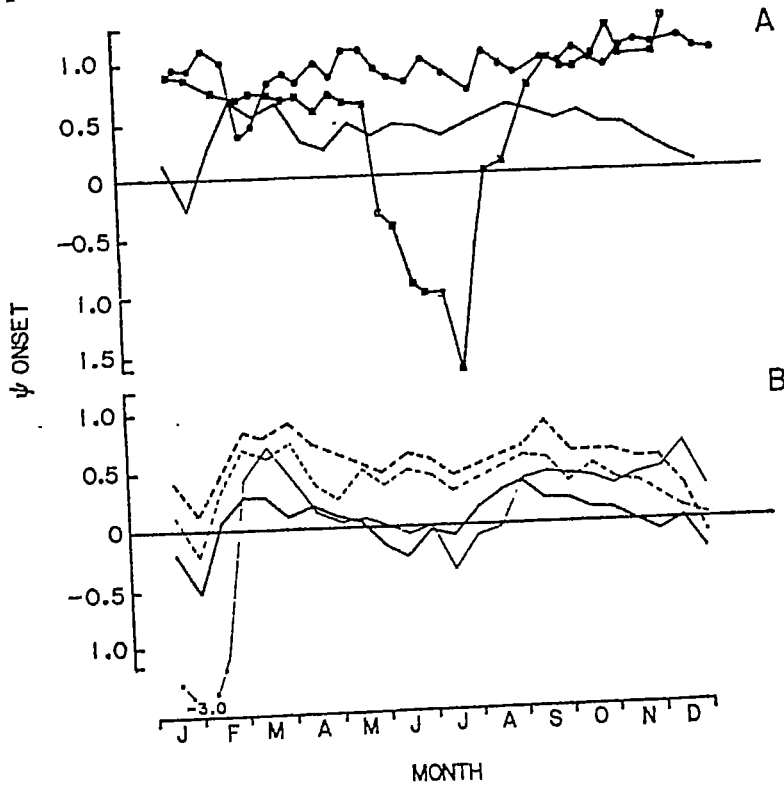


Fig. 2. Seasonal changes in the phase angle difference between the onset of activity and sunrise (Ψ onset) in grey squirrels. A - Nest box activity onset at 3 latitudes. B - Transmitter, nest box and feeding onsets of captive squirrels and onsets of activity of wild squirrels at Cedar Creek.

and largest Ψ end in mid-summer. These differences have been found to be less pronounced in both birds and mammals in lower latitudes.

Values for Ψ onset for all squirrels as a function of season are presented in Figure 2. Records from the photocells on the nest boxes at Kuusamo, Andechs and Cedar Creek are shown in Figure 2A. The largest Ψ onset for the squirrel

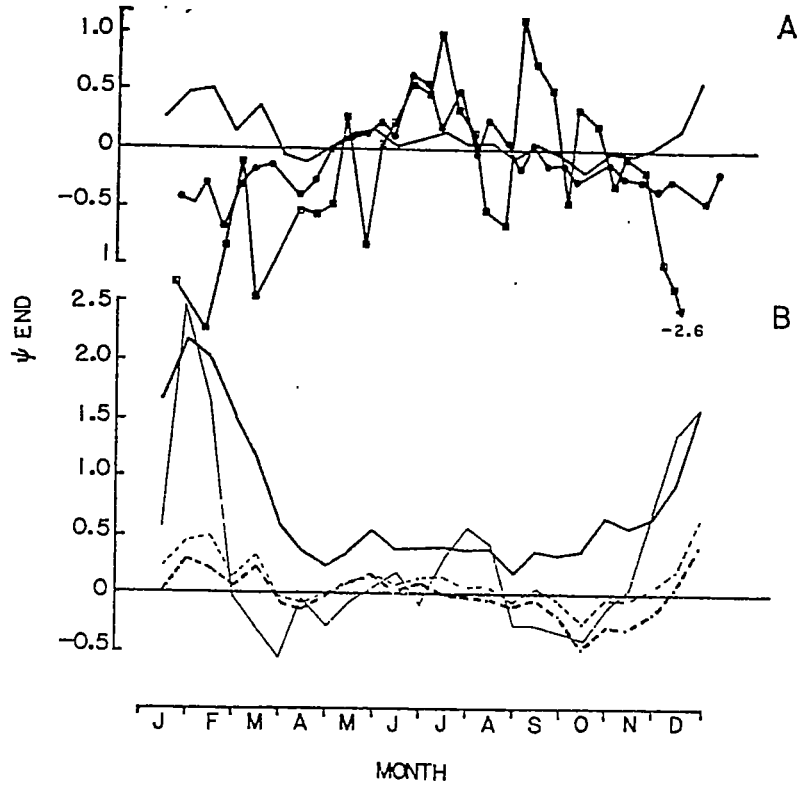


Fig. 3. Seasonal changes in the phase angle difference between the end of activity and sunset (Ψ end) in grey squirrels. A. Nest box activity end at 3 latitudes. B. Transmitter, nest box and feeding ends of captive squirrels and end of activity of wild squirrels at Cedar Creek.

living near the Arctic Circle occurred in mid-summer, which is in direct contradiction to the pattern described by Daan and Aschoff (1975). The Ψ onsets at Andechs and Cedar Creek do not exhibit as wide a change as at Kuusamo. The largest Ψ onset in captive squirrels occurred in late February and March for Cedar Creek and the lowest values were found in January and December. Both the highest and lowest values of Ψ onset at Andechs were found in February. Data from these localities do not appear to support the pattern described by Daan and Aschoff (1975). Aschoff's (1969) earlier evaluation of phase differences as positive or negative seems to be a more appropriate method for evaluating our data.

The four measurements of onset of activity at Cedar Creek, shown in Figure 2B, support using this approach. These curves summarize the averages of

transmitter onset, nest onset and feeding onset for captive squirrels and of transmitter onset for wild squirrels. Though the absolute values are different, these curves reveal a maximum positive spring peak and a less obvious fall peak with minimum values occurring in mid-summer. This pattern of Ψ onset as a function of the season is similar to that reported in several species of day-active birds and mammals (Aschoff 1969, Aschoff et al. 1970 and Daan and Aschoff 1975).

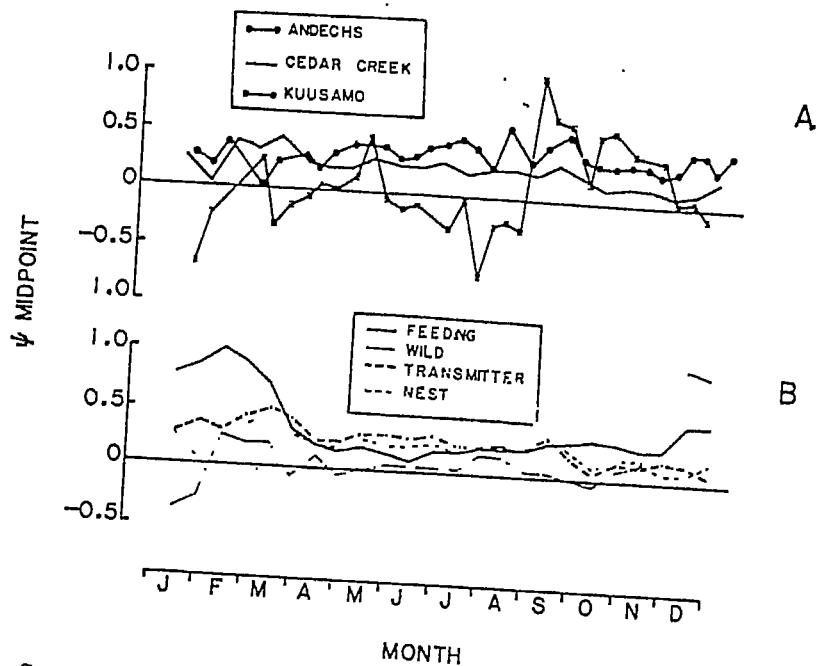


Fig. 4. Seasonal changes in the phase angle difference between the midpoint of activity and true noon (Ψ midpoint) in grey squirrels. A - Nest box activity midpoint at 3 latitudes. B - Transmitter, nest box and feeding midpoints of captive squirrels and midpoint of activity of wild squirrels at Cedar Creek.

A large negative value of Ψ onset in late January and February is especially apparent for the wild squirrels, but also appears in the three curves for the captive squirrels at Cedar Creek. The large shift in the onset of activity after sunrise produces the short activity time.

Data on Ψ end are summarized in Figures 3A and 3B, similar to Ψ onset. The curve from the squirrel at Andechs fits Aschoff's (1969) rules very well, with the largest positive values of Ψ end occurring in summer and the highest negative values in winter. At the Arctic Circle, however, the squirrel exhibited two positive peaks of Ψ end and one negative peak in mid-summer, with the end of activity being 0.6 hours later than sunset (Figure 3A).

In comparing the four measures of activity end at Cedar Creek (Figure 3B), one can observe the end of nest activity fluctuating about the 0 value from spring through fall, but reaching a high positive value in winter. This high

value of Ψ end in winter was even more pronounced in feeding activity and in the activity pattern of the wild squirrels. The ends for feeding activity are 1.5–2.3 hours before the time of sunset, and are almost identical to data from wild squirrels.

Midpoint of activity

The phase angle difference between the midpoint of activity time and the midpoint between sunrise and sunset is usually used as the best value for measuring the entrainment of the circadian system by the light-dark cycle (for details see Aschoff 1969 and Daan and Aschoff 1975). Values for Ψ midpoint of nest activity at Andechs and Cedar Creek are similar (Figure 4B). These values varied from 0.0 to 0.6 hours and do not show trends similar to other day-active animals described in the circadian literature. The curve of Ψ midpoint for the squirrel near the Arctic Circle indicates that both the maximum negative value and the maximum positive value occurred in summer, indicating a very large phase shift at that time of the year.

All values of Ψ midpoint from the four Cedar Creek measurements are extremely stable between April and November (Figure 4B), with a range of less than 0.5 hour. The wild squirrels showed negative values in January but large positive phase shifts in the second half of November through December. Phase of feeding midpoint is shifted by about 1 hour in the winter season. There are no such Ψ midpoint seasonal changes in other day-active species reported in the literature.

Activity time as a function of photoperiod

Activity time (α), the time interval between onset and end of activity, usually follows the length of the photoperiod, i. e., the time interval between sunrise and sunset. Averages for all squirrels are shown in Figure 5. The top 2 data sets represent activity as indicated by nest box photocells for squirrels in Kuusamo and Andechs. The data sets labeled Cedar Creek TA, NA and FA represent transmitter activity, nest activity and feeding activity summarized for all captive squirrels at Cedar Creek. The bottom data set summarizes averages for all wild squirrels monitored by telemetry.

The activity time of the grey squirrel near the Arctic Circle paralleled the photoperiod and was larger or equal to it when day length was between 5 and 19 hours. Length of activity deviated from length of daylight when the photoperiod was 3 to 5 hours and 19 to 22 hours. No S-shape, such as that described by Daan and Aschoff (1975), can be detected in the Kuusamo data. However, the curve is similar to that reported for the Great Spotted Woodpecker (*Dendrocopus major*) (Aschoff 1969, Figs 12–13). Aschoff believed that the pattern was related to the late breeding season of this woodpecker.

All three measurements of nest box activity, at Andechs, Kuusamo and Cedar Creek, and transmitter activity in the nest boxes at Cedar Creek, show that the activity time is longer but parallel to the photoperiod. In addition, the feeding activity of captive squirrels also parallels the length of the photoperiod, but is generally shorter. Feeding time and length of daylight were approximately equal when the day length was 13 to 14 hours. At longer photoperiods the length of feeding again became shorter. There is a strong similarity in the pattern of feeding activity (FA) in captive squirrels and activity of wild squir-

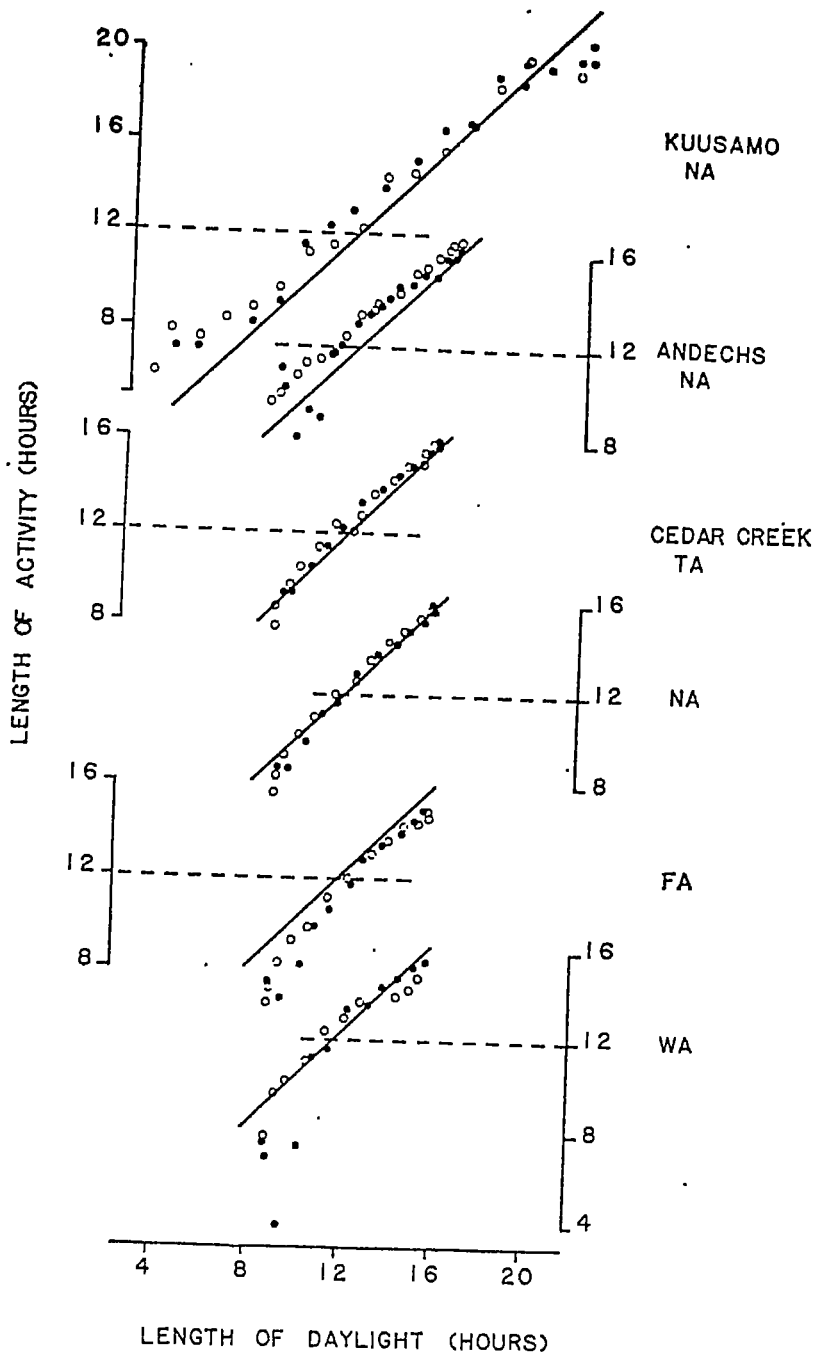


Fig. 5. Length of activity (α) of grey squirrels as a function of the photoperiod at 3 latitudes. Closed circles indicate the first half and open circles the last half of the year. The diagonal line represents a 1:1 ratio between α and photoperiod. Nest activity

rels (WA) measured by radiotelemetry. We did not detect changes in the length of activity time in spring, due to changes in testosterone levels, such as those reported for starlings (*Sturnus vulgaris*) by Gwinner and Turek (1973).

At all three locations activity time deviated greatly from photoperiod during midwinter when days were short. However, the greatest independence was recorded during day lengths shorter than 10 hours in Andechs, on FA of caged

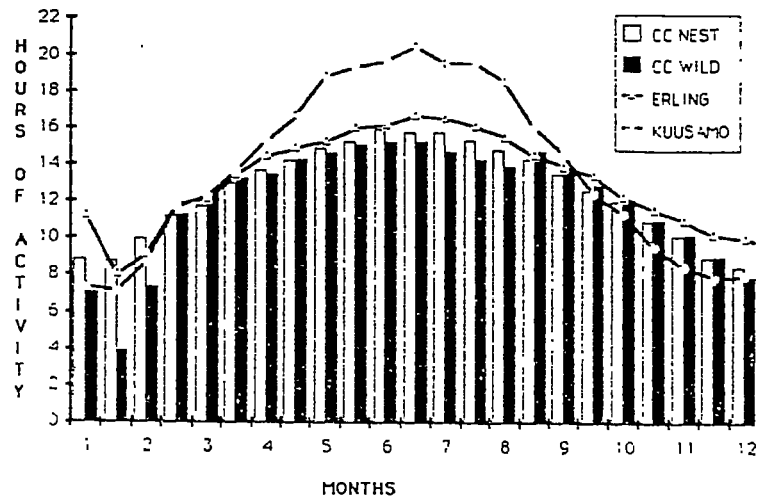


Fig. 6. Comparison of nest box activity of grey squirrels measured at 3 latitudes with transmitter activity of wild squirrels at Cedar Creek.

squirrels, and especially on wild squirrels. As far as we know, such a relation between activity time and photoperiod has not been reported. It appears that the photoperiod is not able to completely fulfill the "role" of the strongest Zeitgeber and force the circadian oscillation to synchrony with the light cycle. In day-active birds, as described by Daan and Aschoff (1975), a "hysteresis" was noted, especially at high latitudes. This did not occur in grey squirrels.

Activity time as a function of the year

Comparison of activity time (α) measured by different techniques and at different locations is presented in Figure 6. As expected, the longest activity time occurs in the summer months at Kuusamo near the Arctic Circle. The second longest activity time occurs at Andechs. Duration of activity in summer at Cedar Creek is shortest because the latitude at Cedar Creek is the lowest, resulting in the shortest photoperiod. Data obtained by radiotelemetry in captive squirrels at Cedar Creek are similar to data recorded from the nest boxes and show similar trends; therefore, they are not included in Figure 6. Feeding activity times were shorter than nest activity, but showed the same trend.

(NA) is shown for all locations and transmitter activity (TA), feeding activity (FA) and wild activity (WA) are also shown for Cedar Creek.

Table 1. Correlation of activity time of grey squirrels to ambient air temperature in east-central Minnesota

Period	Average	min	max	Maximum amplitude/24 hrs	r
Jan 1st half	-14.9	-33.1	0.6	24.1	0.45
Jan 2nd half	-11.7	-35.4	4.4	25.4	0.64
Feb 1st half	-7.9	-31.8	9.2	31.9	0.56
Feb 2nd half	-0.7	-13.9	13.9	18.3	0.41

Activity data on wild squirrels at Cedar Creek differ in several ways from data on captive squirrels. From June to August the activity time of these animals was shorter than for captive squirrels at the same location. An abrupt increase in the activity time of the wild squirrels is observed in late August. From this date until the end of December the curves for both captive and wild squirrels are nearly identical.

At all localities, regardless of latitude, a decrease in the length of activity time in the second half of January was recorded. This decrease was especially pronounced in the wild squirrels. It is likely that the observed decrease was due to the influence of a strong abiotic factor or perhaps more than one. Air temperature could be such a factor. Temperature data from Cedar Creek are given in Table 1. The correlation coefficients suggest a positive relationship between daily activity time and air temperature. This relationship may explain,

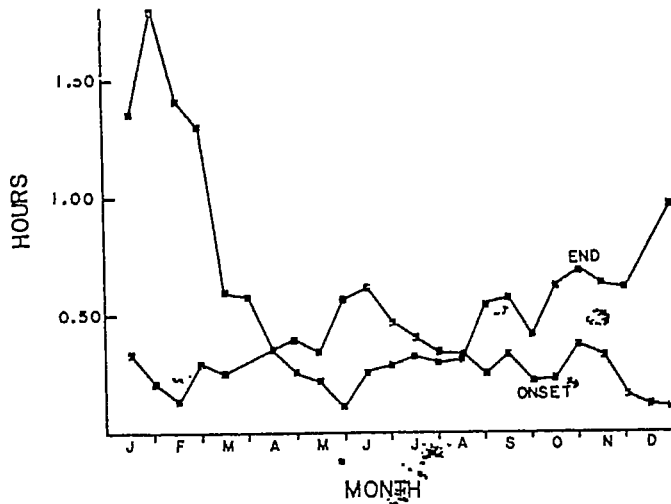


Fig. 7. Seasonal changes in the phase angle difference between onsets and ends of nest box activity and feeding activity in a male and female grey squirrel held in the same pen. The onset curve indicates the time difference between the onset of activity measured as the squirrel left the nest box and the time it began feeding. The end curve shows similar data for cessation of feeding and entering the nest box for the last time in the evening.

at least in part, the breakdown of the coupling between activity time and photoperiod, especially in wild squirrels.

The values of the length of α from all localities and from different types of measurements are most identical in March and September. This is probably evoked by the maximum strength of the Zeitgeber at that time of-year (Aschoff 1969).

Nest box and feeding activity as a function of season

Time between the onset of nest box activity and feeding activity shows a definite seasonal pattern (Figure 7). The shortest time between these two points occurred in February and December, with the pattern showing the smallest values throughout the winter. The largest value, 0.6 hours, occurred in summer. The seasonal pattern in the difference between feeding end and nest box end shows the opposite pattern with the highest value, 1.8 hours, occurring in the second half of January, and the lowest, 0.1 hours, in the second half of May.

Squirrels began foraging soon after awakening in winter. In summer they left the nest box and were active in the pen for long periods before beginning to feed. Identical time intervals between locomotor and feeding activities in the morning and evening occurred in the first half of April, after the spring equinox, and in the first half of August, before the fall equinox. The longest interval between the ends of feeding and locomotor activity occurred in winter, but the shortest intervals for the ends of feeding and nest activity occurred

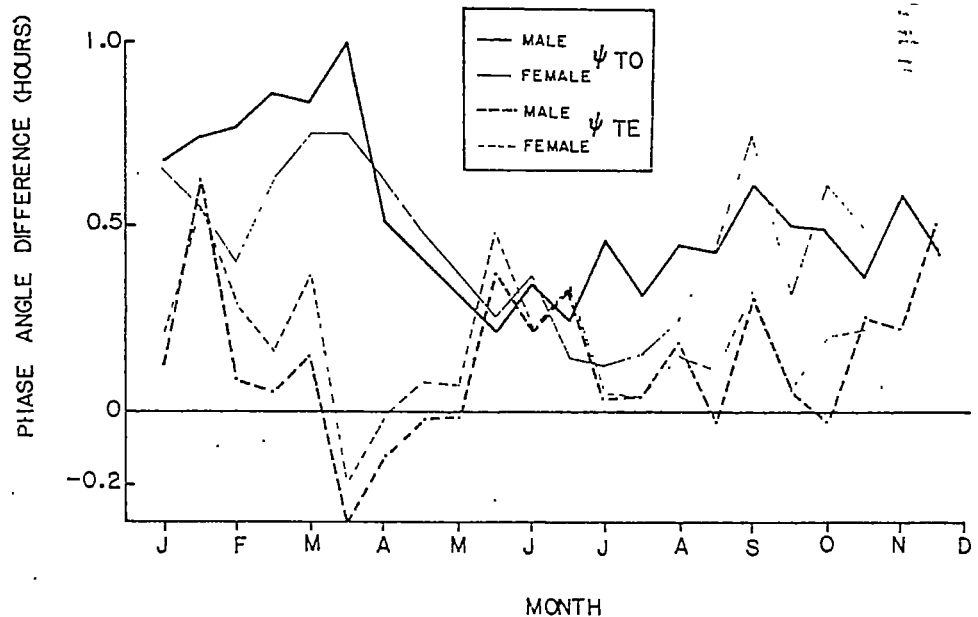


Fig. 8. Seasonal changes in phase angle difference between transmitter activity onset and sunrise and transmitter activity end and sunset in a male and female grey squirrel held in the same pen at Cedar Creek.

Table 2. Sexual differences between beginning and end of activity of captive grey squirrels in east-central Minnesota

			J	F	M	A	M	J	J	A	S	O
Inside nest	Morning ♂	before ♀	+	+	+	-	-	-	+	÷	0	-
	Evening ♂	after ♀	0	+	÷	+	+	+	+	-	0	-
Leaving or entering nest	Morning ♂	before ♀	-	+	0	-	-	-	+	÷	+	+
	Evening ♂	after ♀	-	+	0	-	-	+	+	0	-	-

+ Largest number of days with predominance
 - Largest number of days without predominance
 0 Number of days equal

in late spring and summer. In other words, foraging ended in winter long (more than 1 hour) before the end of locomotor activity. In summer, feeding activity ended about 15 to 25 minutes before the end of nest activity.

Sex differences in activity rhythms

Aschoff and Wever (1962) predicted in Rule 3 that the males of light-active species began activity earlier than females and follow the female to rest in the evening. The design of our experiment at Cedar Creek made it possible to monitor the individual activity of a male and female squirrel kept in the same cage and using the same nest box and feeding box. Data from the photocell on the nest box and from the radio transmitters were used to establish the activity pattern for each squirrel. However, it was sometimes not possible to recognize which individual was the first to leave the nest box in the morning or the last to enter in the evening (see Methods for details). We attempted to evaluate sexual differences on the basis of two types of phase angle measurements, transmitter (TA) onsets and ends and nest box (NA) onsets and ends of the male and female.

Data on phase angle differences in TA (Figure 8) indicate that larger, or more positive, values for the male occurred conspicuously from January through March and from June through mid-August. During these periods the male began activity in the nest box earlier than the female. Shorter, or more negative, Ψ end values for the male occurred from February through May indicating that the male was active in the nest box later than the female. During the remainder of the year, both Ψ ends for the female and male were almost identical.

The number of days in which the male left the nest box before the female in the morning and the number of days the male followed the female in the evening calculated for each month varied from 13-25. The total number of days through the year when the male was known to begin nest box activity first was 114. The female began nest box activity first on 71 days. With respect to the end of activity, the male entered the nest box later on 104 days and the female on 204 days.

The pattern in which the male began activity before and ended after the female did not generally follow the predictions of Aschoff's Rule 3

(Table 2). Full agreement with Rule 3 occurred only in February and July in both types of measured activity, and in March for activity into the nest box. Activity in all other months did not correspond with the predicted model.

DISCUSSION

It is apparent from our data that there are no marked differences in results obtained by the different measurement techniques on either captive or wild squirrels. With regard to the mechanism of entrainment of circadian rhythms by an exogenous Zeitgeber, it appears that some of the major seasonal parameters of the circadian rhythm are not following the predicted models (Aschoff, Wever 1962; Aschoff 1969, Daan and Aschoff 1975).

Activity time (α) as a function of the photoperiod does not show the pronounced S-curve predicted by Daan and Aschoff (1975 page 309-310) as one of the 3 most important generalizations of their study. This is especially noticeable in high latitudes, where activity of squirrels closely follows the extreme length of photoperiod (Fig 5-KUUSAMO). It is important to note that the long and short photoperiods are strong enough to entrain the circadian oscillation at this high latitude.

At Andechs and Cedar Creek, the shortest α occurred in early spring when the length of the photoperiod was increasing (Fig. 5). In most other species, activity time follows the length of photoperiod. Since this did not occur in the squirrels, an additional exogenous factor appears to be influencing the activity time.

The extremely short α that occurred in the wild, as also reported by Bland (1977), differs from α 's of squirrels in captivity. This short α is produced by high negative values of Ψ onset and by high positive values of Ψ end, which are nearly similar. This results in the value of midpoint being close to the 0 line, the time of true noon.

A short activity period in grey squirrels has been observed in natural habitats by several authors. Shorten (1954) stated that in short days activity is restricted to foraging. Thompson (1976) and Bland (1977) found a seasonal winter peak and believed that squirrels may have selected the warmest portion of day in which to be active. Wild squirrels at Cedar Creek are under a strong influence of daily temperature changes in January and February, as shown in Table 1. At that time they either spend their resting time in the trees or in nests built of dry leaves. The protection provided by nests and dens is probably necessary to maintain their critical physiological temperature. The European squirrel, *Sciurus vulgaris*, is able to keep the nest temperature 20-30 °C higher than the ambient air temperature after a warming phase of 10-30 minutes (Pulliainen, 1973) in the coldest winter months.

Low temperature could reduce the sensitivity of the circadian system to light and shorten activity time, but not to the extent shown in Figure 5. The activity time for captive squirrels is longer than for wild squirrels, which might be caused by higher temperatures in the nest boxes. One should also consider daily maximum temperature amplitude, temperature values, and direction and velocity of the wind and its chill factor as possible additional modifying factors (exogenous) which might exert a stronger influence than the photoperiod.

Length of activity time in wild squirrels is markedly increased in the second

half of August. The end of August through November is the period of nut gathering behavior (Bland 1977; Thompson 1976). We believe it is this behavior that shifts the end of activity beyond sunset. This phenomenon did not occur in captive squirrels.

The strongest Zeitgeber (L:D ratio of 1.0 and shortest twilight) (Hoffman 1969, Wever 1967) occurs at the time of the vernal and autumnal equinox and produces the greatest precision of the circadian rhythm (Aschoff et al. 1972). One can presume that the day-to-day variations in timing of the rhythm of activity will be lowest about the time of the equinoxes, and that the length of activity time will be close to the L:D ratio of 1.0. The grey squirrel rhythm meets these conditions in late February and early March, slightly before the time of the vernal equinox, and in early October, slightly later than the autumnal equinox. These findings fully follow the predicted model (Aschoff 1969, Wever 1962).

The "seasonal rule" formulated by Aschoff (1964) predicts that the summer increase in photoperiod should produce an increased phase-angle difference in day-active animals. This increase should be enhanced by the length of twilight in mid-summer (Wever, 1967). The activity patterns of grey squirrels did not follow this rule. Even at the Arctic Circle, a high negative value was recorded in July and August rather than the expected high positive value. We found a high positive value in feeding activity of caged squirrels, emphasized by a high phase-angle difference between the end of feeding activity and sunset from January through March and slightly in December. From late November through late January the values of Ψ midpoint in wild squirrels were first highly positive but then negative. This extremely large negative value in January was produced mainly by a late onset of activity with respect to sunrise, which corresponded with low morning ambient temperatures (see Table I). Conversely, high ambient temperature was probably responsible for the bimodal activity pattern developed in the summer months in both captive and wild squirrels. These results agree with the findings of Bland (1977).

Circadian Rule 3 (Aschoff and Wever 1962) predicts a longer activity time and a higher positive phase-angle difference in day-active animals compared to night-active animals. This was supported by data from many species of day-active birds. The circadian rhythm of activity in grey squirrels does not follow this rule.

The circadian oscillation in day-active mammals and its entrainment by photoperiod in natural habitats show irregularities in comparison to birds. Kenagy (1978) found deviations in the circadian system in the day-active squirrel, *Ammospermophilus leucurus*, and the night-active Kangaroo rat, *Dipodomys meriami*, and stated "... the type of seasonal temporal organization cannot be predicted on the basis of the circadian system."

Daily rhythms could be influenced by internal, time-limited, behavior, such as courtship and nesting of birds, food gathering of squirrels or construction of winter houses by muskrats and beaver. These behavioral activities occur under natural conditions, but usually not in captivity. They could be triggered by exogenous stimuli, such as the length of photoperiod or temperature cycles, or both acting together, and/or by social stimuli as described by many authors (see summaries in Regal and Connolly 1980). Activation of an internal behavioral block usually results in feedback by hormonal pathways which may influence the frequency of the circadian oscillation. This is displayed as an

abrupt or slow change in phase angles. Study of these circadian parameters in wild animals will provide new insights on the circadian organization of animals related to their natural habitats.

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