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Changes in Daily Activity Rhythms of Some Free-ranging Animals in Minnesota

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Activity patterns of many vertebrates have been monitored by an automatic radio tracking system at the Cedar Creek Natural History Area in east-central Minnesota. Activity rhythms of Gray Squirrels (*Sciurus carolinensis*), Red Foxes (*Vulpes vulpes*), Muskrats (*Ondatra zibethicus*), Ruffed Grouse (*Bonasa umbellus*) and Barred Owls (*Strix varia*) show marked seasonal changes which are believed to be responses to environmental conditions or physiological and behavioral requirements of the animal. Variations in number of activity periods, total minutes of activity, timing of activity in relation to sunrise and sunset, and in the amount of rest during the normal active period are shown to be related to changes in such factors as temperature, snow cover, food supply and breeding behavior. These modifications of activity rhythms suggest that controlling mechanisms are sufficiently plastic to allow animals to alter their behavior significantly in response to a changing environment. In contrast, animals in captivity show remarkably precise timing with respect to activity rhythms. This regularity appears to be highly dependent on caging and the uniformity of environmental conditions under which such animals are maintained.

Key Words: Activity rhythms, Gray Squirrel, *Sciurus carolinensis*, *Red Fox*, *Vulpes vulpes*, Muskrat, *Ondatra zibethicus*, Ruffed Grouse, *Bonasa umbellus*, Barred Owl, *Strix varia*, Minnesota.

The daily activity pattern of any free-ranging animal is determined by an endogenous mechanism whose output is modified by both biological and environmental factors, which themselves exhibit seasonal changes. However, the adaptive significance of such changes is not well understood (Daan 1981; Rusak 1981). Data on the activity patterns of wild animals living under natural conditions have often been anecdotal, whereas detailed information has been obtained for many species in captivity. Analyses of these latter data have indicated remarkably precise patterns of activity from day to day for individual species. Experimental studies have revealed an endogenous mechanism of timing which persists in the absence of environmental stimuli.

Development of automatic telemetry techniques for monitoring the activity of wild animals has made it possible to obtain long-term data on rhythms of many species of vertebrates living under natural conditions. This paper uses available data to show that activity rhythms of wild animals living under natural conditions do not exhibit high precision nor do they maintain the same pattern throughout the year, in spite of an endogenous mechanism and an environmental Zeitgeber. Possible explanations for these changes are considered in terms of the abilities of the various species to survive and reproduce. Examples have been chosen from both birds and mammals studied at the Cedar Creek Natural History Area in east-central Minnesota.

Enright (1970) suggested that laboratory studies of endogenous rhythms might have little relevance to ecology. On the other hand, data on activity rhythms of captive animals and of wild animals are often cited together in papers dealing with endogenous rhythms (Daan and Aschoff 1975). Uniformity or consistency of the observed rhythms is often implied. Data in this paper reveal striking seasonal changes and great plasticity in daily activity rhythms of a variety of birds and mammals, suggesting that uniformity or consistency of rhythms is rare in nature. Students of endogenous rhythms in the laboratory, whether or not they are expecting to contribute to ecological understanding, should be well aware of the potential influence of environment on wheel-running, feeding or other measures of activity.

Methods

Study animals were captured in live traps, in drive nets and by a variety of other methods (Keith et al. 1968; Huempfner et al. 1975). Each animal was fitted with a radio transmitter broadcasting on a unique frequency in the 53 mHz range (Tester et al. 1964). The transmitters were designed either with the broadcasting antenna forming a collar, or as a back and breast harness with a whip antenna extending along the back. Transmitters weighed 35 to 42 grams, had an expected life of 180 days, and an effective range of about 1.6 km.

Radio signals from the individual animals were monitored by the Cedar Creek automatic radio tracking system (Cochran et al. 1965; Tester 1978).

Location and activity were determined for each animal from data recorded on microfilm every 45 seconds. Field observations of radio-marked animals confirmed that the recorded data corresponded to activity and rest (Tester 1971).

The radio signal from a motionless animal appeared as a continuous black bar on the microfilm records, whereas signals from a moving animal appeared as broken or interrupted bars. These breaks were caused by modulation of the radio signal due to a change in capacitance of the circuit as the collar changed position on the neck of the animal or as the whip antenna moved or vibrated. The characteristics of the radio signal on the microfilm record provided a means of determining, to the nearest minute, when an animal was active or resting. Specific types of activity, such as running, feeding, or grooming could not be differentiated from the radio signals. However, modifications of selected receivers in the automatic tracking system enabled drumming of male Ruffed Grouse to be monitored. In the analysis, data were summarized for 5 to 15 minute intervals, depending on the quality of data available and length of the study period for each species.

Data from the microfilm records were recorded manually on tabulation sheets and encoded on computer punch cards for further analysis on a Control Data Cyber 74 system. The analysis program was designed to show each daily pattern of rest and activity for an individual animal and to summarize rest and activity over specified time periods, such as weekly or monthly.

Weather data were recorded at the U.S. Weather Bureau Station at the Cedar Creek Natural History Area. Sunrise and sunset times were determined from U.S Naval Observatory Chart 1155 for Minneapolis. Breeding chronologies, types of behavior, and availability of food, such as acorns, were determined by direct field observations.

Results

GRAY SQUIRREL, *Sciurus carolinensis*

Gray Squirrels were monitored over a 15-month period from July 1971 through September 1972 (Bland 1977). Periods of activity and rest were plotted daily for each squirrel. Combining the data for all squirrels for each two week interval produced a series of graphs showing seasonal changes in activity patterns (Figure 1). Because data were obtained on a different number of squirrels during each two-week period, the individual graphs do not always represent identical numbers of animals. Although variations due to differences among squirrels and among days are not accounted for, these graphs provide a generalized picture of the activity waveform throughout the year. Figure 1 shows clearly that a bimodal waveform is characteristic of early spring and summer. During winter, low intensity activity is expressed only during a narrow mid-day window. A square waveform denoting intense continuous activity extending for the entire daylight period is characteristic of fall and late spring. Thompson (1977) also observed a single mid-day peak in winter, and a bimodal pattern showing the seasonal maximum in summer, based on visual field data.

Although Figure 1 shows the general pattern of onset and end of activity with respect to sunrise and sunset, the cumulative nature of the graphs obscures much detail. Because activity onset and end represent critical times frequently used in analysis of circadian rhythms, figures were prepared to illustrate exact onset and cessation time of each animal. Figure 2 presents an example of such data for a juvenile female from 4 August 1971 to 10 September 1972. Though irregularity in onset and cessation times from day to day is apparent, one can also see a general pattern that changes with the season.

Activity onset and cessation times averaged for all squirrels were used to illustrate phase relationships with sunrise and sunset (Figure 3). A marked reduction in the α:p ratio in winter is apparent.

RED FOX, *Vulpes vulpes*

Red Foxes are primarily nocturnal, with activity onset occurring near sunset and activity end near sunrise, but with considerable daily, seasonal and individual variation (Ables 1969; Storm 1965; Tembrock 1958). Individuals monitored at Cedar Creek usually exhibited several periods of movement and rest daily. The typical 24-hour activity waveform was a sequence of relatively long periods of rest during the day followed by relatively long periods of movement at night. Major functions carried out during the active period included foraging and maintaining the territory occupied by the family (A. Sargeant, in preparation). In addition, activities associated with breeding occurred during late winter and spring. Feeding occurred at any time during the active period and did not always appear to be the most important behavioral function. In his analysis of behavior, A. Sargeant (in preparation) indicated that the distance traveled and rate of movement associated with foraging and territory maintenance remained relatively constant from day to day throughout the year. During summer, when nights are short, the intensity of activity was high throughout the period of darkness (Figure 4A). In contrast, during long winter nights when foxes had more time to carry out the required activities, they spent considerable time resting, as shown by the lower intensity of activity (Figure 4B).

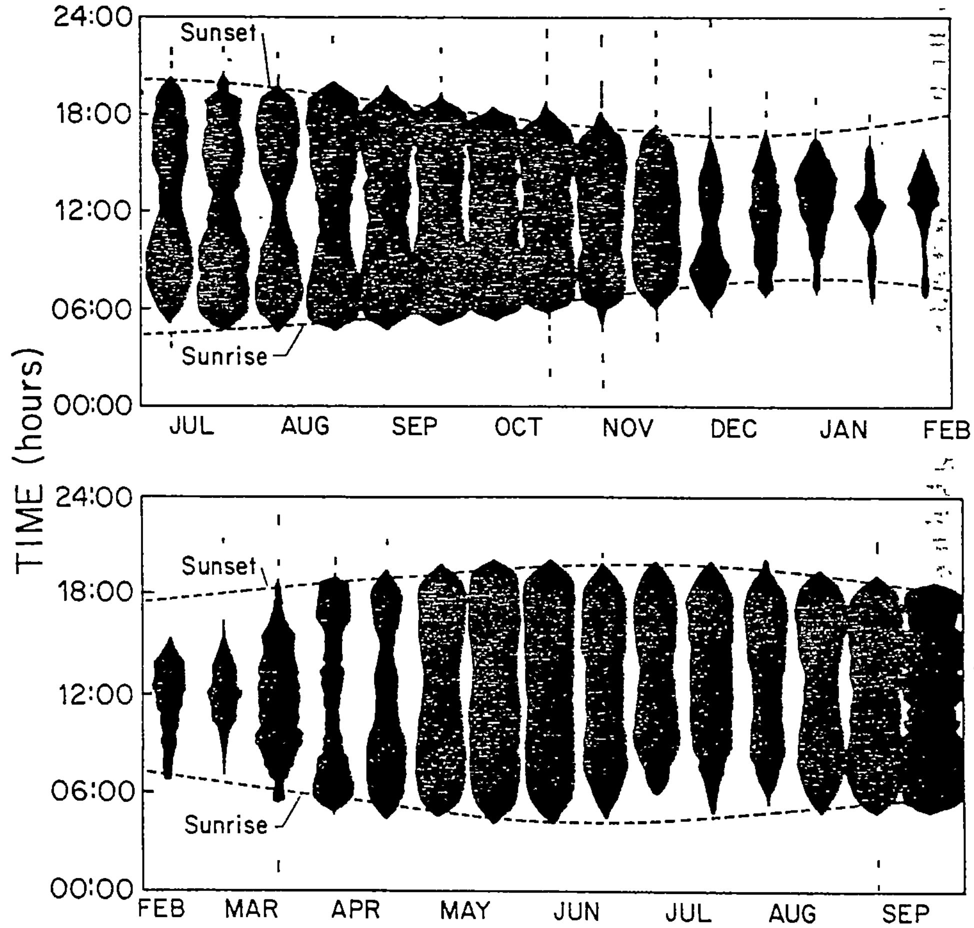

FIGURE 1. Seasonal activity patterns for Gray Squirrels from July 1971 to September 1972 (average for 4-8 squirrels). Full width of each period indicates 100% activity. The curved horizontal lines show sunrise and sunset. Time is Central Standard Time.

MUSKRAT, *Ondatra zibethicus*

In general, Muskrats are considered to be nocturnal. However, O'Neil (1949) and Errington (1963) suggested that high population density and/or certain meteorological conditions might result in increased diurnal activity. Van Horn (1975) reported an increase in diurnal activity after ice formed on his study lake in Wisconsin. Using data from tracks in sand transects, Stewart and Bider (1977) reported that Muskrats had a bimodal waveform with peaks occurring about 1630 h and 2230 h.

Muskrats at Cedar Creek exhibited an activity rhythm quite different from that of Gray Squirrels and Red Foxes. During the period of study, from July 1969 through February 1970, the number of activity periods per 24 hours varied from two to four. From July through about 30 August, four periods of activity were about evenly distributed throughout the 24 hours. In subsequent months the number of activity periods was reduced to three and then to two. In this reduction, which occurred at the time of freeze-up of lakes and streams, the day activity periods were eliminated and Muskrats became essentially nocturnal (Figure 5). Unlike the Red Fox, the total

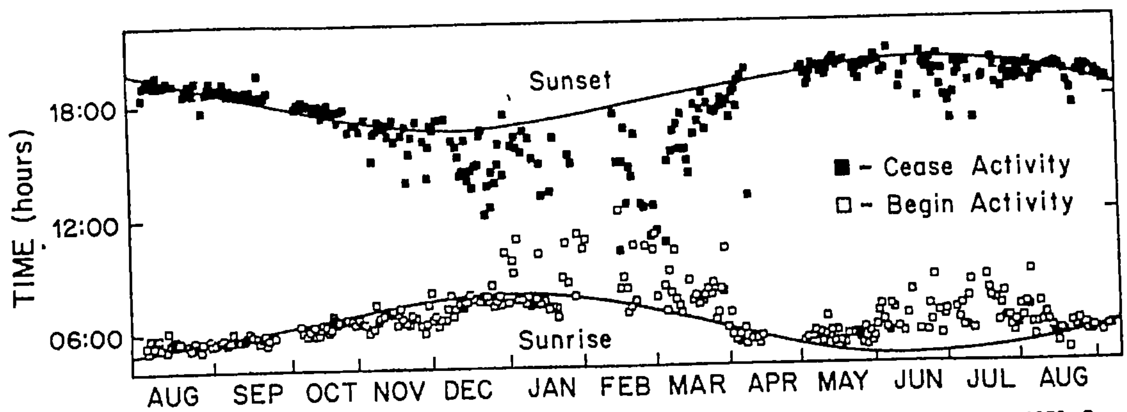

FIGURE 2. Onset and cessation of activity of a female Gray Squirrel from 4 August 1971 until 10 September 1972. Open squares represent onset, black squares represent cessation, and the curved lines show times of sunrise and sunset.

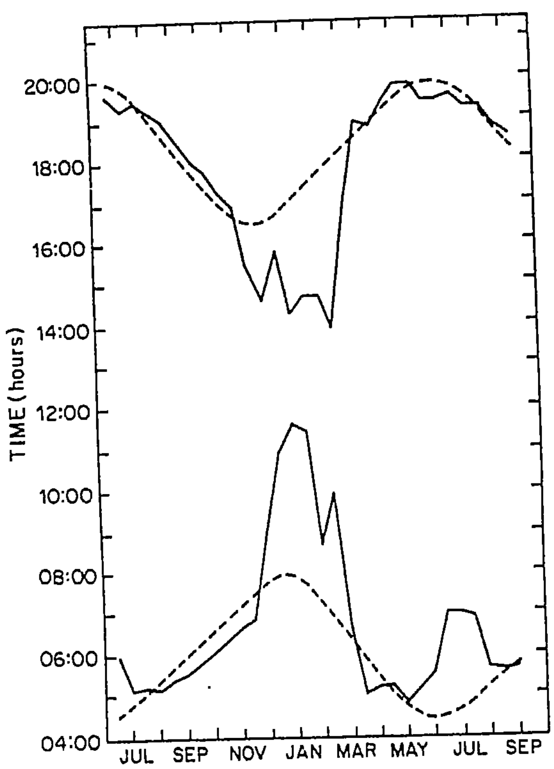

FIGURE 3. Phase relationships between onset and end of activity and sunrise and sunset for Gray Squirrels from July 1971 through September 1972. The solid lines represent activity onset and cessation and the dashed lines represent times of sunrise and sunset

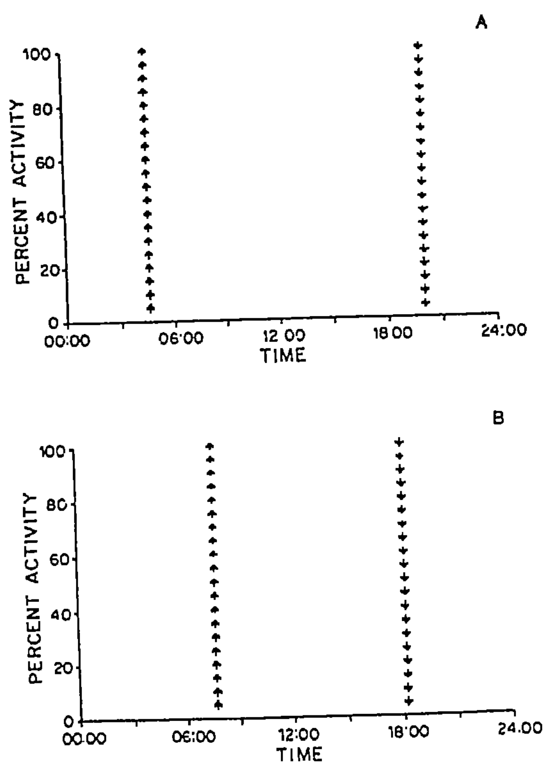

FIGURE 4. Activity patterns for an adult female Red Fox showing the percentage of days the fox was active for any given time during the 24 hours. Arrows show times of sunrise and sunset. A. Activity from 1 through 15 July 1964 illustrating pattern typical of short summer nights. B. Activity from 15 through 29 January 1964 illustrating pattern typical of long winter nights

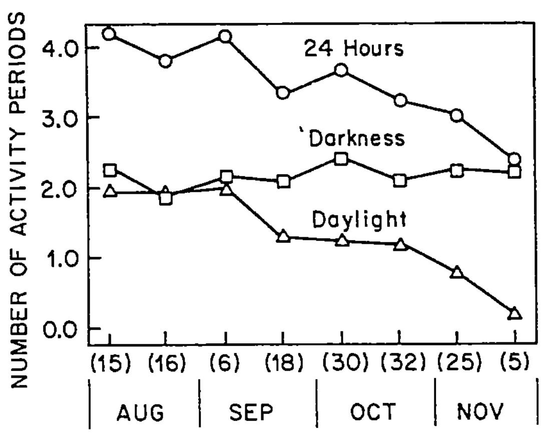

FIGURE 5. Mean number of activity periods for 24 hours, for daylight, and for darkness, for Muskrats from 1 August to 30 November 1969 Sample sizes in Muskrat-days are given in parenthesis

minutes of activity per 24 hours was reduced to approximately half that exhibited in late summer.

While the reasons for this change are not known, it is probably related to the functions which Muskrats must carry out during this period of the year. In late summer and early fall Muskrats are building lodges and storing food in preparation for winter. These activities undoubtedly require that the animals be active for many minutes in each 24-hour period. After ice forms on the lakes and streams, Muskrats are no longer able to construct houses. For the duration of the ice-cover period they rely on stored food supplies and on foraging under the ice. Most activity during winter is probably related to feeding. One might expect this feeding to occur during the warmer temperatures of daytime; however, the temperature of the water under the ice where food is stored remains relatively constant at approximately 4°C until the spring thaw. The fact that the Muskrats were active at night during this period suggests that the species may be basically nocturnal but becomes active during the day when time is required for house building and food storage.

RUFFED GROUSE. *Bonasa umbellus*

Birds studied at Cedar Creek have also exhibited changes in activity rhythms in response to behavioral requirements or environmental stresses. Ruffed Grouse are normally diurnal and both sexes show a bimodal waveform with activity peaks near sunrise and sunset, similar to many other birds (Aschoff 1967). The examples presented below to illustrate plasticity in activity rhythms of Ruffed Grouse are related to breeding and brood rearing behavior.

During spring, male grouse display by drumming, which begins in early April and extends into July. Drumming may occur during either night or day, with the pattern changing as the season progresses. Activity associated with feeding and other daily functions, such as preening and territorial defense, are also carried out during the drumming season. Figure 6A illustrates activity of a male grouse for a two-week period during the peak of the drumming season. Archibald (1976) showed that drumming occurred throughout the day except for brief periods near sunrise and sunset when feeding activity was most pronounced. It is apparent from Figure 6A that this grouse was active nearly 100% of the daylight period. Although this high level of activity must place stress on the physiology of the males, such levels occur for

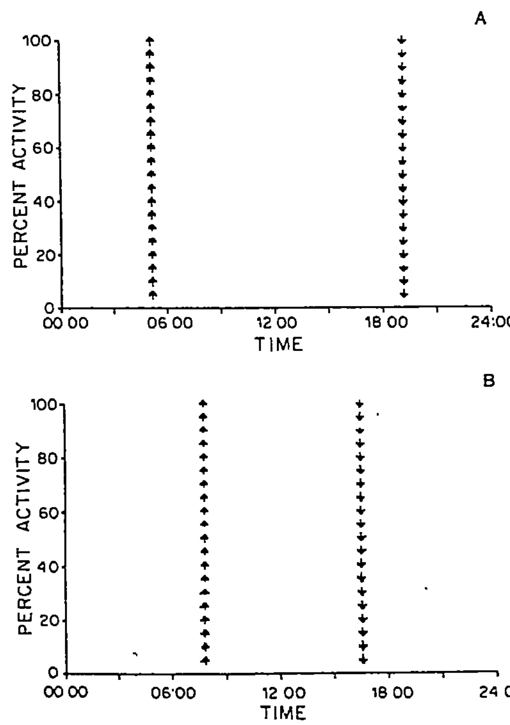

FIGURE 6. Activity pattern for adult male Ruffed Grouse showing percentage of days the grouse was active for any given time during the 24 hours Arrows show times of sunrise and sunset. A. Activity from 23 to 29 April 1970 illustrating the high level of activity throughout nearly the entire 24 hours B Activity from 20 to 27 December 1971 illustrating the typical winter pattern of reduced activity with peaks occurring around sunrise and sunset

only a few weeks during the year (Archibald 1976).

Activity in winter is markedly reduced, with obvious peaks near sunrise and sunset (Figure 6B). At this season activity is related mainly to feeding on buds and catkins of trees and shrubs (Huempfner and Tester, *in press*). Between feeding periods, grouse rest in depressions in the snow or burrow into soft, fluffy snow.

A somewhat similar type of short-term change in activity rhythm was discovered in female Ruffed Grouse (Maxson 1977). Prior to egg laying, hens exhibited the typical bimodal waveform, with activity beginning prior to sunrise and ending after sunset (Figure 7A). During incubation hens were on the nest for nearly the entire 24-hour period, with only brief periods of activity for feeding in early morning and late afternoon (Maxson 1977). Immediately after hatching, the hens altered their activity rhythm, beginning activity as much as several hours later in the morning and ending activity earlier in the evening (Figure 7B). In addition, the level of activity was higher throughout the active period compared with the pre-incubation period. Maxson (1977) believed that this delay of onset and early cessation was related to brooding behavior by the hen. Brooding during the cool, wet morning and evening hours reduced the exposure of chicks to chilling and wetting from heavy dew, thus helping them to maintain their body temperature. As the chicks grew older, activity patterns of the brood hens began to resemble those of the broodless hens.

BARRED OWLS, *Strix varia*

Phase relationships of activity onset and end with respect to sunset and sunrise were highly variable in Barred Owls studied by Fuller (1979). Positive and negative phase differences as great as 60 minutes were observed in a non-breeding female monitored for approximately six months. Non-breeding Barred Owls exhibited nocturnal activity patterns with peaks of activity usually occurring just after sunset and before sunrise; however, some activity was also detected at various times throughout the day.

Activity waveforms of breeding birds changed markedly through the breeding season (Figure 8). During incubation, the female was active less than 3 percent of the time. The male, however, increased his activity at this time, presumably to obtain food for the incubating female. Fuller (1979) believed the marked increase in activity of both the male and female following hatching to be the result of increased hunting.

The time of year when the adults are feeding young corresponds to the time of year with short nights. Fuller observed that the adult Barred Owls were forced to hunt during the day to provide adequate food for their young. However, he also observed non-breeding adult females hunting in daylight during this same time of the year. Similar behavior has also been observed for other owl species (Bunn 1972; Marti 1974).

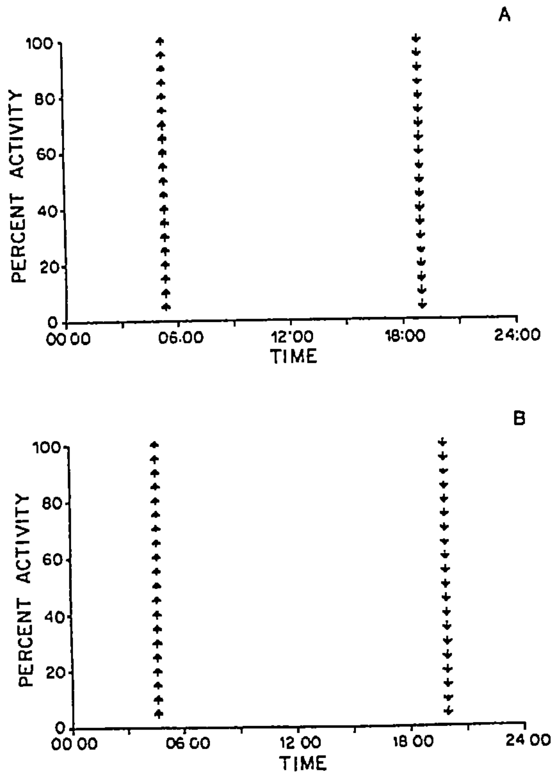

FIGURE 7. Activity patterns for an adult female Ruffed Grouse showing the percentage of days the grouse was active for any given time during the 24 hours. Arrows show times of sunrise and sunset. A. Activity during pre-incubation period illustrating the typical bimodal activity rhythm with onset prior to sunrise and cessation after sunset. B. Activity pattern during post-incubation illustrating the reduction in crepuscular activity associated with brooding.

Discussion

Comparison of these results with published accounts of activity rhythms of many species in captivity revealed that the animals living in the wild showed much variation in the times when activity began and ended in terms of the phase relationship to sunrise and sunset. In contrast, animals held in captivity showed remarkably precise timing from day

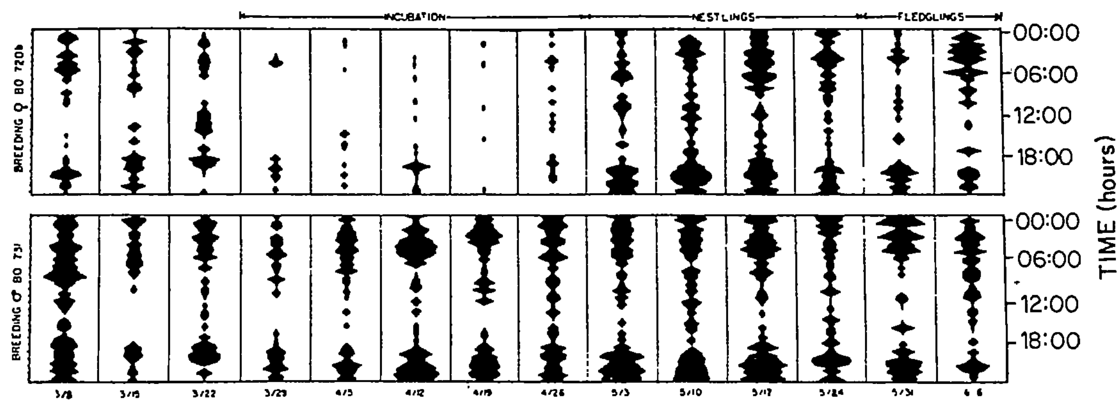

FIGURE 8. Activity patterns of a pair of Barred Owls during part of the breeding cycle in 1973 illustrating decreased activity by the female during incubation and an increase in daytime activity by the male after the young hatched. Full width of each period indicates 100% activity.

to day with respect to the onset and termination of activity as related to the light/dark regimen (Pittendrigh and Daan 1976). In addition, wild animals exhibited marked flexibility in the number of activity periods and total minutes of activity per 24 hours, and showed the ability to shift from night-active to day-active patterns when the need arose.

Much of the theory of seasonality of circadian rhythms assumes that length of twilight and length of day and night are the most important controlling factors (Aschoff 1969; Kenagy 1976; Wever 1967). The data from Cedar Creek, however, indicate that other factors override length of day and/or twilight. Using the data from Gray Squirrels as an illustration, one can see that the phase relationships between activity onset and sunrise (ψ onset) and activity end and sunset (ψ end) both show two maxima and two minima per year (Figure 3). The annual range of change in ψ onset was 294 minutes and in ψ end, 250 minutes. Such large amplitudes have not been reported in the literature, nor has the observed pattern been predicted by theory. It seems likely that ecological and ethological aspects of the biology of the squirrels and changes in environmental factors "damp out" the endogenous control of activity patterns and make data collected from free-ranging squirrels unsuitable for modeling the circadian system.

Data on activity patterns obtained from numerous species at Cedar Creek suggest that the endogenous timing mechanism is modified or overridden by other factors at various times throughout the year. A simple model (Figure 9) illustrates how environmental factors and biological factors may act to modify activity patterns within the framework established by the Zeitgeber and the endogenous mechanism. Linkage of environmental and biological factors,

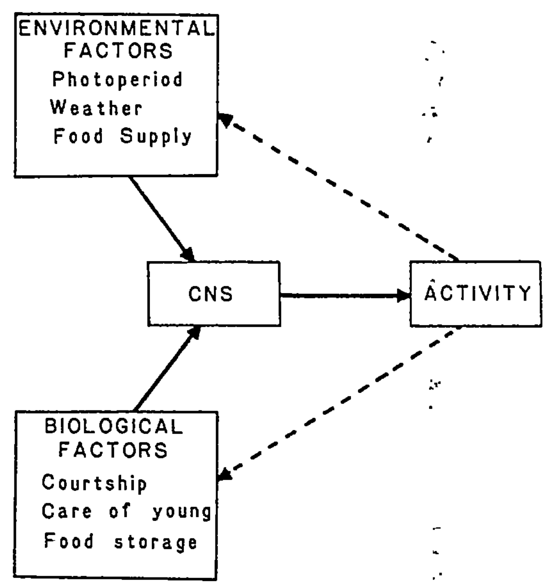

FIGURE 9. Model illustrating the influence of environmental and biological factors on activity rhythms of free-ranging animals. Feedback is shown by dashed lines leading from activity. Examples of environmental and biological factors which act on the central nervous system (CNS) are given in the appropriate compartments.

shown by solid lines, is through the central nervous system "pathway" controlling activity. The combination of these driving forces, mediated and integrated through the central nervous system, determines the activity exhibited by the animal. This activity may result in changes in environmental and biological factors, as indicated by the dashed feedback loops in the model. For example, food supplies in the environment may be reduced by foraging, or courtship activities may cease following mating.

Environmental factors such as day length have been shown by numerous investigations (Aschoff et al. 1982; Erkinaro 1969; and others) to influence activity rhythms. Studies described above indicate strong effects of such factors as ambient temperature and snow cover (Bland 1977), food supply (Bland 1977; Fuller 1979), and breeding behavior (Archibald 1976; Maxson 1977) on activity of free-ranging animals. In addition, A. Sargeant (in preparation) found that Red Foxes at Cedar Creek switched from nocturnal feeding to diurnal feeding during a winter with very thick snow cover. With the snow thickness exceeding 100 cm, Gray Squirrels were forced to burrow to find food. As a result, the squirrels were highly vulnerable and foxes became day-active and captured squirrels at the snow-tunnel entrances. Garshelis (1983) reported that male Sea Otters (*Enhydra lutris*) in Prince William Sound, Alaska, switched from their normal diurnal pattern of feeding and territory defense to nocturnal feeding when they moved to areas of richer food supply. These switches occurred quickly and lasted until the males returned to their territories.

Ecological and ethological factors, such as courtship and care of young by Ruffed Grouse, care of young by Barred Owls, and house building by Muskrats, had marked influences on activity rhythms. Changes in activity patterns were not as rapid as in the case of male Sea Otters, but did occur within a few days.

Rapid changes in activity rhythms suggest that the causative mechanism is neural rather than biochemical. Therefore, the driving forces of environmental and biological factors are given equal weight in the model (Figure 9). However, their individual strengths, as indicated by the solid lines, are not considered as strong as the Zeitgeber.

Many of the environmental and behavioral factors are controlled in laboratory studies, i.e. environmental chambers maintain constant physical conditions and animals in individual cages do not breed, care for young or search for food. Therefore, these driving forces are eliminated and observed behavior is determined by the Zeitgeber through the endogenous mechanism.

The plasticity in activity pattern is a vital part of the adaptive mechanism which enables wild animals to survive in a changing environment. However, the endogenous component must also be considered vital in triggering the animal to become physiologically ready for activity (Dean and Aschoff 1982). In contrast, it appears that the regularity of rhythms of captive animals reflects endogenous control under stable environmental conditions. Researchers must be aware of these fundamental differences in the design of experiments and interpretation of results.

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