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CHRONOBIOLOGY AND AGROECOSYSTEMS

J. Figala and John R. Tester

Department of Environmental Protection,
Agricultural University, Prague, CS (J.F.) and
Department of Ecology and Behavioral Biology,
University of Minnesota, Minneapolis,
Minnesota 55455 (J.R.T.)

INTRODUCTION

In the last four decades agroecosystems in many parts of the world have changed rapidly. In brief, field units have become larger and "green island" habitats in many fields have been removed. Marshes, swamps and other wetlands have been drained and fields have been tilled with larger and heavier machinery. Use of chemicals as fertilizers and pesticides has increased markedly, resulting in increased chemical residuals in food products and in the soil. Changes in management practices and increased use of chemicals have caused interruptions in food chains and food webs, resulting in the disappearance of many plant and animal species. These changes in agroecosystems have contributed to destabilization and decrease in the diversity of native plants and animals.

We believe that diversity and stability could be increased markedly on many farms by reconstructing the landscape using sound ecological and physiological principles. This implies modification in the plant community and subsequently in the associated animal community. From the chronobiological point of view, reconstruction of any agroecosystem must be based upon knowledge of the temporal organization or timing of variables, e.g. foraging, as a function within the circadian (24-hour), infradian (seasonal or annual) and ultradian (< 24 hours) domains for each animal species.

The major contribution of chronobiology may well be in the area of explaining time as a niche factor in relation to either exploitation competition, where one species may reduce the availability of resources to other species (Levins, 1968), or interference competition, whereby one species may reduce the ability of other species to make use of a shared resource (Carothers and Jaksic, 1984).

MONITORING OF SELECTED ANIMAL SPECIES

Ducks

In Europe and North America, numerous species of dabbling ducks (Subfamily Anatinae) and diving ducks (Subfamily Nyrocinae) occur in wetlands in agroecosystems. Two species of dabbling ducks, mallards (Anas platyrhynchos) and gadwalls (Anas strepera), and two species of diving ducks, crested pochards (Aythya ferina) and tufted ducks (Aythya fuligula) were selected to examine interactions between species occupying the same habitat. All dabbling ducks were raised in a group indoors near C. Budejovice, CS (49 0'N, 14 30'E) until approximately one month of age, when they were placed outdoors in separate 3 x 6 m pens. Food was a granulated monodiet used for domestic ducks, available ad libitum in automatic feeding boxes. Water, maintained in basins .5 x .5 x 1 m, was changed every day or every other day, but at different times of the day. Feeding activity was recorded using a system of photo cells placed at the entrance of the feeding boxes (Figala et al., 1989). Food intake was analyzed in one hour intervals.

On April 1, an adult mallard drake was placed in the pen with the mallard hen. The first egg was laid on April 12th. A nest was built and incubation began May 1. On April 29th the drake was transferred to a separate, nearby pen so that visual and acoustical communication was possible. Incubation lasted for 35 days, when the hen abandoned her unfertile eggs (Figala et al., 1989). A similar procedure was followed with the crested pochard. The pair remained together until May 31st, but no eggs were laid.

Stoat (Weasel)

Food consumption and locomotor activity of a captive adult female stoat (Mustela erminea) were studied continuously for 11 months in Andechs, FRG (47 58'N, 11 30'E). The stoat was kept in a outdoor circular 12 x 2 m pen with a sand floor. The walls were opaque laminated glass to prevent disturbance from the outside and the top was covered with wire

The pen contained a sleeping box (30 x 30 x 15 cm) with two 7 cm aluminum tubes with one-way doors. One tube allowed entrance to the nest box and the other allowed exit. The time the stoat spent in the box was considered rest time and the time the animal was out of the box was considered activity time. Visual observations of the stoat confirmed these activity classifications.

Foraging was monitored by interruption of the beam of a photocell placed at the 5 cm diameter entrance to the feeding box (12 X 12 X 8 cm). The food, consisting of homogenized meat mixed with a raw egg and vitamins, was provided ad libitum and was replenished at different times of the day.

Gray Squirrels

Locomotor and feeding activity of captive gray squirrels (Sciurus carolinensis) were monitored both in North America and Europe (Figala and Tester, 1986). Activity of captive squirrels was monitored simultaneously by photocells on the feeding and sleeping boxes and by radio signals from transmitters on each animal.

Activity in free-ranging gray squirrels was recorded automatically on microfilm using radio telemetry. The rhythm of feeding activity was determined by applying the method reported by Müller and Schreiber (1967), in which the percent deviation of the months average value was calculated for one hour intervals (Figala et al., 1984).

Analysis

The time within the 24-hour cycle when the amount of feeding increased sufficiently to rise above the threshold line was selected as the onset of food intake. Similarly, the time when feeding fell below the threshold was selected as the time of cessation (Figala and Müller, 1972). Bimodal rhythms were characterized as bigeminus when the first peak was higher than the second, and as alternans when the second peak was higher (Aschoff, 1962).

FEEDING ACTIVITY PATTERN IN DUCKS

Seasonal changes in food intake by the drake mallard are shown in Fig. 1. Feeding activity by the drake and hen mallard (Fig. 2) appeared synchronized with sunrise, but not with sunset. The rhythm of feeding activity in the hen peaked during the day and total activity time was nearly constant throughout the 18-months of monitoring. The drake also fed primarily during the day, especially in the second year. However, during October and November of the first year of life, a night phase of feeding also occurred. The level of activity was slightly higher during night than during the day, especially in October.

The drake gadwall fed more during the night (Fig. 1) than the mallard. The daylight phase of feeding exhibited a morning peak synchronized by sunrise. The phase angle difference, which was similar to mallards, was nearly constant except in winter.

Reports on feeding activity of free-ranging gadwall from October to April show that over 60 percent of the feeding may occur at night (Paulus, 1984). From October to April, the time used for feeding increased from 44 percent to 77 percent (Paulus, 1984). Those results from free-ranging gadwalls correspond closely with our data on captive gadwalls.

Seasonal changes in food intake in crested pochards and tufted ducks are shown in Fig. 1. Rhythmicity in the feeding activity of crested pochards was synchronized by sunrise and sunset, with negative phase angle differences. Direct observations of free-ranging pochards during winter indicated the beginning of the night phase of feeding in the first half of night (Bauer and Glutz, 1968). The early morning peak occurred shortly before dawn. Similar results have been noted for the winter season, when daily onsets of feeding flight activity were correlated with very low light intensity (< 1 lux) (Galhoff at el., 1984).

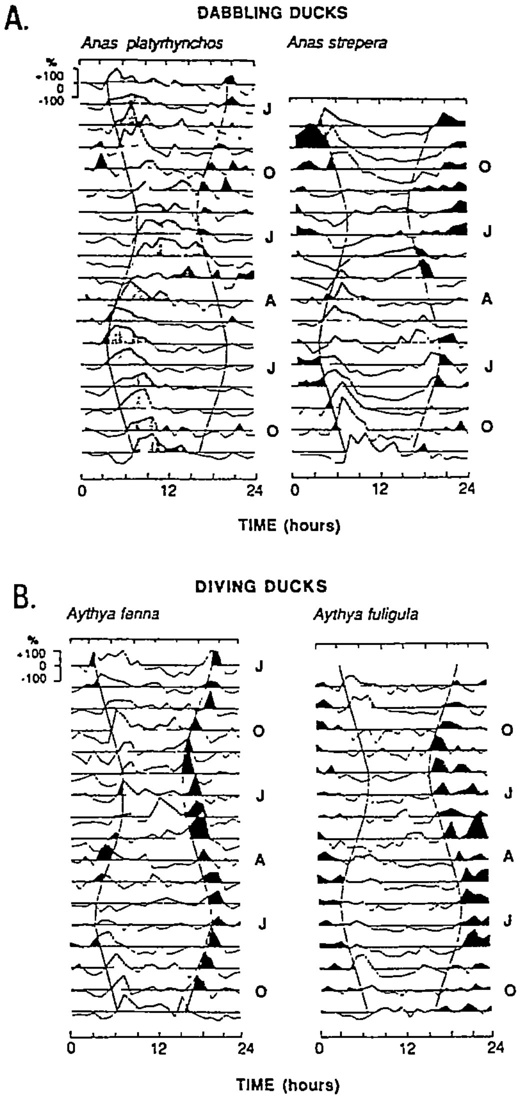

Figure 1. Seasonal changes in feeding activity of captive dabbling ducks (A) and diving ducks (B). For all figures, the horizontal curves show percent deviation from the monthly average for each hour and the curved vertical lines indicate sunrise and sunset. Black areas represent feeding activity higher than the monthly average threshold during the night; hatched areas during the day.

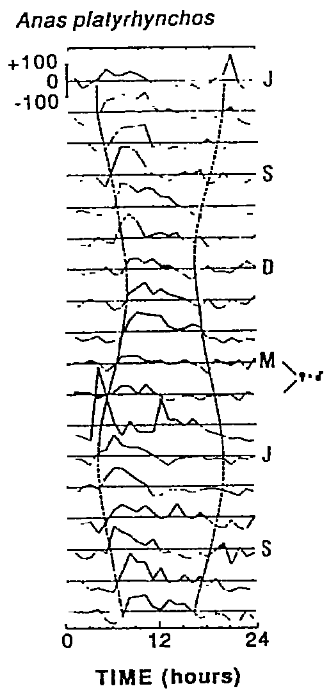

Figure 2. Monthly feeding activity of a captive female mallard. A male mallard was placed with the female during March and April. The shift to an ultradian rhythm during these months is probably related to courtship and breeding behavior. Incubation lasted until May 31.

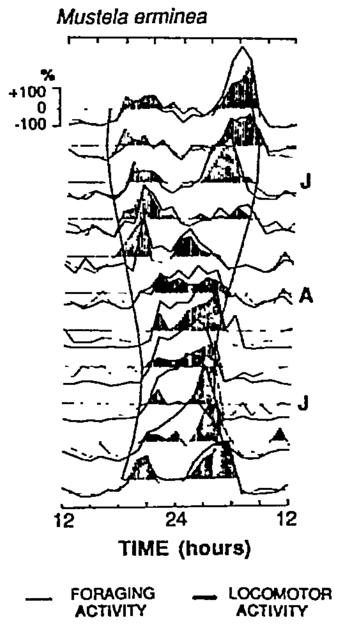

Figure 3. Seasonal changes in feeding and locomotor activity in a stoat.

The feeding activity of tufted ducks exhibited a night peak throughout most of the 16 months of monitoring. During October and November the feeding rhythm appeared to be ultradian.

Little information has been reported on the feeding activity of free-ranging tufted ducks. Food intake may be highest during daylight in summer (Folk, 1971) when the ducks appear to exhibit a bigeminus rhythm (Willi, 1970). Feeding during the night has been observed in October at the time of migration. Low levels of feeding were observed during daylight in September and October (Holzinger, 1977), but no data were collected on feeding activity during the night. In general, it appears that free-ranging tufted ducks commonly feed at night.

CHANGES IN LOCOMOTOR AND FEEDING ACTIVITY PATTERN AS A FUNCTION OF SEASON

Locomotor activity in a stoat occurred mainly during night hours throughout the 11-months of monitoring. A small amount of locomotor activity occurred during daylight (Fig. 3), as also observed in free-ranging stoats (Debrot and Mermov, 1983).

The most common feeding rhythm had the alternans pattern and occurred in summer, fall and the first half of winter. The typical alternans pattern was observed for locomotor activity from November through January, and again in May and September. A striking change in activity patterns for both locomotor and feeding occurred during February and March, when the bigeminus pattern became common. A unimodal pattern in locomotor activity began in April and continued through August.

Rhythms of locomotor and foraging activity were both synchronized by sunset and sunrise. The length of both activities followed the length of the night span and had the same pattern except in late spring and summer. From April through August, but especially during July and August, a tendency for a one-peak pattern of locomotor activity was shown in contrast to the alternans feeding activity pattern. It is quite possible that these different activity patterns are entrained by separate oscillators; one for feeding activities and the second for locomotor activities.

Rhythms of both activities show almost the same phase and pattern during fall and winter months. In late spring and summer, a time space for locomotor activity is available during which the animal could meet ecological or behavioral needs. In contrast, in winter and early spring when energy demands were high nearly all of the activity was related to feeding.

PHASE ANGLE DIFFERENCES BETWEEN LOCOMOTOR AND FEEDING ACTIVITY AS A FUNCTION OF SEASON

It is well known that there are seasonal changes in the relative influence of synchronizers on rhythms of activity (Aschoff, 1969; Hoffmann, 1969). The strongest Zeitgeber usually occurs at the time of the spring and fall equinox (Aschoff and Wever, 1962). The weakest Zeitgeber occurs during mid-summer and midwinter. Assuming that both locomotor and feeding oscillators have the same sensitivity to the LD cycle, they will maintain the same phase angle to sunrise and sunset. Further, the phase angle between the rhythms should remain stable throughout the year.

Gray squirrel data obtained in captivity using photocells on sleeping and feeding boxes are shown in (Fig. 4). All points represent the average of 4 animals (Figala and Tester, 1986). The phase angles between onset and end of locomotor and feeding activities show different seasonal patterns.

Similar seasonal differences were found in starlings (Sturnus vulgaris) by Gänshirt et al., (1984). However, in starlings the phase angle difference for onset was opposite to the phase angle observed in squirrels. Both species are day active. The additional influence of low winter temperatures on the activity rhythm in squirrels must also be considered (Belovsky and Slade, 1986).

The data from gray squirrels and the stoat presented above support the possibility of different levels of sensitivity in the locomotor and feeding oscillators.

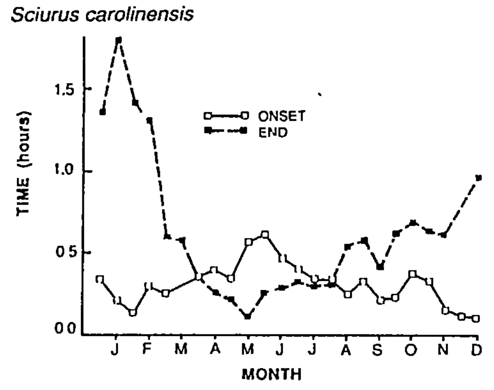

Figure 4. Seasonal changes in the phase angle difference between onsets and ends of nest box activity and feeding activity in a male and female grey squirrel held in the same pen. The onset curve indicates the time difference between onset of activity measured as the squirrel left the nest box and the 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.

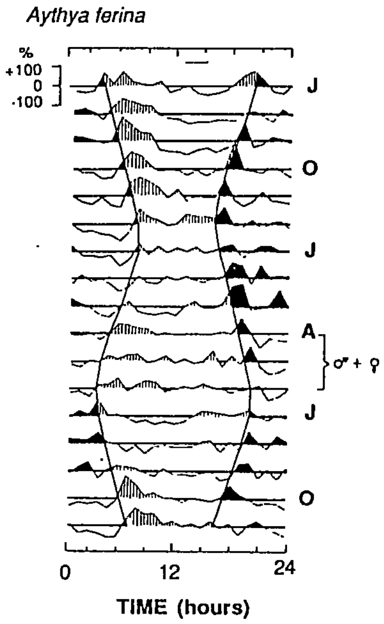

Figure 5. Monthly feeding activity of a captive female crested pochard. A male crested pochard was placed with the female from April through June. The shift to an ultradian rhythm in May and June is probably related to courtship and breeding behavior.

ULTRADIAN, CIRCADIAN AND INFRADIAN COMPONENTS

Ultradian rhythms in paired ducks

The synchronization of ultradian rhythms by social interactions has been reported for several vertebrate species (Regal and Connolly, 1980). However, ultradian rhythms have not been studied with respect to how changes in resting and activity may resynchronize physiological activities.

Feeding rhythms in paired mallards (Fig. 2) and paired crested pochards (Fig. 5) are characterized by short shifts of phase during the 24-hour cycle. Changes from circadian to ultradian activity could be caused by presence of the male, since female pochards kept alone in captivity did not exhibit this change. These results suggest that the changes shown by the pairs were related to courtship. Lesser scaup (Aythya affinis) have also been shown to increase their feeding activity after pair formation (Siegfried, 1974). The number of diving bouts was higher and a change in the phase of the feeding rhythm was observed.

Circadian

A number of circadian characteristics, especially those related to activity pattern, have been examined in this paper. Patterns of feeding and locomotor activity varied among unimodal, bigeminus and alternans. Phase angle differences, expressed as time between onset of activity (or peak of activity) and sunrise, or between cessation of activity and sunset, exhibited a wide range of both positive and negative values. Phase angle differences between feeding activity onset and locomotor activity onset were also highly variable.

DIVERSITY

Agroecosystems have the potential to support a high diversity of both plants and animals. The species discussed in this paper are representative of birds and mammals commonly present on farms in the northern hemisphere.

CONCLUSIONS

Locomotor and feeding rhythms of activity measured in captivity frequently have different characteristics than the same rhythms measured in free-ranging individuals. These differences are due to exogenous biotic and environmental factors. For example, an acorn surplus in fall prolonged the length of activity in gray squirrels and influenced phase angle differences (Figala and Tester, 1986). Changes from circadian to ultradian rhythms of feeding occurred as a result of courtship in two duck species. Other exogenous factors influencing activity rhythms are discussed in Tester and Figala (1989).

Different phases of feeding rhythms in some dabbling and diving ducks species have important ecological consequences for establishing the species in an appropriate time niche. This phenomenon has enabled species to compete successfully and to become established in existing communities (Brandl and Schmidtke, 1983).

The feeding oscillator, as reported by Gänshirt et al., (1984) and Subbaraj and Gwinner (1985), is probably sensitive to seasonally changing exogenous abiotic and biotic synchronizers. For example, the constant food resource for the captive stoat precludes the possible influence of differences in food availability. Therefore, the spontaneous change in activity pattern during February and March could be an endogenous conditioned overt rhythm related to a change in food resources in the natural environment (different prey or change of prey activity pattern) or to behavioral aspects of reproduction. The daily feeding rhythm may be set by the synchrony of both prey availability and the activity rhythm of the prey. Such activity may vary between environments and seasons (Belovsky and Slade, 1986).

Further, the time during which the forager is exposed to predators (Belovsky and Ritchie, 1989) and the activity rhythm of the predators (Masman et al., 1988) must also be considered. A predator depending on a single food resource would be expected to have its feeding rhythm synchronized with the locomotor rhythm of its prey, not only during the 24-hour cycle (Mikkola, 1970) but also throughout the year. Polyphagous predators would synchronize their feeding rhythms with the locomotor rhythms of the specific prey foraged during a specific season.

A large number of biotic and/or abiotic exogenous factors are known to influence bio-oscillators. Rusak (1981) suggests that the responsiveness of this oscillatory complex to environmental events may determine adaptive behavioral flexibility of many vertebrates.

Detailed development of time-energy budgets requires information on many factors, including age, sex and social status of the organisms, as well as seasonal differences in habitat (Moen, 1973). Knowledge of annual, seasonal and daily rhythms of feeding and locomotion measured simultaneously in captivity and in free-ranging animals is necessary to elucidate the structure and function of food chains and webs. This contribution of chronobiology will further our understanding of the niche of selected species in agricultural ecosystems.

AGRICULTURAL APPLICATIONS, IMPLICATIONS, AND NEW DIRECTIONS

The reintroduction of habitat components for the purpose of stabilizing or altering agroecosystems must be based on knowledge of food chains and webs. Patterns of activity of both producers and consumers (predators and prey) during daily and annual cycles are of special concern. Application of knowledge of chronobiological overt rhythms could significantly shorten time of succession and lead to more rapid establishment of diverse and stable agroecosystems.

SUMMARY

Influences of seasonal changes on the circadian system were observed in studies of feeding activity in four species of ducks and of feeding and locomotor activity in two species of mammals kept in captivity in the natural LD cycle. Feeding and locomotor oscillators had different sensitivities to exogenous synchronizers. Changes from a circadian to an ultradian feeding rhythm occurred as a result of courtship and breeding behavior in two duck species. Different phases of feeding rhythms in ducks were shown to have important ecological consequences for

establishing the species in appropriate time niches in agricultural wetlands.

Detailed study of annual, seasonal and daily rhythms of feeding and locomotion measured simultaneously in captivity and in free-ranging animals is necessary to elucidate the structure and function of food chains and webs. Activity rhythms of both producers and consumers (predators and prey) during daily and annual cycles is of special concern. This contribution of chronobiology will further our understanding of the niche of selected species in agricultural ecosystems.

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