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EFFECTS OF BIOLOGICAL AND ENVIRONMENTAL FACTORS ON ACTIVITY RHYTHMS OF WILD ANIMALS

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INTRODUCTION

Activity rhythms of vertebrates, and the biological clocks which control these rhythms, have been of great interest to both laboratory and field biologists. These rhythms have proven to be persistent under a wide variety of experimental conditions. The presence of endogenous oscillators controlling such rhythms is the subject of active research (Edmunds, 1988). In spite of the presence of such oscillators and the exceptional control which they exert on activity under controlled conditions, activity of wild animals in the natural environment does not exhibit high precision nor does it maintain the same pattern throughout the year (Tester, 1987). Pohl (1982) reported that this variability in activity rhythms is probably related to special ecological requirements of the species. The variability is manifested in terms of the time of onset and end of activity and as a result, changes in such circadian characteristics as period and phase relationships (Figala et al., 1984; Figala and Tester, 1985).

Temporal information is provided to the animal through the length and direction of change of the photoperiod. Thus, animals determine time of year and anticipate changes in the environment which enable them to initiate such activities as food storage, migration, and reproduction to enhance survival and the production of offspring. Additional information may be provided by such biological and physical parameters as nutritional state, social status, stress, food availability, temperature or humidity. Recent studies suggest that multiple sources of biotic and environmental information interact with hormonal signals to produce a particular behavior (Moore and Marler, 1988).

Development of radio telemetry techniques for monitoring activity of unrestrained animals living in their natural environment has made it possible to obtain long-term data on rhythms of many species. These data reveal striking changes in seasonal levels of activity and great plasticity in circadian aspects, suggesting that constancy of rhythms is rare in free-ranging animals. This paper reviews information on variability in activity rhythms as a result of such biological factors as courtship, care of young, time since last food intake, and aspects of food storage and fat reserves, and environmental factors such as photoperiod, weather, food supply, and disturbance.

All of the species mentioned in this review may occur in and be a part of agricultural ecosystems. However, none should be considered as domesticated.

METHODS

Most of the research reported in this review was conducted using radio telemetry. Study animals were fitted with radio transmitters broadcasting on a unique frequency. The transmitters were designed with the broadcasting antenna in the form of a collar or as an integral part of a back or breast harness. Radio signals from individual animals were monitored manually or by an automatic tracking system which determined location and activity at specified time intervals. Field observations of radio-marked animals confirmed that recorded data corresponded to activity and rest (Tester, 1971). Data were recorded automatically on microfilm or tape, or manually by observers monitoring audio signals from a receiver. Analyses programs were designed to indicate daily patterns of rest and activity for an individual animal and to summarize rest and activity over specified time periods, such as weekly or monthly (Figala et al., 1984).

BIOLOGICAL FACTORS INFLUENCING ACTIVITY RHYTHMS

Courtship

Ruffed grouse (Bonasa umbellus) studied year around at the Cedar Creek Natural History Area in Minnesota are normally diurnal and both sexes show a bimodal wave form with activity peaks near sunrise and sunset (Tester, 1987), similar to many other birds (Aschoff, 1967). Beginning in early April and extending into July, male grouse carry on their courtship display of drumming. Drumming may occur during either night or day, with the pattern changing as the season progresses. Archibald (1976) showed that during the peak of the courtship season, drumming occurred throughout the 24 hour day except for brief spans near sunrise and sunset when the male grouse were feeding. Combining the minutes spent drumming, feeding and preening indicate that male grouse are active nearly 100 percent of the 24 hours during the peak of the breeding season (Archibald, 1976). In contrast, activity during other seasons of the year indicates a diurnal pattern with distinct crepuscular peaks.

Care of Young

Prior to egg-laying, female ruffed grouse at Cedar Creek Natural History Area exhibited a typical bimodal activity pattern (Maxson, 1977). During incubation hens were on the nest for nearly the entire 24-hour period. 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. Maxson (1977) believed that this delay of onset and early cessation was related to brooding behavior by the hen. Brooding during the cool morning and evening hours reduced the exposure of chicks, helping them to maintain their body temperature.

In studies of barred owls (Strix varia) at Cedar Creek, Fuller (1979) observed that non-breeding owls exhibited nocturnal activity patterns with peaks of activity occurring just after sunset and before sunrise. However, when the female was incubating, the male increased his length of activity time, presumably to obtain food for the female. Fuller (1979) indicated that the marked increase in activity of both the male and female following hatching was the result of increased hunting for food for the growing young.

The demands of caring for young were considered to be responsible for seasonal differences in activity among different sex and age groups of black bears (Ursus americanus) studied in southeastern United States by Garshelis and Pelton (1980). Females with cubs were more active than the other sex and age categories in spring and fall.

Nutritional Status

Activity patterns of goshawks (Accipiter gentilis) studied in Sweden revealed that activity increased as the level of hunger increased. Widen (1982) found that the ratio of activity to rest increased significantly on days following the time of last food intake. Further, the percent of total time active per day increased markedly as hunger level increased.

Food Storage and Fat Reserves

Gray squirrels (Sciurus carolinensis) and muskrats (Ondatra zibethicus) studied at Cedar Creek both showed marked seasonal changes in activity patterns (Tester, 1987). A striking increase in activity of gray squirrels in September and October was related to the collection and storage of food for winter. Similarly, high levels of activity of muskrats in late summer and early fall were believed to be related to the time required to build lodges and store food for winter. After ice formed, preventing further lodge construction and food storage, the minutes of activity per 24 hours were reduced by about half.

ENVIRONMENTAL FACTORS INFLUENCING ACTIVITY RHYTHMS

Weather

The influence of weather on activity rhythms may be manifested in many ways, including energetics of maintaining body temperature, initiation of breeding, availability of food, and change in the environment such as formation of ice on lakes and rivers. Gray squirrels at Cedar Creek showed a marked reduction in activity in winter (Tester, 1987; Figala and Tester, 1986). These squirrels were under a strong influence of cold temperatures in

January and February. During these months they spent their resting time in tree cavities or in nests made of dry leaves. Protection provided by these nests was probably necessary to maintain their critical physiological temperature. The squirrels were active only during the time of day when ambient temperatures were at maximum.

Badgers (Meles meles) in Britain also exhibited a shorter alpha in winter (Harris, 1982). However, no explanation for this change in activity rhythm was given.

The seasonal effects of temperature on the activity of black bears in southeastern North America revealed marked seasonal changes. In spring, increases in level of activity were associated with increases in ambient temperature until the temperature reached approximately 20°C, where activity appeared to stabilize. In summer, activity also increased as temperature increased, until about 23°C when activity declined. In fall, activity increased during warmer periods and decreased when the temperatures exceeded 20°C (Garshelis and Pelton, 1980).

The effect of freezing of lakes can best be illustrated by data on muskrats at Cedar Creek (Tester, 1987). From July 1969 through February 1970, the number of activity periods per 24 hours varied from two to four. In July and 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 at the time of freeze-up of lakes and streams. The day active periods were eliminated and muskrats became essentially nocturnal with the total amount of activity per 24 hours being reduced to approximately half that exhibited in late summer.

Food Supply

The activity rhythm for a breeding male woodcock (Scolopax rusticola) monitored in Britain changed markedly from April to May (Hirons and Owen, 1982). In early spring, woodcock spent the night on pasture where they were active and presumably feeding on worms. They were inactive for most of the day, which was spent in forest. Within one month, as nights became shorter and the grass longer and the ground on pasture fields harder, the birds switched to feeding in the forest during the day and resting at night.

Switches from nocturnal to diurnal feeding during winter in response to a changing food supply were reported for red fox (Vulpes fulva) by Sargeant (in preparation). A switch from a diurnal pattern of feeding to nocturnal feeding was reported for sea otters (Enhydra lutris) in Alaska by Garshelis (1983) when the otters moved to areas of richer food supply.

Seasonal differences in activity rhythms reported for black bears by Garshelis and Pelton (1980) were reported to be due in part to the abundance and nature of the food supply. Bears lost weight during spring, possibly due to the unavailability of nutritious foods or to inability to digest available foods efficiently after winter dormancy. The low energy and poor digestibility of the high-fiber grasses consumed in the spring resulted in a diet with low nutritional value, which may have restricted the amount of energy bears could expend during mid-day. The crepuscular activity pattern exhibited in the spring could reflect an optimal foraging strategy for bears on a low energy diet (Garshelis and Pelton, 1980). During summer bears fed on berries and fruits. The small size and dispersion of this food may have required foraging to continue throughout the middle of the day. Such activity would be possible with a diet high in caloric value. During fall, increased foraging was necessary to increase body fat in preparation for winter dormancy.

Disturbance

In a comparison of the activity rhythms of badgers living in urban and rural sites, Harris (1982) observed that rural badgers had longer active spans per 24 hours. Emergence from the sett was delayed about an hour compared to badgers in the rural study area, but the time of return to the sett was approximately similar. No explanation is given for this difference, but it might be assumed that the disturbance caused by human activities in the urban area resulted in the later initiation of activity.

A more striking example of the effect of disturbance on activity rhythms is illustrated by wild pigs (Sus scrofa) in Europe and Asia. Wild pigs in zoos or in large fenced areas, exposed to much human activity, appeared to have lost their natural shyness and were day active. In

Siberia, Bromlej (1964) observed that Sus scrofa ussuricus was day active, and attributed this to the lack of human disturbance in this region. In contrast, Gundlach (1968) and Briederman (1971) reported that the main peaks of activity in Germany, where the pigs were exposed to much human activity, occurred before dawn and after dusk. Both authors suggested the influence of a "command vector" of human activity which serves as a social interspecific synchronizer. Somewhat similar changes in phase of activity as a result of disturbance by humans have been reported for roe deer (Capreolus europeus) by Bubenik and Bubenikova (1967), crocodiles (Crocodilus niloticus) by Corbet (1970) and pine marten (Martes foina) by Löhrl (1972).

ULTRADIAN, CIRCADIAN AND INFRADIAN COMPONENTS

Untradian

Ultradian oscillations appear to persist in some of the variables monitored in muskrats at Cedar Creek (Tester, 1987) as well as in a number of other small mammals (Gerkema and Daan, 1985). Rate of digestion of food is a potential underlying factor for ultradian rhythms, with smaller organisms being required to alternate feeding activity with periods of digestion more frequently than larger animals. Similarly, an ultradian rhythm would be exhibited by a song bird gathering food for its young, feeding the young, and then gathering food again. However, Gerkema and Daan (1985) believe that the control of the phase of some ultradian rhythms is related to social synchrony.

Ultradian oscillations in the range of 30 to 240 minutes have been singled out as a special group found in many plants and animals (Koukkari, Bingham and Duke, 1987). Observations on muskrats, reported above, and on kestrels (Falco sparverius) (Nunn, 1986) support this conclusion.

Circadian

All studies reviewed were conducted under the natural LD cycle and the activity patterns are referred to as daily rhythms. Circadian rhythms have been observed in many wild species under laboratory conditions. It is important to note that masking caused by biological and environmental factors has been reported to influence rhythms under a wide range of experimental conditions (Minors and Waterhouse, 1989; Page, 1989). The biological and environmental factors discussed in this review can all be considered as potential masking factors.

Infradian

Variable rhythms that display responses to seasonal changes, as reviewed in this paper, might be classified as infradian. For example, courtship, estrous, and care of young are seasonal in timing for many species. Similarly, reduction in total activity due to cold temperature by organisms living in high latitudes or the development of migratory restlessness in birds are seasonal responses to environmental change. Many of these activity patterns are believed to be endogenous and are referred to as circannual rhythms (Gwinner, 1986).

DIVERSITY

This review of investigations of rhythms in free-ranging birds and mammals suggests that wild animals have the ability to quickly adapt their activity patterns to rapid changes in biological and environmental conditions. We believe that such adaptations are widespread in all groups of animals, arising in the context of evolutionary fitness and survival in the complex natural world.

AGRICULTURAL APPLICATIONS, IMPLICATIONS, AND NEW DIRECTIONS

While the species considered in this review may have little direct significance to agriculture, the concept of plasticity in activity rhythms in organisms living in the natural environment is highly relevant. Livestock maintained under ranch conditions may be expected to exhibit activity rhythms quite different from rhythms of livestock maintained in individual cages or pens. These differences may be significant in relation to aspects of management such as time of feeding, forage supplements, exercise and breeding.

SUMMARY

This paper reviews information on the effects of biological and environmental factors on activity rhythms of wild animals monitored by radio telemetry. Variations in radio signals received from free-ranging animals are used to determine the pattern of activity and rest. Telemetry is especially effective for obtaining activity data from wild animals at night and from those living in dense vegetation or underground.

Biological factors such as breeding behavior, care of young, time of last eating, and food storage cause changes in daily activity patterns. Similarly, environmental factors such as temperature, snow cover, food supply and disturbance caused by humans in an urban setting also cause changes in daily activity patterns. The observed modifications of activity rhythms show that controlling mechanisms allow wild animals to quickly respond to changing biological and environmental factors.

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