

Activity time in the flying squirrel, *Pteromys volans*, in central Finland

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Receipt of Ms. 10. 9. 1979

Abstract

Studied the activity time (time spent outside the nesthole) of the flying squirrel, *Pteromys volans*, in central Finland. The recording of activity was performed in natural conditions with wild animals by an automatic system consisting of an electrical clock, a capacitive approach switch, a ciné camera, and a flash unit. The recording continued for three and half years in the main study nest and shorter periods in two other nests.

Five types of activity patterns were found. These and individual and between-year variations in activity time were analyzed using an ecological approach. The total activity time did not follow strictly the length of the night. The male was nocturnal, while lactating female and outdoor active young had in summer also a diurnal component of activity. This was caused by the increased energy demand due to reproduction. From September to April the nocturnal activity was split into two components, which were maximally seven hours apart. Both sexes had an aberrant pattern of activity in spring when displaying.

The ecology of diurnal red squirrel, *Sciurus vulgaris*, and non-obligatorily nocturnal flying squirrel is compared.

Introduction

Circadian activity patterns, especially those of birds and mammals, have been of great interest recently. All mammals and birds studied so far show seasonal and/or latitudinal variations in parameters characterizing circadian activity rhythms. Endogenous and exogenous factors are known to affect the rhythmic behaviour of animals, but the roles and mechanisms of these remain unclear (ASCHOFF 1960, 1969; DAAN and ASCHOFF 1975; BROWN 1976; EDMUNDS 1976).

Based on extensive data gathered so far, many theories concerning the timing and duration of activity periods have constructed since ASCHOFF's and WEVER's (1962) synthesis. A mathematical approach, which assumes the animals respond to the cues from the periodic environment like machines, has revealed some regular features (e.g. WEVER 1962–1964).

A vast majority of the studies of animal activity patterns have been carried out in laboratories, where the possibility of controlling and manipulating the periodic environment (e.g. the proportion of light (L) and dark (D) periods as well as light intensity) enables an experimental approach, which has proved very fruitful in testing hypotheses and developing theories (DECOURSEY 1961; KRAMM 1975; KAVANAU 1976).

Many studies have also been performed in natural light cycles in order to reveal the normal activity patterns of the species concerned. If, however, the animals are kept in captivity, the results and conclusions derived from this kind of experiments are questionable even if natural ambient temperatures are maintained. As a rule the test animals are provided with an excess of food and water, which is seldom the case in the nature. In addition, the animals are usually caged separately to make the interpretation of the data easier. Individual caging pre-

vents the animals from performing many of their natural activities including normal movements, territorial behaviour and social activities in general.

Field studies of mammalian activity patterns encounter many practical difficulties (e.g. LAUFENS 1969, 1973), but only such studies can give a realistic picture of the activity patterns and reveal all factors affecting it. Recent rapid technological developments, e.g. sophisticated telemetry systems, have brought solutions to many of the methodological problems.

The aim of this study was to show the observed seasonal, between-year and individual variations in the activity time of a rodent, *Pteromys volans*, can be explained more soundly by using an ecological approach, than by merely trying to fit the data to different oscillation models. In earlier papers we have described general activity patterns (HOKKANEN et al. 1977) and development of outdoor activity in young flying squirrels (TÖRMÄLÄ et al. 1978).

Material and methods

The eastern flying squirrel, *P. volans*, which is split into several subspecies, has a very wide distribution in Asia. Outside the USSR, Finland is the only European country where it occurs. Due to its recent decline in abundance in Finland, it has been classified as an endangered species (BORG and MALMSTRÖM 1975).

This study was made with wild animals in natural conditions. Most of the data were collected using an automatic recording system consisting of an electrical clock attached above the entrance of the nest-hole, a capacitive approach switch sensitive to objects approaching at a distance of 3 cm, a ciné camera, and a slash unit. Each record (single super 8-mm colour shot) provided date and time of day when a squirrel came out of or went into the nest. In many cases recognition of individual squirrels occupying the same nest was possible because of slight differences in appearance.

The main study nest was situated in the rural community of Muurame (62°10' N, 25°30' E) in central Finland (see HOKKANEN et al. 1977). Recording was started in November 1974 and continued until March 1978. During this period the main study nest was occupied by at least seven individuals, one of which was an old female who stayed in the nest from the beginning of the study until August 1976.

Activity time here, as well as in our other reports, means the actual time that the squirrels spent outside the nest-hole. This approach is the most convenient for hole-dwelling animals and has previously been widely used (e.g. LAUFENS 1969, 1973, 1975). As KRAMM (1975) points out when the animals are inside the nest, they may be involved in a variety of activities including nursing the young and repairing the nest.

For data processing, the calendar year was divided into 37 periods, and means for these ten-day periods were used in analyses of the data and in figures if not otherwise stated. Outdoor visits lasting less than three minutes were not included in the calculations.

Since there were only negligible differences in the activity times of flying squirrels living in the same nest outside the breeding season their mean activity times were used in calculating means for ten-day periods. In summer the activity times of the female and its young were calculated separately.

Results and discussion

The activity patterns of the American flying squirrel, *Glaucomys volans*, are well known from the extensive studies by DECOURSEY (1959, 1960, 1961, 1972) and DAAN and ASCHOFF (1975). According to these authors, this species, which is taxonomically and ecologically close to *Pteromys volans*, is highly nocturnal, both in its natural habitat and in a variety of artificial LD schedules in the laboratory. OGNEV (1966) reports some cases of diurnal activity in *Pteromys* but regards them to be exceptional.

We could distinguish five types of activity patterns in *Pteromys* (Fig. 1). Type 4 was not mentioned in our earlier report based on fewer observations (HOKKANEN et al. 1977). The most surprising phenomenon was the simultaneous occurrence of nocturnal and diurnal components of activity in the main study nest during the summers of 1975 and 1976 but not in 1977.

On the basis of the records for 1975 we put forward a hypothesis that this exceptional type of activity was a response by the pregnant and lactating female to the increased energy de-

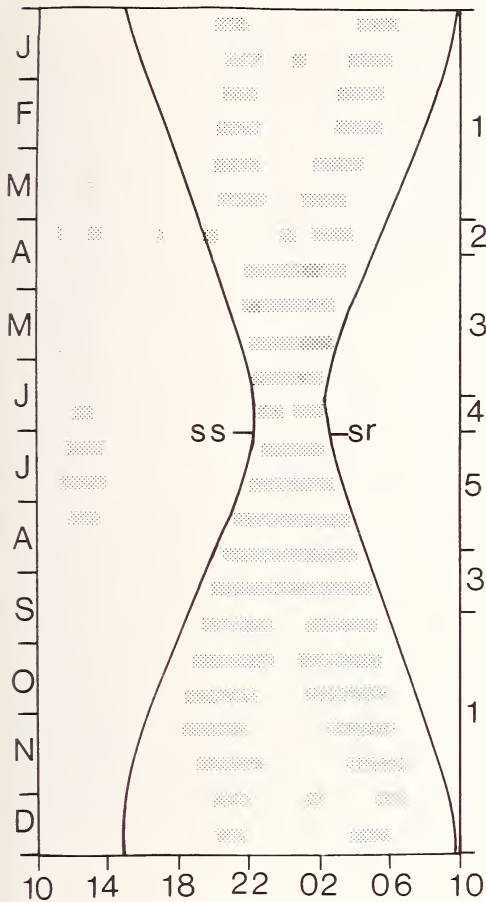


Fig. 1. Activity types of the flying squirrel in central Finland. The figure is a generalized model based on the whole material. Type 1: Nocturnal bimodal (occasionally trimodal), Type 2: Aberrant pattern during display, Type 3: Nocturnal unimodal, Type 4: Nocturnal bimodal-diurnal unimodal, in lactating females before the young are active outdoors, Type 5: Nocturnal unimodal-diurnal unimodal, in lactating females and young when the young are active outdoors. The male lack the diurnal component of activity and it is unimodally nocturnal (Type 3) also in summer. ss is time of sunset, sr is time of sunrise

mand, which could not be met during the short northern nights (HOKKANEN et al. 1977). According to KACZMARSKI (1966), the energy demand of a pregnant and lactating bank vole, *Clethrionomys glareolus*, is increased by an average of 58% compared to a female without young. Energy demand is markedly greater during lactation than during pregnancy (TROJAN and WOJCIECHOWSKI 1967; MYRCHA et al. 1969).

According to our field observations, during outdoor activity the female flying squirrels were almost exclusively engaged in browsing the leaves of *Alnus incana* and to lesser extent *Populus tremula* around the main study nest in the summer time, and we assume a high correlation between activity time and energy intake during this period.

The main study nest was occupied in the summer of 1975 by an old female and three young, in 1976 by the same female and two young and in 1977 by a solitary male. In 1976 the young were born approximately one month later than in 1975, judging from the dates of their first emergence outside the nest. The peak activity time in the female occurred in 1976 about one month later than in 1975 and corresponded to the difference in the time of birth of the young (Figs. 2 and 3). The shape of the curves describing the activity times during the summer is strikingly similar in both years despite the different timing. In 1977 the male was strictly nocturnal in the summer and its activity time correlated ($r = .98^{***}$) with the length of the night (defined as the time between sunset and sunrise).

The total activity time of the female for two ten-day periods preceding and for four following the first emergence of the young was 371h in 1975 and 350h in 1976. These values correspond to 6.19 and 5.83h/day respectively. The slightly smaller value in 1976 may be due to the smaller clutch size (2 vs. 3). The activity of the female was 60% higher in 1975 than that of the male in 1977 during the same period (cf. KACZMARSKI 1966). Outside the breeding season we could not observe significant differences between the activity times of the male and the female.

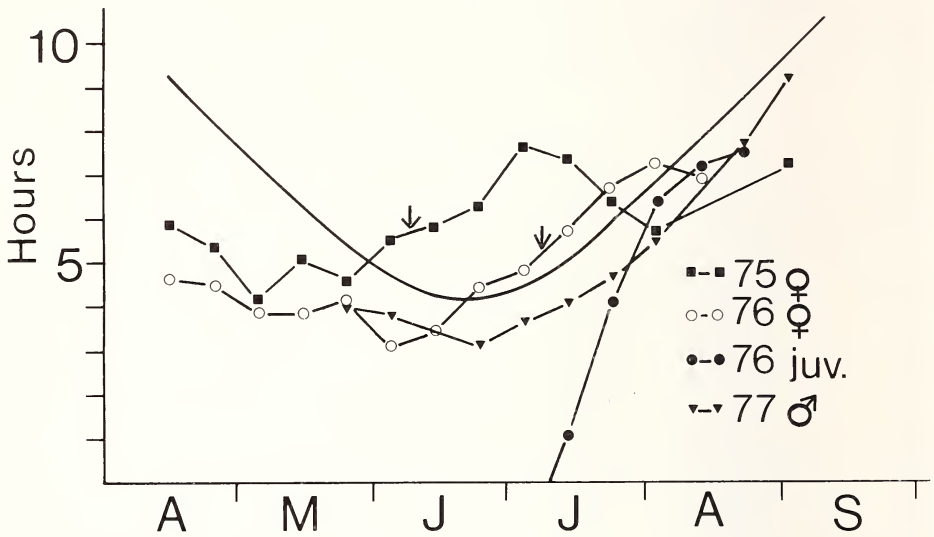


Fig. 2. Total activity time in a female (1975 and 1976), a male (1977) and young (1976 juv.) flying squirrels. Arrows indicate the time of the first emergence of the young outside the nest. The solid line indicates length of the night

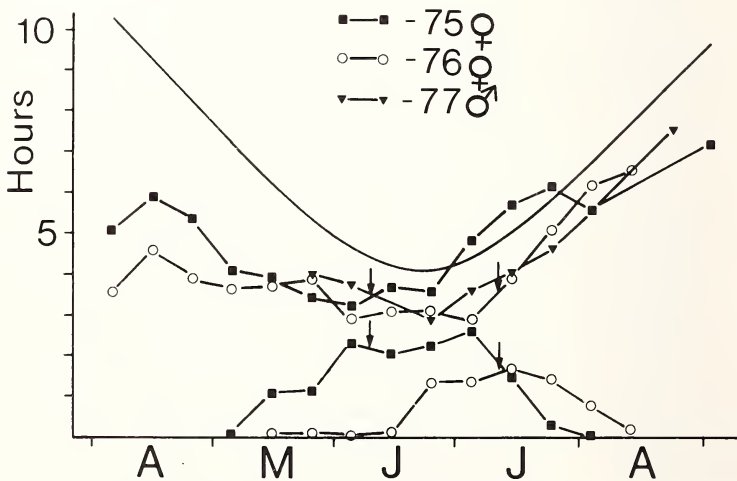


Fig. 3. Nocturnal (upper curves) and diurnal (lower curves) components of activity time in a female and a male flying squirrel. Arrows indicate the first emergence of the young outside the nest. The solid line indicates length of the night

Both in 1975 and 1976 the activity (and browsing) time for the female reached a maximum at the end of the lactation period (Fig. 2), agreeing with the results of e.g. KACZMARSKI (1966). The length of lactation period is not known, but when the young first emerged from the nest they were barely halfgrown. During their outdoor active lives they were nursed about 35 days (TÖRMÄLÄ et al. 1978).

One may ask why the activity time of reproducing female was split into nocturnal and diurnal components. During periods of high energy demand it is more economical to feed twice during the 24 h period at intervals of about 12 hours than to extend the nocturnal activity (feeding) time. As a rule the diurnal activity period was shorter than the nocturnal one. On June 19–28, 1975 the daytime activity was maximum (43% of the total activity time). In addition, the capacity of the stomach sets a limit for maximal energy (leaves) intake at a single feeding.

The nocturnal component of outdoor activity was divided into two components in lactating female before the young started to move outside the nest (Type 4 in Fig. 1, see also Fig. 4). At that time the female left the nest three times a day. At the corresponding time the male had nocturnal unimodal type (3) of activity. The return of females to nest sites to lactate has been observed previously in the Natterer's bat, *Myotis nattereri*, by LAUFENS (1973). After nursing the young, the female bats also went out to catch food for the rest of the night.

The diurnal component of activity time during the breeding season has also been observed in predatory mink, *Mustela vison*, (females but not males) in Sweden (GERELL 1969) and in the pygmy owl, *Glaucidium passerinum*, in Finland (MIKKOLA 1970). It is possible that the phenomenon occurs only in high latitudes where the nights are short or lack during the breeding season.

According to GÓRECKI (1977), it is impossible for a female of the common hamster, *Cricetus cricetus*, or other relatively large rodent species with several young to supply all the energy required for maintenance and growth by lactation. The flying squirrels also started to browse outside the nest when barely halfgrown, and their activity time reached that of the female in about 35 days (Fig. 2 and TÖRMÄLÄ et al. 1978). We suggested earlier that the curve

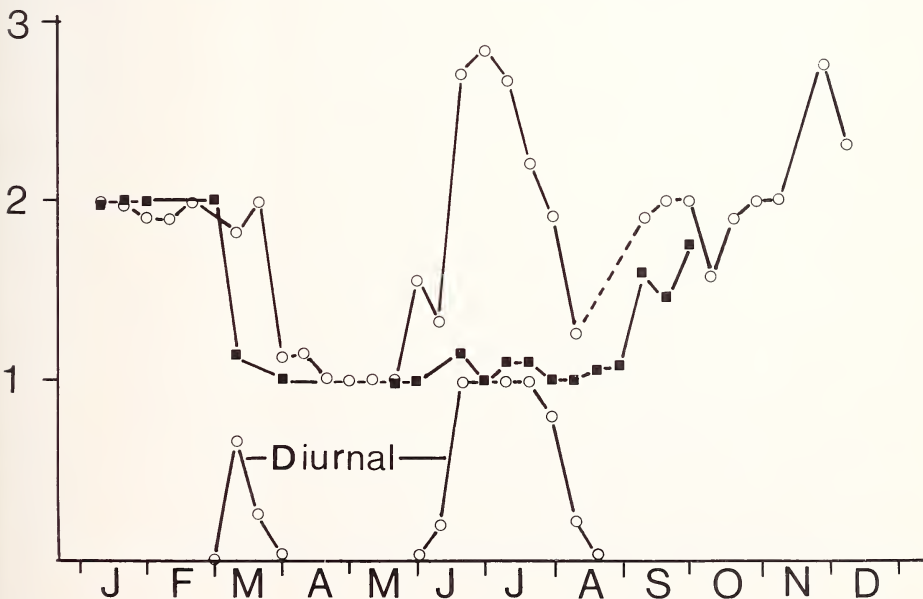


Fig. 4. Number of total and diurnal activity periods per 24 h in a male (squares) and a female (circles) flying squirrel

representing the outdoor activity time of the young as percentage of that of the female is similar or at least proportional to a curve describing the change in proportion of milk and leaves in the nutrition of the young flying squirrels.

During the last days when the female and two young shared the common nest in 1976, the activity time of the young slightly exceeded that of the female. At this time lactation had ceased or was at least negligible, and the energy demand of the growing young was probably greater than that of the old female.

The flying squirrels had a nocturnal component of activity throughout the year (Fig. 1). A positive correlation ($r = .36^{**}$ d. f. = 68) existed between the length of night and the nocturnal activity time. A linear regression model, however, explained only 13.2% of the seasonal variation in activity time. Thus in contrast to many earlier results on nocturnal rodents (e. g. DECOURSEY 1972; DAAN and ASCHOFF 1975), the nocturnal activity time did not follow strictly the length of the night (Fig. 5). This may be partly due to differences in methods of data interpretation. We did not use the time between first and last signs of nocturnal activity but the actual time the squirrels spent outside the nest. For example, in December 1976 the 'activity-end-minus-activity-onset method' (DAAN and ASCHOFF 1975) would give 11.24 hours activity time, while our method gives only 4.40 hours, since the squirrel spent 6.84 hours around midnight in the nest.

The nocturnal activity time exceeded the length of the night only in the summer of 1975, when the female bred early. The total activity time differs from the nocturnal activity time (Fig. 5) only during display and in summer in reproducing females (Figs. 1–3).

The nocturnal pattern of activity was unimodal (Type 3) in male from April to September, while the female had a bimodal pattern at the beginning of lactation (Type 4). During the winter half of the year the nocturnal activity was more or less bimodal in both sexes (Figs. 1, 4 and 6). In midwinter the activity was occasionally split into three components (Figs. 1 and 4). The resting time between active periods during the night was about seven hours maximum in midwinter (Fig. 6).

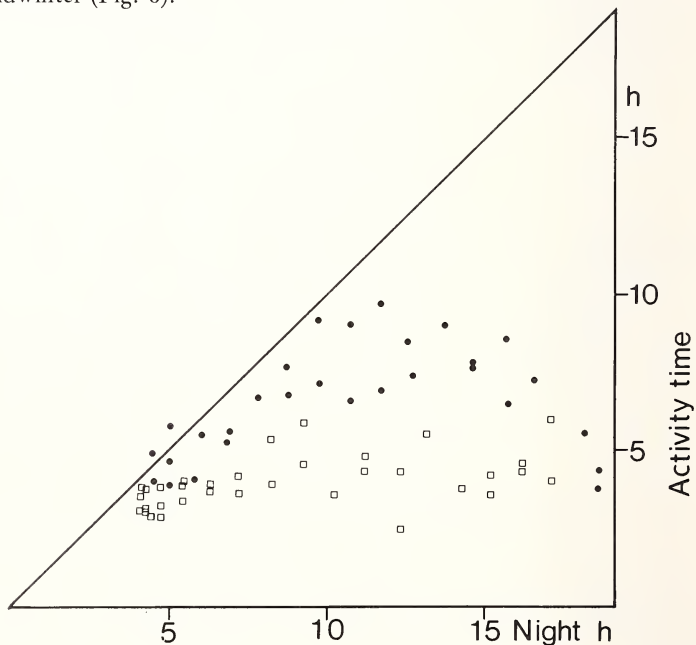


Fig. 5. Nocturnal activity time in flying squirrels in relation to the length of the night. Squares refer to spring (January–June) and dots to autumn (July–December) halves of the year

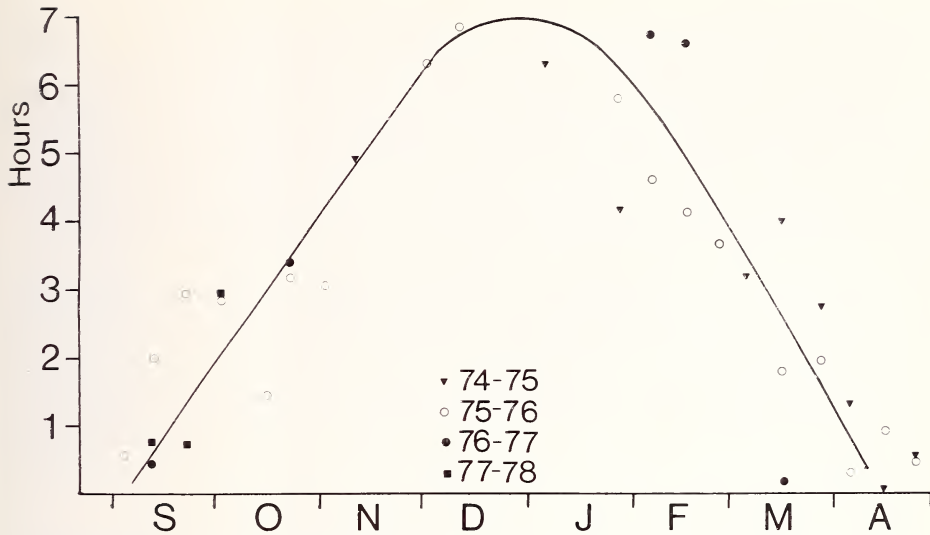


Fig. 6. Resting time between the first and second (occasionally third) activity periods during nocturnal bimodal (trimodal) type of activity. Occupation of the main study nest during winter period: 1974–75 a male and a female, 1974–75 a female whole winter and a male until November, 1976–77 the two young born in summer 1976, and 1977–78 1–2 (mainly 2) individuals

The feeding periods interrupted by a resting interval are energetically more useful than one longer feeding period around midnight. The feeding habits of the flying squirrels are not well known. According to SIIVONEN (1972) and SKAREN (1978), the main winter foods are the catkins of *Alnus* spp. and *Betula* spp. Flying squirrels store these in hollow trees and nest boxes. Of the two components of nocturnal activity the one toward morning was generally longer. The proportion of this morning component (ten-day means) varied from 50.6 to 69.2% ($\bar{x} = 58.3\%$) of the total nocturnal activity. One possible explanation for this may be the gathering of energy for the long resting period. The flying squirrel does not actually gather food into the hole where it spends the inactive period (daytime). The bimodality of activity patterns has been observed in many species (ASCHOFF 1966), e.g. in the diurnal red squirrel, *Sciurus vulgaris* (ZWAHLEN 1975).

At equal photoperiod (length of day) the nocturnal activity time was longer in the autumn than during the spring half of the year (Fig. 5, $t = 7.51^{***}$, d. f. = 14, paired t-test for pooled data). The same was observed in the golden hamster, *Mesocricetus auratus*, and in the American flying squirrel, *Glaucomys volans* (DAAN and ASCHOFF 1975), but the difference was not as clear as in our material. The reverse has been found in most birds studied. DAAN and ASCHOFF (1975) propose that this is a result of endocrine influence connected with the reproductive state in birds. Because the situation is reversed, the explanation is not valid for e.g. the flying squirrel. One possible ecological explanation for the high autumn activity in the flying squirrel may be the collecting of food for storage, and in addition, repairing and insulating the nest for winter. Due to practical difficulties in studying the species during dark autumn nights, we know little about the time required to collect food for winter storage. Our recording method, however, provided useful information about autumn nest building. Both in 1975 and 1976 lichen (*Usnea* sp.) was first carried into nest in early September and then more intensively in late October. Both sexes carried lichen into the nest-hole, maximally ten times per night.

Figs. 2, 3, 5 and 6 indicate between-year difference in activity patterns of the flying squirrels occupying the main study nest. The year to year variation in spring and summer was

above explained to be due to differences in timing of breeding or due to sex. Variations in autumn and winter may be caused by individual endogenous differences, year to year changes in winter food availability, etc., but our material does not allow further analyses.

An aberrant pattern of activity was observed in March and April 1975 and 1976, when the pair living in the main study nest was active irregularly both during the night and day (Type 2 in Fig. 1). During this period the squirrels most probably engaged in sexual display.

From above we can conclude that variations in the activity time of the flying squirrel in natural conditions cannot be explained simply by changes in the length of the night. The species can be classified in central Finland as mainly, but not obligatorily, a nocturnal mammal.

At high latitudes where the seasonal changes in day length are pronounced, nocturnal and diurnal animals encounter different problems. Overwintering birds, such as tits, and e. g. red squirrels have difficulties gathering enough food during the short day to last the long cold nights. They feed from dawn to dusk during winter days, and two consecutive days of bad weather may be hazardous. During the breeding season, on the other hand, they have a long light time for feeding and gathering food for the young. According to our results, during winter the nocturnal flying squirrels have excess time during the long nights to meet the energy demand required to maintain thermoregulation. For example, in midwinter the flying squirrels spent only about 25% of the dark time outside the nest (Fig. 5).

During the reproductive season the night is not long enough for reproducing flying squirrel females in high latitudes. *Pteromys*, however, can feed in broad daylight but the red squirrel is incapable of gathering food during the winter nights.

Timing and duration of active periods also affect survival via predation. According to KAVANAU's (1976) pioneering studies, the potential pressure of carnivores upon their prey is greatest at twilight, since then the hunting times of nocturnal and diurnal predators overlap. In winter, e. g. the red squirrel is exposed to both nocturnal and diurnal predators while they are outside the nest in twilight and daylight (ZWAHLEN 1975; SIIVONEN 1972). In contrast, the flying squirrel is available only to nocturnal predators during a relatively short time during winter nights. In our study area during the summer the female flying squirrel is active (and potential prey) during the night, twilight and even in broad daylight. *Pteromys* has been found to be summer prey for the great owl, *Bubo bubo* (HUHTALA et al. 1976), the Ural owl, *Strix uralensis* (MIKKOLA and MIKKOLA 1974), and also the diurnal goshawk, *Accipiter gentilis* (SULKAVA 1964).

Based on the above discussion we can assume the evolution of the activity-time strategy of the flying squirrel has mainly been affected by two factors: 1) feeding and food gathering and 2) avoidance of predation. The type of activity found in the flying squirrel results in low mortality during the nonbreeding season compared to diurnal but otherwise ecologically similar species. The nonobligatory nocturnalism enables the species to get enough nutrition to raise moderate sized clutches (1–4 young). The activity-time strategy of the ecologically most similar diurnal species, the red squirrels leads in high winter mortality due to starvation and predation (e. g. PULLIAINEN 1973), while this species has plenty of time during the breeding season to gather food for the reproductive effort. The red squirrel has 1–3 clutches of 3–8 young and shows vigorous fluctuations in abundance (SIIVONEN 1972).

Acknowledgements

We are grateful to Professor MIKKO RAATIKAINEN for providing working facilities and for his comments on the manuscript. Our sincere thanks are also due to Dr. EINO ERKINARO and Dr. JUSSI VIITALA for suggestions on the manuscript. Dr. JOANN V. WEISSENBERG kindly revised the English text. The study was financially supported by the Finnish Cultural Foundation.

Zusammenfassung

Die Aktivitätszeit des Flughörnchens, *Pteromys volans*, in Mittel-Finnland

Die Aktivitätszeit (die Zeit, welche die Tiere außerhalb ihrer Nisthöhle verbringen) des Flughörnchens, *Pteromys volans*, wurde in Mittel-Finnland untersucht. Die Aktivität wurde in der freien Natur an wilden Tieren mit Hilfe eines automatischen Systems registriert, zu welchem ein kapazitiver Annäherungsschalter, eine Elektrouhr, eine Schmalfilmkamera und ein Blitzlichtgerät gehörten. Die Registrierung wurde an dem Hauptuntersuchungsnest dreieinhalb Jahre durchgeführt und an zwei anderen Nestern jeweils kürzere Zeit.

Fünf verschiedene Aktivitätstypen wurden beobachtet. Diese sowie die Schwankungen der Aktivitätszeit zwischen den einzelnen Individuen und Jahren wurden unter Heranziehung von ökologischen Verfahren analysiert. Die Gesamtaktivitätszeit folgte nicht genau der Dauer der Nacht. Das Männchen war nachtaktiv mit Ausnahme der kurzen Paarungszeit (März–April), aber das säugende Weibchen und die Jungen waren außerhalb des Nestes sowohl nacht- wie tagaktiv. Es wird vermutet, daß dies mit dem durch die Fortpflanzung bedingten, gesteigerten Energiebedarf zusammenhängt, der in den kurzen Nächten nicht befriedigt werden kann. Von September bis April war die Nachtaktivität in zwei Komponenten aufgeteilt, zwischen denen eine Ruhezeit von sogar sechs Stunden lag.

Die ökologischen Besonderheiten von tagaktiven Eichhörnchen und Flughörnchen (die mit Ausnahme des säugenden Weibchens und dessen Jungen nachtaktiv sind), werden in den nordischen Breiten miteinander verglichen.

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Eine Hypothese zur Evolution microtoider Molaren bei Nagetieren¹

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Eingang des Ms. 7.1.1980

Abstract

A hypothesis on the evolution of microtoid molars in rodents

Demonstrated that during chewing in many rodents M^3 and M_1 are less involved than the other molar teeth. This may be an explanation for the evolution of microtoid molar patterns in which the molar rows are lengthened by an extension of M^3 and M_1 .

Das Backenzahngebiß der Wühlmäuse (Rodentia, Arvicolidae) besteht aus drei Molaren in jedem Kieferast. Die Schmelzschlingenmuster der Kauflächen dieser Molaren sind für die Bestimmung der Arten wichtig. Ihre Variabilität wurde in zahlreichen Arbeiten an inzwischen sehr umfangreichem Material untersucht, für die als Beispiel ANGERMANN (1974) zitiert sei. Dabei fällt auf, daß vor allem M^3 und M_1 inner- und zwischenartlich besonders große Unterschiede aufweisen können, wogegen die übrigen Zähne nur selten wichtige Kennzeichen liefern. Einen Parallellfall bilden die Ohrenratten (Rodentia, Muridae, Oto-

¹ Ergänzte Fassung eines beim 2. internationalen theriologischen Symposium in Brunn 1978 gehaltenen Vortrages.

² Herrn Prof. Dr. BERNHARD RENSCH zum 80. Geburtstag gewidmet.

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Zeitschrift/Journal: [Mammalian Biology \(früher Zeitschrift für Säugetierkunde\)](#)

Jahr/Year: 1979

Band/Volume: [45](#)

Autor(en)/Author(s): diverse

Artikel/Article: [Activity time in the Aying squirrel, Pteromys volans, in central Finland 225-234](#)