# Activity Patterns of Free-Ranging Roe Deer *(Capreolus capreolus)* at Kalø

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JOHNNY LUND JEPPESEN

Med et dansk resumé:
Aktivitetsmønster hos
fritlevende rådyr
*(Capreolus capreolus)*
på Kalø

Резюме на русском языке:
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# DANISH REVIEW OF GAME BIOLOGY

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# Abstract

Jeppesen, J.L., 1989: Activity patterns of free-ranging roe deer *(Capreolus capreolus)* at Kalø. - Dan. Rev. Game Biol. 13 (8).

Automatic recording of the activity patterns of roe deer *(Capreolus capreolus)* took place during 1980-84 at Kalø estate in East Jutland, Denmark. Data from recordings totalled 37,611 hours and involved 8 females and 9 males. Two behavioural states were distinguished: 'active' and 'inactive'. A bimodal pattern of daily activity, with peaks in the level of time active at sunrise and sunset, was most distinct during winter but these peaks had almost vanished in June. Synchronisation of activity by individuals was highest in winter, whereas a low synchronisation was reached in May. Monthly means of daily time active relative to total time showed a marked annual cycle, ranging from below 40% in winter to above 50% in summer. These daily and annual rhythms result from corresponding changes in the duration of activity bouts: maximum median active and inactive bout lengths were recorded during winter and minimum values during summer. Mean number of active bouts per 24-hours was lowest in winter, and varied throughout the year from 9 to 15 (May) for females and from 9 to 18 (August) for males. It is proposed that the duration of cycles (1 active + 1 inactive bout) is related to turnover rate of food in the rumen of roe deer, except for periods of rut and parturition. Short active and inactive bouts reflect that food turnover rate is highest in spring and summer when high quality food plants appear ('rumen fill theory') and basal metabolic rates are high. Relative to sex and age, recorded differences in duration of active-inactive cycles may be related to variations in basal metabolic rates: high metabolic rates probably result in: 1)increased efficiency of filling the rumen (shorter active bouts); and 2)stronger selection for high quality food plants (shorter inactive bouts).

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# Contents

# Introduction

According to Aschoff (1966), 24-hour patterns in activity exhibited by many species under natural conditions may be caused by endogenously controlled physiological rhythms termed 'circadian'. Also, these activity patterns are entrained to the 24-hour day and the calendar year (circannual) by periodically changing environmental stimuli, the so-called 'Zeitgebers' (Aschoff 1954) or synchronisers. Diurnal variation in light intensity is generally the most consistent and reliable of the environmental factors, and light therefore acts as a 'master factor' (Cloudsley-Thompson 1960). Shifts between light and darkness are especially effective Zeitgebers (Georgii 1981).

Food available to roe deer *(Capreolus capreolus)* is usually scarce and of poor quality during winter, and more abundant and of higher quality in spring and early summer (Drozdz & Osiecki 1973, Bobek et al. 1974, Drozdz 1979). Feeding behaviour of roe deer is adapted to these seasonal changes: basal metabolic rate declines during winter (Drozdz et al. 1975, Weiner 1977, Ellenberg 1978), as does food intake (Drozdz & Osiecki 1973, Ellenberg 1978, Drozdz 1979) and activity level (Cederlund 1981). Anatomically, roe deer adapt to winter conditions by a shrinkage of the resorbing surface of the rumen (König et al. 1976), as well as by a reduction of about 20% in the overall volume of the rumen (Hofmann 1979). Similar annual patterns occur in whitetailed deer *(Odocoileus virginianus)* (Silver et al. 1969, Thompson et al. 1973, Holter et al. 1976, Moen 1976, 1978), and are thought to be an adaptation for energy conservation (Moen 1976, 1978).

In free-living cervids, long-term studies of activity patterns have been conducted on red deer *(Cervus elaphus)* by Georgii (1981), Georgii & Schröder (1983), and on roe deer by Cederlund (1981). This paper presents information on daily and seasonal acitivity patterns of free-ranging roe deer at the Kalø estate in East Jutland, Denmark. The purpose is to examine activity patterns among sex and age classes relative to season, in order to determine possible differences. Furthermore, the study intends to evaluate seasonal variations in synchronous activity among individual deer. In addition, the duration of active-inactive cycles is related to turnover rate of food in the rumen, and the possible effects on activity patterns of quality and quantity of food plants, metabolic rate, food intake, hormone level and behaviour, as known from the literature, are analysed.

# Acknowledgements

# Study area and roe deer population

The study area is part of Kalø estate in East Jutland (56°17'N. Lat., 10°30'E. Long.), and consists of 400 ha of fertile land, of which the Ringelmose forest comprises 165 ha (Fig. 1). The remainder is agricultural land divided by hedgerows and coverts. Height above sea level is below 100 m, and the rolling landscape slopes evenly towards the sea. The Ringelmose forest is open with deciduous trees on two thirds of the area.
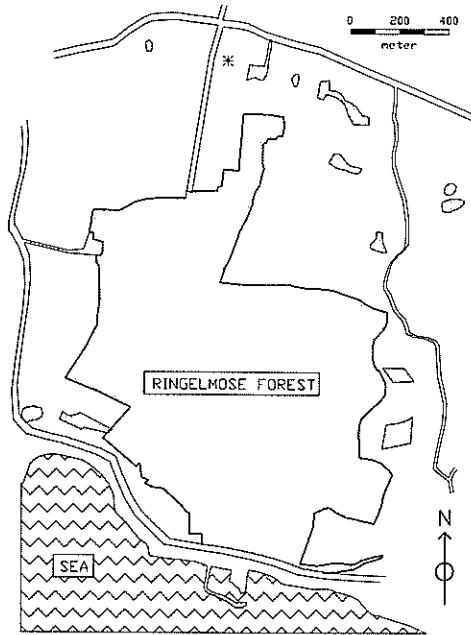
*Fig. 1. Study area. The Ringelmose Forest (shaded) is surrounded by areas with agricultural crops. Asterisk indicates position of the vertical omnidirectional half-wave antenna.*

Among areas of tall stands of mostly beech *(Fagus silvatica)* there are young, dense plantings of oak *(Quercus sp.)* and spruce *(Picea sp.)*, some of which are fenced. Distribution and age of tree species were described by Strandgaard (1972), but after

heavy windfalls in November 1981 about 22 ha of old stands of spruce, fir *(Abies sp.)* and beech have been replaced by open areas of rich herbaceous vegetation. Some of these areas have been subsequently planted with oak and spruce.

The roe deer population at Kalø has been closely studied for more than 25 years and it has not been hunted before or during this study. The size of the spring population has been approximately 100 individuals each year (see Strandgaard 1972) out of which about 90% has been individually collar-marked during the study period. The Kalø roe deer are social and live in groups in winter, but in spring and summer they are solitary (Strandgaard 1972, 1981). This social organisation has been reported for other European populations of roe deer (Kurt 1968A, Bramley 1970, Reichholf 1980, Bideau et al. 1983a, Stüwe & Hendricks 1984). At Kalø, roe deer forage primarily in forested areas from November until January eating buds and shoots of ligneous plants, and again from March to May feeding on wood anemone *(Anemone nemorosa)*; during other seasons they forage mainly on various agricultural crops (Strandgaard 1972, 1977, 1981). Parturition occurs in May and June, centred around June 1st, and the rut lasts about one month encompassing the last week of July and the third week of August.

## Materials and methods

Roe deer at Kalø have been caught each winter for more than 20 years, and capture and marking procedures have been described in detail by Strandgaard (1972). During 1980-1984, 35 roe deer were fitted with radio-collars for tracking purposes and activity recording. Radio transmitters were a Grimsö model (Cederlund et al. 1979), and transmitters as well as modified collars were constructed at the Game Biol-

ogy Station. Radio-collars weighed 200-250 g, and transmitters functioned in the 151 MHz range. Expected battery-life (lithium cells) was 2-3 years. Often the same individual was trapped each winter, and a few deer were fitted with new radio-collars if the battery was expected to expire during the following season.

The system used to record activity automatically has been described by Cederlund

& Lemnell (1980). Signals from up to two study animals were received within a range of at least one km by a vertical omnidirectional half-wave antenna connected to one or (in the case of two transmitters) two LA12 receivers (AVM). These were connected to a Gould Brush 220 two-channel recorder, which could chart signals from two animals simultaneously. Two such recorders were used for several periods of time so that four animals could be registered at the same time.

Any movement of the study animal was indicated by changes in signal strength received as the transmitter position or orientation was altered. This system may allow separation of different activities, such as resting, walking, foraging and running (Cederlund & Lemnell 1980, Cederlund 1981). In the present study, however, such a precise interpretation of the data was considered to be too time consuming. Therefore, this paper only deals with two main behavioural parameters: 'active', which means any registration of movement, and 'inactive' which refers to a motionless state, mainly in a lying position.

To test reliability of recorded signals relative to behaviour, visual observations were made on radio-marked deer within a fenced area, while continuous recordings of variations in signal strength were received simultaneously. Distinction between active and inactive (bedded) states could be achieved with an accuracy of within one minute, as also stated by Cederlund & Lemnell (1980).

This particular activity recording technique may not distinguish between animals that are standing still and those that are bedded. However, standing for periods longer than 3 minutes without movements was seldomly observed and the problem of confounding bedded and standing behaviour is probably negligible since periods of less than 3 minutes duration were not treated separately.

Signals received from free-ranging roe deer were often too strong or too weak to produce decipherable recordings. This was mostly due to variations in distance between study animal and receiving antenna, and to variations in topographic conditions. In 1983, therefore, an automatic gain control was constructed (Gaardmand & Jeppesen 1984) and fitted to the receiver-unit. With this gain control activity-data were produced that could be deciphered 100% of the time, for days and sometimes weeks of continuous recordings. Furthermore, a time-marking device was constructed (Gaardmand & Jeppesen 1984) in order to add accuracy to the system.

Within each month, only samples from individual deer containing more than 100 hours recording were included. Most samples consisted of considerably more hours, although for a few males this was close to the minimum (100 hours).

In order to be included in calculations of weekly means of active time relative to total time, two conditions had to be fulfilled per animal per week; (1) for days of activity recording, more than 50% of the hours had to be decipherable and (2) each hour of the 24-hour period had to be represented on at least two days of the week.

## Results

Seventeen radio-marked roe deer (8 females, 9 males) were included in this study. All adult females were gestating/lactating during spring and early summer, and all adult males were territory-holding. Activity (active/inactive states) was recorded from December 1980 to October 1984, giving a total of 37,611 hours of recordings of

acceptable quality (App. 1). Transmitter failures (mainly in the first years of study), deaths or migrations of roe deer out of range resulted in some gaps in the recordings. Available information was, however, rather evenly distributed over the months of the year, but with most for spring and summer. Females were generally contributing more data than males (3:1), and for both sexes recordings were poorest from October to December. In December, recordings of males were so scanty (a total of only 177 hours) that they were excluded from most calculations. Despite the above-mentioned gaps, 823 complete 24-hour recordings (676 days for females, 147 for males) were obtained.

## Seasonal variation in daily activity

The daily activity pattern was characterised by alternating active and inactive bouts distributed irregularly throughout the 24-hour period (Fig. 2). A polyphasic activity pattern was seen, with active and inactive bouts being longer in winter than in spring (cf. p. 13-14).

Despite an apparent acyclical sequence of active bouts over the 24-hour period, two distinct peaks appeared when mean number of active minutes per hour was calculated over a period of days for each individual deer. The same pattern appeared when samples from several deer were pooled (Fig. 3).

The most striking feature in both sexes was the high level of time active at sunrise and sunset. This bimodal activity pattern was most distinct in winter. For females, these two peaks became less marked from April onwards and almost vanished in June. In June, there was no morning peak and the evening peak was rudimentary, the level of time active fluctuating between 42% and 62% throughout the whole 24-hour period. In July and August the peaks became distinct again, and the contrast be-
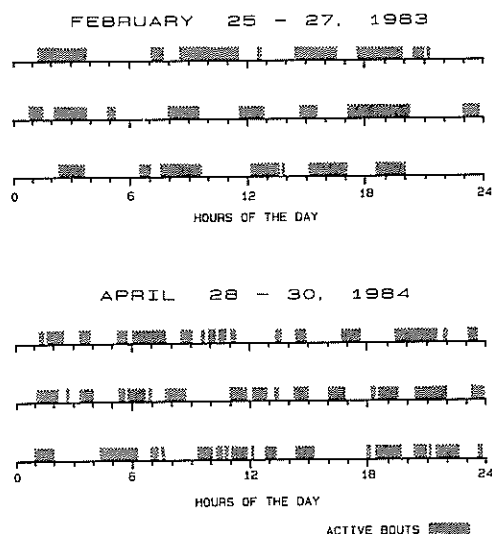


Fig. 2. Activity pattern of female no. 407A, showing active and inactive bouts, for three consecutive days in February 1983 and April 1984.

tween maxima and minima became more pronounced as autumn progressed. Morning peaks of activity coincided with sunrise, except from April to August where the smaller peaks were delayed 1-2 hours relative to sunrise. Evening peaks of activity were delayed one or two hours relative to sunset during October-January, but coincided during the rest of the year.

An additional circadian activity pattern for females was recognised during periods with short days (December-February). A small peak in time active appeared in the afternoon, following the minimum that occurred after the morning peak. During the night, one or two small peaks in time active were discernible for several months, appearing after the minimum that followed the evening peak or before the minimum preceding the morning peak. The level of time active during the night was significantly higher than during the day in September-January (t-tests (Sokal & Rohlf 1981), $p < 0.001$; see App. 3 for details),

7

PERCENT ACTIVE TIME OF TOTAL TIME

JANUARY

FEBRUARY

MARCH

APRIL

MAY

JUNE

JULY

AUGUST

SEPTEMBER

OCTOBER

NOVEMBER

DECEMBER

HOURS OF THE DAY          HOURS OF THE DAY

8
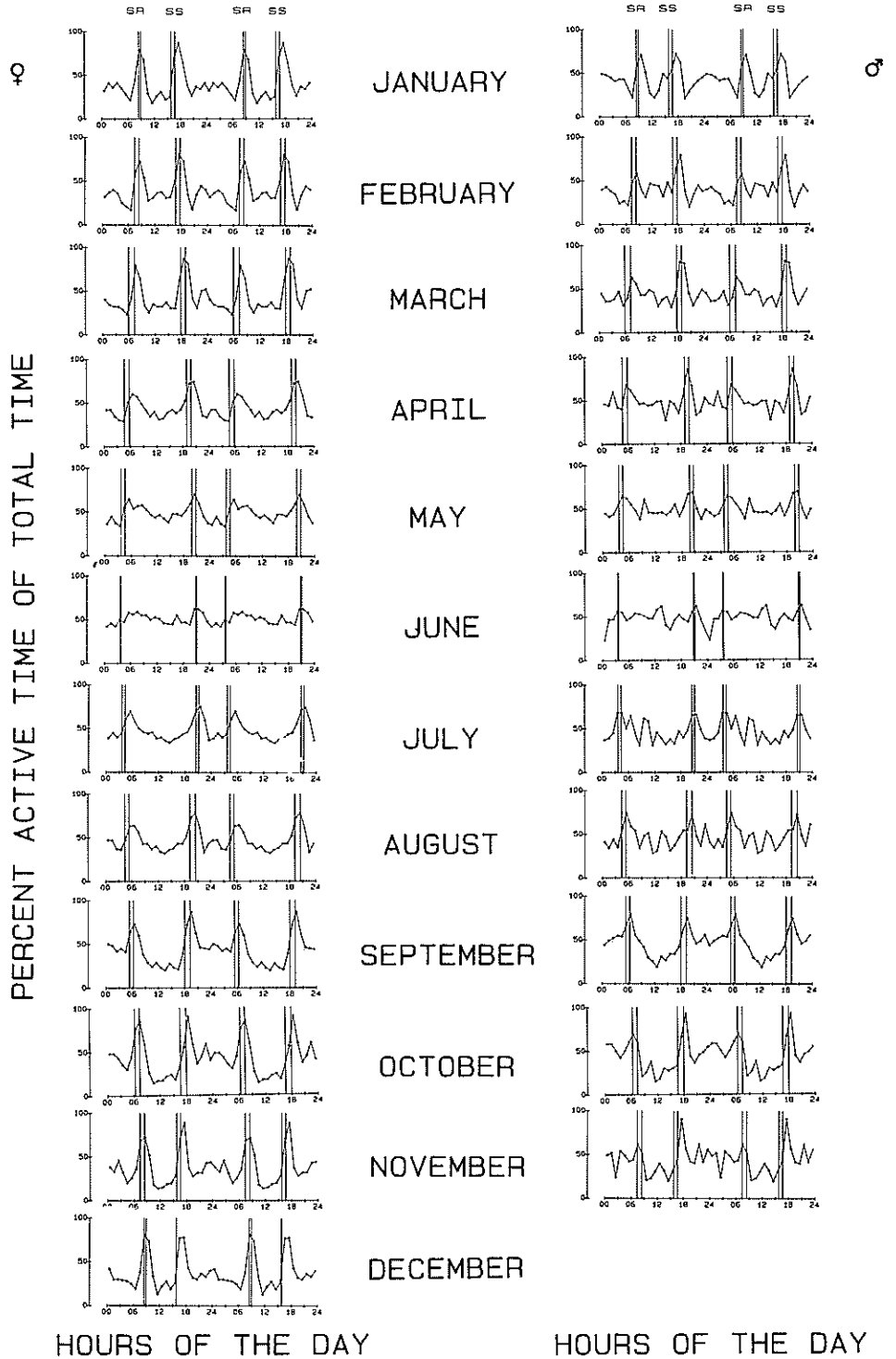
*Fig. 3. Daily distribution of activity and its seasonal variation on the basis of mean number of active minutes per hour (percent active time of total time), in female (left column) and male (right column) roe deer. Each 24-hour period is represented twice in order to facilitate inspection of the pattern at night. Sunrise (SR) and sunset (SS) are indicated. Number of recorded hours and deer per month is provided in App. 2.*

whereas in May females were significantly more active during the day than during the night (t = 5.213, df = 2,543, p < 0.001). During the rest of the year no significant difference between nighttime and daytime levels of time active was observed (Fig. 3).

Circadian activity patterns of males showed much the same seasonal variability as those of females. The 24-hour patterns seemed more serrate during some months, which may possibly be due to the relatively small samples compared to those of females. Patterns in July and August, however, with several maxima for time active

during both day and night in addition to morning and evening peaks, may be due to polycyclic tendencies during rut. In comparison, September showed a much more stable bimodal pattern of activity.

Evening peaks in time active for males were more distinct than morning peaks during October-November and February-April. Morning peaks coincided with sunrise, except in January when they were delayed by one hour. Evening peaks were delayed up to one hour compared to sunset, especially in autumn and winter. As for females, the level of time active for males was
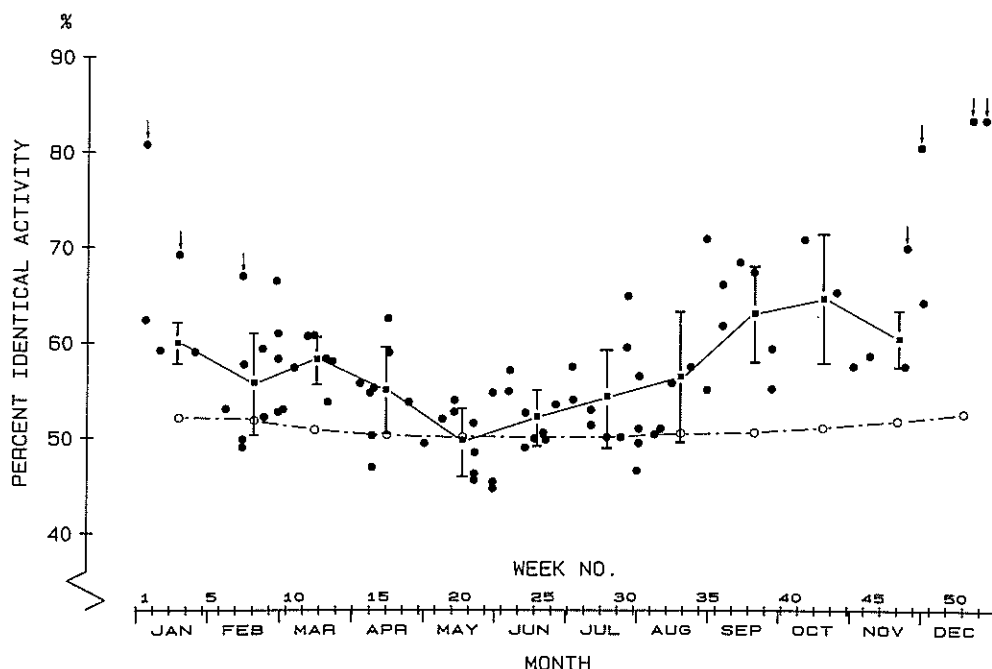


*Fig. 4. Percent of identical activity (active-inactive) of adult deer compared two by two in weekly samples. Squares and vertical lines indicate monthly means and standard deviations. Arrows indicate winter-samples containing comparisons between a mother (312A) and her 1½-year old female offspring (407A), but they are not included in monthly means. Graph with open circles indicates expected values provided that active and inactive bouts appear at random.*

significantly higher (p < 0.001; see App. 3 for details) during the night than during day in September-November (no data in December). During the rest of the year, the hourly proportion of active time to total time was equally distributed between day and night (Fig. 3).

## Synchronisation of activity

Seasonal variations in the double-peaked circadian activity pattern shown in Fig. 3 resulted from individual deer showing identical daily variations. It follows that the patterns of individual deer were most closely synchronised with those of others during winter and least during summer. This is confirmed in Fig. 4. In spite of a large individual variation, there is a clear trend towards a lower synchronisation after the winter and through spring until May, when a minimum mean of 50% identical activity is reached. The mean percentage in May equals the expected value provided

that active and inactive bouts appear at random (Fig. 4). After May the synchronisation gradually increased during summer and autumn. The highest percentages of identical activity occurred in winter between a doe and her 1 1/2-year old female off-spring (Fig. 4). Variation in synchronised activity between mother and fawn in winter-spring is published elsewhere (Jeppesen in prep.,a).

## Total level of time active

Large differences in the total time active per day, not only from day to day, but also from animal to animal, occurred for females. However, a clear seasonal trend became obvious when weekly means of active time relative to total time (in percent) were calculated from all activity-data on females (Fig. 5). A winter level from 35% to 44% active time to total time was recorded from week 47 (mid-November) to week 13 (late March). During April and May (spring) the
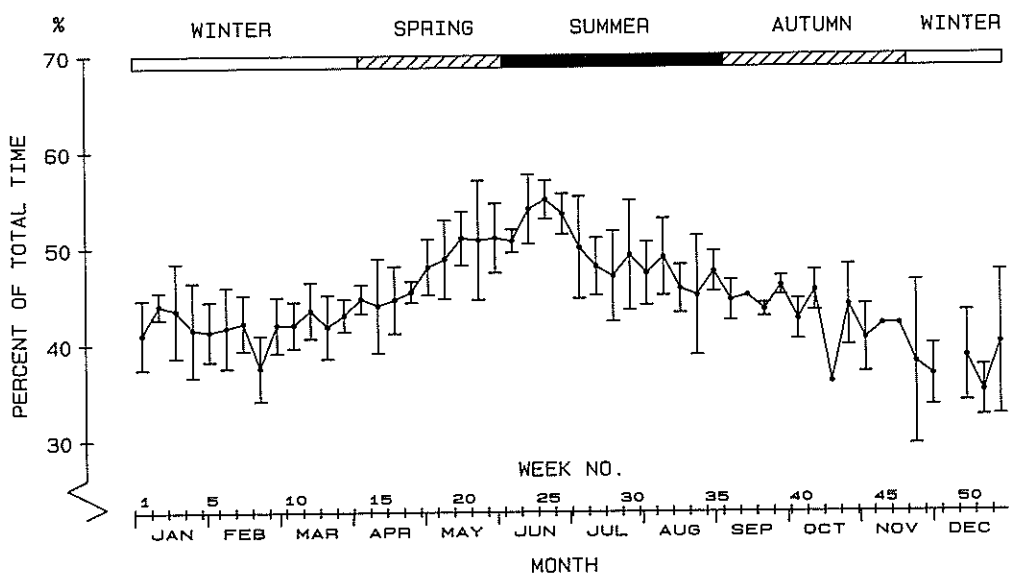


Fig. 5. Annual rhythm in the level of time active by female roe deer. Weekly means of active time relative to total time (in percent) and standard deviations are indicated, and are related to season of the year. Number of deer recorded per week is provided in App. 4.

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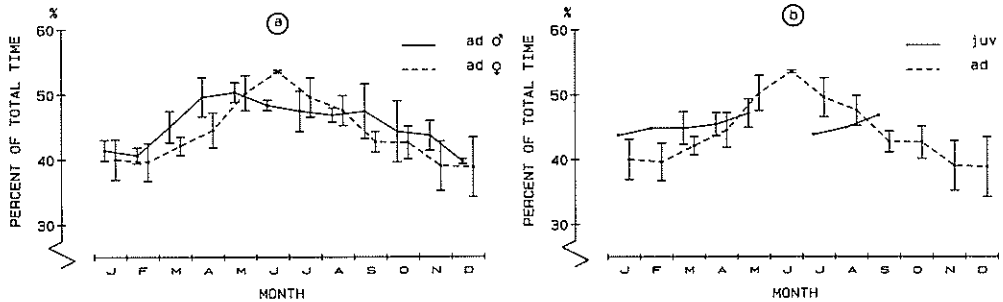
*Fig. 6. Annual cycle in the level of time active by a)adult females compared to males, and b) adult females compared to young females, 7-16 months of age. Monthly means of active time relative to total time (in percent) and standard deviations are indicated. Number of total recorded hours and deer per month is provided in App. 5.*

proportion of active time gradually increased to 51%, and a maximum of 55% was reached in June (week 25). From late June, the level of time active declined to 45-50% and stayed there through August (week 35). During autumn the decline in active time to total time gradually continued to below 45%, and a minimum of 35-40% was reached in November-December.

Data for males only fulfilled the two forementioned conditions (p. 6) concerning weekly means of active time to total time for 29 weeks of the year. Therefore, the recordings of males are presented in terms of monthly mean values, and these are compared to monthly mean values of adult females (Fig. 6a). In January and February the proportion of active time to total time of both males and females was about 40%. After that the level of time active in both sexes increased, but in March, and especially in April, the level of males was higher than that of females (by 6% and 14%, for the two months respectively), although only significantly higher in April (t=2.552, df=2,840, p<0.02). In May the level of time active for both sexes was equal at 50% (annual maximum in males), but in June the proportion of active time to total time for females (54%, the annual maximum of females, and 11% higher than in males) was significantly higher (t=2.427, df=2,537, p<0.02) than that of males. In

June the proportion of active time declined a little in males to a level that persisted until the end of September. From September onwards, the level of time active in males was again above that of females (from 4% to 12% higher during September-November), though only significantly so in September (t=2.014, df=1,991, p<0.05).

Included in the data set for females were recordings from two young females (407A in 1983; 309A in 1984), from 7 to 16 months of age (not including June), and this material has been analysed separately. The level of time active for the young females tended to vary much less in the course of the year than that of adults (Fig. 6b), being higher than adults in winter (13% higher in February), although not significantly, and significantly lower in summer (12% lower in July, t=2.325, df=2,268, p<0.05). The level of time active for adult females was higher than that of yearlings in May, and decreased to below the level of yearlings again in September. Weekly levels of time active for females (combined young and adult) in July (Fig. 5), masks the even higher levels of time active for adults. The level of time active per day of yearling 407A was 2-9% lower than that of its mother during weeks 27-33 1983 (early July-mid August), and 6-13% lower that its own level during the same weeks the following year when it had become an adult with 2 fawns.

11

ACTIVE BOUTS

INACTIVE BOUTS

(a)

DEC.

JAN.

FEBR.

(b)

MAY

JUNE

JULY

LENGTH OF ACTIVITY BOUTS (MINUTES)

FREQUENCY OF BOUT LENGTH (%)

12
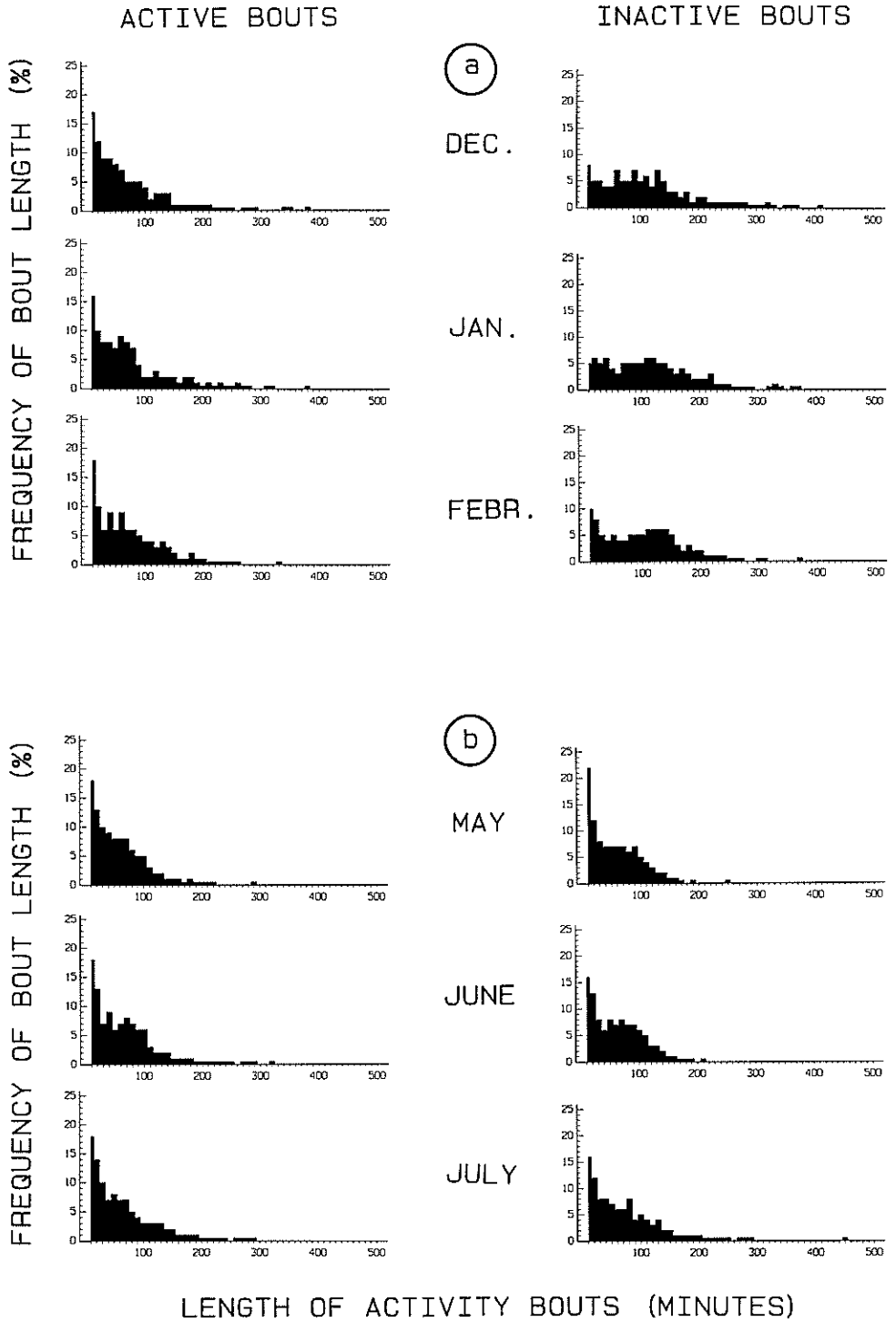
*Fig. 7. Distributions of active and inactive bout lengths in female roe deer during a) 3 winter months and b) 3 spring-summer months.*

In July 1983 the level of time active for yearling 407A over 15 full 24-hour recordings was <50% (31-49%), whereas it was >50% (51-63% over 9 24-hour recordings) in July the following year.

## Seasonal variation in duration of active and inactive bouts

Much variation occurred among individual deer of both sexes in the mean length of active and inactive bouts. Despite distinct seasonal variation, mean bout lengths were consistently longer in some individuals than in others, and each deer showed an individual activity pattern. One-way analysis of variance (Sokal & Rohlf 1981) and t-tests revealed significant differences at a 5%-level within several months (see App. 6), and this was most pronounced for females. Lengths of active and inactive bouts in both females and males were skewed during most months (see Fig. 7 for females). Consequently, distributions were better characterised by the median (Figs. 8 and 9) than by the mean. Distributions of active bouts

were skewed during all months in both sexes whereas the distributions of inactive bouts were skewed only during summer, with many short bouts. During winter, distributions of inactive bouts tended to be more extended, and medians in Figs. 8 and 9 were close to the mean values provided in App. 6.

None of the distributions of active bout lengths in females during November-March differed significantly (median tests, 5%-level of significance (Downie & Heath 1970)). Monthly medians gradually decreased from a maximum of 51 minutes in January and February to 40 minutes in May. The distributions in April and May differed significantly from those during January-March ($p < 0.01$ and $p < 0.001$, respectively). In June the median increased to 50 minutes, and this distribution differed significantly from those of April-May ($p < 0.001$) and from those of July-October ($p < 0.001$), when medians gradually decreased to an annual minimum of 35 minutes. Distributions during July-October did not differ significantly. In No-
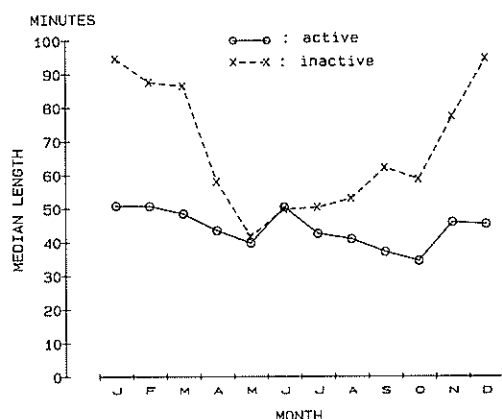


*Fig. 8. Annual cycle of median active and inactive bout lengths in female roe deer. Number of bouts and deer per month are provided in App. 7.*
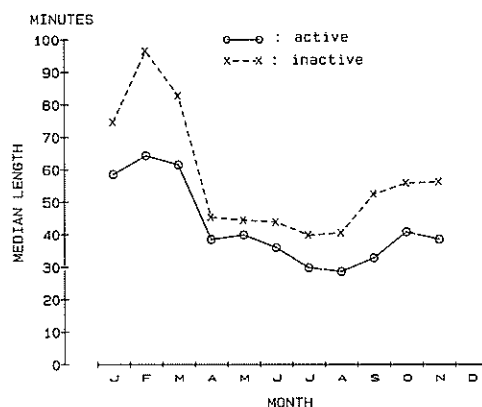


*Fig. 9. Annual cycle of median active and inactive bout lengths in male roe deer. Number of bouts and deer per month are provided in App. 8.*

13

vember and December medians of active bouts again increased, and these distributions differed significantly from that of October (p < 0.05).

Distributions of inactive bout lengths in females varied much more (Fig. 8). Distributions during December-March, with medians from 86 to an annual maximum of 95 minutes in December and January, differed highly significantly (median tests, p < 0.001) from those during the rest of the year. Differences were highly significant between April and May (p < 0.001), and between May and June (p < 0.01), May showing an annual minimum median of 42 minutes. Distributions during June-August showed significantly shorter medians than those during September-October (p < 0.001), and the distribution in November differed highly significantly from all other distributions (p < 0.001).

Seasonal variation in distributions of active bout lengths in males was more distinct than that of females (Fig. 9). The distributions during January-March, with an annual maximum of medians of 64 minutes,

differed highly significantly from those during April-November (p < 0.001), with medians decreasing from 40 minutes in May to an annual minimum of 28 minutes in August. The median then increased to 41 minutes in October and 39 in November. Distributions during April-November did not, however, differ significantly. Insufficient data for males in December made comparison with this month impossible.

As for females, seasonal variations in inactive bout lengths in males were large. The distribution in January differed significantly (p < 0.05) from the one in February, the latter reaching an annual maximum of medians (97 minutes). The distribution in March did not differ significantly from those in January and February. Distributions during January-March, differed highly significantly (p < 0.001) from those during April-November, which reached an annual minimum median (40 minutes) in July and August. In addition, distributions during April-August showed significantly shorter medians than those during September-October (p < 0.01).

Tab. 1. Comparisons between adult and young females (7-16 months of age) of monthly median values (in minutes) of active and inactive bouth lengths. Data from yearlings are missing in June. Asterisk indicate significant differences at the 5%-level, median tests.

| | JAN. | FEB. | MAR. | APR. | MAY | JUN. | JUL. | AUG. | SEP. |
|---|---|---|---|---|---|---|---|---|---|
| **Active bouts** | | | | | | | | | |
| Adults | 50.8 | 49.7 | 47.8 | 42.2 | 37.7 | 50.4 | 40.1 | 38.2 | 31.9 |
| Young | 51.3 | 57.2 | 49.8 | 47.0 | 45.1 | | 50.0 | 55.0 | 54.7 |
| Disparity | +0.5 | +7.5 | +2.0 | +4.8* | +7.4* | | +9.9 | +16.8* | +22.8* |
| –Percent | +1.0 | +15.1 | +4.2 | +11.4 | +19.6 | | +24.7 | +44.0 | +71.5 |
| **Inactive bouts** | | | | | | | | | |
| Adults | 97.2 | 88.3 | 87.0 | 55.3 | 36.3 | 49.8 | 46.0 | 51.0 | 59.5 |
| Young | 84.9 | 84.1 | 84.8 | 65.0 | 56.0 | | 69.6 | 66.3 | 70.8 |
| Disparity | –12.3 | –4.2 | –2.2 | +9.7* | +19.7* | | +23.6* | +15.3* | +11.3 |
| –Percent | –12.7 | –4.8 | –2.5 | +17.5 | +54.3 | | +51.3 | +30.0 | +19.0 |
| **(Active + inactive) cycles** | | | | | | | | | |
| Adults | 148.0 | 138.0 | 134.8 | 97.5 | 74.0 | 100.2 | 86.1 | 89.2 | 91.4 |
| Young | 136.2 | 141.3 | 134.6 | 112.0 | 101.1 | | 119.6 | 121.3 | 125.5 |
| Disparity | –11.8 | +3.3 | –0.2 | +14.5 | +27.1 | | +33.5 | +32.1 | +34.1 |
| –Percent | –8.0 | +2.4 | –0.1 | +14.9 | +36.6 | | +38.9 | +36.0 | +37.3 |

14

Distributions of both active and inactive bout lengths of males compared to those of females differed for several months (Figs. 8 and 9). Medians of active bouts for males were significantly higher than those for females in February and March ($p < 0.01$, and $p < 0.001$, respectively), whereas medians of active bouts for females were significantly higher than those for males during June-August ($p < 0.001$). Medians of inactive bouts for females were significantly higher than those for males in January ($p < 0.02$), April ($p < 0.01$), during July-September ($p < 0.01$), and in November ($p < 0.001$).

Data were achieved for two young females: 309A during the period February-May 1984, and 407A during January-September 1983 (except June). Median active and inactive bout lengths of the young females diverged considerably during several months from those of the adult females (Tab. 1). Both active and inactive bout lengths of young females tended to vary much less in the course of the year than those of adults. In late winter when fawns still occur within the home range of their mothers, and to a large extent still accompany her (Jeppesen, in prep.,a), median length of active bouts of fawns were longer than those of adult females, whereas inactive bouts were shorter (Tab. 1). These differences, however, were not significant

(median tests). During May-September, median active and inactive bouts were significantly shorter for adult females than for fawns (Tab. 1).

Females seemed to alter their activity pattern when parturition neared. Continuous activity recording was rendered possible by one pregnant female (402A) during the week of birth in May 1984 as she stayed within the same small area in the forest during those days (Tab. 2). During the days preceding the date of birth both active and inactive bouts became gradually shorter, and the number of active bouts per day increased considerably. A few days after the birth she moved to a greater extent within her home range.

## Daily frequency of active bouts

The number of active bouts per 24-hours relates to the length of active and inactive bouts by varying throughout the year in a manner inversely proportional to mean duration of active-inactive cycles (Fig. 10). In both sexes, mean daily frequency of active bouts was 9-10 during January-March, after which it increased sharply to 15 in May (14 in April for males) (Fig. 10). For females the daily number of bouts dropped from this maximum in May to about 12 in September-October and 9 in November-December. Assuming Poisson distribution

Tab. 2. Activity pattern of female 402A during the days preceding and following the date of birth of two fawns, May 15, 1984.

| Date | Total time active per 24-hours: % | No. of active bouts per 24-hours | Mean length of bouts (in minutes): | |
|------|------|------|------|------|
| | | | Active | Inactive |
| May 12 1984 | 46.0 | 15 | 44 | 50 |
| – 13 – | 49.7 | 24 | 30 | 30 |
| – 14 – | 51.4 | 24 | 31 | 28 |
| – 15 – | **52.2** | **35** | **21** | **20** |
| – 16 – | 46.2 | 29 | 22 | 27 |
| . . . . | | | | |
| – 18 – | 53.3 | 19 | 40 | 37 |
| – 19 – | 45.6 | 17 | 39 | 40 |

15

*Fig. 10. Monthly mean numbers of active bouts per 24 hours. Vertical lines indicate standard deviations. Number of deer and number of days per month are provided in App. 9.*

of the mean daily number of active bouts, the mean daily frequency for males was significantly higher than that for females in April (t = 2.735, df = 240, p < 0.01) and during July-September (p < 0.001, see App. 3 for details). The maximum of means over the year for males was 18 daily bouts in August. Furthermore, males showed significantly more daily active bouts in November than females (t = -5.70, df = 99, p < 0.001).
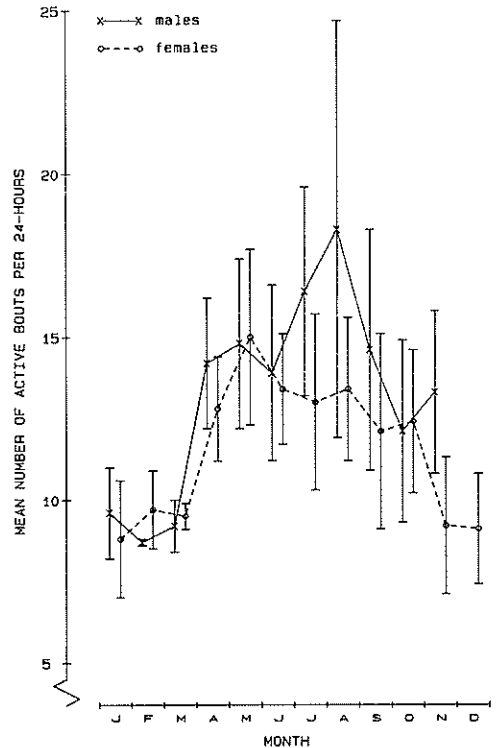
# Discussion

## Two-peaked activity pattern

The activity pattern with peaks in time active at dawn and dusk as reported in the present study has previously been documented for roe deer (Bubenik 1960, 1965, von Berg 1978, Ellenberg 1978, Vincent et al. 1979, Cederlund 1981, van Bemmel & van Den Oord 1982, Putman 1986), red deer (Bubenik 1965, Bubenik & Bubenikova 1967, Bützler 1974, Georgii & Schröder 1978, 1983, Georgii 1981), elk *(Cervus elaphus)* (Craighead et al. 1973, Collins et al. 1978, Bowyer 1981, Lieb 1981), white-tailed deer (Jackson et al. 1972, Kammermeyer & Marchinton 1977), fallow deer *(Dama dama)* (Jackson 1977), moose *(Alces alces)* (Geist 1963, Belovsky & Jordan 1978), and reindeer *(Rangifer tarandus)* (Erriksson et al. 1981).

Several authors emphasise that the two peaks of activity coincide with peaks in

movements, and Mauget & Sempéré (1978), Bideau et al. (1983b), and Vincent et al. (1983) noted that 'travelling activity' in roe deer peaked at dawn and dusk. This pattern also applies to roe deer at Kalø, the largest travel movements being those to and from preferred feeding areas (Jeppesen in prep.,b).

Bubenik (1960) reported that the highest daily level of time active for roe deer was reached when the sun passed 20° above the horizon. Consequently, deer were most active in the middle of the day in December-January. At other times of the year two daily maxima for time active occurred. In most other studies, including the present one, peaks in the level of time active occurred during twilight periods.

Distinct peaks in time active in winter, with the relative height of the peaks

16

diminishing from winter to summer, were previously reported for roe deer (Ellenberg 1978, Putman 1986) red deer (Georgii 1981, Georgii & Schröder 1983), and reindeer (Erriksson et al. 1981). These same trends occurred in Danish red deer (Jeppesen 1987b, and unpubl.). Bubenik (1960) also noted for roe deer that the double-peaked activity pattern was broken down in June. Peaks in time active at sunrise and sunset in winter were not strongly expressed by Swedish roe deer (Cederlund 1981).

The 1-2 hours delay in the morning peaks in time active compared to sunrise shown by females at Kalø during April-August may be due to the endogenous rhythm not being able to follow the more extreme oscillations of sunrise (the peaks disappeared in June). The same interpretation may apply to the delay of evening peaks compared to sunset during winter. For reindeer, Erriksson et al. (1981) suggested that the longer photoperiod caused a later onset of morning activity.

It is not obvious why male roe deer at Kalø show a delay in both the morning and evening time active peaks in winter. For elk, Lieb (1981) reported a correlation between the subtle shifts in the timing of morning/evening feeding bouts and ambient air temperature, which appeared to be an energy conserving response to changes in temperature associated with transitions between day and night. Bowyer (1981), however, did not find any significant correlation between elk activity and temperature.

Apart from the two distinct time active peaks at dawn and dusk, no further cyclic activity was recognised in the 24-hour pattern, such as von Berg (1978) reported for roe deer on the basis of a few three-day samples.

The reason for the higher level of time active at night in both sexes during autumn may be that during this season roe deer prefer to forage on open fields with little or no cover, and therefore do so mainly during darkness (own observations). Furthermore, hunting for other game species during autumn and winter may have disturbing effects on roe deer (Jeppesen 1987a), causing them to be less active during the day.

Photoperiodic control of the activity patterns by dawn and dusk synchronises the circadian rhythm of individual deer most strongly during winter, and thus causes a higher inter-individual synchronisation at this time. This higher synchronisation within the population may be reinforced by deer feeding in groups from October/November until March/April, the active-inactive cycles for periods of time being synchronised. With the shift towards more solitary behaviour in summer, the feeding bouts of different animals are less synchronised.

## Total level of time active

Based on monthly means the daily level of time active in females and males in winter was 27% and 21%, respectively, lower than the maximum summer level for each category; based on weekly means the difference between these winter and summer values for females was 36%, (data unavailable for males). These figures correspond very well with seasonal differences observed for roe deer living in a more severe climate in central Sweden, i.e. 31% in males and 27% in females (Cederlund 1981). It may be misleading, however, to correlate the Swedish figures directly with figures achieved in the present study, as data are missing for Swedish females from the season with lowest activity in Swedish males. In comparison, activity during winter was 50% lower than during summer in female red deer and 30% lower in males (Georgii 1981, Georgii & Schröder 1983). In elk, the seasonal difference was 27% (Lieb 1981).

17

## Active and inactive states

Excluding nursing and rutting activities, active and inactive states are related to food intake and processing. Most behavioural elements within the active state are interspersed among feeding bouts, and Turner (1979) noted that feeding (and movements in connection with feeding) and 'orienting' took up more than half the active time, whereas other elements were of minor quantitative importance. During the rut, however, 'social behaviour' made up the quantitatively most important behavioural element in adult males (Turner 1979). In adult female roe deer, Turner (1978) reported a constant relationship between time spent feeding and standing (active) in winter and spring, and Cederlund (1981) assumed the proportion of feeding behaviour in relation to the active state to be constant. The number and duration of behavioural elements exhibited by an animal when active are not constant, however, but are influenced by sex, age, and season, as well as group size and social status within the group (Turner 1979, Büttner 1980). Human disturbances also influence activity patterns (Turner 1979, Jeppesen 1987a & b).

Ruminants usually lie down when ruminating (Moen 1973). In captive reindeer more than 90% of rumination took place during resting (inactive) periods (Erriksson et al. 1981), and Bowyer (1981) noted that almost all rumination in elk occurred when bedded. Cederlund (1981) emphasised that roe deer, too, usually combine rumination with resting. Within the inactive state, periods of rumination alternate with periods of proper resting, occasionally including sleep. Sleep, however, only occupies a small proportion of the total inactive time in roe deer (Bubenik 1960) and red deer (Georgii 1978). In tame elk rumination took place in well over half of the inactive time (Collins et al. 1978). No data

are available on the proportion of rumination in relation to the duration of inactive bouts in roe deer, but Cederlund (1981) assumed the proportion to be constant throughout the year.

Assuming that an average daily active bout length represents a (re-)filled rumen, and an average inactive bout represents an emptied rumen (see 'rumen fill theory', below), then median bout length in the present study indexes the efficiency of food intake (filling the rumen), and rumination (emptying the rumen), respectively. A consequence is that the highest level of time active does not necessarily reflect the highest food intake. Instead, the duration of active-inactive cycles acts as a relative measure of turnover rate of food in the rumen.

## 'Rumen fill theory', metabolism and turnover rates

The 'rumen fill theory' (Moen 1973, Westoby 1974) is crucial in understanding the mechanisms underlying activity patterns in roe deer. The theory suggests that ruminants must keep their guts filled constantly, and that they are limited by how fast they can process food rather than by how fast they can obtain it. The animal stops ingesting food when the rumen is filled to its capacity. The more digestible the food mass is, the sooner the rumen will be emptied and the sooner the animal will be able to eat again (Moen 1973).

Small animals have greater basal metabolic rates per unit of body weight than do larger ones (Kleiber 1961) and small ruminants, such as the roe deer, have e relatively small rumen compared to larger ones (Prins & Geelen 1971). Therefore, turnover rate of food in the rumen of small ruminants must be higher than in larger ruminants. In order to achieve this, it is necessary that the food is easily digestible and of high quality (low fibre, high protein). Thus, small ruminants must select for

18

this type of food. Based on stomach morphology, Hofmann et al. (1976) classified the roe deer as a 'concentrate selector' (see Hofmann & Stewart 1972), whose feeding 'strategy' is to select for the most digestible food, producing a high turnover rate in the rumen. Turner (1978) showed that female roe deer avoided less digestible food types and selected easily digestible ones in spring. Further, Drozdz (1979) emphasised the importance of selection for herb layer plants (or leaves rather than stems and twigs) rather than for browse, also in cases of identical digestibility, because the rate of passage of herb layer plants through the alimentary tract is more rapid than that of browse.

Accordingly, it is to be expected that the daily number of active bouts in roe deer will be higher than in larger cervids. This certainly seems to be the case. Bubenik (1960) reported 8-12 active bouts per 24 hours in roe deer, and Cederlund (1981) noted 7-13. These figures correspond to the monthly means of 9-15 active bouts per 24 hours shown in the present study (up to 18 in rutting males). In comparison, Mitchell et al. (1977) reported 6-9 foraging periods per 24 hours for red deer, and Georgii (1981) and Georgii & Schröder (1983), providing monthly mean numbers of daily active bouts for red deer, found between 5 and 10. Elk show 5-7 active bouts per 24 hours as derived from figures in Lieb (1981).

Furthermore, as basal metabolism of roe deer is at its highest during spring and early summer (Drozdz et al. 1975, Weiner 1977, Ellenberg 1978), a higher turnover rate of food, and thus a higher number of active bouts per 24 hours, is to be expected during this time of year. This is confirmed in the present study in Fig. 10, and has been demonstrated earlier in roe deer (von Berg 1978, Ellenberg 1978, Cederlund 1981). The high turnover rates in spring and early summer are concomitant with and dependent on a high quality and quantity of food

plants, as well (see Bobek et al. 1974, Drozdz 1979). The high number of active bouts shown by males during July-August (Fig. 10) cannot, however, be explained by the rumen fill theory, but was probably due to rutting activities, (see p. 22).

## Adult females

Turner (1978) reported no variation in duration of average standing (active) bouts from January until April in free-ranging adult female roe deer, but during the same period recorded a decrease in average lying (inactive) bout duration. The latter resulted from higher turnover rates of the selected food as daylength progressed.

In the present study, lengths of active bouts for females were not constant throughout the year, but varied significantly. Therefore, as food quality and quantity increase during spring (especially from April when sprouts become available in large amounts), the efficiency of filling the rumen probably increases, resulting in shorter active bouts. Thus, according to the assumption of a filled rumen per median active bout (cf. p. 18), daily food intake increases even more than it would if active-bout duration remained constant. The increase in the total amount of time active (Fig. 5) during spring chiefly results from the steep decrease in inactive-bout duration (Fig. 8), and this, in turn, reflects the higher digestibility of the selected food, as spring progresses. As already emphasised, the increase in basal metabolism during spring probably intensifies food intake and selection for high quality food plants, so that the resulting activity pattern is not merely a response to higher digestibility of available food plants (see below as well).

Digestibility of food plants declines gradually from May until October (Drozdz & Osiecki 1973, Drozdz 1979), and the gradual increase in the duration of inactive bouts during this period (Fig. 8) is probably

19

directly caused by this; deer require more time to process a rumen full of food. However, the duration of inactive bouts in adult lactating females was shorter in July than in June (Tab. 1), which probably indicates that the very large maintenance metabolism of lactating females during July (Ellenberg 1978) forces them to select more specifically for food plants of higher quality than in June. Accordingly, a faster turn-over rate in the rumen is induced. Following this, the duration of inactive bouts increased, and the only possible way for adult females to sustain a high energy-intake was to intensify feeding, thus shortening the active bouts. The duration of active bouts, although increasing in June, gradually did decrease until October (Tab. 1, Fig. 8). High availability of food plants in summer probably makes a more efficient food intake possible in adult females. Thus, median duration of active-inactive cycles in adult females was shorter during July-October than in June, suggesting a high food intake.

From September/October maintenance metabolism decreases (Ellenberg 1978). The high turnover rates of food that are still maintained, as indicated by the short active-inactive cycles, make a deposition of fat reserves possible, which Hoffmann (1977) reported to be initiated as from September.

After leaf fall, at the shift from October to November, the digestibility of browse abruptly decreases (Drozdz 1979). According to the rumen fill theory, this may explain the marked increase in duration of inactive bouts in females during November and December. The simultaneous increase in duration of active bouts may result from a lower efficiency in filling the rumen, caused by the drop in quantity (and quality) of food. Accordingly, the number of active bouts dropped to winter level (Fig. 10).

The decrease in level of time active, however, should not merely be regarded as an automatic response to the reduction in quality and quantity of food plants. Enclosed roe deer also reduce activity and food intake during winter, despite identical food supply at all seasons (Barth et al. 1976, Eisfeld 1977, Ellenberg 1978). Roe deer adapt physiologically and anatomically to winter conditions by reducing basal metabolism (Drozdz et al. 1975, Weiner 1977, Ellenberg 1978) and by diminishing the volume and absorbing surface of the rumen (König et al. 1976, Hofmann 1979).

## Young versus adults

Sex and age dependent variation in activity patterns indicate that digestibility of food plants is not the only factor influencing the patterns. Seasonal differences in basal metabolism between young and adult deer, and between the sexes, are probably essential physiological adaptations. Fasting heat production (FHP) during winter was more than 20% higher in fawns, 6-8 months old, than in adults (Weiner 1977). Fawns grow until winter and have smaller fat reserves than adults (Hofmann 1979). Additionally, Hartfiel et al. (1985) reported that radiant heat loss at low temperatures in February was higher in a fawn than in an adult female. The higher energy-requirements of young deer may explain the observed higher level of time active during winter of young females compared to adults (Fig. 6b). However, as activity patterns of mother and infant are highly synchronous during winter (Jeppesen, in prep.,a) fawns may gain energy by feeding more than adults when active, as demonstrated by Büttner (1980).

During spring and summer the situation is reversed: FHP in adult (gestating, lactating) females is much higher than in yearling females. Thus, in non-breeding females maintenance metabolism increases by 50% from winter to summer (Ellenberg 1978); but in gestating/lactating females FHP is

particularly large (Weiner 1977, Ellenberg 1978). In gestating females energy intake (per metabolic weight of unity) increased compared to non-gestating females from 4-2 weeks prior to parturition (Ellenberg 1978). In the present study the difference in median inactive-bout duration between yearlings and adult females became obvious already from April (Tab. 1). The energy-intake increases during lactation to an average of 2.5 times the energy-intake of nonlactating females (in females supporting two fawns in mid July, op. cit.).

From May until September median active-inactive cycles were 27-34 minutes shorter in adult (gestating/lactating) females than in yearling females (Tab. 1; no data from yearling females in June). As already emphasised, the high FHP in adults during this period probably forces them to perform a much more efficient food intake, including a strong selection for food plants of high digestibility, compared to food intake in yearlings, and this is reflected in very short median active and inactive bouts (fast turnover rate).

Especially during the last month of gestation and during lactation, however, factors additional to metabolic rate, digestibility of food plants, and light influence the activity patterns, although probably to a lesser extent. Adult females are more cautious during this particular period and spend more time 'orienting' (Turner 1979). Aggressive interactions are common among mothers (Kurt 1968b, Espmark 1969), but are usually of short duration (Jeppesen, unpubl.). Females spend much time caring for the fawns (Espmark 1969). Newborn roe deer fawns are 'hiders' (Lent 1974) and are nursed several times per day (Bubenik 1965, Espmark 1969). Care periods, however, seem to be integrated in the rhythm of feeding and ruminating (own observations).

The change in activity pattern prior to and after parturition (Tab. 2) was very likely due partly to physiological alterations before giving birth, and partly to very frequent contacts between mother and offspring immediately after birth in connection with establishment of a mother-young bond (Bubenik 1965, Espmark 1969). Furthermore, increased alertness towards potential predators may influence activity patterns during this period.

## Males

Male roe deer exhibit territorial behaviour during spring and summer, with peaks in March/April and during the rut in July/August. High levels of aggression follow high concentrations of testosterone in blood plasma (Barth et al. 1976, Sempéré et al. 1980), and peaks in manifestations of territorial behaviour in male roe deer, such as scrapes, fraying of vegetation, and chasings of other males are in parallel to the testosterone curve (see Kurt 1968a, Davies & Davies 1968, Bramley 1970, Strandgaard 1972, Cumming 1974, Barth et al. 1976, Ellenberg 1978, Sempéré et al. 1980). Similarly, increases in male movements within territories follow the increases in the testosterone curve (monthly means of 'travelling activity'; Bideau et al. 1983b).

French studies revealed increased movements of males in spring (Mauget & Sempéré 1978, Sempéré 1979a, Bideau et al. 1983b), as well as enlarged daily ranges (Sempéré 1979a, Bideau et al. 1983b). Male roe deer at Kalø behaved similarly, although the increase was significant only from autumn to spring, with intermediate figures in winter (Jeppesen in prep.,b). Mauget & Sempéré (1978) concluded that increased movements in March were due to territorial activity, whereas the total amount of time active per 24 hours, that did not increase until April, corresponded to the sprouting vegetation in April. This is part of the conclusion for the present study also. The earlier increase in the daily level

21

of time active for males during spring compared to females (Fig. 6a), however, is probably the result of a faster turnover rate of food in the male gut: the decrease in duration of both active and inactive bouts in males from March to April is more abrupt than in females (Figs. 8 and 9), thus suggesting that basal metabolic rates per unit of body weight in males are higher than in females at this time of year. Therefore, with reference to the rumen fill theory (p. 18), it seems probable that males show a more efficient food intake and a stronger selection for food plants of high digestibility in March-April than do females. Reports on a high food intake in males in spring (Barth et al. 1976, Eisfeld 1977, Ellenberg 1978) support this conclusion. In spring, energy requirements for maintenance are certainly very high in male roe deer (Ellenberg 1978).

The increased testosterone level in blood plasma of males during the rut in July/August, causing increased territorial and courting activities, does not manifest itself in a higher level of total amount of time active per 24 hours (Fig. 6a). During rut, however, median duration of active and inactive bouts were at their minimum (Fig. 9), causing a maximum in the number of active bouts per 24 hours (Fig. 10). The rumen fill theory does not explain the short active and inactive bouts during the rut. Coincident with the peak in rutting activities, food intake is at its minimum (Barth et al. 1976, Eisfeld 1977, Ellenberg 1978). Fat deposits that were built up during the spring were depleted during the rut, causing a weight depression of 20-25% in fenced deer; Ellenberg (1978) reckoned that it led to a weight loss of up to 40% in free-ranging roe deer. Activity patterns of males during the rut, therefore, were probably strongly influenced by courting and mating activities. Adult males spend more time on social behaviours during the rut than at other times of the year (Turner 1979).

After the rut, the testosterone concentra-tion, and accordingly the level of aggression, drops drastically (Short & Mann 1966, Barth et al. 1976, Sempéré et al. 1980). During autumn and winter males abandon territoriality and join smaller groups of roe deer, feeding together (see p. 17). As occurs for females, fat deposits of males are built up from September until mid-winter (Hoffmann 1977), and the higher daily level of time active in males compared to females during autumn (Fig. 6a) may be ascribed to higher nutritive needs as a consequence of their heavy weight loss during the rut.

The reason why the median duration of bouts in males did not increase from October to November, as it did for females, is not obvious. Ellenberg (1978) reported a peak in fights in October among fenced males, and Sempéré (1979b) gave accounts of exceptionally rapid movements in males in November and December. Some specific male behaviours, therefore, may influence activity patterns in autumn.

# Conclusions

Several endo- and exogenous factors influence the activity patterns of roe deer. Basically, the patterns are constrained by the anatomical structure of the digestive organs. Secondly, the patterns are influenced by seasonal physiological changes, such as are associated with mating, gestation, lactation, growth of antlers, body growth, and moulting. These factors, in turn, affect basal metabolic rates. Seasonal changes in quality, as well as quantity, of food plants also influence activity patterns. The timing, however, of physiological events and of digestibility of food plants is probably affected by changes in daylength, and the photoperiod helps to entrain the entire activity schedule.

Quality and quantity of food plants probably exert the same overall effect on

the activity patterns of all roe deer within a population, and do so according to the rumen fill theory. Activity patterns of different sex and age classes, however, are not identical throughout the seasons, and with the exceptions of rut and parturition, differences in activity patterns are probably mainly caused by variations in basal metabolic rate among sex and age classes and between seasons.

Periods of high metabolic rate per unit of body weight necessitate a high turnover rate of food in the rumen of roe deer. This is probably achieved by: 1)increased efficiency of filling the rumen, resulting in shorter average active bouts, and 2) stronger selection for high quality food plants, resulting in shorter average inactive bouts. Indeed, short median active-inactive cycles were noted in those sex and age classes that are known to have higher metabolic rates per unit of body weight, compared to those with lower rates. Energy-intake, however, is rarely in accordance with maintenance metabolic rates, and the roe deer has a cycle of deposition and mobilisation of body fat reserves (see Weiner 1975, Ellenberg 1978).

During the rut food intake in male roe deer is at a minimum, and a peak in courtship behaviour is probably the main reason for very short active and inactive bouts during this period. Also, prior to and after parturition the rumen fill theory is an unlikely explanation for short active and inactive bouts in adult females. Selection has favoured the maximisation of reproductive success. Rates of feeding, selection of diet, rates of food passage, and overall activity are only important insofar as they assure successful reproduction.

## Dansk resumé

### Aktivitetsmønster hos fritlevende rådyr *(Capreolus capreolus)* på Kalø

De fleste dyr udviser en eller anden form for rytmisk aktivitet, som dels beror på indre fysiologiske rytmer (circadiane eller cirkannuale), dels på periodiske forandringer i de omgivende stimuli, de såkaldte »Zeitgebere«, hvoraf de daglige skift mellem lys og mørke er særlig afgørende. Som hos andre drøvtyggere påvirkes aktivitetsmønsteret hos rådyr *(Capreolus capreolus)* endvidere af fordøjelsesprocesserne og af kvaliteten og mængden af den indtagne føde. Af andre faktorer, der kan påvirke rådyrets aktivitetsmønster, kan nævnes vejrforandringer, tilstedeværelse af andre rådyr og menneskelige forstyrrelser.

Formålet med denne undersøgelse er at belyse såvel det daglige som det årlige aktivitetsmønster hos fritlevende rådyr på Kalø i Østjylland. Aktivitetsmønstrenes årscyklus er desuden forsøgt relateret til de sæsonmæssige variationer i basalstofskifte, fødeoptagelse, hormonniveau og adfærd, der er omtalt i litteraturen.

Ved hjælp af automatisk aktivitetsregistrering blev der i perioden fra december 1980 til oktober 1984 indsamlet i alt 37.611 timers dechifrerbare aktivitetsdata fra 8 råer og 9 bukke (App. 1). Dyrenes bevægelser registreredes som forandringer i de modtagne radiosignalers styrke. Aktivitet blev registreret som to adfærdsparametre: »aktiv« som omfattede alle typer bevægelser i terrænet, og »inaktiv« som betegnede de perioder, hvor dyret ikke bevægede sig, og hvor det hovedsageligt var liggende.

Rådyrs daglige aktivitetsmønster var karakteriseret af hyppige skift mellem aktive og inaktive perioder (Fig. 2), i en tilsyneladende ikke-cyklisk sekvens. Når det gennemsnitlige antal aktive minutter pr. time blev udregnet over flere dage, fremtrådte dog to tydelige aktiv-toppe, én ved solopgang og én ved solnedgang. Det to-toppede aktivitetsmønster var tydeligst i vintermånederne, mens toppene, der var mindre markante i april og maj, i juni næsten var forsvundet

(Fig. 3). Fra juli blev aktiv-toppene atter tydelige, og forskellene mellem maxima og minima blev mere udprægede mod slutningen af året. I nogle måneder forekom sekundære maxima omkring de to toppe.

Om sommeren registreredes 1-2 timers forsinkelse i morgentoppen i forhold til solopgang hos råerne, og om vinteren en forsinkelse på op til 1 time af aften-toppen i forhold til solnedgang. Dette kan måske skyldes, at dyrenes indre cirkadiane rytme ikke helt kan kompensere for svingningerne i tidspunktet for henholdsvis solopgang og solnedgang i yderpunkterne om sommeren og vinteren.

Fotoperiodisk kontrol af aktivitetsmønsteret ved hjælp af »Zeitgeberne« solopgang og solnedgang synkroniserer den cirkadiske rytme hos rådyrene i bestanden mest udpræget om vinteren (Fig. 4). Det større sammenfald i aktivitet inden for bestanden forstærkes desuden af, at dyrene fra oktober/november til marts/april lever i mindre flokke, hvor aktiv-inaktiv cyklerne ofte er synkrone.

Der var stor forskel i rådyrenes totale aktive tid pr. døgn, ikke blot fra dag til dag, men også fra dyr til dyr. Der var dog en tydelig årlig cyklus (Fig. 5 og 6). Om vinteren var aktivniveauet for voksne dyr 35-45% af den totale registrerede tid. Niveauet steg gradvist om foråret, hurtigst hos bukkene (Fig. 6a), hvis maximum på 50% registreredes i april/maj. Råernes maximum, 55%, blev nået i juni, hvorefter niveauet gradvist aftog gennem resten af året. Fra september var bukkenes aktiv-niveau 4-12% højere end råernes. Unge (7-16 måneder gamle) råers aktiv-niveau varierede mindre end de voksnes, med et højere niveau om vinteren og et lavere om sommeren (Fig. 6b).

Der var tydelige sæsonmæssige forskelle i den gennemsnitlige varighed af aktive og inaktive perioder. Der var hos begge køn stor årlig variation i fordelingerne af inaktive periodelængder, (Fig. 7) med store medianværdier om vinteren (95 (♀) og 97 (♂) minutter) og små forår-sommer (42 (♀) og 40 (♂) minutter) (Fig. 8 og 9). Fordelingerne af de aktive periodelængder hos råerne varierede betydeligt mindre, mens der hos bukkene var temmelig stor variation (medianer fra 28 til 64 minutter). Hos unge råer varierede længden af både aktive og inaktive perioder året igennem meget mindre end hos voksne råer (Tab. 1). Især om sommeren var perioderne

hos de unge betydelig længere end hos voksne råer.

Antallet af aktive perioder pr. døgn er en funktion af længden af aktive og inaktive perioder og varierer året igennem omvendt proportionalt med den gennemsnitlige varighed af aktiv-inaktiv cyklerne. Hos begge køn var der 9-10 aktive perioder pr. døgn i januar-marts, hvorefter det steg til 15 i maj (Fig. 9). Dette udgjorde et maximum hos råerne, hvor niveauet indtil oktober gradvist faldt til 12, og til 9 i november-december. Hos bukkene derimod forekom det højeste antal aktive perioder (18) i brunsttiden i august.

»Vomfyldeteorien« (Moen 1973, Westoby 1974) er væsentlig for fortolkningen af de mekanismer, der bestemmer rådyrenes aktivitetsmønster. Den foreslår, at drøvtyggere må holde deres mavetarm-system fyldt konstant, og at de er begrænset af, hvor hurtigt de kan forarbejde føden, snarere end af hvor hurtigt de kan indtage den. Jo mere fordøjelig føden er, jo hurtigere vil vommen blive tømt og dyret være parat til at æde igen.

Med undtagelse af brunsttiden og tiden omkring fødslen antages det, at en gennemsnitlig daglig aktiv periode repræsenterer den tid, det tager at fylde vommen, og at en gennemsnitlig inaktiv periode repræsenterer den tid, det tager at tømme vommen. Derved vil en median periodelængde henholdsvis indeksere effektiviteten af fødeindtaget (fyldning af vommen) og af drøvtygningen (tømning af vommen). En konsekvens er, at det højeste aktivitetsniveau ikke nødvendigvis reflekterer det højeste fødeindtag. I stedet virker varigheden af aktiv-inaktiv cyklerne som et relativt mål for fødens omsætningshastighed i vommen.

Omsætningshastigheden af føden er størst (korte aktive og inaktive perioder) forår og sommer, hvor fødeplanternes fordøjelighed og næringsværdi er størst, og hvor basalstofskiftet er højest. Registrerede forskelle i varigheden af aktiv-inaktiv cykler (Fig. 8 og 9, Tab. 1) efter køn og alder kan relateres til variation i basalstofskiftet: Et højt basalstofskifte resulterer formodentlig i: 1) forøget effektivitet ved fyldning af vommen (kortere aktive perioder), og 2) en stærkere selektion af fødeplanter af høj kvalitet (kortere inaktive perioder).

Små dyr har højere basalstofskifte pr. kg kropsvægt end større dyr, og små drøvtyggere

24

som rådyret har en forholdsvis lille vom sammenlignet med større drøvtyggere. Derfor må fødens omsætningshastighed i vommen være større hos små drøvtyggere, og for at opnå det

må små drøvtyggere udsøge sig let fordøjelig føde af høj næringsværdi. Dette er grunden til, at rådyret har flere aktive perioder pr. døgn, end det er tilfældet hos større hjortearter.

Резюме на русском языке:
Характеристика активности вольно живущих косуль (Capreolus capreolus) на землях имения Калё.

Большинство животных выказывают какой нибудь вид ритмической активности, отчасти основанной на внутренних физиологических ритмах (круглосуточных или круглогодовых), и отчастью на периодических изменениях окружающих стимулов, так называемых "цейтгеберов", из которых ежедневная смена света и темноты особенно решительна. Как у других жвачных, у косуль (Capreolus capreolus) на характеристику их активности кроме того влияет принятая пища. Из прочих обстоятельств, могущих воздействовать на характеристику активности косуль, можно принять в учет перемены погоды, присутствие других косуль и беспокойство, вызванное человеком.

Целью настоящего исследования было выяснение как суточного, так и годового ритма активности живущих на воле косуль на Калё в Восточной Ютландии. Годовой цикл характеристик активности кроме того пытались привести в связь с сезонными вариациями обмена основных веществ, принятием пищи, уровнем гормонов и поведением, описанным в литературе.

При помощи автоматической регистрации активности в периоде с декабря 1980 г. по октябрь 1984 г. были собраны дешифруемые данные об активности за итого 37.611 часов от 8 самок и 9 самцов (Приложение I). Движения животных регистрировались при помощи изменений силы принятых радиосигналов. Активность регистрировалась в виде двух параметров поведения: "активность" включала всякие типы передвижения по местности, а "бездеятельность" означала периоды, в которых животные не передвигались, и главным образом оставались лежа.

Ежедневный образ активности косуль характеризовался частыми сменами активных и бездеятельных периодов (Фиг. 2), в порядке, непосредственно казавшемся не циклическим. Однако, когда среднее число активных минут за час было вычислено за несколько дней, выявлялись два четких максимума активности, один при восходе, другой при заходе солнца. Эта характеристика активности "с двумя верхушками" наиболее четко различалась в зимние месяцы, в апреле-мае эти "верхушки" были менее заметны, а в июне их едва-ли было возможно различить (Фиг. 3). С июля максимумы активности снова становились четкими, и разницы между максимумами и минимумами всё сильнее увеличивались к концу года. В некоторые месяцы наблюдались вторичные максимумы вокруг двух "верхушек".

Летом регистрировалось запоздание утреннего максимума на 1-2 часа по отношению к восходу солнца, а зимой запоздание вечернего максимума до одного часа по отношению к заходу солнца. Причиной этого может быть, что внутренний суточный ритм животных не полностью способен компенсировать изменения времени восхода и захода солнца, когда эти времена летом и зимой достигают крайних значений.

Фотопериодический контроль характеристики активности при помощи "цейтгеберов" восхода и захода солнца наиболее близко синхронизирует суточные ритмы косуль популяции зимой (Фиг. 4). Более близкому соответствию активности разных особей популяции кроме того способствует то, что косули с октября/ноября по март/апрель живут небольшими стайками, в которых циклы активности/бездеятельности часто бывают синхронными.

Была большая разница между общими длительностями активности косуль за сутки, не только со дня на день, но и с одного животного на другое. Однако, выявлялся четкий годовой цикл (Фиг. 5 и 6). Зимой уровень активности взрослых животных составлял 35-45% всего зарегистрированного времени. Весной уровень постепенно повышался, быстрее у самцов (Фиг. 6 а), у которых максимум = 50% был зарегистрирован в апреле/мае. Максимум у самок, 55%, достигался в июне, после чего уровень в течение остальной части года постепенно понижался. С сентября уровень активности самцов был на 4-12% выше, чем у самок. Уровень активности молодых самок (возраста с 7 по 16 месяцев) колебался меньше, чем взрослых самок, причем этот уровень зимой был выше, а летом ниже (Фиг. 6 b).

Были четкие сезонные разницы средней длительности периодов активности и бездеятельности. У обоих полов была значительная годовая вариация распределения бездеятельных периодов (Фиг. 7), с высокими медианными величинами зимой (95 минут у самок и 97 у самцов) и небольшими весной и летом (42 минуты у самок, 40 у самцов) (Фиг. 8 и 9). Распределения длительностей активных периодов у самок колебались значительно меньше, а у самцов была довольно сильная вариация (медианы от 28 до 64 минут). У молодых самок длительность как активных, так и бездеятельных периодов в течение всего года колебалась намного меньше, чем у взрослых самок (Табл. I). Особенно летом, периоды у молодых были значительно длительнее, чем у взрослых самок.

Число активных периодов за день является функцией длительности активных и бездеятельных периодов, и в течение года вариирует обратно пропорционально средней длительности циклов активности/ бездеятельности. У обоих полов было по 9-10 активных периодов за сутки с января по март, после чего число повышалось до 15 в мае (Фиг. 9). Это было максимумом у самок, у них уровень до октября постепенно понижался до 12, и в ноябре-декабре до 9. У самцов, напротив, наблюдалось наивысшее число активных периодов (18) в периоде течки в августе.

"Теория наполнения рубца" (Moen 1973, Westoby 1974) важна для объяснения механизмов, определяющих характеристику активности косуль. В этой теории предлагается, что жвачным необходимо содержать систему желудка-кишек постоянно наполненной, и что ограничением является быстрота, которой они способны переваривать пищу, а не быстрота, которой они могут принимать её. Чем более удобоварима пища, тем быстрее рубец опорожняется, и животное снова будет способно есть.

За исключением времени течки и периода родов, предполагается, что средний суточный период активности представляет собой время, необходимое для наполнения рубца, а средний период бездеятельности – время, нужное для его опорожнения. Следовательно, высший уровень активности не обязательно указывает на принимание наибольшего количества пищи. Вместо этого, длительность циклов активности/бездеятельности служит относительной мерой скорости оборота пищи в рубце.

Скорость оборота пищи наиболее высока весной и летом (краткие активные и бездеятельные периоды), когда удобоваримость и питательность пищевых растений наиболее высоки, и когда обмен основных веществ наиболее высок. Зарегистрированные разницы длительности активных/бездеятельных циклов (Фиг. 8 и 9, Табл. I) по полу и возрасту можно рассматривать в связи с обменом основных веществ: высокий обмен основных веществ вероятно вызывает: 1) повышение эффективности при наполнении рубца (более краткие активные периоды), и 2) повышенную разборчивость при выборе пищевых растений высокого качества (более краткие бездеятельные периоды).

У небольших животных, обмен основных веществ за кг веса тела выше, чем у больших, и у небольших жвачных, таких как косуль, рубец относительно небольшой по сравнению с более крупными жвачными. Поэтому, скорость оборота пищи в рубце у небольших жвачных должна быть выше, и, для достижения этого, небольшие жвачные принуждены выбирать себе удобоваримую пищу высокой питательности. Это является причиной того, что у косули больше активных периодов за сутки, чем у более крупных видов оленей.

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*Appendix 1. Known age of roe deer and the total time each year of decipherable activity recordings.*

| Specimen No. | Year of birth | Number of hours per year | | | | | Total |
|---|---|---|---|---|---|---|---|
| | | 1980 | 1981 | 1982 | 1983 | 1984 | |
| Females | | | | | | | |
| 302B | before 1977 | 70 | 139 | | | | 209 |
| 212A | 1974 | | 1,062 | 167 | | | 1,229 |
| 310A | 1979 | | | 639 | 5 | | 644 |
| 312A | 1977 | | | 5,583 | 5,714 | 1,826 | 13,123 |
| 404A | 1976 | | | | 159 | | 159 |
| 407A | 1982 | | | 149 | 3,734 | 3,086 | 6,969 |
| 309A* | 1983 | | | | | 2,027 | 2,027 |
| 402A | | | | | | 3,465 | 3,465 |
| Total | | 70 | 1,201 | 6,538 | 9,612 | 10,404 | 27,825 |
| Males | | | | | | | |
| 208A | 1979 | | 479 | | | | 479 |
| 209A | 1974 | | 232 | | | | 232 |
| 301A | 1979 | | 428 | 2,642 | 801 | | 3,871 |
| 309A* | 1981 | | | 362 | | | 362 |
| 110A | 1981 | | | 1,673 | 47 | | 1,720 |
| 211A | 1979 | | | | 556 | | 556 |
| 202A | 1975 | | | | 1,964 | 153 | 2,117 |
| 410A | before 1982 | | | | | 346 | 346 |
| 412A | 1980 | | | | | 103 | 103 |
| Total | | | 1,139 | 4,677 | 3,368 | 602 | 9,786 |

* Same transmitter, different animals

*Appendix 2. Total number of recorded hours and deer per month. Additional data to Fig. 3.*

| | Females | | Males | |
|---|---|---|---|---|
| | No. of hours | No. of deer | No. of hours | No. of deer |
| Jan. | 1,579 | 5 | 505 | 4 |
| Feb. | 2,498 | 7 | 644 | 2 |
| Mar. | 2,870 | 6 | 1,870 | 5 |
| Apr. | 3,156 | 8 | 828 | 3 |
| May | 3,578 | 6 | 706 | 3 |
| Jun. | 2,167 | 5 | 667 | 2 |
| Jul. | 2,270 | 5 | 689 | 3 |
| Aug. | 2.673 | 5 | 538 | 2 |
| Sep. | 1,733 | 4 | 702 | 3 |
| Oct. | 1,135 | 3 | 468 | 2 |
| Nov. | 1,110 | 3 | 472 | 2 |
| Dec. | 1,488 | 4 | | |

*Appendix 3. Results of statistical tests*

t-tests (Sokal & Rohlf 1981) indicate that the level of time active during night was significantly higher than during day for females in:

| | | | | | |
|---|---|---|---|---|---|
| September | : t = | 7.319, | df = | 1,158, | p<0.001 |
| October | : t = | 6.979, | df = | 812, | p<0.001 |
| November | : t = | 5.025, | df = | 872, | p<0.001 |
| December | : t = | 3.508, | df = | 1,277, | p<0.001 |
| January | : t = | 3.297, | df = | 1,215, | p<0.001 |

t-tests (Sokal & Rohlf 1981) indicate that the level of time active during night was significantly higher than during day for males in:

| | | | | | |
|---|---|---|---|---|---|
| September | : t = | 4.269, | df = | 536, | p<0.001 |
| October | : t = | 4.641, | df = | 367, | p<0.001 |
| November | : t = | 3.568, | df = | 365, | p<0.001 |

t-tests (Sokal & Rohlf 1981) indicate that mean daily frequency of males was significantly higher than that for females in:

| | | | | | |
|---|---|---|---|---|---|
| July | : t = | 5.86 , | df = | 205, | p<0.001 |
| August | : t = | 6.81 , | df = | 203, | p<0.001 |
| September | : t = | 3.90 , | df = | 164, | p<0.001 |

*Appendix 4. Number of deer recorded per week. Additional data to Fig. 5.*

| Week no. | 1 . . . 5 . . . . 10 . . . . 15 . . . . 20 . . . . 25 . . . . 30 . . . . 35 . . . . 40 . . . . 45 . . . . 50 . . |
|---|---|
| No. of deer | 3 2 2 2 3 3 6 4 4  4 6 5 3 3  5 7 5 5 6  6 4 3 3 4  3 2 3 3 4  5 4 3 3 4  2 2 1 2 3  2 2 1 2 2  1 2 2 3   3 3 3 |

*Appendix 5. Total number of recorded hours and deer per month. Additional data to Fig. 6a+b.*

| | Males | | Adult females | | Young females | |
|---|---|---|---|---|---|---|
| | No. of hours | No. of deer | No. of hours | No of deer | No. of hours | No. of deer |
| Jan. | 304 | 2 | 1,524 | 5 | 212 | 1 |
| Feb. | 644 | 2 | 2,348 | 7 | 299 | 1 |
| Mar. | 1,870 | 5 | 1,967 | 4 | 903 | 2 |
| Apr. | 924 | 4 | 1,918 | 5 | 970 | 2 |
| May | 723 | 3 | 2,480 | 4 | 1,098 | 2 |
| Jun. | 788 | 3 | 1,751 | 3 | | |
| Jul. | 689 | 3 | 1,731 | 4 | 539 | 1 |
| Aug. | 538 | 2 | 2,133 | 4 | 540 | 1 |
| Sep. | 702 | 3 | 1,291 | 3 | 442 | 1 |
| Oct. | 468 | 2 | 1,135 | 3 | | |
| Nov. | 472 | 2 | 911 | 2 | | |
| Dec. | 131 | 2 | 1,102 | 3 | | |

31

*Appendix 6. Monthly means and standard deviations of active and inactive bout lengths (in minutes) in female and male roe deer.*

| Month | Females | | | Males | | |
|---|---|---|---|---|---|---|
| | n | active bouts min | inactive bouts min | n | active bouts min | inactive bouts min |
| January | 7 | 66±17* | 104±22* | 5 | 65±12 | 89±11 |
| February | 9 | 60± 9 | 91±12 | 2 | 68± 1 | 98± 4 |
| March | 6 | 65± 4 | 87± 5 | 6 | 72±10 | 87± 5 |
| April | 8 | 50± 6 | 65±10* | 5 | 50± 6 | 54±10 |
| May | 6 | 48± 9* | 51± 9* | 3 | 46± 9* | 50± 7 |
| June | 5 | 55±11* | 54± 5 | 4 | 50±10 | 58±13 |
| July | 5 | 55±14* | 60±12* | 3 | 41±11* | 49± 7 |
| August | 6 | 50±11* | 60± 8* | 2 | 38±14* | 47±15* |
| September | 5 | 54±14* | 70±15* | 3 | 48± 5 | 55±20* |
| October | 3 | 49±10 | 70±10 | 2 | 57±11* | 66±16* |
| November | 3 | 61±12 | 101±30* | 3 | 48± 6 | 62±16* |
| December | 4 | 63±17 | 107±16 | | | |

* Significant differences at the 5%-level among individual deer in mean length of active and inactive bouts (analysis of variance and t-tests, Sokal & Rohlf 1981).

*Appendix 7. Number of bouts (active and inactive) and female deer per month. Additional data to Fig. 8.*

| | No. of females | No. of active bouts | No. of inactive bouts |
|---|---|---|---|
| Jan. | 7 | 607 | 683 |
| Feb. | 9 | 1,049 | 1,136 |
| Mar. | 6 | 1,080 | 1,130 |
| Apr. | 8 | 1,615 | 1,677 |
| May | 6 | 2,193 | 2,274 |
| Jun. | 5 | 1,124 | 1,209 |
| Jul. | 5 | 1,116 | 1,214 |
| Aug. | 6 | 1,448 | 1,534 |
| Sep. | 5 | 820 | 905 |
| Oct. | 3 | 536 | 577 |
| Nov. | 3 | 419 | 430 |
| Dec. | 5 | 524 | 597 |

*Appendix 8. Number of bouts (active and inactive) and male deer per month. Additional data to Fig. 9.*

| | No. of females | No. of active bouts | No. of inactive bouts |
|---|---|---|---|
| Jan. | 4 | 189 | 225 |
| Feb. | 2 | 213 | 236 |
| Mar. | 6 | 715 | 757 |
| Apr. | 5 | 560 | 623 |
| May | 3 | 408 | 481 |
| Jun. | 4 | 500 | 571 |
| Jul. | 3 | 428 | 504 |
| Aug. | 2 | 323 | 380 |
| Sep. | 3 | 341 | 373 |
| Oct. | 2 | 217 | 250 |
| Nov. | 2 | 244 | 265 |
| Dec. | | | |

*Appendix 9. Number of deer and days per month. Additional data to Fig. 10.*

| | No. of deer | No. of days | No. of deer | No. of days |
|---|---|---|---|---|
| Jan. | 7 | 123 | 4 | 47 |
| Feb. | 9 | 165 | 2 | 36 |
| Mar. | 6 | 155 | 6 | 112 |
| Apr. | 8 | 165 | 5 | 77 |
| May | 6 | 180 | 4 | 75 |
| Jun. | 5 | 132 | 4 | 74 |
| Jul. | 5 | 139 | 3 | 68 |
| Aug. | 6 | 163 | 2 | 42 |
| Sep. | 5 | 119 | 3 | 47 |
| Oct. | 3 | 70 | 2 | 41 |
| Nov. | 3 | 66 | 2 | 35 |
| Dec. | 5 | 134 | | |

Vol. 13