

Reindeer 24-hr within and between group synchronicity in summer *versus* environmental variables

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Abstract: The impact of abiotic stimuli on the circadian activity rhythm of *Rangifer* has long been debated. Their highly gregarious and mobile behaviour presupposes synchronized behaviour within a group, while a predominant abiotic influence would be expected to synchronize separate, independent groups subjected to the same environment. We tested within and between group synchronization of semi-domestic reindeer during summer observing 6 independent groups located in close proximity to each other. We also tested how some external environmental factors affected the animals' behaviour. Activity of all individuals (3 females in 6 groups, $n = 18$ reindeer) was recorded every 10 minutes 24-hrs a day, along with weather variables and biotic factors such as insect harassment. Data were divided into two periods of 8 and 6 days, respectively, separated by a period of 6 days. Animals within a group showed highly synchronized behaviour, reflected in overlapping periods of grazing and ruminating. There was little or no synchronization between groups, reflected by little or infrequent overlapping of activities amongst some of the groups. Rarely were all 6 groups active or inactive simultaneously. There was no consistent or significant influence on the reindeers' behaviour by any of the environmental variables recorded. Thus, and as expected, in the absence of external environmental stimuli, the activity of individuals within a group was synchronized. However, there was no synchronization amongst independent groups. This supports the claim that during summer, in the absence of disturbance from stimuli such as insect harassment or anthropogenic activities, reindeer have a 24-hr polycyclic activity rhythm independent of climatic variables. Instead of abiotic factors, such as light, reindeers' activity rhythms were defined by internal physiological processes and intra-specific group interactions reflected in almost complete within group synchronization and lack of between group synchronization.

Key words: activity, behaviour, circadian rhythm, feeding, light, *Rangifer tarandus*, solar radiation.

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Introduction

During the growing season, reindeer, like all northern ungulates, attempt to maximize their energy input. Reindeer are highly gregarious and social animals that most often live in groups. Group synchronization logically minimises interruptions in an individual's feeding and ruminating rhythm, and many factors likely support within-group synchroni-

zation, or work against the lack of it. Although it has long been claimed and observed that reindeer groups operate in apparent synchronization (Thomson, 1977; Skogland, 1984), *i.e.*, timing their activities to each other, this has never been tested at an individual or group level.

Selection forces have likely reinforced synchronized

behaviour within a group, but does synchronized behaviour between independent groups exist and if so, how and why would this occur? The impact of abiotic stimuli on the circadian activity rhythm of *Rangifer* has long been debated (see Colman *et al.*, 2002). A predominant abiotic influence would be expected to synchronize separate, independent groups subjected to the same environment. The theory that reindeer are mostly crepuscular (Roby, 1978, 1980; Eriksson *et al.*, 1981; Russell & Martell, 1986; Smith & Collins, 1989), *i.e.* concentrate their feeding behaviour during the twilights, maintains that changes in light (sun rising or setting, or the strength of solar radiation during the arctic summer) “triggers” feeding behaviour and produces synchronicity amongst reindeer within a group. If this were true, we maintain that this would also produce synchronization amongst all reindeer groups within the same geographical area. We tested these theories using data from groups of semi-domestic reindeer in separate enclosures. We tested both within group synchronization and between group synchronization amongst 6 separate reindeer groups within the same geographical area and during two periods. We also tested whether environmental variables such as light intensity “triggered” reindeers’ feeding behaviour.

Table 1. Pearson’s correlation (synchronization) among the 6 groups, Finnmark, June 1999 for a) period 1 and (b) period 3. Correlation coefficients ($P < 0.05$ shown in bold).

a) Period 1

| | Group 1 | Group 2 | Group 3 | Group 4 | Group 5 |
|---------|---------|-------------|---------|---------|-------------|
| Group 1 | -0,11 | -0,09 | 0,01 | -0,17 | -0,18 |
| Group 2 | | 0,39 | 0,13 | -0,23 | -0,14 |
| Group 3 | | | 0,17 | -0,02 | -0,11 |
| Group 4 | | | | 0,06 | -0,19 |
| Group 5 | | | | | 0,36 |

b) Period 3

| | Group 1 | Group 2 | Group 3 | Group 4 | Group 5 |
|---------|---------|---------|---------|-------------|---------|
| Group 1 | 0,07 | -0,04 | -0,21 | 0,2 | -0,18 |
| Group 2 | | 0,18 | -0,17 | 0,44 | -0,03 |
| Group 3 | | | 0,19 | 0,28 | -0,01 |
| Group 4 | | | | -0,09 | 0,22 |
| Group 5 | | | | | 0,02 |

Methods

The study was conducted 9-29 June 1999, in an open farm landscape in Bognelvdalen, approximately 5 km from Langfjordbotn, Finnmark County (22°19'E, 69°59'N; Fig. 1). The experimental area was a level 2 ha field at sea level. This area had not been cul-

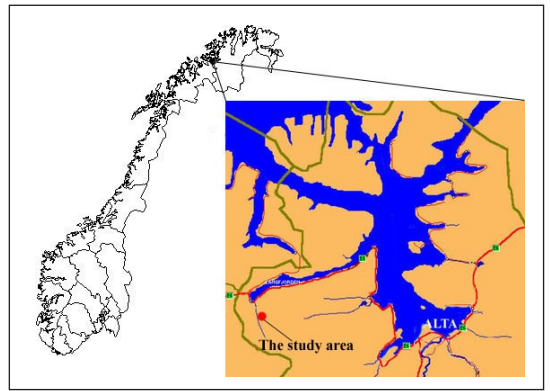


Fig. 1. Location of the study area in Bognelvdalen, West-Finnmark, Norway.

tivated during the last 25 years and consisted of a homogenous mixture of natural and earlier planted grass species. The experiment’s location in an open agricultural area, combined with a short distance from the ocean and a cold-water river system, provided an almost constant wind over the experimental area. This, in combination with the timing of the experiment in June, probably reduced harassment on animals from parasitic flies compared to inland areas and later in the summer season, an important factor for the outcome of the experiment. No insect avoidance/disturbance behavior was registered for any of the animals for the duration of the experiment (Eidesen, 2002).

Six 40 m × 50 m enclosures were built, and the fences between the enclosures were cased with fabric to prevent visible contact between the animals in different enclosures. All corners out to 3 m along the fence were covered with the same fabric to provide animals with shelter and shade. To provide the animals with drinking water, two buckets with running water were placed opposite each other in the middle of the 50 m sides in each enclosure. The animals foraged on natural vegetation.

Three out of eighteen female reindeer yearlings were released into each of 6 separate enclosures and observed during two independent periods; period 1 was 9-16.6.99 (8 days) and period 3 was 24-29.6.99 (6 days). The second period was excluded from this study, and thus, we consider the first and third periods independent of each other. All animals were individually numbered with collars for identification. Altmann’s (1974) instantaneous scan sampling technique was used for data collection at 10 minutes intervals 24-hrs a day. Observations were taken from 3 m high observation towers placed between enclosure 1 and 2, 3 and 4 and between 5 and 6. To avoid possible bias caused by the activities of observers taking their positions in the towers, they sat still for at

Table 2. Pearson's correlation (Corr.) and probability values (*P*) between the feeding behavior for each group and the environmental variables solar radiation (light), temperature (temp.), wind speed (W. speed), and wind direction (W. dir. 1 is wind direction different than from the north and W. dir. 2 is wind direction different than that from the west) during periods 1 and 3.

| Group | Period | Light | | Temp. | | W. speed | | W. dir. 1 | | W. dir. 2 | |
|-------|--------|-------|----------|-------|----------|----------|----------|-----------|----------|-----------|----------|
| | | Corr. | <i>P</i> | Corr. | <i>P</i> | Corr. | <i>P</i> | Corr. | <i>P</i> | Corr. | <i>P</i> |
| 1 | 1 | -0.02 | 0.85 | -0.07 | 0.50 | -0.04 | 0.72 | -0.08 | 0.42 | 0.16 | 0.12 |
| | 3 | 0.14 | 0.21 | 0.08 | 0.46 | 0.02 | 0.86 | -0.06 | 0.61 | -0.21 | 0.06 |
| 2 | 1 | -0.01 | 0.95 | -0.10 | 0.32 | 0.06 | 0.56 | -0.02 | 0.82 | 0.00 | 0.97 |
| | 3 | -0.21 | 0.07 | -0.17 | 0.13 | -0.10 | 0.37 | -0.04 | 0.73 | 0.00 | 0.97 |
| 3 | 1 | 0.11 | 0.28 | -0.03 | 0.80 | -0.04 | 0.71 | 0.03 | 0.76 | -0.07 | 0.49 |
| | 3 | -0.03 | 0.81 | -0.10 | 0.37 | 0.05 | 0.64 | -0.01 | 0.96 | 0.07 | 0.53 |
| 4 | 1 | 0.04 | 0.71 | -0.09 | 0.39 | -0.02 | 0.82 | -0.14 | 0.17 | 0.10 | 0.34 |
| | 3 | -0.04 | 0.70 | -0.02 | 0.84 | 0.02 | 0.86 | 0.13 | 0.27 | -0.11 | 0.32 |
| 5 | 1 | 0.08 | 0.44 | 0.13 | 0.22 | 0.08 | 0.42 | 0.08 | 0.43 | 0.03 | 0.81 |
| | 3 | 0.03 | 0.79 | 0.04 | 0.73 | 0.01 | 0.96 | -0.08 | 0.50 | 0.05 | 0.68 |

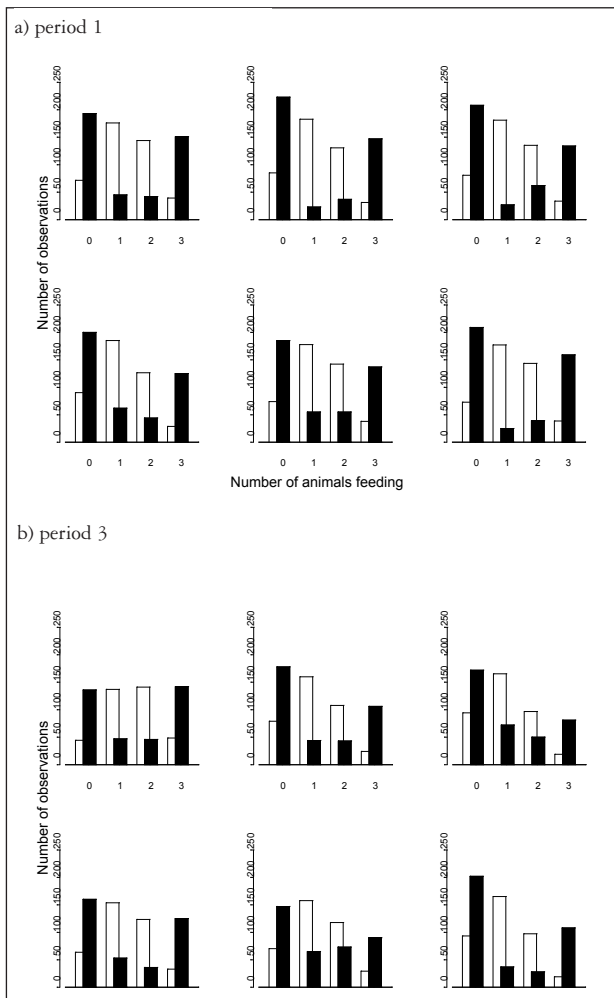


Fig. 2. Synchronization amongst individuals within each of the 6 groups during a) period 1 and b) period 3. All (3) or no (0) animals feeding much more often than expected.

least 10 minutes before observations began. Observations were conducted simultaneously in all six enclosures. Usually, observations were taken using eyesight only, but binoculars (8×21 or 8×40) were used when necessary. Type of activity: *feeding, lying head up, lying head down, standing, walking and running* were recorded on prepared field sheets for every individual. Only feeding activities were used in the present analyses. The use of succeeding samples of all animals for every 10 minutes was expected to produce a high degree of autocorrelation. Correlations between observations with different time intervals were tested, and between two observations of a one-hour interval the degree of autocorrelation was acceptable. Furthermore, there was only a minimal decrease in correlation if the interval was increased to more than one hour. Thus, mean values of all samples in one-hour intervals were calculated (6 samples with 3 animals each, equaled 18 samples per hour). Due to unforeseen problems, some of the one-hour periods had fewer samples, and in the analyses, each one-hour period was weighted according to the number of samples it was based on.

A Grant Squirrel data logger model 1200 was used together with five different meteorological sensors to record the following climatic parameters; *wind speed, wind direction, air temperature, and solar radiation*. The data logger and all sensors were mounted on a Grant Instruments mini-meteorological station located between enclosure 3 and 4, 10 m from the enclosure. The data logger was supplied with a 12V battery. *Wind speed* was measured with a Vector Instruments switching

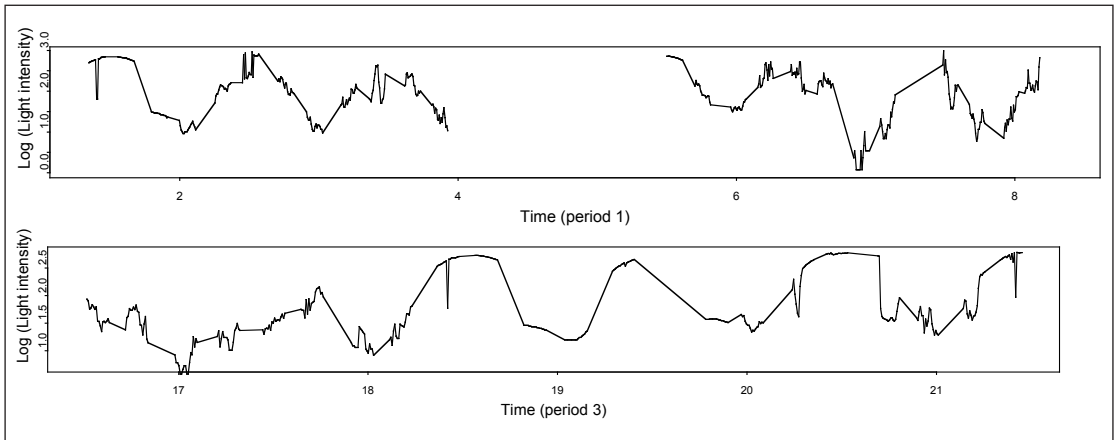


Fig. 3. The 24-hour cycle of solar radiation (light intensity) during periods 1 and 3, Finnmark, June 1999. The change in day (the numbers along the x-axis) represent midnight. Missing data between day 4 and 6 in period 1 was caused by a storm.

anemometer A100R with a threshold of 0.3 m/s, and an accuracy of ± 0.1 m/s. *Wind direction* was measured with a Vector Instruments Porton Windvane W200 with a threshold of 0.3 m/s, and an accuracy of ± 4 °C. *Air temperature* was measured with a Y.S.I. HS thermistor sensor with a maximum deviation from the actual temperature of 0.2 °C in the range of 0 °C to 70 °C. This sensor was placed 1.5 m above ground, and was not covered. Thus, when there was sun, the temperature recorded was in the sun, and when there was shade, the temperature recorded was in the shade. *Solar radiation* was monitored directly by means of a Skye Instruments pyranometer sensor with a 300-1100 nm silicon diffused photocell. All parameters were measured continuously and an average for every 10 minutes period was logged. Although there is 24-hrs of "daylight" during the polar summer, solar radiation continues to have a similar cycle as throughout the rest of the year (Krüll *et al.*, 1985). Because of this, we were able to test the reindeers' feeding cycles with changes in light intensity, similar to (Krüll *et al.*, 1985). Once a week, the data from the logger was transferred to a computer and later imported into a Microsoft Excel worksheet.

Results

As expected, the reindeer within each group behaved as a group, lying and ruminating together, feeding and moving together, and generally, were well synchronized throughout the entire experimental period.

We have plotted the expected number of animals feeding simultaneously per group/period, assuming that they are not synchronized, *versus* their true behavior (the observed number of simultaneously feeding animals). The expected number is the total

number of observations per group multiplied by the binomial distribution (based on the actual recorded percentage of feeding behavior in each group and period). For instance, each animal in group 1, period 1 were feeding on average in 45% of the observations (431 observations). If the animals were behaving independently, we would expect to observe two or three animals feeding simultaneously most (74%) of the time, while we actually observed zero or all three animals feeding together most of the time (80% of the observations). The results support that for all 6 groups during both periods, none or all three individuals tended to feed simultaneously, supporting strong within-group feeding synchronicity (Fig. 2a & b).

Between the groups, there was very little synchronization, reflected by the fact that out of 30 possible group correlations, all coefficients were below 0.5 and only 4 correlations were significant ($P < 0.05$) (Table 1a & b). We consider these 4 statically significant correlations as random events that do not represent any biological tendencies. The existence of an external, environmental stimulus simultaneously triggering all 6 groups was further dismissed by the lack of any effect found for the recorded environmental variables on the reindeers' feeding behaviour (Table 2). As expected, solar radiation (light intensity) maintained a 24-hour cycle throughout the study period (Fig. 3). When testing specifically for light intensity, there was no effect of light on any of the groups feeding activities independently or during either period (Table 2; Fig. 4).

Discussion

Semi-domestic reindeer in separate enclosures showed within group synchronicity with no dependence of feeding behaviour on external abiotic stimulus. The

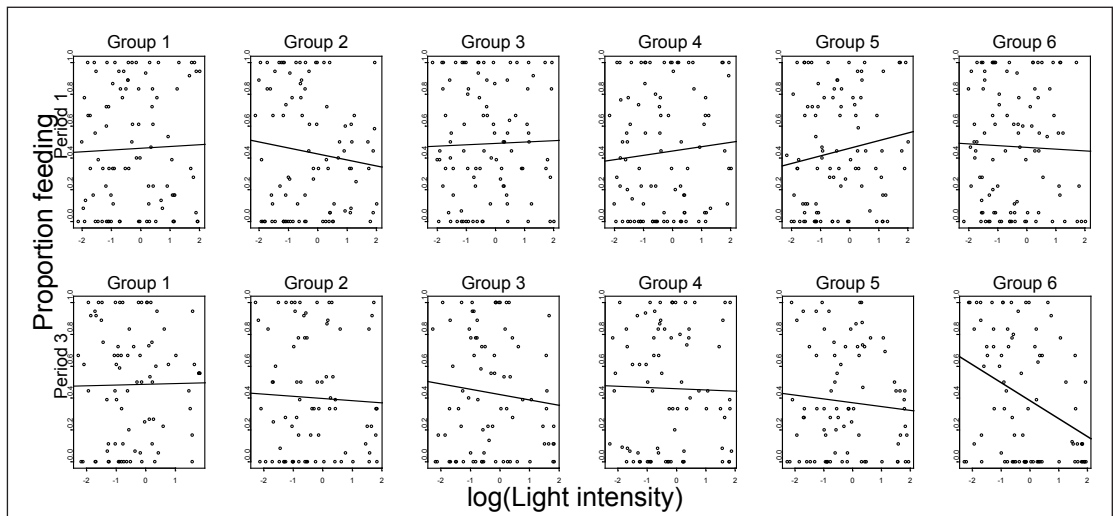


Fig. 4. Linear regression lines indicating that feeding did not depend on light intensity during the arctic summer, Finnmark, June 1999.

lack of “zeitgebers” (Krüll *et al.*, 1985) was further supported by the low level of synchronicity between separate groups located in the same geographical area. Individual reindeer are indeed dependent upon “the group”. The group feeds, moves, reacts, learns, and probably evolves as an entity. Yet equally so, and most likely vital to survival in the challenging and variable environment reindeer inhabit, the group is, or tries to be, independent of unnecessary restrictions any dependence on light or other zeitgebers would place on them. One group also operates independent from other surrounding groups, regardless of whether individuals of two separate groups are of the same sex or age as was recorded here. The existence of within and lack of between group synchronization may play an important role in connection with intra-specific competition. Further studies are needed to investigate sexual segregation of adult male groups from female post-calving groups during summer and whether this may reflect intra-specific competition or different feeding capacities and thus, the need for separate, more synchronized groups during the growing season in order to maximise intake.

Numerous studies have claimed that *Rangifer* are essentially a diurnal animal that attune their feeding rhythm to set points of sunrise and sunset (crepuscular), and that their total amount of activity over 24-hr periods is controlled by photoperiod (Roby, 1978, 1980; Eriksson *et al.*, 1981; Russell & Martell, 1986; Smith & Collins, 1989). However, similar to Maier & White (1998) and Colman *et al.* (2002), we found no effect of light on reindeer feeding activity during summer, despite the clear 24-hour cycle for solar radiation. Thus, we maintain that reindeer groups

should not be dependent on light or other Zeitgebers during the growing season when the opportunity for maximum forage intake and energy input exists. Rather, reindeer (groups) appear to be 24-hr time maximizers, ultimately limited by intake and digestion. Group movements and coordinated reactions towards stimuli presuppose the need for behavioural synchronization. *Rangifer* appear to be adapted to a polycyclic activity rhythm during summer (Maier & White, 1998; Colman *et al.*, 2002), maintaining a regular feeding routine that maximizes foraging efficiency and is independent of external Zeitgebers. In addition to light, the other environmental variables varied considerably during and between the two periods. This variation provided the basis for testing the actual effects those variables had on the reindeers’ behavior. Similar to light, the reindeers’ feeding cycles and within and between group synchronicity were not influenced by any of the recorded environmental variables during either period separately or combined.

The most important factor influencing the feeding rhythm for female reindeer in our experiment was the activities of the other two reindeer in her group. The influence of the group placed upon individuals is likely a driving force in daily decisions made at the individual level amongst *Rangifer* in specific, but also other social organisms in general. Group cohesion in terms of movements, reactions towards disturbances, calving, or other events, may rely on an optimal level of intra-specific and intra-group synchronization. Other elements of group interactions, such as an individual’s size, sex, or age, could play a major role in the time related allocation of activities for the entire

group and thus, other individuals. Optimizing group synchronization should therefore reduce suboptimal foraging, competition and ultimately, improve both individual and herd survival and production.

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Abstract in Norwegian / Sammendrag:

Betydningen av abiotiske variabler på reinens døgnrytme har lenge vært diskutert. Med sin gruppeadferd og mobilitet forventer man samhandling innenfor ei gruppe, mens abiotiske variabler forventes å synkronisere adferden mellom adskilte grupper i samme miljø. Vi testet adferdssynkroniseringen innenfor og mellom grupper av tamrein ved å observere aktiviteteter i seks uavhengige grupper hver med tre simler. Vi testet også hvordan noen miljøvariabler påvirker dyrenes adferd. Aktiviteten til alle individene ble observert hvert tiende minutt hele døgnet sammen med klimatiske forhold og biotiske variabler som insektplage. Dyrene innenfor ei gruppe viste klart felles adferd med samme beite- og liggeperioder. Det var lite

eller ingen synkronisering mellom grupper, idet det var lite eller tilfeldig sammenfall av aktiviteter. Sjelden var alle seks gruppene aktive eller inaktive samtidig. Aktiviteten til individer innenfor en gruppe var synkronisert som forventet, uten eksterne miljøvariabler. Derimot var det ingen synkronisering mellom uavhengige grupper. Dette støtter teorien at reinsdyr har en 24-t polisyklisk aktivitetsrytme uavhengig av klimatiske variabler på sommeren og uten sterke påvirkninger utenfra som parasittiske insekter eller menneskelige aktiviteter. Vårt forsøk viste at reinens aktivitetsrytme tydeligvis var definert av interne fysiologiske prosesser og interaksjoner innen gruppen.