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Where clocks are redundant: weak circadian mechanisms in reindeer living under polar photic conditions

**Bob E. H. van Oort · Nicholas J. C. Tyler ·
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Abstract Biological rhythms are a result of interplay between endogenous clocks and the ambient light–dark (LD) cycle. Biological timing in resident polar organisms presents a conundrum because these experience distinct daily LD cycles for only a few weeks each year. We measured locomotor activity in reindeer, *Rangifer tarandus platyrhynchus* (SR, $n=5$ and 6) and *R. tarandus tarandus* (NR, $n=6$), ranging freely at 78 and 70°N, respectively, continuously throughout 1 year using data loggers. NR, but not SR, are gregarious which enabled us to examine the integrated effects of differences in social organisation and the photic environment at two different latitudes on the organisation of activity. In both sub-species, ultradian bouts of activity and inactivity alternated across the 24-h day throughout the year. This pattern was modified by the LD cycle in NR but barely at all in SR. Periodogram analysis revealed significant ultradian rhythmicity in both sub-species; the frequency of daily cycles of activity increased from three per day in winter to nearly five in summer. We conclude that this increase, and a concomitant increase in the level of daily activity, reflected the seasonal increase in the animals' appetite and the quality of their forage. Secondly, the combination, most evident in SR, of a weak photic response, weak circadian mechanisms and a weak social synchronization reduces the constraints of biological timing in an environment which is effectively non-rhythmic most of the year and permits expression of the basic ultradian pattern of ruminant activity. Third, the weaker 24-h rhythmicity in SR compared to NR indicates a latitudinal decrease in circadian organization and photic responsiveness in *Rangifer*.

Introduction

The cycle of the solar day creates the temporal framework to which plants and animals have adapted through the evolution of 'biological rhythms'. These rhythms are driven by endogenous genetic 'clocks' (e.g. King and Takahashi 2000) which enable organisms to anticipate and, hence, to prepare for predictable changes in their environment. This occurs as a result of an interplay between the clocks and exogenous time cues (Zeitgebers), the most prominent of which is the 24-h (diel) light–dark (LD) cycle. This cycle, besides signalling the passing of the day, also varies throughout the year in an entirely predicable manner at any given latitude. As latitude increases, however, there is a corresponding reduction in the amplitude of the LD cycle for an increasingly large part of the year. At 78°N in Svalbard, for example, the sun remains >6° below the horizon from mid-November until the end of January; in this period, the 'polar night', there is continuous darkness

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(DD) during which light intensity never reaches civil twilight (10 lx). In contrast, from April until September, there is a 'polar day' when light intensity remains continually above civil twilight (LL). Terrestrial organisms resident at this latitude, therefore, only experience distinct LD cycles for approximately 18 weeks each year, 9 weeks in spring and 9 weeks in autumn. The presence of circadian clocks is ubiquitous and independent of environmental conditions. Their expression, however, is not self-evident and, consequently, biological timing in polar species presents a conundrum owing to the extreme range of photic conditions characteristic of high latitudes.

Recently, we have reported that reindeer (*Rangifer tarandus* L.) display only weak circadian organisation in their daily pattern of activity. Remarkably, the animals remained active throughout the 24-h day throughout the year, and the pattern of their activity changed only slightly in response to the very large seasonal changes in photoperiod (van Oort et al. 2005). In the present study, we investigated the degree of ultradian and seasonal organisation of locomotor activity in free-living reindeer in relation to their photic environment. We studied sub-species living at 70°N (*R. tarandus tarandus* 'NR') and 78°N (*R. tarandus platyrhynchus* 'SR'). The photic regime at 70°N shares features in common with that at 78°N; the sun remains above the horizon from late May until the end of July (polar day). In winter, it remains between 0 and 6° below the horizon from the end of November until the middle of January. Thus, though there is no true polar night at 70°N, for 7 weeks in the middle of winter, the light intensity never exceeds twilight. In addition to living under different photic regimes, NR are highly gregarious while SR are not (Skogland 1989). Our comparative approach, therefore, allowed us to examine the integrated effects of differences in social organisation and photic environment at two different latitudes on the temporal pattern of daily activity in reindeer.

Materials and methods

Animals

Trials were conducted in two sub-species of reindeer using animals ranging freely in their natural habitat: Svalbard reindeer (*R. tarandus platyrhynchus*, Vrolik 1829), a high Arctic resident, in Adventdalen on the Svalbard archipelago (78°N, 16′E) and sub-Arctic Eurasian mountain reindeer (*R. tarandus tarandus*, L., 'Norwegian reindeer') in northern Norway (70°N, 23′E).

Six female NR were monitored from December 1998 until November 1999. These animals belonged to a herd of approximately 700 semi-domesticated reindeer herded by

Sámi pastoralists. All the NR had entered their third year, and their age in December 1998 was therefore 31 months. Six male SR were monitored from October 1997 to May 1998 and a further five from April to October 1999. The animals were selected singly and at random from small groups (<5 animals) in a population of approximately 700 reindeer (Tyler and Øritsland 1999). All the SR were sub-adults: their estimated ages at the start of each trial, based on the pattern of eruption and wear of their incisiform and molariform teeth (Miller 1974; Leader-Williams 1979), were 28 and 22 months in the two groups, respectively. Consequently, there was neither any pronounced difference in body size (associated with sexual dimorphism) between the NR and the SR nor any likelihood that the SR (males) participated to any significant extent in the rut (as was subsequently evident from the actograms). In the absence of these factors which might potentially have influenced the daily patterns of activity, the sex difference between the two experimental groups was not considered further. The capture and instrumentation of the animals are described by van Oort et al. (2004).

Permission to work with reindeer was granted by the Norwegian Committee on Ethics in Animal Experimentation and, in the case of the SR, also by the Governor of Svalbard.

Recording and presentation of data

Activity was recorded continuously on each animal using small data loggers (Actiwatch AW4, Cambridge Neurotechnology, UK; van Oort et al. 2004). The loggers measured motion-induced voltage changes at 32 Hz, converted these into values (counts) integrated over sampling periods (bins) of 10 and 15 min for SR and NR, respectively, and stored the data as total counts per bin. On recovery, the data were downloaded from the loggers and the counts were decoded in two general categories of behaviour, 'activity' (1) and 'inactivity' (0), by the method of van Oort et al. (2004). This procedure yielded time series consisting of alternate, discrete bouts of activity and inactivity in continuous records lasting between 5 and 12 months.

Individual data were presented as double-plotted actograms created in Circadia software (Behavioral Cybernetics, Cambridge, MA, USA) which provided a qualitative description of temporal (24 h) patterns of activity. The average monthly pattern of daily activity was described using line plots based on pooled samples for each subspecies. The plots presented the median rate of activity (minute per hour) across 24 h in periods of 10 days centred on the 15th of each month.

Quantitative presentations of data included the rate of activity (hour per 24 h) and the median duration (h) of bouts (*sensu* Metz 1975) of activity and inactivity deter-

mined for each animal each day. Data were pooled for all animals by sub-species and plotted as weekly (rate) and monthly (duration) medians (range) throughout 1 year. Annual fluctuations in the rate of daily activity were quantified using a cosine function:

$$C(t) = m + A \cdot cos((2\pi(t - \varphi))/P) \qquad (1)$$

where t is time in Julian days (day 1=1 January) and P is the period of the cycle. Assuming annual cycles, P was set equal to 365. Parameters m [midline estimating statistic of rhythm (mesor), hour per 24 h], A (amplitude, hour per 24 h) and φ [acrophase, Julian day (day 1=1 January)] were fitted by least-square approximation of the data using nonlinear regression (SPSS 1998) after which φ was converted back to Gregorian date. The data for one SR, selected at random, were discarded from the cosinor analysis to make the sample size homogeneous at $n=5$.

In all presentations, the data for the two trials in SR (October–May and April–October) were combined in single plots to illustrate the pattern of activity across one full year. In addition, plots of daily rate of activity and bout lengths in both NR and SR were folded at 1 January to facilitate comparison between the two sub-species.

Periodogram analysis

The presence and periodicity of rhythms of activity were determined by F-periodogram analysis based on the algorithm of Dörrscheidt and Beck (1975). Analyses were performed on data from one to three consecutive 10-day periods in each reindeer each month using Circadia. Periodicity was recognised where peaks in the circadian ($\tau \approx 24$ h) or ultradian ($\tau' \approx 4$–9 h) ranges exceeded the 95% confidence limits. Ultradian periods that were harmonics of circadian periods, or vice versa, were rejected. The validity of τ and τ' was determined by comparing their respective amplitudes (Q); τ' was accepted as valid where $Q\tau' > Q\tau$, and τ was accepted as valid where $Q\tau' < Q\tau$. The relative amplitude of rhythms [$d(Q)p$] was calculated according to Gerkema et al. (1994).

We used interval (bin) samples, and, consequently, any period of x h could have fallen within the range of $x \pm$ one sampling interval (10 min for SR and 15 min for NR). We therefore established critical ranges at both the solstices and the equinoxes with which to distinguish potential circadian from diel rhythms (van Oort et al. 2005, supplementary information).

Statistical analysis

Values of parameters m, A and φ generated by the cosine model (Eq. 1) were compared between NR and SR using t tests assuming unequal variances. The duration of bouts of activity and inactivity, respectively, was compared between the two sub-species using Mann–Whitney U tests. The periodicity of the ultradian rhythms was compared across months using Kruskal–Wallis tests. H_o was rejected at P (two-tailed) <0.05 in all tests. All analyses were performed in SPSS for Windows Release 9.0.0 (SPSS 1998).

Terminology

In the high Arctic where, even at sea level, snow may lie for 10 months of the year, the common nomenclature for different seasons is potentially misleading. At the 'spring' equinox (21st of March), for example, ambient temperatures may frequently fall below −20°C and reindeer and forage plants alike are still fully winter-adapted. Likewise, in some years, the 'spring' melt may not occur until after the summer solstice, even though the animals will already have been exposed to LL for several weeks by this time. In this paper, therefore, the terms 'spring', 'summer', 'autumn' and 'winter' refer to the photic environment only and bear no connotation regarding ambient temperature, snow cover or the growth of plants. Moreover, the morning and evening periods of twilight are greatly extended at high latitudes; at 70 and 78°N, for example, there are 14 h, 20 min and 16 h, 18 min daylight (>10 lx), respectively, at the spring and autumn 'equinoxes'. By convention, however, we have chosen to include the dates of the equinoxes as points of reference.

Results

Trials in NR yielded six continuous records each lasting 329 days. These included 126,155 bins classified as 'activity' and 63,919 bins classified as 'inactivity'. Trials in SR yielded five continuous records in winter (October to April) each lasting 202 days and six continuous records in late winter, summer and early winter (April to October) each lasting 161 days. Combining these included 159,565 bins classified as 'activity' and 120,513 bins classified as 'inactivity'.

Both sub-species of reindeer displayed a typical ruminant pattern of behaviour consisting of alternating ultradian bouts of activity and inactivity. Both were active throughout the 24-h day around the year (Figs. 1 and 2). In each, however, the 24-h organisation of the bouts was modified whenever there was a distinct LD cycle. Under LD, the reindeer tended to be less active for some hours preceding dawn and following dusk. This was apparent for approximately 9 months of the year, from late July until early May, in NR but for only 5 months of the year, from early February until mid-April and from late August until mid-November, in SR, in which, in any case, the 24-h organisation of the bouts was much weaker.

The diel rhythm of activity in NR was clearly defined with respect to transitions between L and D phases (Figs. 1 and 3). The onset of activity in the morning and the offset in the evening were closely associated with dawn and dusk, respectively. From late November until mid-January, when the interval between the onset and offset of civil twilight was short (<7 h), NR displayed a bout of activity which lasted throughout the twilight day and a longer, though less clearly defined, bout of activity at night. From mid-January, when the sun first broke the horizon, in most individuals the daytime bout of activity split into a morning bout and an evening bout divided by a period of inactivity. Later, as day length increased, these two bouts became increasingly separated until, early in April, the reindeer once again became active in the middle of the day. Parallel with this, their nighttime bout of activity became progressively compressed until, early in April, it fused with the advancing morning bout. From the beginning of May, when the sun remained above the horizon, the animals became inter-mittently active around the clock. In autumn the pattern was reversed: early in August, when the sun dropped below the horizon at midnight, the animals began again to display a daily rhythm in which their continuous activity was interrupted by a conspicuous period of inactivity preceding dawn and another one following dusk, respectively.

SR, by contrast, displayed only faint daily rhythmicity when exposed to the LD cycles of spring and autumn (Figs. 2 and 3). There was no sharp onset of activity in the morning nor sharp offset in the evening associated with dawn and dusk, respectively, nor any clear bouts of inactivity preceding dawn and following dusk.

Both sub-species displayed a high degree of organisation at the ultradian level. Regularly recurring bouts of activity and inactivity created conspicuous bands in the actograms which advanced or retreated from day to day (Figs. 1 and 2). These bands were most pronounced in SR during DD. They were apparent, though weaker, in both sub-species during LD but were largely absent under LL.

Consistent with visual inspection of the actograms, periodogram analysis revealed that diel and circadian rhythms were all but absent in both NR and SR in June. NR displayed diel rhythmicity in September, January and March; SR, by contrast, displayed only a low level of diel rhythmicity and only in March (van Oort et al. 2005). Both sub-species displayed sustained ultradian rhythmicity in all months of the year, though the prevalence of this was lower in summer (June–August) in NR (Table 1). The average (median) periodicity of the ultradian rhythms varied significantly across months (range=5–8 h; Kruskal–Wallis, NR $\chi^2=$ 52.7, df=11, P<0.001; SR χ^2=101.5, df=11, P<0.001), being shortest in summer in both sub-species (Table 1).

NR were generally more active than SR: the average (mesor) activity time across the year was 15.8 h·24 h^{-1} in

NR compared to 13.7 h·24 h^{-1} in SR (t=7.11, P<0.001; Table 2). Both sub-species displayed a clear annual cycle in daily activity (Fig. 4). The amplitude of the cycle was significantly greater in SR (2.3 h·24 h^{-1}) than in NR (1.5 h·24 h^{-1}, t=4.37, P<0.001; Fig. 4, Table 2). In both sub-species, the rate of daily activity increased from a nadir in winter to a peak in summer and thereafter declined. The acrophase in the cosine model (Eq. 1) occurred significantly earlier in NR (29 July) compared with SR (13 August; t=−7.90, P<0.001; Fig. 4, Table 2).

Bouts of activity were significantly longer in NR (median=2.75 h, interquartile range=1.75–4.00 h) com-pared with SR (median=2.00 h, interquartile range=0.67–3.00 h, z=−42.5, P<0.001). Their duration, however, was highly variable in all months and displayed no clear seasonal fluctuation in either sub-species (Fig. 5). Bouts of inactivity were also significantly longer in NR (median= 1.25 h, interquartile range=0.75–2.00 h) compared with SR (median=1.17 h, interquartile range=0.50–2.17 h, z=−9.2, P<0.001), although the difference was quite small, and tended to be shorter in summer and autumn (June to October) than during the rest of the year (Fig. 5).

Discussion

Daily (≈24 h) rhythms of activity in free-living reindeer do not persist across the year (van Oort et al. 2005; Figs. 1 and 2). Instead, they are periodically absent, and their successive appearance and disappearance is related to the unusual characteristics of the photic environment at high latitudes. Thus, the pronounced daily rhythm of activity displayed by NR in autumn, winter and spring (LD) all but disappeared during LL in summer. In SR, daily rhythms were also absent during LL, during DD when free-running circadian rhythms might have been expected, and even during LD (van Oort et al. 2005). Both NR and SR were generally active around the clock throughout the year and,

Fig. 1 Pattern of the daily activity of Norwegian Reindeer (NR) ▶ across 1 year; individual data. The figure includes double-plotted actograms running from December to the following November for each of the two free-ranging sub-adult female NR. *Each row* represents two consecutive days; scale of the abscissa=time of day (hour). Bouts of activity (*black horizontal bars*) are interspersed with bouts of inactivity (*open spaces*). *Lines* indicating the beginning and end of civil twilight (*black*) and sunrise and sunset (*white*) are superimposed on each actogram. Graphs (**a**–**h**) show F-periodograms for rhythms of activity measured over 10-day periods around the mid-summer and mid-winter solstices (June, December) and the spring and autumn equinoxes (March and September); scale of the abscissa=time of day (hour). *Upper panels* Strength of rhythms (Q); *curved line* 95% confidence limit. *Lower panels* Relative amplitude of rhythms [d(Q)p]; significant diel (τ=24 h), circadian (τ≈24 h) and ultradian (τ'≈4–9 h) rhythms are indicated by *stars*. For reference to the sequence of days denoted '*i*', see text
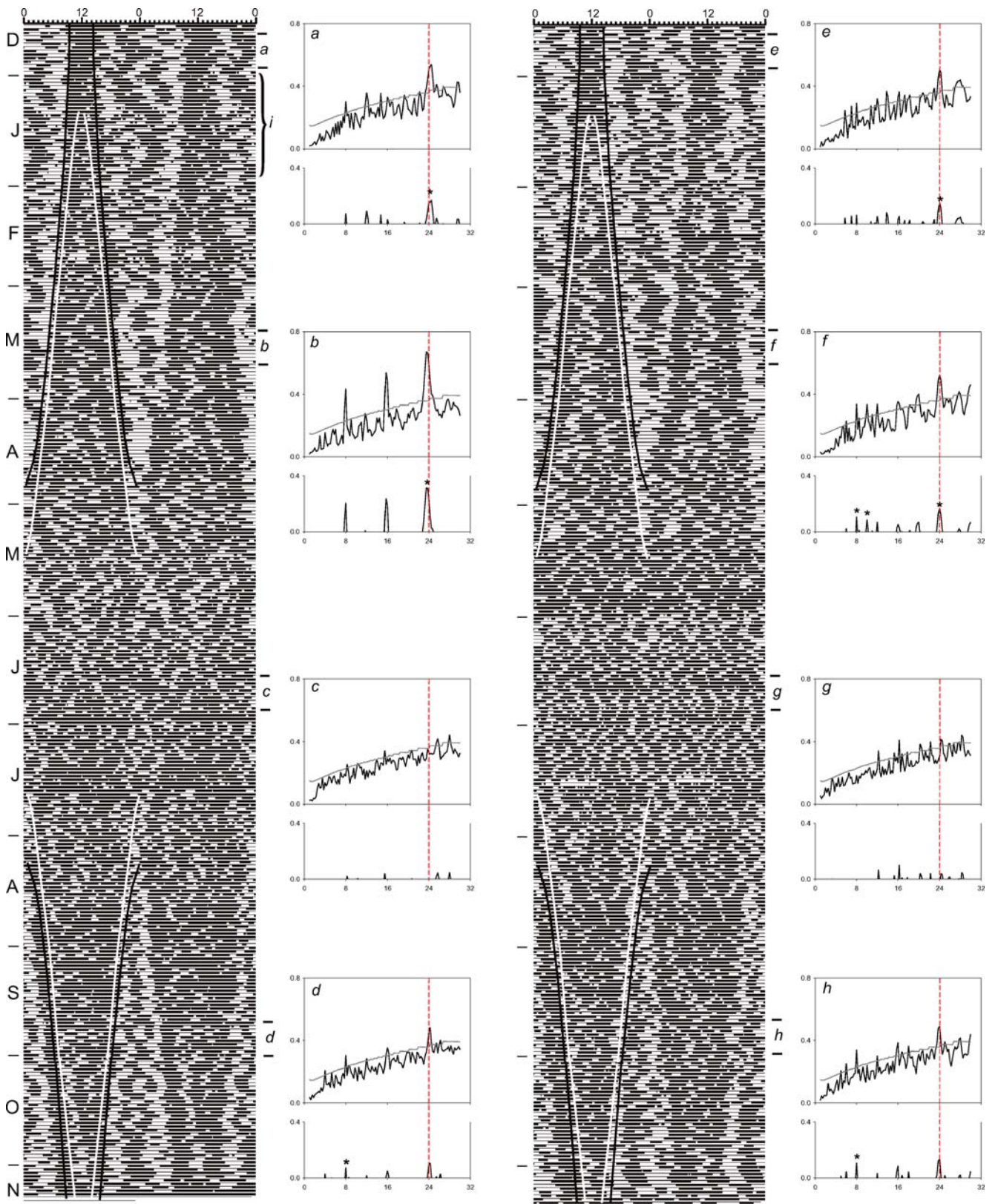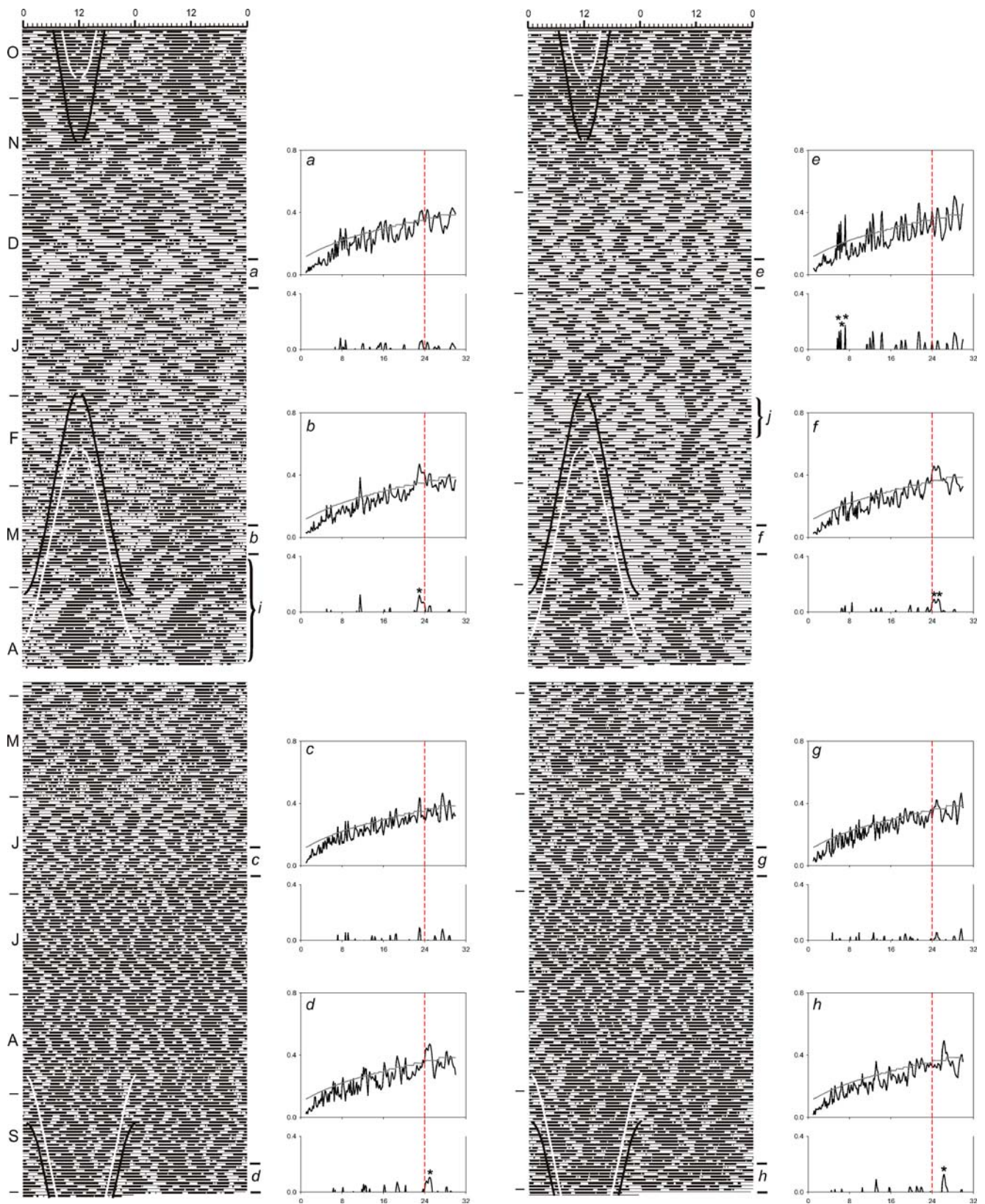
Fig. 2 Pattern of the daily activity of Svalbard Reindeer (*SR*); individual data. The figure includes double-plotted actograms and corresponding F-periodograms presented in the same format as Fig. 1. Data are records from free-ranging sub-adult male SR lasting from October to April (*n*=2) and from May to September (*n*=2). Each actogram is a composite from trials in two animals, selected at random, plotted consecutively to depict the pattern of activity across 1 year. For reference to the sequences of days denoted '*i*' and '*j*', see text
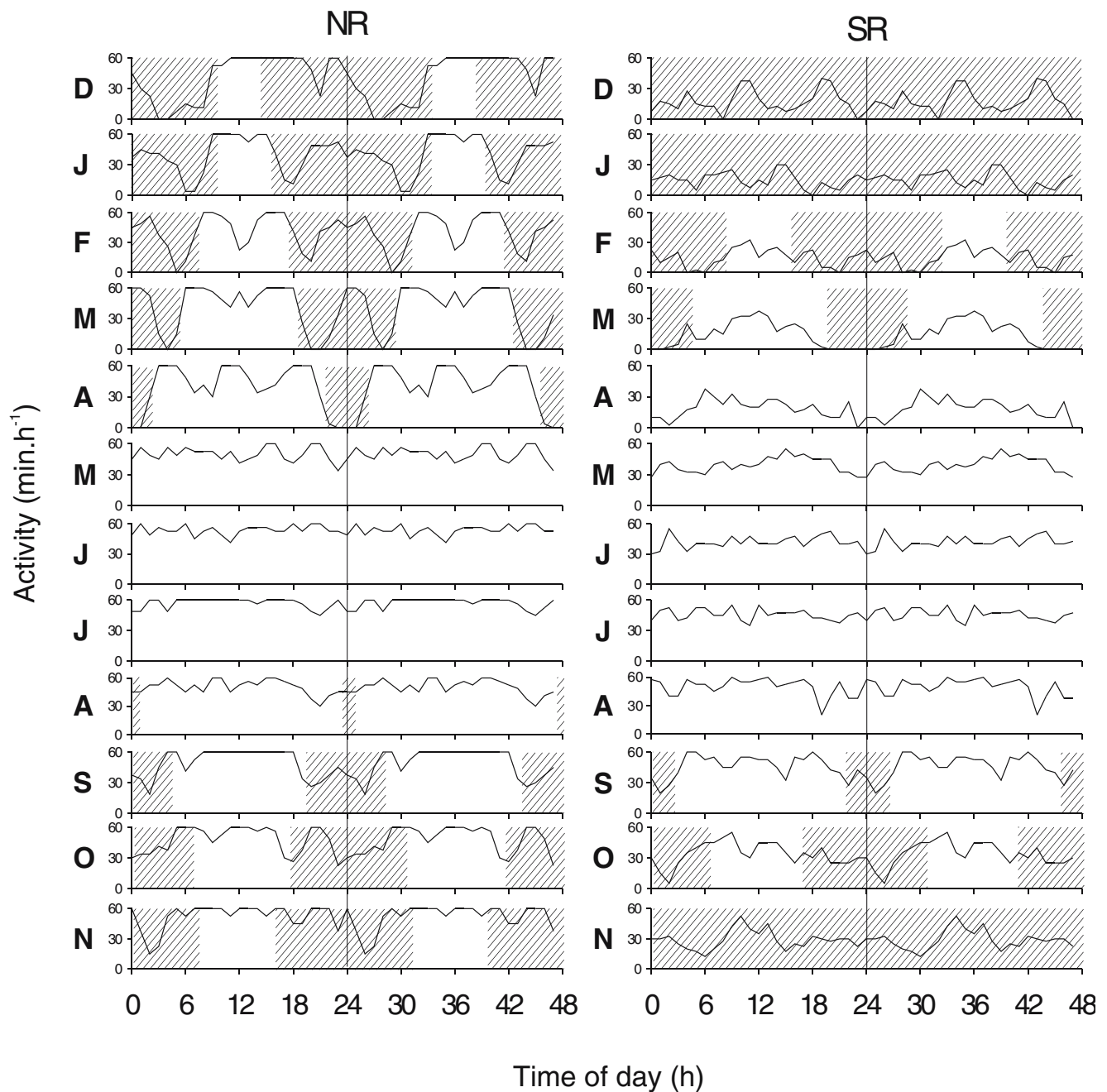
Fig. 3 Pattern of the daily activity of Norwegian Reindeer (*NR*, *left panel*, *n*=6) and Svalbard Reindeer (*SR*, *right panel*, *n*=6 (October to May) and *n*=5 (April to September) across 1 year. The *line plots*, double-plotted for clarity, show the median rate of activity (minute per hour) across 24 h in periods of 10 days centred on the 15th of each month; the *hatched blocks* indicate darkness (light intensity below civil twilight)

in this respect, were 'nycthemeral' like the caribou described by Maier and White (1998). In contrast with the caribou, however, the organisation of daily activity in reindeer varied systematically with respect to the LD cycle whenever it was present. NR, in particular, displayed a clear reduction of activity before dawn and after dusk (Figs. 1 and 3) similar to that reported in a number of studies of

both reindeer (Eriksson et al. 1981) and caribou (Roby 1980; Roby and Thing 1985; Collins and Smith 1989; Russell et al. 1993). The anticipation of dawn indicates the involvement of a circadian oscillator in the regulation of activity. Together, however, these observations suggest that the daily pattern of activity in *Rangifer* is subject only to weak endogenous control for which the LD cycle acts as a

Table 1 The period of ultradian rhythms (τ') of activity in free-ranging Norwegian (NR, $n=6$) and Svalbard reindeer [SR, $n=5$ or 6 (see "Materials and methods" section)] each month across 1 year

	NR			SR		
	Periodograms analysed	Periodograms showing rhythmicity	Period	Periodograms analysed	Periodograms showing rhythmicity	Period
	n	n'	τ' (h)	n	n'	τ' (h)
Jan	18	14	7 (5–8)	15	15	7 (5–11)
Feb	18	16	8 (5–8)	15	15	7 (6–9)
Mar	18	17	8 (6–8)	15	14	8 (6–9)
Apr	18	17	7 (5–8)	18	15	8 (6–9)
May	18	15	6 (4–6)	18	17	6 (4–9)
Jun	18	8	5 (4–6)	18	16	5 (4–8)
Jul	18	7	5 (3–7)	18	17	5 (3–9)
Aug	18	9	6 (4–7)	18	17	5 (4–8)
Sep	18	12	6 (4–6)	18	15	6 (5–9)
Oct	18	17	8 (5–8)	10	8	6 (5–9)
Nov	6	5	8 (6–8)	15	15	7 (6–10)
Dec	6	6	8 (6–8)	15	15	7 (6–9)

F-periodogram analysis was performed on data from one to three consecutive 10-day periods in each reindeer each month. Periodicity is expressed as the median (range) for each month. All harmonics are excluded and only true rhythmicity, therefore, is considered. τ' varied significantly ($P<0.001$) across months in both sub-species.
n Number of periodograms (pooled for all animals), n' number of significant rhythms in the pooled sample for each month

weak Zeitgeber. Although the LD cycle in spring and autumn seems to synchronise the pattern of daily activity, at least in NR, we have little evidence of strong entrainment.

The evidence for the weak endogenous control of activity is, moreover, equivocal. Consistent with the onset of activity being governed by an oscillator entrained to dawn, NR appeared to anticipate dawn earlier in autumn than in spring (Fig. 3). The onset of dawn is progressively delayed as day length decreases in autumn and is advanced as it increases in spring. The onset of activity would therefore be expected to show a larger phase difference with respect to dawn in autumn than in spring, which is exactly what we observed. Identifying anticipation, however, is complicated by the fact that neither dawn nor dusk is sharply defined under natural light conditions. The morning and evening periods of twilight are greatly extended at high latitudes and could, therefore, themselves trigger the dawn increase or dusk decrease in activity. SR, moreover, showed no free-running circadian rhythms under DD, which is the photic condition in which such rhythms are normally expressed (Daan and Aschoff 2001). Sheep, for example, displayed free-running circadian rhythms under experimental exposure to DD although these did not persist (Ebling et al. 1988). On the other hand, the continuous series of alternating bouts of activity and inactivity in SR displayed a high degree of ultradian organization which extended from DD into the LD period (Table 1). The onset and offset of particular bouts were not fixed but shifted from day to day (Fig. 2j). NR displayed a similar pattern (Fig. 1) and in

both sub-species the timing of particular bouts maintained sufficiently stable phase relationships from one day to the next to suggest that they were phase-locked to a pacemaker (e.g. Figs. 1i and 2j). Some of the median values of τ', however, were multiples not only of 24 (6 or 8 h; Table 1) but also of 16, 18, 30 and 32. The observed patterns, therefore, represent no argument either for or against a circadian clock. The evident organisation of ultradian rhythms under LD demonstrates that although the putative endogenous clock failed to entrain, the daily pattern of the behaviour of reindeer is clearly modulated by the LD cycle. The synchronisation of activity with the L phase (Fig. 3) in conjunction with the free-running ultradian rhythms during the D phase, clearly apparent in NR (Fig. 1i) but also present in SR even under LD (Fig. 2i), might indicate a positive masking by light (Aschoff et al. 1982). Light appears to increase the level of activity without influencing the putative oscillators. Consistent with this, there were no signs under DD of any circadian rhythmicity originating from the preceding L phase as would be expected where there is entrainment (Moore-Ede et al. 1982). SR did display traces of a temporary, weak entrainment; two of five animals showed clear transients during the transition from DD to LD in which, over the course of approximately 1 week, free-running ultradian components were 'captured' by and briefly became associated with the L phase (Fig. 2j). The weak endogenous regulation of activity in reindeer is consistent with the view that circadian control is generally less robust in ruminants, in which microbial digestion

Table 2 The mesor (*m*, hour per 24 h), amplitude (*A*, hour per 24 h), and acrophase [φ, date (days)] of daily activity in free-living Norwegian (NR, *n*=6) and Svalbard reindeer (SR, *n*=5) throughout 1 year (median; range)

	m	*A*	φ
NR	15.8 (15.2–16.4)	1.5 (1.2–2.0)	29 July (2)
SR	13.7 (13.0–14.3)	2.3 (2.2–3.2)	13 August (20)

For each parameter the difference between NR and SR is significant *P*<0.001

generates a relatively constant supply of nutrients, than in monogastric species (e.g. Andersson et al. 2005).

In the emerging model, the daily activity of reindeer is subject to weak endogenous regulation and possibly also masking by light. These, however, are not the only factors that influence the animals' pattern of behaviour. Social cues can act as powerful organisers of activity (Davidson and Menaker 2003), albeit their role as true Zeitgebers differs widely between species (Mistlberger and Skene 2004). The organising effect of social cues is nicely illustrated in reindeer. In this species, a group, whether consisting of just a few (<5) or many individuals, is a highly coordinated entity in which, at any instant, the majority of animals perform the same behaviour, usually either grazing or lying down (Skogland 1984; Boertje 1985; Roby and Thing 1985; Collins and Smith 1989; Russell et al. 1993). The fact that NR displayed a higher degree of organisation of daily activity than SR may reflect differences in the gregariousness of the two sub-species. The tight relationship between the activity and the LD cycle in gregarious NR may result from social synchronisation enhancing masking and weak entrainment by light. SR, by contrast,

are not gregarious, and it is most unlikely that two or more of our experimental animals ever occurred together in the same group. The absence of social cohesion probably contributes directly to the low overall degree of organisation of daily activity throughout the year in this sub-species.

Activity around the clock has important consequences for the nutritional ecology of reindeer. Like most ungulates (Hudson 1985), reindeer devote most (70–90%) of their active time to grazing (SR: Nyholm 1976; Tyler 1987; NR: Skogland 1984), and, consequently, the temporal pattern of logged activity approximates the temporal pattern of grazing. The uniform distribution of daily activity (Figs. 1 and 2), therefore, indicates that reindeer graze around the clock throughout the year and, in the same way, the activity time series (Fig. 4) indicates that the animals show a pronounced annual cycle in the amount of time spent grazing each day. These two features of daily activity are functionally related. The annual cycle of daily activity (Fig. 4) reflects variation in the animals' metabolic requirements. Reindeer, like all northern species of cervids investigated so far, show a clear annual cycle in growth and fattening (Leader-Williams and Ricketts 1982; Reimers et al. 1983; Tyler 1987). Their metabolic demands and, hence, also their appetite are correspondingly high in summer but much reduced in winter (Nilssen et al. 1984; Larsen et al. 1985; Tyler et al. 1999; Mesteig et al. 2000), fluctuating in accordance with an endogenous rhythm that represents a major adaptation to seasonal variation in the quality, abundance and availability of forage (see Barry et al. 1991 for a review). Consequently, the reindeer were active for around 17 h·day⁻¹ in summer (Fig. 4), maximising their food intake during those few weeks when growth and fattening were physiologically permissible. The
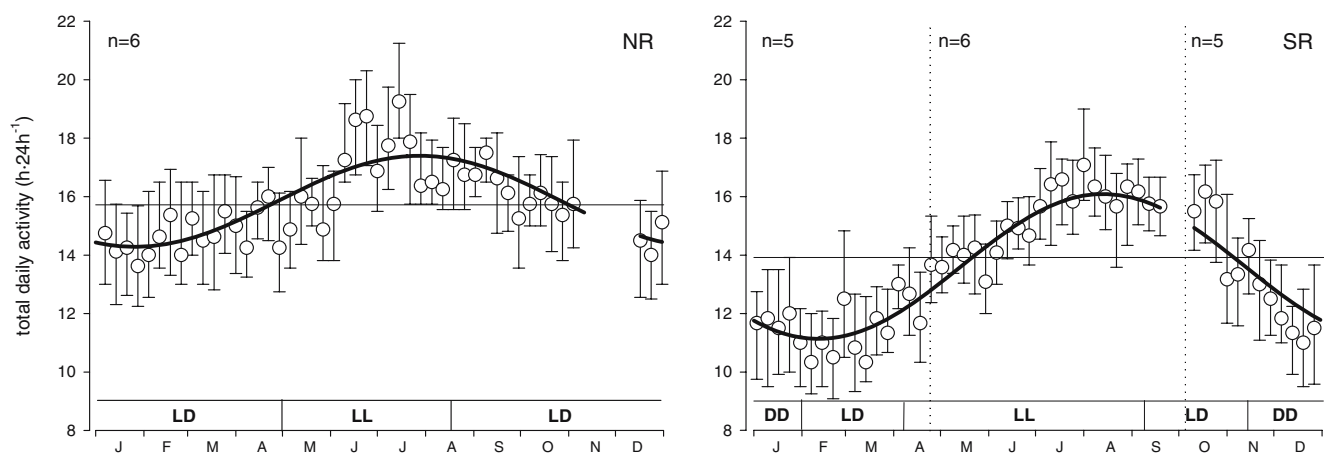

Fig. 4 The rate of activity (hour per 24 h) across 1 year in free-ranging female Norwegian (*NR*, *n*=6) and male Svalbard (*SR*, *n*=5) reindeer. Data are plotted as weekly medians (quartiles) and fitted to a cosine model (Eq. 1; *thick black line*; Table 2). Data for the two trials in SR (October to May and April to October) are combined to illustrate

the pattern of activity across one full year. Ambient light conditions are indicated *in the bar beneath each graph* (*DD* continuous darkness, *LL* continuous light, *LD* daily light–dark cycle; *D*<10 lx<*L*). Both plots are folded at 1 January
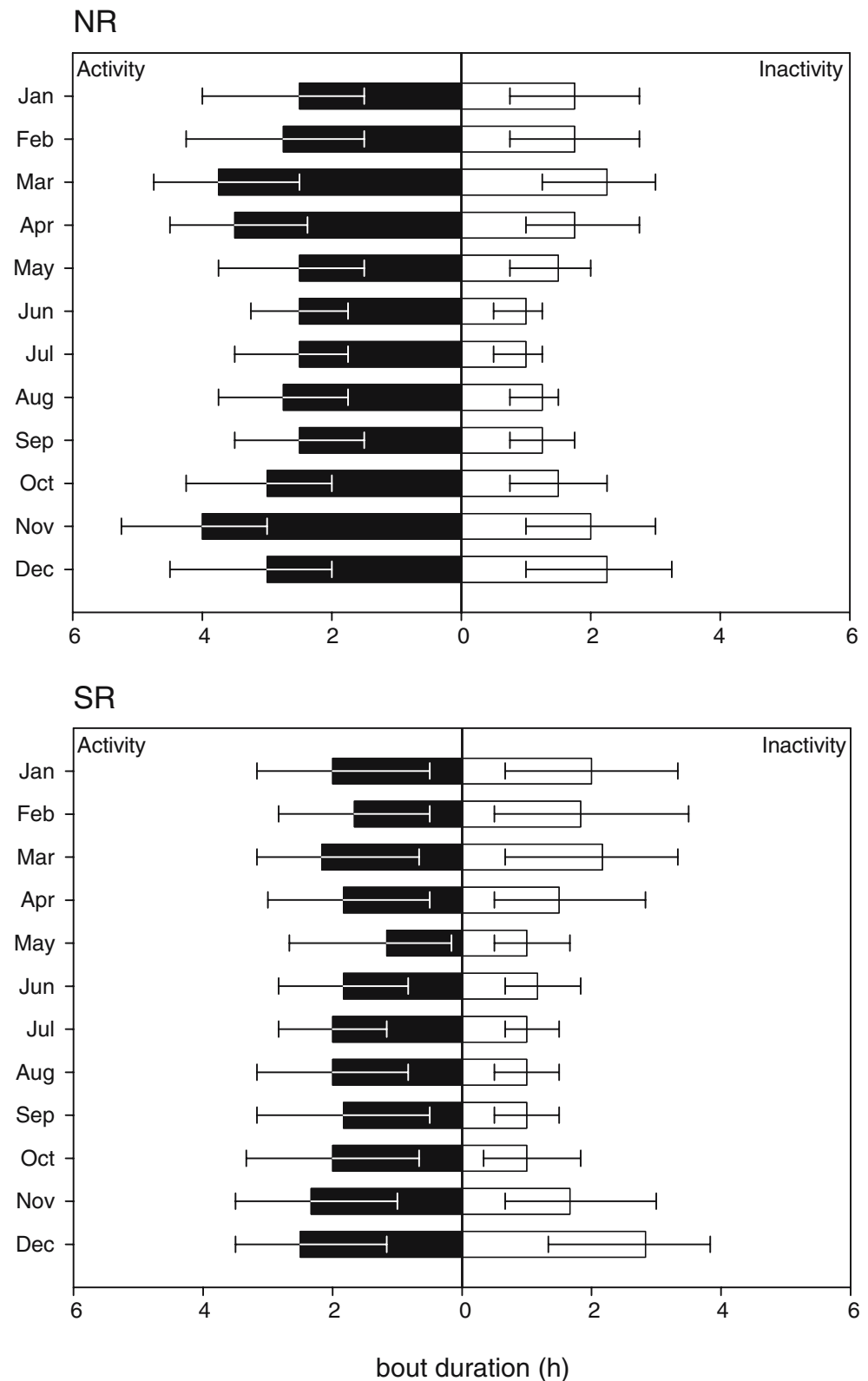
amplitude of the annual cycle of daily activity increased with latitude, reflecting the greater amplitude of the appetite cycle in SR compared with NR (Larsen et al. 1985). The quality of the forage on Arctic ranges, moreover, is very high in summer (White and Staaland 1983; Klein 1990; Sørmo et al. 1997; Larter and Nagy 2001) and the rates of fermentation of fibre and of passage of digesta increase as a result (Orpin et al. 1985; Mathiesen et al. 1987; Sørmo et

al. 1999). Reflecting this, the bouts of activity and of inactivity and the period (τ') of the ultradian rhythms were shorter in summer. In both sub-species, the frequency of cycles of activity increased from three in winter and spring to nearly five per day in summer (see also Hofmann 1989 for a review). This is similar to the situation in voles in which the predominance of ultradian organisation over circadian timing changes across the year (Hoogenboom et al. 1984; Gerkema et al. 1993). Reindeer pursue a different strategy in winter. The small mouths which enable reindeer to feed selectively, plucking only the most nutritious parts of diminutive tundra forage plants, presumably also restrict them to taking small bites (Mathiesen et al. 2000). Consequently, even setting aside the inherent constraints of ruminant digestion, reindeer are precluded from compensating for decreased abundance of forage by feeding in bulk. Instead, they continue to feed selectively in winter, maintaining relatively high concentrations of nutrients in their diet (e.g. Storeheier et al. 2002) though at a cost of very low absolute rates of intake (<4 g DM·min^{-1} in calves, Storeheier et al. 2003) for which they compensate by grazing at night even under the daily LD cycle of spring and autumn. The continuous pattern of feeding in reindeer may, in addition, enhance digestive efficiency by maintaining substrate supply and, hence, stabilizing the environment of microorganisms in the rumen (Leedle et al. 1982; but see also Dehority and Tirabasso 2001 for a review).

Seasonal absence of rhythmicity in the circadian range has previously been observed in the circulating levels of the hormone melatonin in reindeer (Stokkan et al. 1994). The present observations on activity complement and expand this information. Year-round, continuous records of activity in reindeer, now available across a gradient of latitudes ranging from 64°N (Eriksson et al. 1981) to 78°N (van Oort et al. 2005), show that the ≈24-h organisation of activity in this species decreases with increasing latitude. The ultradian organisation of activity, by contrast, appears to increase with latitude (this study). The combination, most evident in SR, of a weak photic response, weak circadian mechanisms and a weak social synchronization reduces the constraints of biological timing in an environment which is effectively non-rhythmic most of the year and permits strong expression of the basic ultradian pattern of ruminant activity. The evident weakness of circadian mechanisms is an adaptation which enables reindeer to feed around the clock around the year irrespective of very large changes in photoperiod. Clocks are presumably present in reindeer but seem not to be used and hence may be considered redundant.

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