Biological rhythms in Arctic vertebrates

B. E. H. van Oort[1], N. J. C. Tyler[2], E. Reierth[1] & K.-A. Stokkan[1]

[1] Department of Arctic Biology and Institute of Medical Biology, University of Tromsø, N-9037 Tromsø, Norway (bob@fagmed.uit.no).
[2] Department of Biology, University of Tromsø, Norway.

Abstract: Many biological processes show regular cyclical fluctuations that persist throughout an organism's life; these range from the transcription of DNA to patterns of behaviour. Persistent, cyclical phenomena of this kind are a fundamental feature of all organisms. They are governed primarily by endogenous rhythms generated by a 'biological clock' situated in the brain. Normally, however, the expression of the clock is modulated to a greater or lesser extent by environmental cues. This paper reviews the physiological control of the temporal organisation of cycles in vertebrates and, in particular, explores their regulation in arctic species like reindeer (*Rangifer tarandus* L.). We emphasise how exposure to the photoperiodic conditions that characterise polar regions places special demands on timing mechanisms and how arctic species, therefore, are of particular interest for the study of biological rhythms. Thus far, behavioural and physiological studies of these species show that arctic reindeer (and ptarmigan) appear to be truly opportunistic in summer and winter, seemingly without any active biological clock and that they are, instead, driven directly by photoperiod. This situation, if confirmed, would be unique among vertebrates.

Key words: caribou, cervid, endogenous rhythm, melatonin, muskox, photoperiod, reindeer, ruminant, Svalbard.

Introduction

Many biological processes show regular cyclical fluctuations that persist throughout an organism's life; these range from the transcription of DNA to patterns of behaviour. Persistent, cyclical phenomena of this kind are a fundamental feature of all organisms. They are governed primarily by endogenous rhythms generated by a 'biological clock' situated in the brain. Normally, however, the expression of the clock is modulated to a greater or lesser extent by environmental cues. This paper reviews the physiological control of the temporal organisation of cycles in vertebrates and, in particular, explores their regulation in arctic species, like reindeer (*Rangifer tarandus* L.), which are exposed to the photoperiodic conditions that characterise polar regions.

The basic problem

In many species, daily and annual cycles in physiological and behavioural parameters are closely correlated with daylength, usually referred to as 'photoperiod' (Table 1). Organisms can extract two kinds of information by monitoring the duration of the daily photoperiod: the daily light/dark cycle provides them with a 24 hour clock and changes in daylength provide them with a calendar indicating the changing of the seasons. In these two ways photoperiod provides an absolutely secure, predictable signal for keeping track of time in what are otherwise often unpredictable environments. Plants and animals living at 30-60°N lat. in the northern temperate zone experience a strongly rhythmic and dynamic photoperiodic environment with clear daily light/dark cycles and pronounced seasonal changes in daylength (Fig. 1). Not surprisingly, therefore, photoperiod plays a major role in the regulation of temporal organisation in temperate species. Arctic species, such as reindeer and muskox (*Ovibos moschatus*), by contrast, live in regions where photoperiodic information is much reduced or even absent for considerable periods of the year. These animals are exposed to continuous daylight, the

Table 1. Glossary.

Terminology	Explanation
Circadian cycle	A cycle with a frequency ≈24 h., i.e. with a length of approximately (*circa-*) a day (*diem*).
Entrainment	Synchronisation of the phase of the biological clock with the correct phase of the environment. Entrainment ensures the proper phase-relationships between particular body rhythms and the appropriate rhythmic changes in the environment.
Free-running rhythm	Biological rhythm expressed under constant conditions.
Infradian cycle	A cycle with a frequency >>24 h., i.e. with less than (*infra-*) one cycle a day (*diem*).
Photoperiod	Duration of night and day.
Pineal gland	Endocrine gland in the brain. Innervated by sympathetic nerves from the SCN. Produces the hormone melatonin.
Polar day	Period of continuous light in summer when the sun is continuously above the horizon.
Polar night	Period of continuous darkness in winter when the sun is continuously below the horizon.
SCN	Suprachiasmatic nucleus. Structure in the hypothalamus where the mammalian biological clock is situated.
Temperature compensation	Independence of the frequency of a cycle from ambient temperature.
Ultradian cycle	A cycle with a frequency <<24 h., i.e. many (*ultra-*) cycles occur within a day (*diem*).
Zeitgeber	Time cue which signals the setting or resetting of the biological clock to the correct phase with respect to the time of the day or of the year. Light is the most important, but not the only, zeitgeber.

'polar day', in summer and continuous darkness, the 'polar night', in winter. Nevertheless, they display pronounced, highly predictable annual cycles of metabolism, growth and behaviour. This simple observation suggests that the regulation of cyclical phenomena may be different in Arctic compared to temperate species.

The role of self-sustained, clock-driven, endogenous rhythms in the regulation of annual cycles of growth and behaviour is well documented in temperate ungulates such as red deer (*Cervus elaphus:* Loudon & Jabbour, 1994), white-tailed deer (*Odocoileus virginianus:* Brown *et al.,* 1978) and sheep (*Ovis aries:* Lincoln, 1992; 1998). However, there is no convincing evidence for the role of a biological clock in the control of the corresponding cycles in reindeer and muskoxen. One way to identify the presence of an endogenous rhythm is to demonstrate that a cycle - the daily cycle of the production of melatonin or the annual cycle of coat growth, for instance - persists while the animals are maintained under constant daylight conditions. However, this has not been investigated for arctic ungulates.

In a sense, of course, the necessary experiments are performed twice a year every year, for these are exactly the conditions to which animals living in their natural environment are exposed in mid-winter and mid-summer. Thus, the clear daily rhythms of behaviour which Svalbard reindeer (*R. t. platyrhynchus*) display in February and March and September and October disappear under the continuous light conditions of May, June and July and December and January (van Oort *et al.,* 1998 and unpubl. data). A similar situation is observed in Svalbard ptarmigan (*Lagopus mutus hyperboreus:* Reierth & Stokkan, 1998). Both organisms fail to show persistent rhythms of behaviour when exposed to continuous light conditions. The possibility
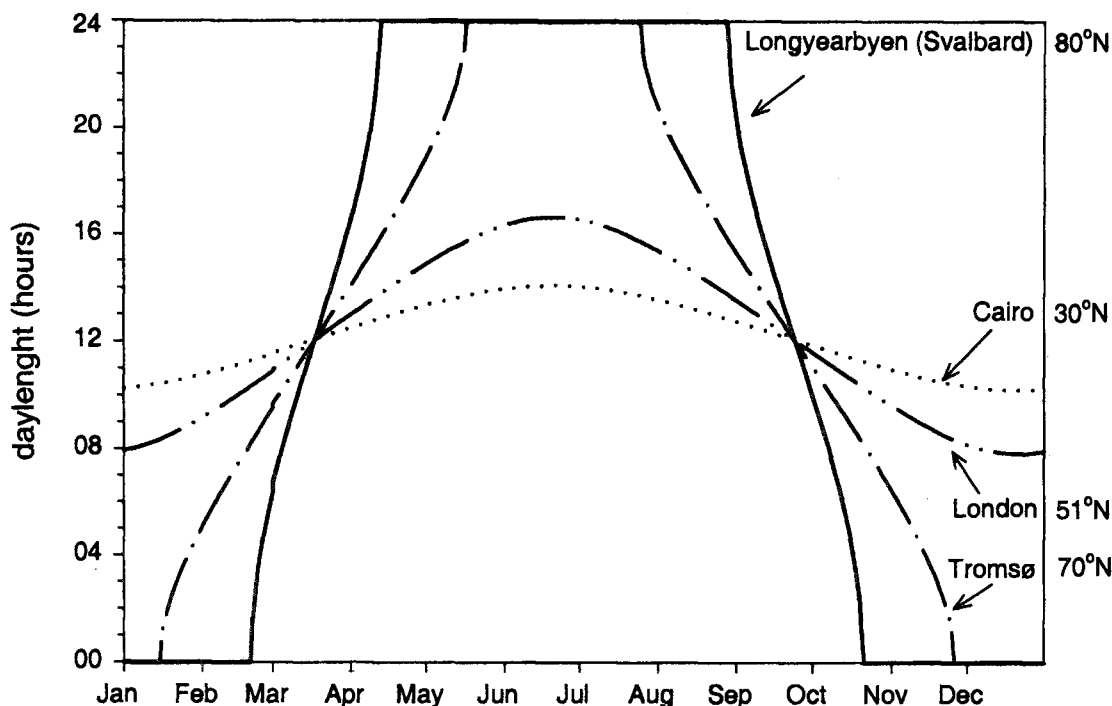
Fig. 1. Comparison of daylength at different latitudes. Note both the long period of continuous light and darkness at 80°N and also the much higher speed of changes here in daylength in spring and autumn compared to more southerly latitudes.

exists, therefore, that the annual cycles of growth and metabolism of reindeer and muskoxen might be regulated directly by daily changes in photoperiod while the clock itself has become virtually vestigial. In support of this, there is evidence that the clock function which governs daily patterns of behaviour and the secretion of melatonin in reindeer is much reduced, if not completely absent, during the polar day and the polar night.

Characteristics and functions of rhythms

Biological rhythms are regular, cyclic events of any length of time which are under the control of endogenous oscillators. Such rhythms are generally recognised on three time scales: ultradian (<<24 h), circadian (~24 h) and infradian rhythms (>>24 h). The latter include rhythmical phenomena with frequencies of months or years.

Examples of ultradian rhythms include the spontaneous beating of the heart, breathing, the alternating bouts of REM and non REM sleep, the secretion of many hormones (e.g. Orth *et al.,* 1979; Moore-Ede & Sulzman, 1981), feeding bouts in ruminants (Squires, 1971) and in daily bouts of

activity in animals living in the intertidal zone. Examples of circadian rhythms include the daily rhythms of body temperature, the secretion of melatonin and the sleep/wake and activity cycles (Akerstedt, 1979; Orth *et al.,* 1979). Infradian rhythms include arousal during hibernation (e.g. ground squirrels *Spermophilus lateralis:* Ruby *et al.,* 1996), menstruation, the annual cycle of growth and fattening in northern cervids (Leader-Williams & Ricketts, 1982; Suttie *et al.,* 1983; Tyler, 1987; 1995; Lincoln & Baker, 1995; Suttie & Webster, Hewison *et al.,* 1996), the antler cycle in reindeer (Lincoln & Tyler, 1994), the annual moult of hair and feathers (Meijer, 1989; Stokkan & Sharp, 1990), breeding and migration (e.g. Lundberg & Eriksson, 1984). All these cyclical fluctuations occur regularly and spontaneously. They are not prompted by exogenous environmental cues but are triggered, instead, by endogenous signals that arise independent of, but may become modified by, the animals' environment.

An important test of the endogenous basis for an overt rhythm is the persistence of cyclicity even when the environment is held constant. To identify the endogenous basis of a rhythm one should, in

addition, be able to demonstrate (i) that its phase can be altered by the manipulation of light/dark signals (Aschoff, 1964a; 1999) and (ii) that it's expression is temperature compensated (Table 1). Golden hamsters' (*Masocricetus auratus*) daily cycle of wheel-running and the sleep/wake pattern of humans, for example, persist when the experimental subjects live in constant darkness (Jorgens, 1967; Aschoff, 1985). Had these cycles of activity been driven directly by the light/dark cycle, they would have been abolished immediately following the onset of constant light (or dark) conditions.

While the functional role of biological clocks has been demonstrated in a wide range of organisms, there is little direct experimental evidence of the adaptive significance of the circadian organisation which the clocks regulate. Nevertheless, it is generally accepted that organisms benefit from the temporal organisation of physiological functions and behaviour, chiefly because it enables them to anticipate daily and seasonal changes in their environment (Aschoff, 1964b). Thus, in plants, protein synthesis and the orientation of leaves anticipate the onset of daylight as well as the movement of the sun across the sky (Stayton *et al*, 1989; Levy & Moore, 1993). Honey bees (*Apis mellifera*) have a sense of time which allows them to anticipate the peak of the daily production of floral nectar and even find their way back to previously detected food stores by means of time-compensated sun-compass orientation (Aschoff, 1986; Frish & Aschoff, 1987; Moore *et al*, 1989). The immune function of deer mice (*Peromyscus maniculatus*) is enhanced (Demas & Nelson, 1998), reindeer fatten and grow a thick coat (Suttie & Webster, 1995) and Arctic waders migrate south all in advance of the onset of winter. Accurate timing of estrus and mating in northern species of deer ensures that the burden of lactation many months later coincides with the period when the females have access to abundant high quality forage. When aberrations in timing result in conceptions outside the normal breeding season, the unusually early-born or late-born calves suffer heavy mortality (Clutton-Brock *et al*, 1982).

The biological clock(s)

In mammals, the clock which generates circadian rhythmicity is situated in a region of the hypothalamus called the suprachiasmatic nucleus (SCN). The SCN consists of groups of neurons whose activity oscillates spontaneously with a frequency close to 24 hours. The oscillating frequency of the SCN as a whole is the mean of the activity of the individual cells. Neither the way in which the activity of the different cells is integrated, nor the way in which the net circadian rhythmicity of the SCN is translated into the regulation of the body's rhythmic functions is known, but the pineal hormone melatonin evidently plays an important role in this.

While the SCN plays a central role in generating endogenous circadian rhythms and, for this reason, is often referred to as *the* biological clock, it is not unique: there is a variety of oscillators in mammals which, singly or in combination, are involved in driving different behavioural and physiological rhythms. There are also different classes of oscillators, even within a single cell (Hoffmans-Hohn *et al.*, 1984). Some are normally entrained by the light/dark cycle while others are entrained by other stimuli, such as the cyclical presentation of food. One such is the oscillator which regulates feeding activity in rodents (Boulos & Terman, 1980), pigeons (*Columba livia*: Phillips *et al.*, 1993) and house sparrows (*Passer domesticus*: Hau & Gwinner, 1992). The existence of oscillators of this kind is easily overlooked because in nature the availability of food is often closely linked to the light/dark cycle (e.g. the abundance of insects eaten by insectivorous birds). Thus, while the activity of the birds, for example, is tightly correlated to light conditions, the relationship may be only indirect. The role of multiple or compound clocks in regulation of the temporal organisation of behaviour has been demonstrated by the experimental separation of rhythms that were apparently inextricably linked and by recording the subsequent independent persistence of each (Mrosovsky & Hallonquist, 1986). The mammalian SCN, therefore, is better considered not as *the* clock but as the *master clock*, the chief among many. This view represents a widely accepted model for the hierarchical regulation of rhythmic phenomena in many classes of organisms including plants, insects, amphibians and mammals (Hagemayer & Waisel, 1987; Turek & Losee-Olson, 1988; Grandin & Charbonneau, 1991; Reinberg & Touitou, 1996; Heintzen *et al*, 1997; Turek, 1998; Weaver, 1998).

Control of rhythms in temperate species

Though biological rhythms are, by definition, driven by endogenous mechanisms, this in no way denies the role of the environment in modulating
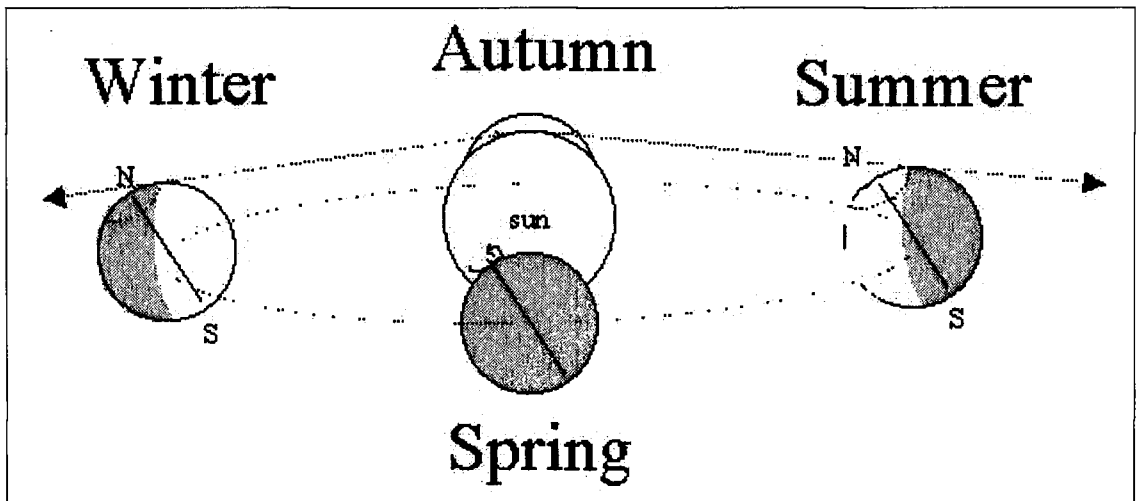
Fig. 2. The figure shows the revolution of the Earth around its axis and the consequential occurence of night and day. Seasons are a result of the tilting of the Earth's axis which causes different parts of the Earth, in turn, to face predominantly towards or away from the sun. The seasons are indicated for the northern hemisphere. The arrows show how sunlight is absent north of the Arctic circle in winter, while there is continuous daylight there in summer.

their expression. Environmental input is essential: the rhythms evolved to synchronise the physiological and behavioural functions of the organism to its environment, not to isolate the organism from that environment. The indispensable role of environmental input is nicely illustrated by considering the function of the SCN itself. The master clock has an endogenous frequency of only *approximately* 24 hours. Most animals, however, live in an environment with a light/dark cycle of *exactly* 24 hours. The discrepancy is small but significant. To the extent that the role of the SCN is to synchronise the animal to its environment, the clock must be reset from time to time. The resetting of the phase of the clock is called 'entrainment' (Table 1) and the environmental cues which serve to entrain it are called 'zeitgebers' (Table 1). The best known zeitgeber is the daily light/dark cycle which, at any given latitude, varies in an entirely predictable manner throughout the year.

The light/dark cycle
The occurrence of day and night is due to the rotation of the planet around its axis as a result of which every point of the surface of the Earth moves alternatively into and out of direct view of the sun. The Earth completes one rotation every 24 hours. In addition, it revolves around the sun, completing

one cycle approximately every 365 days. The occurrence of seasons, which so influence the life history of temperate and polar species, is a consequence of the fact that the axis of the Earth is tilted at 23.5° relative to the plane of its orbit. The poles, therefore, alternately face mainly towards or mainly away from the sun (Fig. 2). In the northern hemisphere, we enjoy the long days of summer when the North Pole is tilted towards the sun while in winter, when the situation is reversed, the days are short. Seasonal variation in daylength increases with increasing latitude. At high latitudes, the daily light/dark cycle disappears both in mid-summer when the sun remains continually above the horizon (the 'polar day') and in mid-winter, when the sun remains continually below the horizon (the 'polar night'). At Tromsø, 70°N lat., the polar day lasts 69 days and the polar night lasts 51 days (Fig. 1). Information on daylength at different latitudes is available at *http://aa.usno.navy.mil/AA/data/.*

Receiving and conveying photoperiodic information to the rest of the body
No animal can be entrained by the light/dark cycle unless it posseses a superficial photoreceptor (although see Campbell & Murphy, 1998; Yamazaki *et al*, 1999). In mammals, photoperiodic information is transmitted to the SCN via neural relays

from photoreceptors in the retina which, independent of the visual pathway, are concerned only with entrainment of the circadian clock (Miyamoto & Sancar, 1998). An animal can, therefore, be visually blind but still receptive to photoperiodic information. The retinohypothalamic tract - a projection with no visual function - is believed to be the major route along which photic information is fed into the circadian system although other inputs from the primary and accessory optic tracts also exist (Hofmann, 1981; Menaker & Binkley, 1981).

Adjusting the clock
Diurnal mammals seem to entrain to the daily light/dark cycle through dynamic adjustments in SCN function which result in alteration of the phase and the frequency of the clock (Pittendrigh, 1981; Beersma *et al.*, 1999). The phase of the clock may be advanced or delayed relative to the real (solar) time of day and its frequency may, likewise, be accelerated or decelerated. Adjustment of the phase of the clock appears to be a rapid response, while alteration of the clock's frequency seems to occur continually while the animal is awake (Beersma *et al*, 1999).

The sensitivity of the clock to the different kinds of temporal information to which it can become entrained varies throughout the day and is described in so-called 'phase response curves' (e.g. Pittendrigh, 1981). Sensitivity to photoperiodic information is characteristically high at the beginning and the end of the daily period of activity and low, or even absent, during the middle. These responses are species specific: for example, golden hamsters are highly responsive to photic information while white-footed mice (*Peromyscus leucopus*) are much less responsive (Pittendrigh & Daan, 1976). The functional significance of these differences is unclear. It may be that low sensitivity to environmental zeitgebers enhances opportunistic behaviour. This might be highly beneficial, for example, in animals moving from one rhythmic environment into another. Birds appear to reduce their zeitgeber sensitivity while migrating across many degrees of longitude (Gwinner *et al*, 1997); the pineal gland of lampreys (*Petromyzon marinus*) altogether ceases to synthesise melatonin while the animals are switching hosts (Menaker & Tosini, 1996). Whatever the adaptive significance of these differences in zeitgeber sensitivity, they are reflected in the amplitude of the daily cycle in the plasma concentration of the hormone melatonin (Hau & Gwinner, 1997).

The role of melatonin
The information represented by the output of the SCN, which integrates an endogenous component with photoperiodic modulation, is presumably transmitted to the rest of the body by the daily fluctuation in the plasma concentration of melatonin. This hormone appears to be a key intermediate between the biological clock - the SCN - and rhythms of behaviour and physiological function. Melatonin is secreted by the pineal gland which lies between the cerebral hemispheres above the third ventricle of the brain where it receives sympathetic innervation from the SCN (Lincoln, 1998; Fig. 3). Changes in the plasma concentration of melatonin convey two kinds of information. The daily fluctuation in concentration makes distinction between day (low melatonin) and night (high melatonin) while, in species living in the temperate zone, the duration of the night-time peak of melatonin indicates season, varying from summer (short duration) to winter (long duration). Thus, the duration of the nighttime peak of melatonin shortens as the days grow longer in spring, reaches a minimum in summer, lengthens as the days grow shorter in autumn and reaches a maximum in winter.

Melatonin is a hormone of darkness: it is secreted at night and its secretion is suppressed by light during the day. This can be misleading, because the secretion of melatonin is a response to the endogenous rhythm of the SCN, not to darkness itself. In most mammals, the rhythmic secretion of melatonin persists during exposure to several days of constant darkness (Scott *et al.*, 1995). Light does, however, play a role in the regulation of the secretion of melatonin by inhibiting the SCN from stimulating the pineal production of the hormone (Reiter, 1993).

The role of melatonin in the regulation of biological rhythms has been well demonstrated in ungulates, particularly with regard to the timing of reproduction in seasonal breeders. Photoperiod has clear inductive effects on reproduction in both red deer and sika deer (*Cervus nippon*). An artificial change from long to short days induced premature reactivation of the reproductive axis owing to its signalling the early onset of autumn (Goss, 1969). Treatment with melatonin in spring and summer gives the same signal and the same result. Artificially increasing the duration of exposure to

the hormone induces autumnal (short-day) responses such as the premature reactivation of testicular acrivity and the early onset of ovulatory cycles in red deer (e.g. Lincoln *et al*, 1984; Webster & Barrell, 1985; Adam *et al.,* 1986).

There is one important caveat. The alteration of the timing of reproduction by the manipulation of photoperiod or of circulating levels of melatonin or in response to dietary and social factors (Martin, 1984) demonstrates ways in which environmental cues can modulate the overt expression of an underlying, endogenous rhythm. None of these observations, however, preclude the central role of the clock in establishing the basic seasonal (or daily) rhythm. Clear evidence for this is provided by the persistence of physiological cycles in animals maintained under constant photoperiod, such as the seasonal

rise in blood levels of luteinizing hormone in ovariectomised ewes kept on short days for 2.5 years (Bronson, 1989: 118), or the persistence of the antler, pelage and other cycles in deer (Goss, 1969; 1974; Loudon & Brinklow, 1992). Consistent with this, the characteristic seasonality of reproduction in different species of cervids remains unaltered despite major changes in their photoperiodic regime. Gerald Lincoln illustrated how tropical Axis deer (*Axis axis*), originating from 15°N lat. in India, continued to breed and calve throughout the year; mule deer (*Odocoileus hemionus*), originating from 40°N lat., calved from June to September; and reindeer, from 60-70°N, showed a restricted calving season lasting approximately four weeks at the beginning of summer, even though all these animals were maintained in captivity in London Zoological
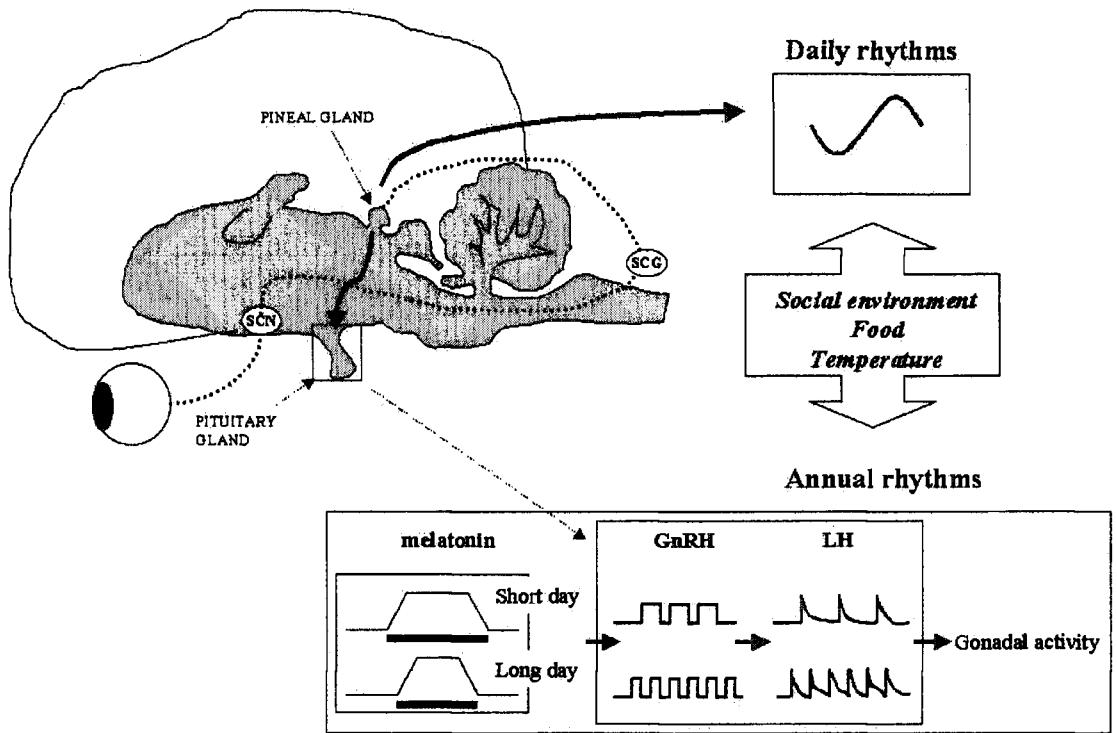

Fig. 3. Schematic plan of the brain illustrating the circadian and circannual axis after a model for a tempetate zone long-day breeding mammal. The dotted line shows the pathway along which photoperiodic information is transmitted to the pineal gland. Light acts both to entrain the phase of the daily endogenous rhythm of the SCN and to suppress melatonin secretion in the pineal gland. The two bold arrows show the pathways along which photoperiodic information, translated into a melatonin rhythm, is believed to influence daily and annual rhythms of physiological function and behaviour. The duration of melatonin secretion acts, for example, via the pituitary gland to modulate the pulsatile secretion of GnRH, thus regulating the activity of the reproductive axis. Daily and annual rhythms are also modulated by non-photic environmental input. (SCN = suprachiasmatic nucleus, SCG = supracervical ganglion, LH = Luteinising hormone, GnRH = Gonadotropin releasing hormone).

Gardens (51°30'N lat.: Lincoln, 1985). The expression of the endogenous rhythms which regulated the breeding season in these deer persisted and was not modified by the characteristics of the photoperiod to which they were latterly exposed.

Rhythms in the Arctic

The life-history of arctic animals exemplifies biological timing in an extreme form. Accurate timing of breeding, rearing young, moulting etc. is particularly important in the Arctic where the ambient temperature may rise above freezing for just a few weeks in summer. Consequently, the degree of synchrony of these and other life-history events within populations generally increases markedly with increasing latitude (e.g. Lincoln, 1998). How is this timing achieved at latitudes characterised by the absence of any marked light/dark rhythm in midsummer and mid-winter which might regulate clock function? We can explore this question using two groups of animals: summer visitors and arctic residents. Visitors, such as migratory birds, are exposed to daily light/dark cycles throughout the year except in mid-summer when they breed and rear their young before departing south. Residents, on the other hand, are exposed to a daily light/dark cycle in late winter and late summer but live under continuous light conditions for the remainder of the year.

Activity rhythms in summer visitors

Snow buntings (*Plectrophenax nivalis*) visit Svalbard (74-81°N lat.) in summer to breed. Their daily rhythms of locomotor activity persist throughout the summer and appear to be entrained by the solar cycle (Krüll, 1976). The birds are evidently able to extract photoperiodic information from the continuous daylight conditions of the arctic summer. Similar observations have been made in a variety of birds and mammals exposed to summer light conditions near the Arctic circle (66°N lat.), including species which do not normally penetrate so far north (Daan & Aschoff, 1975). All species which perform in this manner must have a strong sensitivity to the zeitgeber, thereby being able to extract photoperiodic information even under the continuous daylight conditions of the polar day. The exact nature of the cue is unknown; it might be the changing azimuth of the sun or the changes in the spectral composition of light which occur during the course of the 24 hour day (Krüll, 1976).

Humans, by contrast, behave quite differently. Unlike snow buntings, the summer visitors to Svalbard studied by Johnsson *et al.* (1979) displayed free-running rhythms of body temperature and sleep-wake cycles which soon fell out of phase with the solar, 24 hour day. Humans, therefore, appear to be less sensitive to the photic zeitgeber than snow buntings and are unable to extract photoperiodic information during the continuous daylight conditions of the high arctic summer. Human subjects at 70°N lat. (Tromsø) have been shown to synchronise their melatonin rhythm to the 24 hour day both in summer and winter (Stokkan & Reiter, 1994) but the resultant rhythmicity of the sleep-wake cycle is not strong and sleep disturbances are frequently reported at this location (Lindgjærde *et al.*, 1985). Clearly, sensitivity to continuous light conditions is species specific.

Activity rhythms in arctic residents

High arctic residents respond quite differently to continuous light conditions. Two sub-species have been studied in considerable detail while living under natural light conditions: Svalbard ptarmigan, the only herbivorous bird permanently resident on the high arctic archipelago of Svalbard, and Svalbard reindeer. Both these sub-species behave similarly in response to changes in their photoperiodic environment. As expected, they display daily rhythms of activity while exposed to the daily light/dark cycles of late summer (September-October) and late winter (February-March). In midsummer and mid-winter, by contrast, the animals become intermittently active around the clock (Stokkan *et al.*, 1986; Reierth & Stokkan, 1998; van Oort *et al.*, 1998; 1999a; b; van Oort, unpubl. data). These results indicate that Svalbard reindeer and Svalbard ptarmigan have weak circadian mechanisms: either weak endogenous pacemakers or low sensitivity to the subtle changes in photic conditions which entrain snow buntings in summer. Consequently, these animals are able to feed opportunistically around the clock during the polar night and the polar day as conditions permit, unconstrained by any endogenous cont ol of the temporal pattern of their daily activity. Similar results have been observed in tundra voles (*Microtus oeconomus*) and red-backed voles (*Clethrionomys rutilus*) at 70°N (Swade & Pittendrigh, 1967). In every case, the animals failed to show any free-running or entrained rhythms of activity under continuous light conditions, indicating either loss of the normal coupling

between clock function and behaviour or between the rhythm generating cells within the SCN or even a 'switching-off' of the clock.

In contrast to this, most, though not all, individual arctic ground squirrels (*Spermophilus undulatus*) and brown lemmings (*Lemmus trimucronatus*) maintained rhythmic cycles of activity when exposed to natural summer light conditions at 70°N (Swade & Pittendrigh, 1967). The behaviour of these individuals, therefore, was governed endogenously as in snow buntings and humans (Krüll, 1976; Johnsson *et al.*, 1979). It is evident that considerable variation exists both within and between species in the ways in which the biological clock responds to the special photic conditions which characterise high latitudes.

Rhythms in arctic ungulates
Many cyclic phenomena have been described in Arctic ungulates. These include seasonal variation in activity rhythms (muskoxen: Jingfors, 1982; Oakes *et al.*, 1992; Schaefer & Messier, 1996; Côté *et al.*, 1997; reindeer: Eriksson *et al.*, 1981; Skogland, 1984; van Oort *et al.*, 1998; 1999b), growth (McEwan, 1968; Leader-Williams & Ricketts, 1982), appetite (McEwan & Whitehead, 1970; Ryg & Jacobsen, 1982; Larsen *et al.*, 1985; Tyler *et al.*, 1999), the antler cycle in reindeer (McEwan & Whitehead, 1980; Leader-Williams, 1979; Ryg, 1983; Lincoln & Tyler, 1991; 1994; Bubenik *et al.*, 1997), heart rate (Nilssen *et al.*, 1984; Fancy & White, 1986; Sokolov, 1990; Mesteig *et al.*, submitted), testis function (Leader-Williams, 1979) and a variety of reproductive and metabolic hormones (e.g. Whitehead & McEwan, 1973; Ringberg *et al.*, 1978; Ryg & Jacobsen, 1982; Nilssen *et al.*, 1985; Suttie *et al.*, 1991; Bubenik *et al.*, 1997; 1998).

Notwithstanding the variety of phenomena which have been described, little is known about the regulation of these cycles. Recent work on two sub-species of reindeer, however, provides some intriguing clues. Like in Svalbard reindeer (above), the marked daily rhythms of activity which mainland reindeer (*R. t. tarandus*) living at 70°N lat. show in late winter also break down under the continuous light conditions of summer. Their daily bouts of activity become evenly distributed across the 24 hour day such that they are just as likely to be active at midnight as at noon (van Oort *et al.*, 1998; 1999b). Like Svalbard reindeer, therefore, mainland reindeer seem to have only weak circadian mechanisms in summer.

Interestingly, these two sub-species of reindeer

seem to respond differently to the continuous darkness of winter in their respective natural evironments. While Svalbard reindeer become arrhythmic during the polar night, showing activity around the clock as in summer, mainland reindeer living freely at 70°N lat. remain synchronised with the 24 hour day. Their main bout of activity occurs in the middle of the day and the timing of the onset of activity early in the morning remains highly predictable throughout the winter (van Oort *et al.*, 1998; 1999b). In both situations where these studies were carried out (at 70° and 78°N lat.) the sun remains permanently below the horizon in the middle of winter: mainland reindeer, nevertheless, were capable of responding to the weak diurnal fluctuation in the level of twilight that occurs during December and January at 70°N lat. These results can be intetpreted in one of two ways. Either mainland reindeer are entrained by the weak photic information which is available in winter, or their clock function is suppressed and activity is regulated, instead, directly by changes in light intensity. The key difference between these alternatives may be the level of SCN activity and the functional significance of the clock in winter. This can be explored by studying the pattern of secretion of melatonin which lies closer to the clock than the rhythm of activity and which might, therefore, mote accurately reflect clock function.

Melatonin rhythms in arctic ungulates
Only three groups have investigated the roles of photoperiod and melatonin in the control of endogenous mechanisms in arctic ungulates (muskoxen: Tedesco *et al.*, 1992; reindeer: Eloranta *et al.*, 1992; 1995; Stokkan *et al.*, 1994). A null hypothesis in all these studies is that clock function is maintained throughout the year and, reflecting this, the citcadian rhythm of the secretion of melatonin persists throughout the polar night and the polar day. Were this the case, the observed breakdown of the daily rhythms of locomotor activity in mid-summer and mid-winter in reindeer would be attributable to an uncoupling of the influence of the melatonin cycle from the regulation of activity. If the null hypothesis is rejected, i.e. if the circadian rhythm of the sectetion of melatonin is lost in mid-summer and mid-winter, two alternative explanations for the arrhythmicity of activity arise. Either clock function must be shut down or it persists while the link between the SCN and the pineal is somehow interrupted.

The daily cycle of the secretion of melatonin has been studied in reindeer living under natural light conditions at 70°N lat. Both Eloranta *et al.* (1992) and Stokkan *et al.* (1994) demonstrated the presence of robust daily rhythms in the plasma concentration of melatonin in spring and autumn while in summer the cycle disappeared altogether and the daily production of melatonin fell to an annual minimum. The results from mid-winter trials diverged slightly. Eloranta *et al.* (1992) apparently detected a weak daytime reduction in the plasma concentration of melatonin. Stokkan *et al.* (1994), however, were unable to replicate this result and detected no daily rhythm in the secretion of melatonin in reindeer in December. Taken together, these studies suggest that the breakdown of the daily rhythmicity of activity in reindeer in summer is associated with the suppression of the daily rhythm of the secretion of melatonin, while leaving aside the question of the level of clock function at this time.

Eloranta *et al.* (1995) took a first step towards investigating clock function with an important experiment in which reindeer were put into a dark room in the middle of the day in mid-summer. The animals, which had been exposed to continuous, natural daylight for several weeks, responded with an immediate rise in the plasma concentration of melatonin. Clearly, the abrupt and unprecedented onset of darkness (i.e. 'night') triggered the SCN which was at once capable of stimulating the pineal gland to secret melatonin. This result offers strong evidence that the link between the SCN and the pineal gland remains uninterrupted in summer.

The outstanding question, therefore, is whether the SCN of reindeer sustains circadian rhythmicity in the absence of environmental (photoperiodic) input. Clearly, in mid-summer it cannot owing to the animals' exposure to continuous bright light, but what is the situation in late winter and late summer when the animals are exposed to a daily light/dark cycle? Is it the case that the SCN can sustain a daily rhythm at these times - just as in temperate species of mammals - and that this ability is lost in summer or, alternatively, is the SCN just a passive partner in the system, with its activity being triggered literally every day? Results from a recent series of trials conducted in Tromsø favour the latter model. No evidence has been found of any persistent daily cycle in the secretion of melatonin in reindeer exposed to several days continuous darkness in spring and autumn (K.-A. Stokkan, unpubl. data). Thus far, therefore, it seems possible that the daily rhythm of melatonin secretion in reindeer is generally driven by the daily light/dark cycle and not by an endogenous mechanism. This situation, if confirmed, would be unique among vertebrates.

Conclusion

Reindeer and muskoxen display a rich variety of daily and annual rhythms in their behaviour and their physiological function which, through accurate timing, ensure that the animals' requirements are adapted to the challenges imposed by the environment. The driving force behind this rhythmicity, however, has as yet not been identified. Remarkably, it is not even certain to what extent the rhythms are driven by endogenous mechanisms. The criteria for identifying circadian rhythmicity have not been met in reindeer. Neither their daily rhythms of activity nor their daily cycle of the secretion of melatonin persist under constant photoperiodic conditions. The rhythms quickly become reestablished on exposing the animals to a light/dark cycle but it is not clear whether this is a result of resetting the phase of an endogenous clock or, instead, merely a passive response to an exogenous rhythm. A few shreds of evidence indicate clock function. For example, the phase of the daily onset and end of activity of free-living reindeer deviates asynchronously from sunrise and sunset both in late-summer and late-winter (van Oort, unpubl. data). Nevertheless, in reindeer, which show a higher degree of synchrony in seasonal timing than probably any other cervid, clock function remains largely unknown.

Failure to demonstrate clock function begs many questions. The disappearance of an overt rhythm can be explained in several ways; either as a 'stopping' of the circadian pacemaker, or as an uncoupling of the rhythm from its pacemaker, or as a desynchronisation among the multiplicity of oscillators which control the rhythms (Aschoff, 1981; 1986). The endogenous basis of daily and annual rhythms has been clearly established in several species of temperate ungulates and for this reason alone we would expect to find it in reindeer. The most parsimonious interpretation of the evidence to date, therefore, is that the observed arrhythmicity is due to some kind of uncoupling of the clock rather than its 'stopping'.

The circadian timing mechanism shows great flexibility in vertebrates. We have already indicated in this review that subtle differences exist along a

latitudinal gradient in the ways in which different sub-species of reindeer respond to changes in photoperiod. It is tempting to suggest that the strength of circadian mechanisms varies across a latitudinal gradient in different species of cervids with reindeer, the most northerly, showing the weakest mechanisms rather as Pittendrigh & Takamura (1989) suggested for different sub-species of *Drosophila* flies. We have emphasised how exposure to continuous photoperiodic conditions places special demands on timing mechanisms and how arctic species, therefore, are of particular interest for the study of biological rhythms. Reindeer, of course, are not the only mammals which live under a continuous photoperiod; subterranean blind mole rats (*Spalax ehrenbergi*: Goldman *et al* , 1997) live in constant darkness. Unlike reindeer however, these animals have persistant rhythms, indicating the presence of strong oscillators. Rigid temporal organisation, therefore, remains, even in the absence of temporal information. High arctic reindeer and ptarmigan, however, appear to be released from the grip of the biological clock in summer and winter which enables them, instead, to become truly opportunistic at these times.

Acknowledgement

References

Adam, C. L., Moir, C. E. & Atkinson, T. 1986. Induction of early breeding in red deer (*Cervus elaphus*) by melatonin. – *J. Reprod. Fertil.* 76: 569–573.

Aschoff, J. 1964a. Die Tagesperiodik licht- und dunkelaktiver Tiere. – *Rev. Suisse Zool.* 71: 528–558.

Aschoff, J. 1964b. Survival value of diurnal rhythms. – *Zoological society of London, Symposia* 13: 79–98.

Aschoff, J. 1985. On the perception of time during prolonged temporal isolation. *Human Neurobiology* 4 (1): 41–52.

Aschoff, J. 1986. Anticipation of a daily meal: A process of «learning» due to entrainment. – *Monitore Zoologico Italiano* 20 (2): 195–220.

Aschoff, J. & Tokura, H. 1986. Circadian activity rhythms in squirrel monkeys: Entrainment by temperature cycles. – *J. Biol. Rhythms* 1 (2): 91–99.

Aschoff, J. 1999. Masking and parametric effects of high-frequency light/dark cycles. – *Jap. J. Physiol.* 49 (1): 11–18.

Akerstedt, T. 1979. Altered sleep-wake patterns and circadian rhythms: Laboratory and field studies of sympathoadrenomedullary and related variables. – *Acta Physiol. Scand. Suppl.* 469: 1–48.

Beersma, D. G. M., Daan, S. & Hut, R. A. 1999. Accuracy of circadian entrainment under fluctuating light conditions: Contributions of phase and period responses. – *J. Biol. Rhythms* 14 (4): 320–329.

Boulos, Z. & Terman, M. 1980. Food availability and daily biological rhythms. – *Neurosci. Biobehav. Rev.* 4: 119–131.

Bronson, F. H. 1989. *Mammalian Reproductive Biology.* Chicago, The University of Chicago Press. 325 pp.

Brown, R. D., Cowan, R. L. & Kavanaugh, J. F. 1978. Effect of pinealectomy on seasonal androgen titres, antler growth and feed intake in white-tailed deer. – *J. Anim. Sci.* 47: 435–440.

Bubenik, G. A., Schams, D., White, R. G., Rowell, J., Blake, J. & Bartos, L. 1997. Seasonal levels of reproductive hormones and their relationship to the antler cycle of male and female reindeer (*Rangifer tarandus*). – *Comp. Biochem. Physiol.* B116 (2): 269–277.

Bubenik, G. A., Schams, D., White, R. G., Rowell, J., Blake, J. & Bartos, L. 1998. Seasonal levels of metabolic hormones and substrates in male and female reindeer (*Rangifer tarandus*). – *Comp. Biochem. Physiol.* C 120: 307–315.

Clutton-Brock, T. H., Guiness, F. E. & Albon, S. D. 1982. *Red deer: Behaviour and ecology of two sexes.* Edinburgh University Press, Edinburgh. 378pp.

Campbell, S. S. & Murphy, P. J. 1998. Extraocular circadian phototransduction in humans. – *Science* 279 (5349): 396–399.

Côté, S. D., Schaefer, J. A. & Messier, F. 1997. Time budgets and synchrony of activities in muskoxen: the influence of sex, age and season. – *Can. J. Zool.* 75: 1628–1635.

Daan, S. & Aschoff, J. 1975. Circadian Rhythms of Locomotor Activity in Captive Birds and Mammals: Their variations with Season and Latitude. – *Oecologia* (Berl.) 18: 269–316.

Demas, G. E. & Nelson, R. J. 1998. Photoperiod, ambient temperature, and food availability interact to affect reproducrive and immune function in adult male deer mice, (*Peromyscus maniculatus*) – *J. Biol. Rhythms* 13 (3): 253–262.

Eloranta, E., Timisjärvi, J., Nieminen, M., Ojutkangas, V., Leppäluoto, J. & Vakkuri, O. 1992. Seasonal and daily patterns in melatonin secretion in female reindeer and their calves. – *J. Endocrin.* 130 (3): 1645–1652.

Eloranta, E., Timisjärvi, J., Nieminen, M., Leppäluoto, J. & Vakkuri, O. 1995. Seasonal onset and disappearance of diurnal rhythmicity in melatonin secretion in female reindeer. – *Amer. Zool.* 35: 203–214.

Eriksson, L. O., Källqvist, M. L. & Mossing, T. 1981. Seasonal development of circadian and short-term activity in captive reindeer, *Rangifer tarandus* L. – *Oecologia* 48: 64–70.

Fancy, S. G. & White, R. G. 1986. Predicting energy expenditures for activities of caribou from heart rates. – *Rangifer,* Special Issue No. 1: 123–130.

Frisch, B. & Aschoff, J. 1987. Food entrainment in bees. – *Physiol. Entomol.* 12: 41–48.

Grandin, N. & Charbonneau, M. 1991. Intracellular free calcium oscillates during cell division of *Xenopus* embryos. – *J. Cell Biology* 112 (4): 711–718.

Goldman, B. D., Goldman, S. L., Riccio, J. & Terkel, J. 1997. Circadian patterns of locomoter activity and body temperature in blind mole-rats, *Spalax ehrenbergi.* – *J. Biol. Rhythms* 12 (4): 348–361.

Goss, R. J. 1969. Photoperiodic control of antler cycles in deer. I. Phase shift and frequency changes. – *J. Exp. Zool.* 170: 311–324.

Goss, R. J., Dinsmore, C. E., Grimes, L. N. & Rosen, J. K. 1974. Expression and suppression of the circannual antler cycle in deer. – *In:* Pengelley, E. T. (ed.). *Circanual Clocks, Annual Biological Rhythms.* Academic Press, New York, pp. 393–422.

Hagemeijer, J. & Waisel, Y. 1987. An endogenous circadian rhythm of transpiration in *Tamarix aphylla.* – *Physiologia plantarum* 70 (2): 133–138.

Hau, M. & Gwinner, E. 1992. Circadian entrainment by feeding cycles in house sparrows, *Passer domesticus.* – *J. Comp. Physiol.* A 170: 403–409.

Hau, M. & Gwinner, E. 1997. Adjustment of house spatrow circadian rhythms to a simultaneously applied light and food zeitgeber. – *Physiol. Behav.* 62 (5): 973–981.

Heintzen, C., Nater, M., Apel, K. & Staiger, D. 1997. AtGRP7, a nuclear RNA-binding protein as a component of a circadian-regulated negative feedback loop in *Arabidopsis thaliana.* – *Proc. Nat. Ac. Sci.* 94 (16): 8515–8520.

Hewison, A. J. M., Angibault, J. M., Boutin, J., Bideau, E., Vincent, J. P. & Sempéré, A. 1996. Annual variation in body composition of roe deer, *Capreolus capreolus,* in moderate environmental conditions. – *Can. J. Zool.* 74 (2): 245–253.

Hoffman, K. 1981. Photoperiodism in vertebrates. – *In:* J. Aschoff (ed.). *Handbook of Behavioural Neurobiology. Vol. 4. Biological Rhythms.* Plenum press. New York and London, pp. 449–473.

Hoffmans-Hohn, M., Martin, W. & Brinkmann, K. 1984. Multiple periodicities in the circadian system of unicellular algae. – *Zeitschrift für Naturforschung section C Biosci.* 39 (7–8): 791–800.

Jingfors, K. T. 1982. Seasonal activity budgets and movements of an introduced Alaskan muskox herd. – *J. Wild. Manage.* 46: 344–350.

Johnsson, A. Engelmann, W., Klemke, W. & Eske, A.T. 1979. Free-running human circadian rhythms in Svalbard. – *Z. Naturforsch.* 34: 470–473.

Jorgens, H. 1967 Beobachtungen über die Rhythmik vegatativer Funktionen während eines mehrtagigen Bunkeraufenthaltes. – *Verh. Dtsch. Ges. Inn. Med.* 73: 650–654.

Krüll, F. 1976. Zeitgebers for animals in the continuous daylight of high Arctic summer. – *Oecologia* (Berl.) 24: 149–158.

Larsen, T. S., Nilsson, N. O. & Blix, A. S. 1985. Seasonal changes in lipogenesis and lipolysis in isolated adipocytes from Svalbard and Norwegian reindeer (*Rangifer tarandus* ssp.). – *Acta Physiol. Scand.* 123(1): 97–104.

Leader-Williams, N. 1979. Age related changes in the testiculat and antler cycles of reindeer, *Rangifer tarandus.* – *J. Reprod. Fert.* 57: 117–126.

Leader-Williams, N. & Ricketts, C. 1982. Seasonal and sexual patterns of growth and condition of reindeer introduced into South Georgia. – *Oikos* 38: 27–39.

Levy, F. & Moore, D. 1993. Popularion variation of leaflet sleep movements in *Oxalis grandis* (Oxalidaceae). – *Am. J. Botany* 80 (12): 1482–1493.

Lincoln, G. A., Fraser, H. M. & Fletcher, T. J. 1984. Induction of early rutting in male red deer (*Cervus elaphus*) by melatonin and its dependence on LHRH. – *J. Reprod. Fert.* 85: 687–704.

Lincoln, G. A. 1985. Seasonal breeding in Deer. – *Royal Soc. N. Z. Bull.* 22: 165–179.

Lincoln, G. A. & Tyler, N. J. C. 1991. Antler growth in male and female reindeer calves occurs in the absence of the gonads. – *In:* Brown, R. D. (ed.). *The Biology of Deer.* Springer verlag, New York, pp. 493–498.

Lincoln, G. A. 1992. Biology of seasonal breeding in deer. – *In:* Brown, R. D. (ed.). *The Biology of Deer.* Springer verlag, New York, pp. 565–574.

Lincoln, G. A. & Tyler, N. J. C. 1994. Role of gonadal hormones in the regulation of the seasonal antler cycle in female reindeer, *Rangifer tarandus.* – *J. Reprod. Fert.* 101: 129–138.

Lincoln, G. A. & Baker, B. I. 1995. Seasonal and photoperiod-induced changes in the secretion of alpha-melanocyte-stimulating hormone in Soay sheep: Temporal relationships with changes in beta-endorphin, prolactin, follicle-stimulating hormone, activity of the gonads and growth of wool and horns. – *J. Endocrin.* 144 (3): 471–481.

Lincoln, G. A. 1998. Photoperiod-Melatonin relay in Deer. – *Acta Veterinaria Hungarica* 46 (3): 341–356.

Lindgjærde, O., Bratlid, T. & Hansen, T. 1985. Insomnia during the «dark period» in Northern Norway. – *Acta Psychiatr. Scand.* 71: 506–512.

Loudon A. S. I. & Brinklow, B. R. 1992. Reproduction in deer: Adaptations for life in seasonal environments. – *In:* Brown, R. D. (ed.). *The Biology of Deer.* Springer verlag, New York, pp. 261–278.

Loudon, A. S. I. & Jabbour, H. N. 1994. Seasonal rhythms in the physiology of deer: endogenous clocks and target tissues. – *In:* Milne, J. A. (ed.). *Recent Developments in Deer Biology.* Edinburgh, U.K., pp. 197–207.

Lundberg, P. & Eriksson, L. O. 1984. Postjuvenile molt in 2 northern Scandinavian starling, *Sturnus vulgaris,* populations: Evidence for difference in the circannual time program. – *Ornis Scand.* 15 (2): 105–109.

Malpaux, B., Viguié, C., Skinner, D. C., Thiéry, J. C. & Chemineau, P. 1997. Control of the circannual rhythm of reproduction by melatonin in the Ewe. – *Brain Res. Bull.* 44 (4): 431–438.

Martin, G. B. 1984. Factots affecting the secretion of luteinizing hormone in the ewe. – *Biol. Rev.* 59: 1–87.

McEwan, E. H. 1968. Growth and development of barren-ground caribou. – *Can. J. Zool.* 46: 1023–1029.

McEwan, E. H. & Whitehead, P. E. 1970. Seasonal changes in the energy and nitrogen intake in reindeer and caribou. – *Can. J. Zool.* 48: 905–913.

McEwan, E. H. & Whitehead, P. E. 1980. Progesreron levels during anestrus, estrus and pregnancy in reindeer and caribou (*Rangifer tarandus*). – *In:* Reimers E., Gaare E. & Skjenneberg S. (eds.). *Proc. 2nd. Int. Reindeer/Caribou Symp., Røros, Norway,* pp. 324-328.

Meijer, T. 1989. Photoperiodic control of reproduction and moult in the kestrel, *Falco tinnunculus.* – *J. Biol. Rhythms* 4 (3): 351–364.

Menaker, M. & Binkley, S. 1981. Neural and endocrine control of circadian control in vertebtates. – *In:* J. Aschoff (ed.). *Handbook of Behavioural Neurobiology. Vol. 4. Biological Rhythms.* Plenum press. New York and London, pp. 243–255.

Menaker, M. & Tosini, G. 1996. The evolution of vertebrate circadian systems. – *In:* Honma, K. S. & Honma, I. (eds.). *Circadian Organisation and Oscillatory Coupling.* Hokkaido University Press, Sapporo, pp. 39–52.

Mesteig, K., Tyler, N. J. C. & Blix, A. S. (submitted). Seasonal changes in heart rate and food intake in reindeer (*Rangifer tarandus tarandus*). – *Acta Physiol. Scand.*

Moore-Ede, M.C. & Sulzman, F. 1981. Internal temporal order. – *In:* J. Aschoff (ed.). *Handbook of Behavioural Neurobiology. Vol. 4. Biological Rhythms.* Plenum press. New York and London, pp. 215–241.

Moore, D., Siegfried, D.,Wilson, R. & Rankin, M. A. 1989. The influence of time of day on the foraging behaviour of the honeybee, *Apis mellifera.* – *J. Biol. Rhythms* 4 (3): 305-326.

Miyamoto, Y. & Sancar, A. 1998. Vitamin B2-based blue-light photoreceptots in the retinohypothalamic tract as the photoactive pigments for setting the circadian clock in mammals. – *Proc. Nat. Ac. Sci.* 95 (1): 6097–6102.

Mrosovsky, N. & Hallonquist, J. D. 1986. Colliding of activity onset and offset: evidence fot multiple circadian oscillators. – *J. Comp. Phys. A* 159: 187–190.

Nilssen, K. J., Johnsen, H. K., Rognmo, A. & Blix, A. S. 1984. Heart rare and energy expenditure in resting and running Svalbard and Norwegian reindeer. – *Am. J. Physiol.* 246: 963–967.

Nilssen, K. J., Bye, K., Sundsfjord, J. A. & Blix, A. S. 1985. Seasonal changes in T3, T4 and Cortisol in Free-ranging Svalbard reindeer (*Rangifer tarandus platyrhynchus*). – *Gen. Comp. Endocrin.* 59: 210–213.

Oakes, E. J., Harmsen, R. & Eberl, C. 1992. Sex, age and seasonal differences in the diets and activity budgets of muskoxen (*Ovibus moschatus*). – *Can. J. Zool.* 70: 605–616.

Orth, D. N., Besser, G. M., King, P. H. & Nicholson, W. E. 1979. Free-running circadian plasma cortisol rhythm in a blind human subject. – *Clinic. Endocr.* 10 (6): 603–618.

Phillips, D. L., Rautenberg, W., Rashotte, M. E. & Stephan, F. K. 1993. Evidence for a separate food-entrainable oscillator in the pigeon. – *Physiol. Behav.* 53: 1105–1113.

Pittendrigh, C. S. 1981. Circadian rhythms: Entrainment. – *In:* J. Aschoff (ed.). *Handbook of Behavioural Neurobiology. Vol. 4. Biological Rhythms.* Plenum press. New York and London, pp. 95–124.

Pittendrigh, C.S. & Daan, S. 1976. A functional analysis of circadian pacemakers in nocturnal rodents. IV. Pacemaker as clock. – *J. Comp. Physiol.* 106: 291–331.

Pittendrigh, C. S. & Takamura, T. 1989. Latitudinal clines in the properties of a circadian pacemaker. – *J. Biol. Rhythms.* 4 (2): 217–235.

Reierth, E. & Stokkan, K.-A. 1998. Activity rhythm in high Arctic Svalbard prarmigan (*Lagopus mutus hyperboreus*). – *Can. J. Zool.* 76: 2031–2039.

Reinberg, A. E. & Touitou, Y. 1996. Human circadian rhythms. Synchronization and dyschronism. – *Pathology Biology.* 44 (6): 487–495.

Reiter, R. J. 1993. The melatonin rhythm: both a clock and a calendar. – *Experientia* 49: 654–664.

Ringberg, T., Jacobsen, E., Ryg, M. & Krog, J. 1978. Seasonal changes in levels of growth hormone, somatomedin and thyroxine in free-ranging semi-domesticared Norwegian reindeer (*Rangifer tarandus tarandus* L.). – *Comp. Biochem. Physiol. B* 60: 383–386.

Ruby, N. F., Dark, J., Heller, H. C. & Zucker, I. 1996. Ablation of the suprachiasmatic nucleus alters timing of hibernation in ground squirrels. – *Proc. Nat. Ac. Sci.* 93 (18): 9864–9868.

Ryg, M. & Jacobsen, E. 1982. Seasonal changes in growth, feed intake, growth hormone and thyroid hormones in young male reindeer (*Rangifer tarandus tarandus*). – *Can. J. Zool.* 60: 15–23.

Ryg, M. 1983. Effect of testostetone on antler growth in yeatling male reindeer. – *Rangifer* 3 (2): 6–9.

Schaefer, J. A. & Messier, F. 1996. Winter activity of muskoxen in relation to foraging conditions. – *Ecoscience* 3: 147–153.

Scott, C. J., Jansen, H. T., Kao-Chen, C., Kuehl, D. E. & Jackson, G. L. 1995. Disruption of reproductive rhythms and patterns of melatonin and prolactin secretion following bilateral lesions of the suprachiasmatic nuclei in the ewe. – *J. Neuroendocrinol.* 7 (6): 429–443.

Skogland, T. 1984. Wild reindeer foraging-niche organization. – *Holarctic Ecology* 7: 345–379.

Sokolov, A. Ya. 1990. Heart tate of the unrestrained reindeer *Rangifer tarandus*. – *J. Evol. Biochem. Physiol.* 26 (2): 182–185.

Squires, V. R. 1971. Temporal patterns of activity in a small flock of Merino sheep as determined by an automated recording technique. – *Animal Behav.* 19: 657–660.

Stayton, M. M., Brosio, P., Dunsmuir, P. 1989. Photosynthetic genes of *Petunia* (Mitchell) are differentially expressed during the diurnal cycle. – *Plant Physiol. Bethesda.* 89 (3): 776–782.

Stokkan, K.-A., Mortensen, A. & Blix, A. S. 1986. Food intake, feeding rhythm and body mass regulation in Svalbard rock ptarmigan. – *Am. J. Physiol.* 251: R264–R267.

Stokkan, K.-A. & Sharp, P. J. 1990. Seasonal breeding in High Arctic Ptarmigan. – *In:* Wada, M. *et al.* (eds.). *Endocrinology of birds: Molecular to behavioral.* Japan Sci. Soc. Press, Tokyo/Springer-Verlag, Berlin, pp. 251–258.

Stokkan, K.-A. & Reiter, R. J. 1994. Melatonin rhythms in Arctic urban residents. – *J. Pineal Res.* 16 (1): 33–36.

Stokkan, K.-A., Tyler N. J. C. & Reiter, R. J. 1994. The pineal gland signals autumn to reindeer (*Rangifer tarandus tarandus*) exposed to the continuous daylight of the Arctic summer. – *Can. J. Zool.* 72: 904–909.

Suttie, J. M., Goodall, E. D., Pennie, K. & Kay, R. N. B. 1983. Winter food restriction and summer compensation in red deer stags (*Cervus elaphus*). – *Brit. J. Nutr.* 50 (3): 737–748.

Suttie, J. M., White, R. G., Breier, B. H. & Gluckman, P. D. 1991. Photoperiod associated changes in insulin-like growth factor-1 in reindeer. – *Endocrin.* 129: 679–682.

Suttie, J. M. & Webster, J. R. 1995. Extreme seasonal growth in Arctic deer: Comparisons and control mechanisms. – *Am. Zool.* 35 (3): 215–221.

Swade, R. H. & Pittendrigh, C. S. 1967. Circadian locomotor rhythms of rodents in the Arctic. – *Am. Nat.* 101: 431–466.

Tedesco, S. C., Flood, P. F., Morton, D. J. & Reiter, R. J. 1992. Seasonal melatonin and luteinising hormone rhythms in muskoxen at 52°N. – *Rangifer* 12: 197–201.

Turek, F. W. & Losee-Olson, S. 1988. The circadian rhythm of LH release can be shifted by injections of a benzodiazepine in female golden hamsters. – *Endocrin.* 122 (2): 756–758.

Turek, F. W. 1998. Circadian rhythms. – *Hormone Res. Basel.* 49 (3-4): 109–113.

Van Oort, B. E. H., Tyler, N. J. C., Tobler, I., Barnes, B. M. & Stokkan, K.-A. 1998. Lack of circadian rhythms in free-living Arctic reindeer during winter. – *VI Meeting Soc. Res. Biol. Rhythms. May 6-10 1998,* Amelia Island Plantation, Florida, USA., p. 59.

Van Oort, B. E. H., Stokkan, K.-A., Reierth, E. & Tyler, N. J. C. 1999a. Biological rhythms in Arctic vertebrares. – *Rangifer* Report No. 4: 13.

Van Oort, B. E. H., Stokkan, K.-A. & Tyler, N. J. C. 1999b. Long-term patterns of activity in relarion to photoperiod in free-ranging reindeer and sheep. – *Rangifer* Report No. 4: 87.

Weaver, D. R. 1998. The suprachiasmatic nucleus: A 25-year retrospective. – *J. Biol. Rhythms* 13 (2): 100–112.

Webster, J. R. & Barrell, G. K. 1985. Advancement of reproductive activity, seasonal reducrion in prolactin sectetion, and seasonal pelage changes in pubertal red deer hinds (*Cervus elaphus*) subjected to shortened daily photopetiod or daily melatonin treatment. – *J. Reprod. Pert.* 73: 255–260.

Whitehead, P. E. & McEwan, E. H. 1973. Seasonal variation in plasma testosterone of reindeer and caribou. – *Can. J. Zool.* 51: 651–658.

Yamazaki, S., Goto, M. & Menaker, M. 1999. No evidence for extraoculare photoreceptots in the circadian system of the Syrian Hamster. – *J. Biol. Rhythms* 14 (3): 197–201.