

Photoperiod and the regulation of annual and circannual cycles of food intake

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For wild animals, food availability usually exhibits considerable seasonal fluctuations and as a result dramatic seasonal variations in body weight, fatness and food intake are often observed. Birds and mammals living in the temperate zones or higher latitudes, therefore, time the onset of reproductive activity each year with great precision so that young are produced at the most propitious time of year. Numerous studies have now demonstrated that in such animals seasonal physiological changes governing the reactivation of the reproductive axis are tuned by external environmental change, principally photoperiod (for review, see Bronson, 1988; Bronson & Heideman, 1994). The annual daylength cycle, thus, represents the most reliable noise-free proximal factor available to entrain seasonal reproductive cycles.

Food intake and body condition are seasonally and photoperiodically regulated in many mammals (Mrosovsky & Sherry, 1980). The phenomenon has been most extensively investigated in ruminants, scuirid rodents and small mammals, including several species of voles and hamsters (Bartness & Wade, 1985; Kay, 1985). The present brief review seeks to highlight aspects of the photoperiodic and seasonal regulation of food intake and metabolic cycles by examining their endogenous nature and considering the manner of their photoperiodic regulation. Two related topics will be considered. First, the role of photoperiod change and the endocrine transduction of the photoperiodic signal will be examined in relation to seasonal changes in metabolism and food intake. Second, the endogenous nature of these processes in many organisms will be emphasized. Since the field has now developed a voluminous literature, reviews and major articles are cited for further reference where appropriate.

SEASONAL CHANGES IN BODY CONDITION AND FOOD INTAKE

Deer

Wild red deer (*Cervus elaphus*) undergo marked seasonal changes in body condition, laying down fat during the late summer which is mobilized by males in the autumnal rut and by females over the winter (Mitchell *et al.* 1976). However, the seasonal cycle of body condition of such animals is not due entirely to the alteration in abundance and scarcity of forage. In red deer, seasonal changes in body condition are also observed when animals are farmed on productive grass pastures (Fennessey *et al.* 1981; Atajaya *et al.* 1989). Studies of enoused deer provided with *ad lib.* access to consistent diets reveal that the body-weight cycle is associated with an underlying cycle of voluntary food intake (VFI), the VFI cycle (Pollock, 1975; Simpson *et al.* 1984; Suttie & Simpson, 1985; Loudon *et al.* 1989; for review, see Barry *et al.* 1991). Similar cycles of body condition and food intake have been shown to occur in other temperate or boreal species including reindeer (*Rangifer tarandus tarandus*; McEwan & Whitehead, 1970; Ryg & Jacobsen,

1982a), moose (*Alces alces*; Gasaway & Coady, 1974) and roe deer (*Capreolus capreolus*; Drozd *et al.* 1975). They are also observed in feral and domesticated breeds of sheep, although in the latter case the cycles are attenuated and do not exhibit the high amplitude seen in wild ruminants (Simpson *et al.* 1984; Kay, 1985).

Under natural conditions the annual peak of VFI in red deer occurs in mid-summer, with a trough in mid-winter (Loudon *et al.* 1989). The food-intake cycle, therefore, matches the energy requirements for peak lactation in females (Loudon & Kay, 1984) and deposition of fat reserves before the rut in stags (Mitchell *et al.* 1976). In intact stags the cycle has a 2–3-fold amplitude; in females a less than 2-fold amplitude (Loudon & Brinklow, 1992).

Photoperiod is known to regulate the VFI cycle of seasonal deer (Brown *et al.* 1979; Fig. 1). For instance, red deer maintained on an artificial 6-month photoperiod such that two cycles of long or short daylength occur in one calendar year exhibit two cycles of food intake and body weight gain, i.e. two rhythms of peak intake followed by a trough (Kay, 1979; Simpson *et al.* 1984). When the cycle is compressed by manipulating the frequency of the photoperiod signal, the peak in appetite lags behind the peak in daylength such that food intake reaches a maximum at a time when photoperiod has started to decrease (Kay, 1979). These seasonal cycles are capable of further photoperiodically-mediated compression. For instance, red deer stags maintained on alternating 2-month periods of artificial photoperiods of 16 h light (L)–8 h dark (D; 16L:8D) followed by 8L:16D show a cycle of food intake and antler growth every 4 months (Suttie *et al.* 1984). Here, the phase-delay in the rhythms of intake is even more marked. (This problem is discussed in more detail (p. 502) in relation to the issue of circannual rhythmicity.)

A number of authors have reported a seasonal reduction in metabolic rate and estimated maintenance energy requirement for deer maintained on winter photoperiods (Silver *et al.* 1969; McEwan & Whitehead, 1970; Thompson *et al.* 1973; Simpson *et al.* 1978). However, in a recent study of growing red deer calves no significant seasonal difference in resting energy expenditure was detected (Sibbald *et al.* 1993). In this latter study general energy expenditure was closely correlated with animal activity and animals were generally more active in the summer than the winter. These observations are consistent with other recent studies of metabolic rates in white-tailed deer (*Odocoileus virginianus*) in which no significant seasonal variation was detected (Pekins *et al.* 1992). Thus, for deer it remains unclear whether metabolic rate exhibits significant seasonal variation or whether earlier reports in the literature of seasonal variation in metabolic rate merely reflected seasonal differences in animal activity and behaviour.

The phasing of the seasonal VFI cycle of deer is largely independent of seasonal changes in gonadal steroid secretion associated with re-activation of the reproductive axis (Fig. 1). For instance, castrated males also exhibit seasonal VFI cycles (Kay, 1979; Ryg & Jacobsen, 1982b). However, gonadal steroids do modulate the amplitude of the VFI cycle since castrated red deer stags exhibit low-amplitude VFI cycles similar to those observed in females (Kay, 1979; Loudon *et al.* 1989; Loudon & Brinklow, 1992). Similarly, in females, ovariectomized oestradiol-implanted female red deer continue to exhibit a normal seasonal body-weight cycle with a peak in late summer and a trough in late winter (A. S. I. Loudon & H. N. Jabbour, unpublished results).

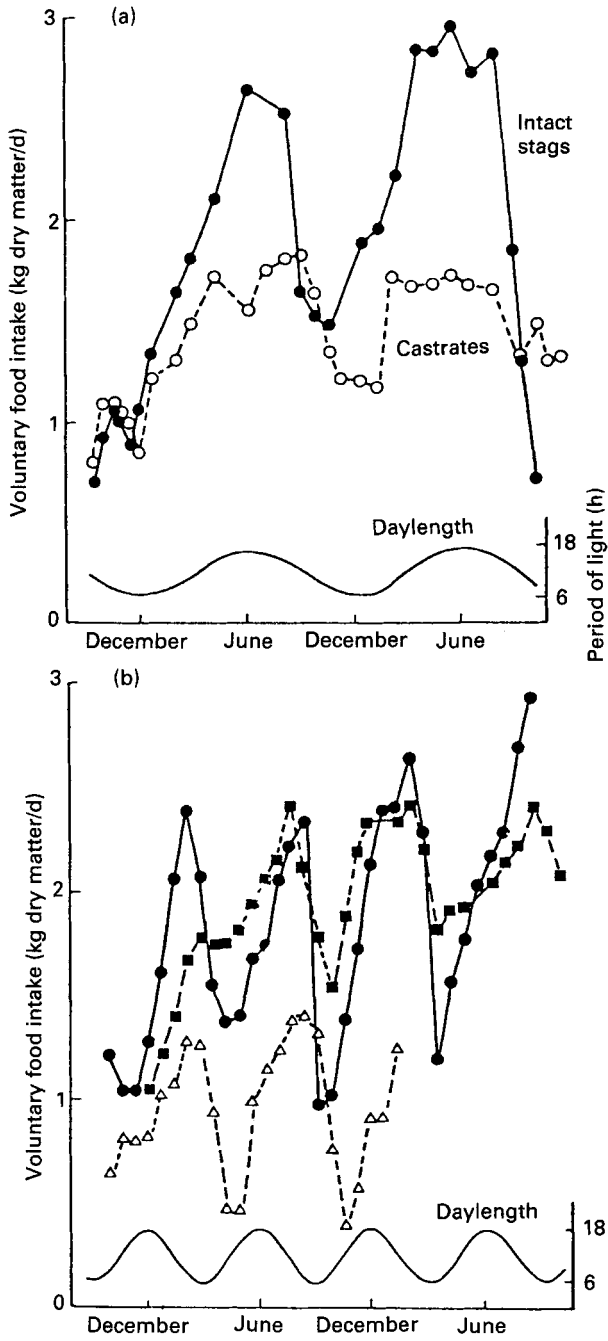


Fig. 1. (a), Voluntary intake of pelleted concentrate by intact (●) or castrate (○) stags penned in natural lighting. (b), Voluntary intake of stags (●), Suffolk × rams (■) and Soay rams (△) subjected to a 6-month photoperiod cycle. From Kay, 1979.

Involvement of the pineal gland

The pineal gland and its hormone melatonin is a key element in the transduction of the photoperiodic signal in mammals (for review, see Reiter, 1980). The synthesis of melatonin is controlled by light, with the neural transmission of this signal following a circuitous route from the retina to the pineal gland. Light stimulates the retina which in turn transmits information to a number of neural structures, most importantly the hypothalamic suprachiasmatic nuclei (SCN). The SCN in mammals is responsible for the generation of circadian rhythmicity, including the daily secretion of a nocturnal pineal melatonin signal (Rusak & Zucker, 1979). Seasonal changes in the duration of photoperiod, therefore, result in an alteration in the duration of melatonin secretion providing the animal with an accurate estimate of the duration of night-length throughout the year. A large number of studies have now demonstrated that artificial administration of melatonin to pinealectomized animals can mimic the effects of photoperiods on reproduction (sheep, Bittman *et al.* 1983; hamsters, Carter & Goldman, 1983). It is now clear that the pineal gland is a neutral agent, transmitting seasonal photoperiodic information via the melatonin signal which can be used to cue a variety of neuroendocrine responses, including inhibition or activation of the gonadal axis, changes in body weight or the initiation of moulting. The actual response to the signal, therefore, is appropriate to the species and the environment in question.

Treatment of red deer with melatonin alters the annual pattern of growth and food intake. Stags treated with subcutaneous implants of melatonin in spring exhibit an advance in the timing of the breeding season, also reaching their peak weight earlier and losing weight earlier than untreated animals (Webster *et al.* 1991). Similar observations have been made for female deer. Milne *et al.* (1990) treated housed adult female red deer with a daily oral melatonin dose from mid-summer and induced a phase shift of approximately 1 month in the timing of the autumnal decline in VFI. The effect of melatonin in advancing the timing of the VFI cycle was also observed in the timing of the moult cycle and onset of the breeding season. These observations are consistent with the view that exogenous melatonin serves to phase-shift all seasonal physiological rhythms.

Few studies have attempted to examine the effects of manipulation of the seasonal appetite cycle of free-ranging mammals. In one such study, grazing red deer were maintained on pastures offering different levels of food availability and treated with melatonin (Heydon *et al.* 1993). Food intake of grazing animals was measured in the autumn by use of the *n*-alkane marker technique (Mayes *et al.* 1986) and their grazing behaviour studied. Melatonin treatment resulted in a significant depression by approximately 20% of VFI for animals grazing on high-availability pastures but had little effect on animals grazing on a more-restricted pasture (Heydon *et al.* 1993). The reduction of food intake in melatonin-treated deer grazing high-herbage biomasses during the autumn was similar to effects observed in enoused melatonin-treated animals fed on *ad lib.* artificial diets (Milne *et al.* 1990).

Studies of grazing behaviour failed to reveal any significant differences between treated and control animals with respect to feeding rate (bites per minute). In such circumstances, melatonin-dependent reductions in food intake may be modulated by variation in the duration of time spent grazing per day rather than the instantaneous feeding rate which may be optimized for any given level of food availability. Melatonin also advanced the timing of the onset of the breeding season, as has previously been shown for this species (Adam & Atkinson, 1984; Adam *et al.* 1986; Milne *et al.* 1990). In this study the timing of the offset of the breeding season was also advanced such that the

total duration of the breeding season was not significantly different from that of untreated animals. These observations provide further support for the idea that melatonin treatment serves to phase-shift underlying circannual rhythms (Loudon & Brinklow, 1992). A general conclusion is that the expression of seasonal appetite changes in free-ranging grazing animals may depend upon a complex interaction between food availability and feeding behaviour such that appetite cycles may only be manifested in wild populations under conditions of high food availability or at certain stages of the annual cycle.

Rodents

In muroid rodents the photoperiodic regulation of appetite and body weight exhibits considerable species variation (Dark & Zucker, 1985). The Syrian hamster (*Mesocricetus auratus*) has been extensively investigated (for review, see Bartness & Wade, 1985). In common with other hamster species, this animal is a long-day breeding mammal with a re-activation of the gonadal axis in response to lengthening photoperiods. Syrian hamsters exhibit their minimal body weight during long photoperiods, at which time they have low fat reserves. Following exposure to short photoperiods, their gonads regress and body weight increases (Hoffman & Reiter, 1966; Bartness & Wade, 1984; Bartness *et al.* 1985). This photoperiodically-mediated increase in body weight is almost entirely associated with the deposition of fat and is largely independent of changes in gonadal steroid secretion since castration reduces the amplitude of the photoperiodic effect by only 10–15% (Bartness & Wade, 1984; Wade & Bartness, 1984a). These changes in body condition are associated with a photoperiodically-mediated overall change in energy metabolism; somewhat paradoxically, short photoperiods stimulate brown adipose tissue growth and thermogenic potential in Syrian hamsters (McElroy & Wade, 1986). Short daylengths also cause an increase in food intake, although the amplitude of the increase over long photoperiods is less than 20%. Here, in contrast to deer (see p. 496), seasonal changes in body weight are primarily attributable to alterations in energy metabolism (Bartness & Wade, 1984), rather than high-amplitude VFI cycles. Treatment of long-day-housed hamsters with melatonin is effective in mimicking the effects of short photoperiods on weight gain and energy metabolism (Bartness & Wade, 1984; Wade & Bartness, 1984a).

In contrast to the Syrian hamster, Siberian hamsters (*Phodopus sungorus*) and meadow voles (*Microtus pennsylvanicus*) lose weight and have a reduced food intake and energy expenditure when placed in short photoperiods (Heldmaier & Steinlechner, 1981a; Dark & Zucker, 1983; Dark *et al.* 1983). These changes can also be mimicked by treatment with melatonin (Bartness & Wade, 1985). Siberian hamsters commonly lose 20–25% of their body weight on short photoperiods, with almost all of this weight loss being in the form of lipid reserves (Wade & Bartness, 1984b). At first sight these differences appear to be paradoxical. However, a key feature of the biology of the smaller Siberian hamsters is that unlike Syrian hamsters they do not hibernate. *Phodopus* reduces its body mass at a time when food supply is decreasing and the harsh Siberian winter is approaching, but by so doing may be able to reduce overall winter maintenance requirements.

The scaling effects of metabolic rate with body size would result in stored fat reserves providing only very short-term energy stores for such an animal. However, short-photoperiod-housed Siberian hamsters exhibit the phenomenon of daily torpor, whereby

body temperature is reduced to approximately 17° for up to 8 h resulting in significant energy savings (Heldmaier & Steinlechner, 1981*b*). Such photoperiodically-mediated inductions of torpor can be blocked by the injection of prolactin (Ruby *et al.* 1993), a hormone normally secreted only during long photoperiods in seasonal mammals (for review, see Curlew, 1992). In addition, Siberian hamsters are avid stors of seeds in their burrows and, therefore, may be able to counteract the effect of depleted body energy stores (Bartness & Wade, 1985). Thus, by storing food, engaging the mechanisms controlling torpor biology and by reducing food intake and body weight, Siberian hamsters are able to survive in extreme winter conditions.

In short-lived muroid rodents, food intake and seasonal metabolic changes are primarily regulated by photoperiodic change. Such species are generally characterized by long breeding seasons with the production of several sequential litters. Under long photoperiods animals remain continuously reproductively active and do not exhibit spontaneous changes in food intake and metabolism. The only expression of an endogenous rhythm is seen if animals are housed under persistent short photoperiodic stimulation. Initially such photoperiods cause gonadal regression, but after 2–3 months animals will spontaneously undergo full gonadal recrudescence with concomitant changes in metabolism, and remain reproductively competent thereafter. Thus, endogenous rhythmicity is confined to a uni-directional change.

An intriguing feature of the biology of many rodents such as voles is that the pattern of postnatal growth and development is partially entrained by photoperiodic influences experienced by the fetus *in utero* (Horton, 1984, 1985; Lee & Zucker, 1988). Vole pups born at the beginning of the breeding season undergo rapid somatic and reproductive development, achieve puberty by 2 months of age and produce several litters before undergoing reproductive involution in response to shortening photoperiods. In contrast, offspring born at the end of the breeding season exhibit slowed growth rates, deposit fat reserves, grow a thick winter pelage and remain reproductively inactive until the commencement of the next breeding season. The underlying mechanisms involved have been revealed in experiments in which montane voles (*Microtus montanus*) were gestated under either long (18L:6D) or short photoperiods (10L:14D) and then switched to an identical intermediate photoperiod (14L:10D) at birth (Horton, 1984). Pups exhibited a pattern of growth reflecting the photoperiod experienced by the mother during gestation. In these and other experiments on meadow voles (Lee & Zucker, 1988), vole mothers clearly communicated information about the daylength to their pups, influencing pup responsiveness postnatally. It has now been established that a major component of the prenatal entraining signal is maternal melatonin, which may be assumed to cross the placental barrier. Treatment of long-day-housed females with melatonin mimics the effects of gestational short photoperiods and results in a decrease in preweaning weight gain, delays testicular development and causes early growth of winter pelage (Lee *et al.* 1989).

THE SEASONAL REGULATION OF BODY WEIGHT AND CIRCANNUAL RHYTHMS

Compensatory weight change

Although seasonal cycles of body-weight gain and loss are characterized by photoperiodically-mediated hyperphagia and anorexia, several lines of evidence support the

idea that changes in body weight and fat content of mammals are not simply a direct consequence of changing food intake. This phenomenon is most strikingly demonstrated in scuirid rodents such as the ground squirrels which exhibit endogenous seasonal rhythms of body mass, food intake and hibernation, even when kept under constant conditions (Pengelley, 1957; Davis, 1976). For instance, ground squirrels deprived of food for extended intervals either side of the weight gain or loss portion of the cycle and then allowed to re-feed will overeat until they have recovered a seasonally appropriate body mass (Heller & Poulson, 1970; Mrosovsky & Fisher, 1970; Barnes & Mrosovsky, 1974), at which point they will then continue to exhibit appropriately-phased cycles. In red deer the spring-time rise in VFI is largely suppressed by treatment with the dopamine agonist bromocriptine, but treated animals still show a seasonal rise in body weight (Curlewis *et al.* 1988b). Seasonal cycles of food intake and body weight are generally observed to be out of phase with each other, with body weight either lagging behind the VFI cycle (deer; Loudon *et al.* 1989) or being in advance of the cycle (ground squirrels, Pengelley & Admundson, 1974; Siberian hamsters, Bartness & Wade, 1985), lending further support to the idea that weight changes are not necessarily a direct consequence of changing VFI. Ground squirrels prevented from increasing food intake from the nadir of the winter appetite cycle still gain weight (Dark *et al.* 1986), while surgical removal of fat pad stores in mid-summer results in spontaneous increase in food intake and the rapid restoration of a seasonally appropriate body weight (Dark *et al.* 1984). Taken together, these findings suggest that wild animals are capable of remarkable precision in the regulation of the phase of seasonal metabolic cycles and that rapid adjustment of body weight and conditions can take place as a result of altered patterns of energy expenditure or VFI.

Circannual rhythms

Long-lived species, including non-human primates, ruminants, squirrels, marmots, bats and seasonal carnivores, differ from short-lived rodents in that they manifest persistent rhythmicity even when maintained under constant conditions. These rhythms have a period of approximately 12 months and have been described as circannual rhythms (Gwinner, 1986a). They have been most extensively investigated in birds (Gwinner, 1986b; Gwinner & Dittami, 1990); in general the neuroanatomical basis for the control of these rhythms is very poorly understood (Zucker & Dark, 1986; Zucker *et al.* 1992). It is appropriate to regard seasonal cycles of food intake and body condition as manifestations of circannual rhythms, tuned by an external photoperiodic signal. For example, red deer calves kept from birth on constant long days (18L:6D) for 18 months exhibit seasonal rhythms of VFI and prolactin secretion which have similar phasing to those of control animals housed on natural photoperiods (Brinklow & Loudon, 1990). Thus, although seasonal rhythmicity of reproduction and metabolism in deer can be manipulated by photoperiod change and melatonin treatment, rhythmicity is endogenous and does not depend on environmental change. The nature of the linkage between seasonal reproductive and metabolic changes is revealed in a comparison between two closely-related species, the red deer and Père David's deer (*Elaphurus davidianus*). These two species will hybridize and have an identical chromosomal karyotype. Although both species have an identical duration to the breeding season, the onset and termination of the season are phase-advanced in the Père David's deer by about 90 d (Curlewis *et al.*

1988a). This advance in breeding season is associated with significant advances in the phase of the VFI cycle, prolactin secretion and the pelage cycle (Loudon *et al.* 1989). The Père David's deer has undergone a phase-advance in the entire circannual physiological axis.

The body-weight cycles and food intake of hibernating ground squirrels have been extensively studied (Pengelley & Amundson, 1974; Davis, 1976). Although these animals exhibit high-amplitude seasonal-weight cycles associated with the deposition of substantial fat reserves, an unexpected feature of their biology is their apparent resistance to artificial photoperiodic manipulations (Pengelley & Amundson, 1974). In contrast to most seasonal mammals, ground squirrels do not respond to the abrupt artificial transitions from long to short photoperiods but persist in showing endogenous seasonal rhythms of body weight and reproductive activity (Davis, 1976). In their natural state, golden-mantled ground squirrels (*Spermophilus lateralis* and *Spermophilus saturatus*) live above ground for approximately 6 months and then hibernate underground in complete darkness for a further 6 months (Kenagy, 1987). It is now known that the body-weight cycle of these animals can be entrained by photoperiod, but only when they are subjected to a close mimic of the natural environmental changes of photoperiod for 6 months followed by 6 months of complete darkness (Zucker *et al.* 1992). Here, the endogenous circannual rhythm is of such strength that it can only be entrained by carefully managed photoperiod cycles.

In contrast to ground squirrels, the conspicuous seasonal rhythms of deer are more amenable to photoperiodic manipulation and this has enabled the relationship between the entraining environmental signal (Zeitgeber) and the underlying circannual rhythm to be explored. In experiments with sika deer (*Cervus nippon*) the annual rhythms of testis development and the growth of the antler (a steroid-dependent process) can be altered by manipulation of the photoperiodic environment. Under constant conditions the antler cycle of the sika deer exhibits a period of approximately 11 months (Goss, 1984). This cycle can be entrained to artificial photoperiod changes (Goss, 1969a,b). As the driving cycle frequency is increased progressively to 6, 4 and 3 months so the antler cycle becomes progressively phase-delayed (i.e. it lags behind the entraining signal). Conversely, when the entraining signal is extended to 24 months, the antler cycle of sika deer exhibits a phase-advance. Similar observations have been made for appetite change of red deer stags driven by high-frequency Zeitgebers (see p. 496). These results in deer are exactly as would be predicted from the operation of an underlying circannual oscillator (Gwinner, 1986a). As the oscillator is driven faster by a more-frequent entraining signal it phase-lags behind the Zeitgeber; driven slower it phase-advances.

An impressive example of the operation of a circannual rhythm is seen in the Axis deer (*Axis axis*), the most southerly of the old-world deer species. In a study of a captive population maintained at latitude 52°N, individual animals within the population exhibited free-running circannual antler cycles but out of phase with other members of the herd (Loudon & Curlewis, 1988; Fig. 2). The cycles of individual animals were resistant to melatonin treatment and, therefore, may provide an example of circannual rhythms of reproduction and body weight which have become uncoupled from the influence of a pineal-dependent photoperiodic Zeitgeber. In this population, free-running circannual rhythms may persist for the life-time of individual animals but in an asynchronous manner and out of phase with other individuals in the herd.

The persistence of circannual rhythmicity in seasonal mammals and the recognition

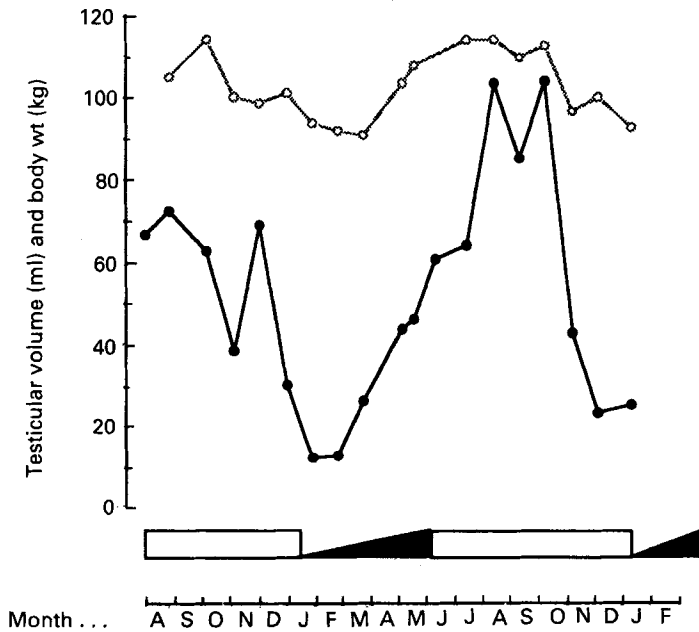
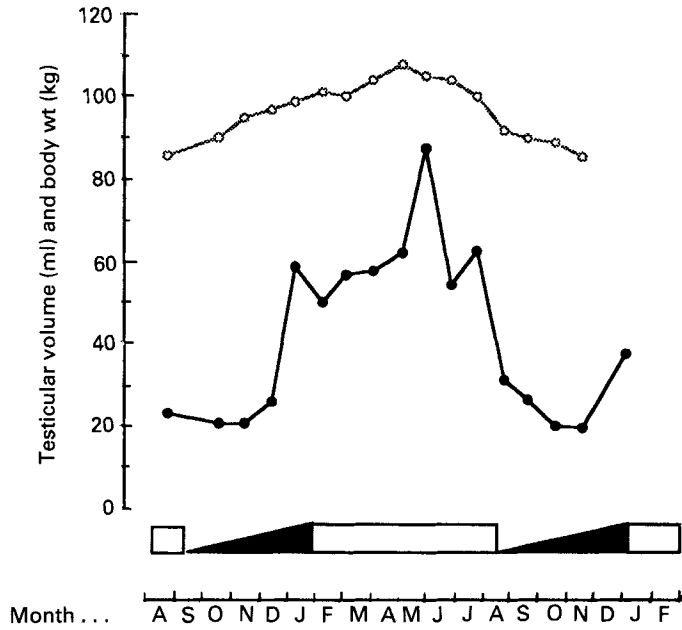


Fig. 2. Circannual rhythms in testis size (●) and body weight (○) in two adult Axis deer stags maintained out of doors at 52°N and studied over the same time period. The antler cycle is shown as period of growth (■) and hard horn (□). Data from Loudon & Curlewis (1988).

that such rhythms are a feature of the biology of many tropical organisms raises a final important issue. Hair growth is one of the most conspicuous rhythms in seasonal mammals. In man, hair growth is also seasonal (Randall, 1991). This begs the question as to whether studies of seasonal biology in animals may have more general significance for the physiology of man (see Prentice & Cole, 1994).

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