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Seasonal regulation of deer reproduction as related to the antler cycle - a review

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ABSTRACT

The antler cycle in male deer is closely associated with the photoperiodic regulation of its reproduction. In most boreal cervids antlers grow during the late spring and early summer, they mineralize before the rut and are cast thereafter. A cascade of events involving several hormones such as melatonin, prolactin (PRL), luteinizing hormone (LH) and testosterone (T) mediates the primary effect of the photoperiod. The pineal gland serves as a neuroendocrine transducer of circadian and circannual variation of photoperiod, producing melatonin in response to the onset of darkness. Peak melatonin levels occur in December while lowest levels are observed in June. Declining melatonin concentrations in the blood after winter solstice unblock the production of PRL which increases until the peak levels are reached in mid June. High PRL levels block LH receptors on the testicular Leydig cells and thus prevent them from producing T too early, at a time not yet suitable for reproduction. The decline of PRL after June unblocks the LH receptors and allows ever stronger stimulation of T production by LH. Experimental manipulations of the photoperiod, exogenous administration of melatonin or blockade of PRL secretion by bromocriptine induce a distinct seasonal shift of reproductive patterns and the antler cycle. In addition to T, the female sex hormone estradiol appears to be also involved in the development of antler bone by being involved in the formation of the ivory compact bone.

Key words: deer, reproduction, photoperiod, antler cycle, melatonin, luteinizing hormone, testosterone, estradiol

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In boreal cervids antler growth is a strictly seasonal event (GOSS, 1969). Except for roe deer (*Capreolus capreolus*), who grow antlers during the winter time, other boreal deer grow antlers in late spring and early summer (BUBENIK, 1990). The antler cycle of boreal cervids is closely related to the seasonal variation of sexual steroids (Fig. 1).

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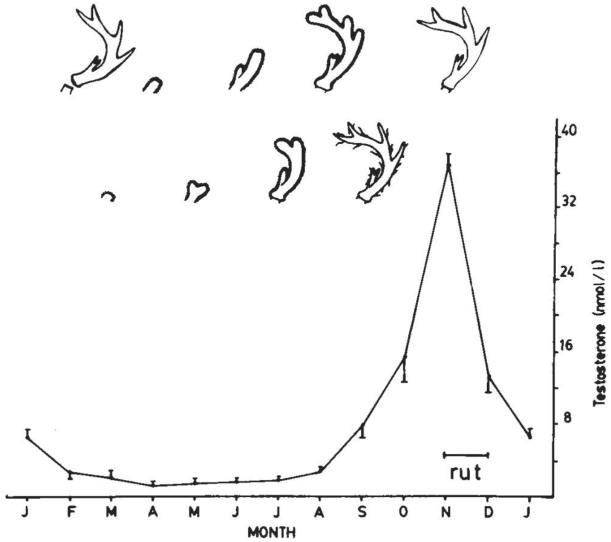

Fig. 1. Seasonal variations of blood testosterone concentrations in white-tailed deer in relationship to their antler cycle

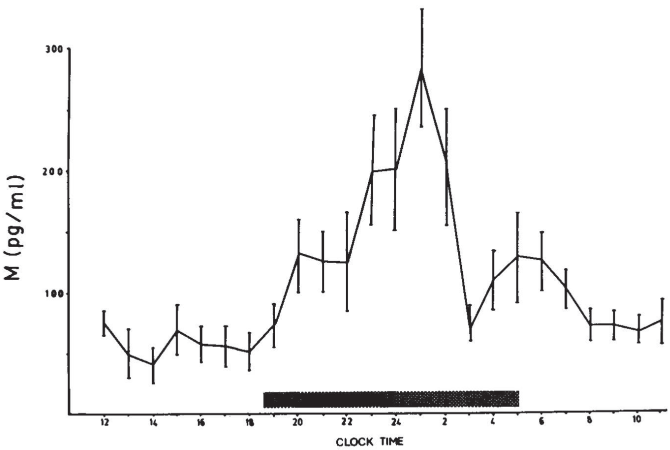

Fig. 2. Circadian variation of melatonin in plasma of male white-tailed deer during September. Horizontal bar indicates the night period (from BUBENIK and SMITH, 1987).

The antlers grow during the period of low concentrations of reproductive hormones. Antler mineralization will follow during the period of rising testosterone (T) levels closer to the rut. Finally, antlers are cast after a rapid decline of T observed at the end of the rut (BUBENIK, 1983; GOSS, 1983). Pioneering studies of Zbignew Jaczewski in the early 1950's demonstrated that the antler cycle of boreal deer is regulated by photoperiodicity (JACZEWSKI, 1952), which is a primary regulator of deer reproduction. The circannual cycle is regulated by a cascade of events involving several hormones. The primary ''zeitgeber'' driving the timing of the mammalian reproduction is the circannual variation of photoperiodicity (REITER, 1980). The effect of light is registered by the retina which then sends a signal to the pineal gland, which acts as a neuroendocrine transducer converting the photic energy of light into a chemical signal called melatonin. Melatonin (M) levels in the blood are low during the day, but increase sharply with the onset of darkness (REITER, 1991) (Fig. 2). Changes in daily production of melatonin depend on the circannual variation of night length. In addition the seasonal concentrations of melatonin also vary with the changes in the night length. Therefore the pineal gland serves as both, the "clock" and the "calendar". Peak melatonin levels in blood of white-tailed deer (Odocoileus virginianus) were detected in December and minimal concentration occurred in June (BUBENIK and SMITH, 1987) (Fig. 3). Although the removal of the pineal gland (pinealectomy) did not abolish seasonality in white-tailed deer, the initiation of antler growth, molt and the rutting behavior was delayed by several months (BROWN et al., 1978). Pinealectomy also disrupted the seasonal pattern of another important hormone, prolactin (PRL) (SNYDER et al., 1983). PRL is a pituitary hormone which is closely tied to the seasonal variation of day length. Its pattern is in reverse order from the pattern of melatonin. Seasonal peak levels are observed during the longest days of June and troughs are detected in mid winter (Fig. 4). Declining concentrations of M in the spring allows PRL to rise. Experimental manipulation of seasonal melatonin concentrations in the blood invariably altered reproductive and antler cycles in white-tailed deer. Exogenous administration of melatonin in the spring (given several hours before the natural rise in the evening) induced a seasonal switch and placed the deer on the path toward the autumn. The antlers of M-treated deer were polished in July (instead of September) and the deer acquired winter coat and became aggressive as being in the rut (BUBENIK et al., 1986) (Fig. 5).

The next step in the cascade of seasonal regulation of deer reproduction is the effect of PRL on another pituitary hormone, luteinizing hormone (LH) which stimulates secretion of testosterone (T) from the Leydig cells of the testes. As high blood concentrations of PRL block LH receptors on the Leydig cells, LH levels increase rapidly during the summer, without causing a corresponding elevation of T. As a result, in most boreal cervids LH peaks several months before peak levels of T are achieved (Fig. 6).

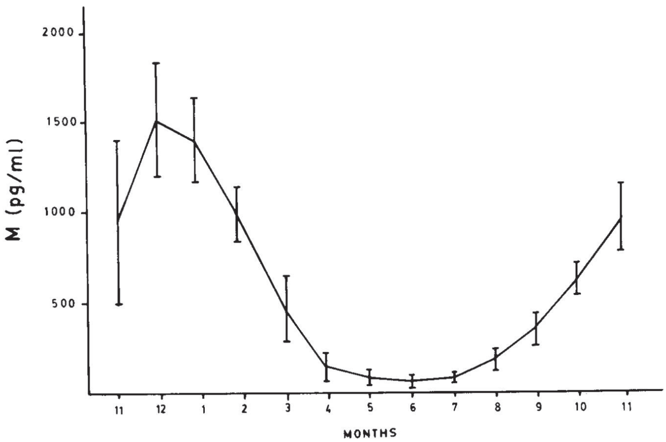

Fig. 3. Circannual variation of peak midnight concentrations of melatonin in the plasma of male white-tailed deer. (from BUBENIK and SMITH, 1987).

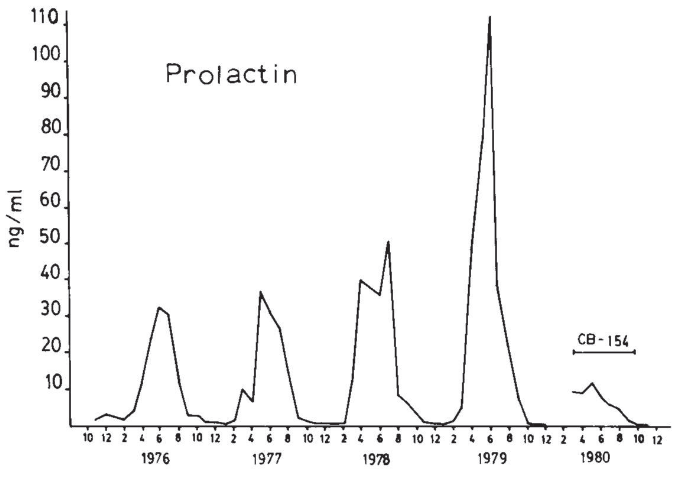

Fig. 4. Seasonal variation of prolactin in the plasma of control and bromocriptine (CB-154)-treated male white-tailed deer. (from BUBENIK et al., 1985).

Fig. 5. Control (left) and melatonin-treated (right) white-tailed deer. Note the polished antlers and the winter coat in the deer treated with melatonin in the spring.

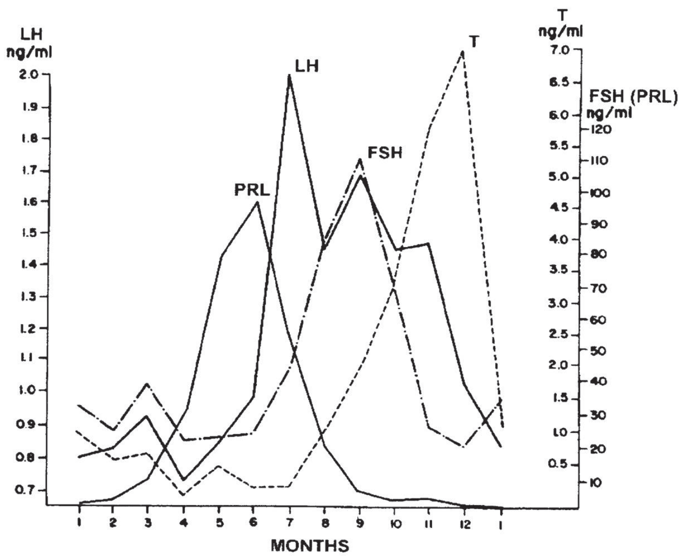

Fig. 6. Seasonal concentrations of PRL, LH, FSH and T in the plasma of male white-tailed deer.

When early in the spring blood levels of PRL were severely reduced by PRL blocker bromocriptine (Fig. 4), receptors on Leydig cells were unblocked and T concentrations began to rise. They peaked in June-July period, (instead in November- December). At this time T increased simultaneously with concentrations of LH (Fig.7). Therefore bromocriptine-treated deer experienced rut several months prematurely (BUBENIK et al., 1985). The sensitivity of receptors on Leydig cells to LH changes throughout the year. In the spring and early summer, relatively high levels of LH are associated with low levels of T; conversely, in the summer or early autumn, even declining levels of LH stimulate rapid production of T leading to the rut (SUTTIE et al., 1984).

Besides producing the male sex hormone T, deer testes also convert some T into the female sex hormone, estradiol (E2). In some cervids, such as caribou, E2 levels during the rut reach concentrations which almost exceed the levels of T (BUBENIK et al., 1997). In adult white-tailed bucks seasonal concentrations of E2 exhibit two peaks, one in the spring, another in the autumn. It has been hypothesized that because E2 has a blocking effect on testicular activity, the high E2 levels in the spring prevent a rapid stimulation of spermatogenesis at a time unsuitable for deer reproduction (BUBENIK et al., 1979). The role of estradiol in the formation of antlers has not been entirely elucidated. It is well established, that besides being produced in the testes, a substantial proportion of E2 is produced in other tissues, such as the adrenal gland and the fat (KETCH et al., 1972; MARTIN, 1978). Estradiol is up to 50 times more effective in the mineralization of antlers than T (BLAUEL, 1935; TACHEZY, 1956; GOSS, 1968; MORRIS and BUBENIK, 1982). In addition, E2 receptors were detected in the velvet of growing antlers (BARREL et al., 1987). Furthermore, antlers of castrates mineralized only by E2 exhibited a higher proportion of compact bone than comparable antlers on intact bucks (BUBENIK, 1990) (Fig 8). Conversely, administration of estradiol receptor blockers (such as CI-628 or MER-25) to intact bucks resulted in the disruption of the formation of Haversian systems and the drastic reduction of the thickness of the compact ivory bone (BUBENIK and BUBENIK, 1978).

Finally, most recently seasonal concentrations of T and E2 in the serum were measured in velvet and growing antler bone of male white-tailed deer (BUBENIK et al., 2005). Their results strongly indicate that in addition to other body tissues, growing antlers are also producing E2 from T.

Testosterone appears to be an essential hormone for the formation and mineralization of antlers. However, low and high concentrations of T in the blood have different functions. Whereas low concentrations of T in the spring (produced mostly in the adrenal gland) stimulate antler growth (BUBENIK et al., 1974; BARTOŠ et al., 2000), high concentrations of T (produced in the testes in the late summer, early autumn) induced massive mineralization of the antlers (BUBENIK, 1990).

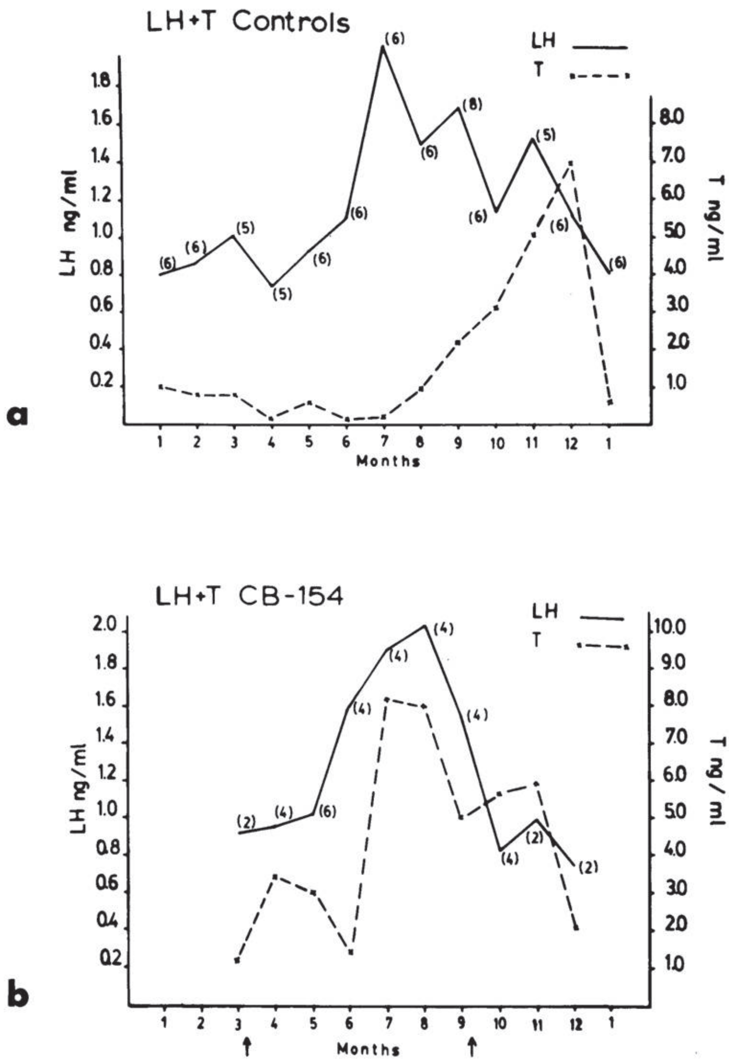

Fig. 7. Seasonal levels of LH and T in control (top) and PRL-suppressed male white-tailed deer (bottom). Note the left shift of T in deer where PRL secretion was suppressed by bromocriptine (CB-154). Arrows indicate the treatment period. (From BUBENIK et al., 1985).

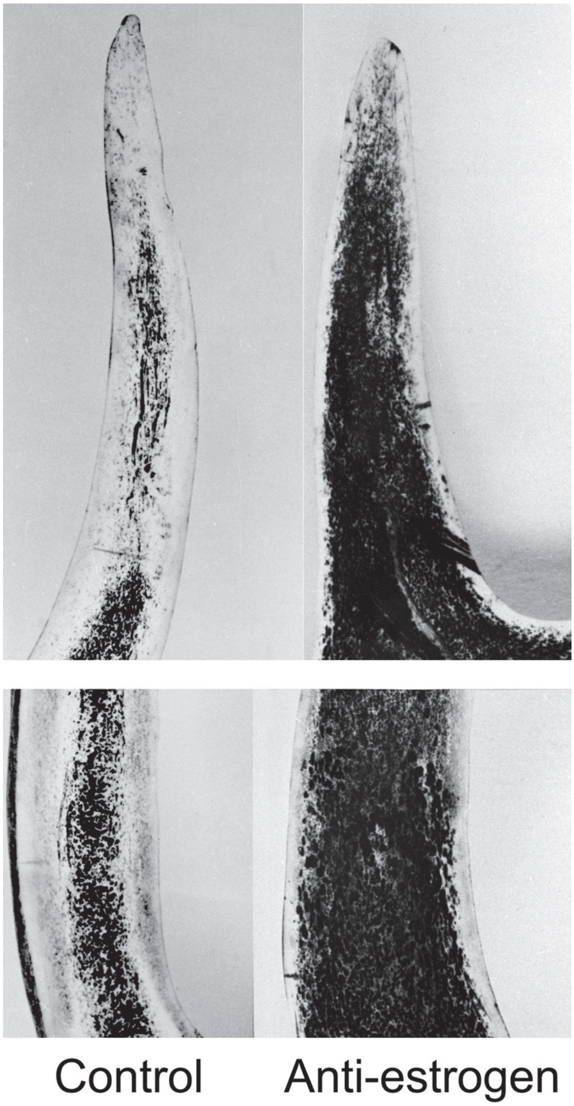

Fig. 8. Cross-section of control and antiestrogen-treated antlers of white-tailed deer. Note the thin cortical ivory bone in the anti-estrogen treated deer as compared to control. (from BUBENIK and BUBENIK, 1978).

In conclusion, the deer antler cycle is coincidental to the reproductive cycle, which in boreal Cervids is primarily regulated by the photoperiod. Testosterone and estradiol are particularly important in the formation and mineralization of antler bones.

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SAŽETAK

Ciklus rasta roga jelenske divljači putem fotoperioda je usko povezan s regulacijom rasplođivanja. U većine punorožaca rogovlje raste u kasno proljeće ili početkom ljeta, okoštava prije razdoblja parenja nakon kojega biva odbačeno. Primarni učinak dnevnoga svjetla prenosi se kroz čitavu kaskadu događaja, uključujući sudjelovanje nekoliko hormona poput melatonina, prolaktina (PRL), luteinizirajućeg hormona (LH) i testosterona (T). Epifiza, kroz produkciju melatonina kao odgovor na manjak količine svjetla, služi kao neuroendokrini prijenosnik dnevnih i godišnjih kolebanja količine dnevnoga svjetla. Najvišu razinu melatonin dostiže u prosincu, a najnižu u lipnju. Pad koncentracije melatonina u krvi nakon zime rezultira lučenjem PRL-a, čija koncentracija raste sve do vrhunca koji postiže sredinom lipnja. Visoka razina PRL-a blokira receptore Leydigovih stanica za LH te time priječi prerano lučenje T. Tek nakon lipnja, pad koncentracije PRL-a omogućava jaki podražaj za lučenje testosterona. Umjetno izazvane promjene u trajanju dnevne svjetlosti, egzogenim aplikacijama melatonina ili kočenjem sekrecije PRL-a bromokriptinom, rezultiraju promjenom reproduktivnih mehanizama i ciklusa rasta roga. Osim T, u razvoju mineraliziranog roga, konkretno kroz oblikovanje kompakte roga, uključen je i ženski spolni hormon estradiol.

Ključne riječi: jeleni, rasplođivanje, fotoperiod, ciklus rasta roga, melatonin, luteinizirajući hormon, testosteron, estradiol