Physiological control of growth, reproduction and lactation in deer.

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Abstract: The physiological mechanisms controlling the growth, lactation and reproductive cycles of cervids, and the control of allocation of energy to different organs are discussed. The growth cycle may be secondary to an appetite cycle, regulated by changes in the secretion of prolactin, gonadal steroids, and possibly unknown factors. The reproductive cycle is controlled by changes in the release at the hypothalamic hormone GnRH, and by changes in the feedback effect of gonadal steroids. These cycles are probably the result of the timing effects of nutrition and changing photoperiod on an endogenous, circannual rhythm. The effect of photoperiod is mediated by the pineal hormone melatonin. The physiological mechanisms controlling the partitioning of substrates between milk production, fetal growth and the tissues of the mother are poorly understood, but may involve changes in the secretion of growth hormone, insulin and triiodothyronine.

Key words: cervidae, seasonal cycles, endocrine regulation

Introduction

In the northern latitudes, where the supply of food changes annually, the rate of production must necessarily change. However, production in these animals does not passively follow changes in food intake, instead the whole physiology of the deer changes seasonally, to be adapted to the environmental conditions. The energetically most costly processes - growth and lactation - take place during the period of highest plant production, whereas fetal growth, which requires less energy, occurs during winter. When various productive processes do occur at the same time, they must compete for energy and substrates.

This review is concerned with how the productive processes of deer are regulated in such a manner as to make best use of the annual cycle of plant production, by correct timing, and by sharing available resources.

Growth

Cervids have a cyclic growth pattern, with rapid weight gain in summer, followed by a winter growth stasis (Ryg, 1983). The annual growth cycle may passively follow an appetite rhytm, although this is not firmly established. Nilssen *et al.* (1984) reported that basal metabolic rate does not change throughout the year. Maintenance requirements of reindeer, measured by the amount of food required to maintain body weight, do not change from winter to early summer (Ryg and Jacobsen, 1982a), and weight gains per unit of food above maintenance is the same in early summer as in winter (M. Ryg, unpublished data). On the other hand, when maintenance requirements of roe deer (Ellenberg, 1978) and white-tailed deer (Holter *et al.*, 1979) was calcuated from energy balance trials, a seasonal cycle was apparent. It is not clear whether these differences are due to methodology or species.

In studies of seasonal appetite, grain-based concentrates have commonly been used as feed. With such diets, the appetite of ruminants is regulated by metabolic signals. The significance of these studies for natural conditions, in which roughage intake is limited more by gastrointes-

tinal factors (Freer, 1981), is unclear. On roughage diets, seasonal appetite could be explained by changes in gastrointestinal capacity (Milne et al., 1978; Mitchell et al., 1976; Staaland et al., 1974.). However, the seasonal regulation of that capacity is unknown, and there may be interactions with metabolic factors.

Although the seasonal growth pattern is entrained by photoperiod (Brown et al., 1979) the controlling mechanisms are unknown. Pinealectomy of white-tailed bucks had no effect on either growth or food intake cycles (Brown et al., 1978), but this could be attributed to the age of the animals, or the limited duration of the experiment. Pinealectomy of young animals affects the seasonal changes in prolactin and gonadal steroids, both of which have been implicated in the control of appetite cycles (Ryg, 1983; Suttie, 1980).

Although cervids may start gaining weight in spring, fat is mostly deposited in autumn and late summer (Dauphiné, 1976; Mitchell et al., 1976). Lipogenic capacity of isolated fat cells parallels changes in food intake (Larsen, Nilsson and Blix, 1985), but from data presented it appears that for a given intake, lipogenic capacity of the fat cells is highest in autumn. This change could be hormonally mediated, since in spring, levels of growth hormone (GH) (which is protein anabolic and lipolytic) are high (Ryg, 1983) and triiodothyronine (T3) levels increase markedly with increasing food intake, at least in young males (Ryg, 1984b; Ryg and Jacobsen, 1982a). Insulin levels also increase in summer (Larsen, Lagercrantz, Riemersma and Blix, 1985), possibly the result of an increse in food intake. During late summer and autumn, GH leves are usually low in adults, and level of food intake has only a minor effect on T3 concentrations (Ryg, 1984b). High insulin, and low GH and T3 levels, in combination with a sustained high food intake, could promote fat deposition. The high GH levels occationally found in calves in autumn might limit lipogenesis. Seasonal changes in T3 levels in adult females are strikingly different from those found in young males (Bahnak et al., 1981; Nilssen et al., 1984), but whether this is related to differences in metabolic patterns is not known.

Skeletal growth of reindeer is regulated to some degree independent of the appetite cycle. After an obligatory growth stasis from October to January, skeletal growth commences and with good nutrition, the rate of growth may be faster in winter than in summer (Ryg, 1983; Ryg and Jacobsen, 1982a). Food restriction had less effect on skeletal growth in summer than in winter, suggesting that skeletal size may be determined more by winter than summer nutrition. This agrees with the observation of Skogland (1983) that mandible length of free ranging reindeer correlated better with winter than summer conditions, although his results may also be interpreted as an effect of maternal winter nutrition on fetal and early postnatal growth (Skogland 1983, 1984).

Gonadal function and reproduction

Seasonal reproductive cycles are regulated by changes in the secretion of the hypothalamic gonadotrophin releasing hormone (GnRH) (Lincoln and Short, 1980), and by changes in the sensitivity of the hypophysis to the negative feed-back action of gonadal steroids (Karsch and Foster, 1981). Before the rutting season, the secretion of GnRH increases and the feedback effect of steroids decreases, resulting in increased hypophyseal and gonadal activity. Frequently there is a peak of gonadotrophin and steroid secretion in spring (Buhenik et al., 1979; 1982; Ryg, 1984a; Sempere and Lacroix, 1982), suggesting a semiannual cycle of reproductive function. The secondary gonadotrophin peak in spring is possibly attenuated by the negative feedback effect of gonadal steroids, since it was much more pronounced in castrates than in intact white-tailed bucks (Bubenik et al., 1982).

High prolactin (PRL) levels are often associated with infertility, and it has been suggested that sexual quiescence in summer is caused by the seasonal increase in PRL secretion. However, suppression of PRL secretion with bromocryptine did not stimulate gonadal function in the ewe (McNeilly and Land, 1979). Possibly the inverse relation between PRL and gonad function is regulated by the hypothalamus. Recently, it was found that the precursor peptide for GnRH contains a peptide that inhibits PRL secretion (Nikolics et al., 1985). GnRH and the prolactin-inhibiting peptide are located in the same hypothalamic nerve terminals (Phillips et al., 1985) and presumably are released at the same time. Increased activity in these neurons could simultaneously stimulate gonadotrophins and inhibit PRL secretion.

The most important external stimulus to gonadal development and regression is the photoperiod; the response is probably mediated by melatonin from the pineal gland. Melatonin administered orally or intramuscularly advances the rutting season of red deer (*Cervus elaphus*) (Adam and Atkinson, 1984; Webster and Barrell, 1985) and white-tailed deer *(Odocoileus virginanus)* (Bubenik, 1983). The effects of pinealectomy on the reproductive cycle are variable. It has little effect on old animals (Brown et al., 1978). In young animals, the testicular cycle may be suppressed, although usually gonadal and hypophyseal cycles persist, but become irregular and out of phase with intact animals (Plotka et al., 1984; Schulte et al., 1981; Snyder et al., 1983). This indicates that the annual cycle is timed, but not generated by, the pineal gland. This suggestion is supported by the classical studies of Goss (1969a, 1969b) which showed that an endogenous, circannual rhythm was involved in the control of antler growth in Sika deer *(Cervus nippon)*.

As with other mammals, female deer must reach a critical body weight, or fat content, in order to conceive (Albon et al., 1983; Ellenberg, 1978; Hamilton and Blaxter, 1980; Lenvik et al., 1982; Reimers, 1983; Thomas, 1982.) The effect is most likely on ovulation rates (Leader-Williams and Rosser, 1983). It is not clear, however, what the metabolic signal is. The critical body weight, as a percentage of mature body weight varies between species and subspecies. Albon et al., (1983) reported that the critical body size in red deer hinds increased with increasing populations density, and Lenvik et al., (1982) reported that reindeer *(Rangifer tarandus)* hinds conceived at a later age when 1½ year old bulls were used as breeding males, than when older males were used. So it appears that the metabolic signal can be modulated by other factors, which are at present poorly understood. Finally, it has been suggested that frequent suckling, associated with poor nutrition, could delay or suppress estrus in red deer (Loudon et al., 1983). Whether this mechanism would apply to reindeer, whose «follower» calves normally suck more frequently than red deer calves, is questionable.

Pregnancy

Maintenance of pregnancy depends on the presence of progesterone, secreted by the placenta, or by one or more corpora lutea. In white-tailed deer, the corpus luteum of pregnancy is the most important source of progesterone. Ovariectomy induces abortion as late as 156 days of pregnancy (Plotka et al., 1982). Whether the maintenance of the corpus luteum of pregnancy depends on luteotropic hormones from the hypophysis or the placenta in deer is not known, but a luteotropic and lactogenic hormone (placental lactogen, PL) is apparently secreted by the placenta of fallow deer *(Dama dama)* (Forsyth, 1973). Parturition is probably initiated by a declining luteal function. It is preceded by a decline in maternal progesterone leves (Blom et al., 1983), and injection of the luteolytic substance prostaglandin $F_2\alpha$ induces parturition (Langvatn, 1986). The exact timing of birth is influenced by the nutritional status of the dam; poor nutrition delays birth (Reimers et al., 1983; Skogland, 1984). Since parturition is initiated by factors related to the degree of maturity of the fetus (Nathanielsz, 1978), this effect is probably a result of slower fetal growth.

The growth of the fetus depends, of course, on the transfer of substrates across the placenta, and may be regulated by the substrate supply to the feto-placental unit, by the size of the placenta, or by endocrine factors. Inadequate nutrition affects the growth of the fetus. Under a wide range of experimental and natural conditions, the weight of the fetus or newborn calf is correlated with the body weight of the dam (Rognmo et al., 1983; Skogland, 1984; Varo and Varo, 1971), indicating that the energy flow to the fetus is a more or less constant part of total metabolic turnover of the dam. The effects of severe undernutrition in early pregnancy, which could inhibit placental development, has not been studied. Fetal growth may be influenced by hormones from the fetus itself, or from the placenta, e.g. placental lactogen (PL), which affects fetal glucose metabolism (Freemark and Handwerger, 1984) and somatomedin production (Adams et al., 1983) and could act as a fetal growth hormone. However, no studies on the effects of maternal nutrition on plasma levels of PL have been conducted.

Lactation

The development of the milk gland is induced by the presence of a conceptus, but little is known about the endocrine regulation in cervids. Progesterone and estrogen, produced in increased

amounts during pregnancy in deer (Blom *et al.*, 1983; McEwan and Whitehead, 1980; Ringberg and Aakvaag, 1982) are probably important. Peptide hormones secreted by the hypophysis (PRL and GH) or placenta (placental lactogen) may participate as well.

Milk secretion by the fully developed gland is partly under nutritional and partly endocrine control. As with other mammals, progesterone probably inhibits milk secretion in deer. When birth of red deer fawns was induced prematurely by prostaglandin injections, the fawns grew normally (Langvatn, 1986). This suggests that the milk secretion started as soon as the corpus luteum, the most important source of progesterone, regressed.

The energy and substrates needed for milk production must be taken from increased food intake or, especially in early lactation, from the body reserves of the dam (Sadleir, 1984). Both the size of the dam at birth (Jacobsen *et al.*, 1981; Rognmo *et al.*, 1983; Skogland, 1983) and nutrition during lactation (Loudon *et al.*, 1984) affects milk yield and calf growth. It has been pointed out that, since the fertility of the female is related to her condition, extended suckling would diminish the chances of conceiving in the fall. White and Luick (1984) presented some evidence that the growth of the mother may have priority over that of the calf; when food was restricted in mid lacation, milk yield and calf growth rate declined, whereas the restriction had little effect on the growth of the dams. The growth rate of red deer dams was scarcely affected by range quality after midsummer. However, up to 40 days of lactation (about mid July), nutrition strongly affected body weight of the females (Loudon *et al.*, 1984), indicating a shift of priorities about mid summer. Before this time the body condition of the dam will decline when nutrition is poor, in order to maintain milk yield as much as possible, whereas in late lactation, poor nutrition will cause diminished milk yield.

The control of milk secretion in cervids is poorly understood. The declining milk yield in late summer might be a result of the seasonal decline in PRL levels. Although PRL is not considered necessary to maintain established lactation in domestic ruminants (Forsyth and Hayden, 1977) Loudon *et al.*, (1983) found a positive correlation between PRL levels and milk yield of red deer hinds throughout lactation, and

results from animals selected for high milk yield may not be applicable to wild ruminants. PRL may simultanously stimulate food intake (Ryg and Jacobsen, 1982b), thus ensuring a sufficient substrate supply, an so, growth and lactation may have some endocrine control in common.

The question then becomes how the flow of energy and substrates is partitioned between the milk gland and the tissues of the mother in early lactation. White and Luick (1984) suggested that, since lactose synthesis may be the pace-setter of milk secretion, the control is exerted via the glucose metabolism of the dam, and endocrine control of glucose metabolism may be important. Growth hormone, which is necessary for maintaining lacation in domestic ruminants (Forsyth and Hayden, 1977), and in the lactating cow shifts nutrient flow from the tissues of the female to the milk gland (Tyrrell *et al.*, 1982) is elevated during lactation in white-tailed does (Bahnak *et al.*, 1981) and reaches maximum levels later than what is seen in males (Ryg, 1983).

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