

# Endocrine control of reproduction in Cervids: the enigma of temperate vs. tropical species

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## Summary

There has been considerable recent advances in our understanding of factors controlling reproductive processes in cervids. Perhaps one of the more interesting facets has been the apparent enigmas between temperate and tropical species located in temperate environments. All cervids studied to date exhibit patterns of prolactin secretion correlated closely with the prevalent photoperiod cycle, indicating that at least some tropical species have retained vestiges of photoperiodism despite their equatorial origins. Luteal cyclicality in non-pregnant females is confined largely to autumn/winter in temperate "short-day" breeders. However, some tropical species exhibit apparent "reverse seasonality" (spring/summer cyclicality), indicating the possibility that they are cued to different regions of the photoperiod curve. Other tropical species exhibit continuous luteal cyclicality in temperate environments. While males from temperate species exhibit profound circannual changes in testicular function, including testicular quiescence and aspermatogenesis that appears related to antler casting/regeneration, tropical species display only modest fluctuations in testicular size and can produce viable spermatozoa throughout the year. Interestingly, these species also exhibit circannual cycles of antler production (albeit not always in a synchronous manner) despite continuous testicular function. Resolution of such enigmas will tell us much about the exogenous and endogenous control of cervid reproduction, and will necessitate further endocrine studies on tropical species to provide information on pituitary function and the effects of gonadectomy and light control on hormone secretion.

## Introduction

Intensive husbandry of several cervid species within the last two decades has precipitated dramatic advances in our understanding of their patterns of reproduction and in the development of artificial breeding technologies. In particular, the more commonly farmed species, such as red deer (*Cervus elaphus scoticus*) and European fallow deer (*Dama dama dama*), have been the focus of detailed studies on reproductive physiology and controlled breeding. However, research on other farmed or captive species has contributed greatly to our insights into reproductive processes; including studies on Pere

David's deer (*Elaphurus davidianus*), chital deer (*Axis axis*), brow-antlered Eld's deer (*Cervus eldi thamin*), white-tailed deer (*Odocoileus virginianus*), roe deer (*Capreolus capreolus*), reindeer (*Rangifer tarandus*), rusa deer (*Cervus timorensis*), sambar deer (*Cervus unicolor*) and Reeve's muntjac (*Muntiacus reevesi*) to name but a few. Rather than reviewing fully the endocrine control of cervid reproduction, we would like to focus on apparent enigmas that emerge when one compares exogenous and endogenous control of reproductive processes in temperate species (i.e. those cervids occurring at latitudes  $>20^\circ$ ) with those of tropical origin ( $<20^\circ$ ), especially tropical

cervids transposed to temperate latitudes. Previous, more general, reviews on reproductive physiology include those by Fisher & Fennessy (1985), Thimonier & Sempere (1989) and Asher & Fisher (1991).

## Seasonality of reproduction

The necessity of most cervid species to give birth at an appropriate time of year for optimal survival and growth of offspring (Lincoln & Short, 1980) has exerted considerable influence on their reproductive physiology. Species of northern temperate origin typically conceive in autumn and calve in summer, while species of tropical origin often exhibit limited seasonality or are completely aseasonal (Lincoln, 1985). The endogenous mechanisms governing seasonal reproductive patterns in temperate species are robust, being manifest rigorously when animals are transferred between localities despite subtle regional variations in seasonal feed supply. Furthermore, transference across the equator results in an exact six-month phase change (Marshall, 1937; Lincoln, 1985) even though the relationship between season and feed production differs considerably between continental northern hemisphere and insular southern hemisphere environments (Asher *et al.*, 1993). Interestingly, tropical species transferred from equatorial (0-15°) zones may exhibit either pronounced "reverse seasonality" (i.e. spring conceptions and autumn/winter calving, e.g. Javan rusa deer, brow-antlered Eld's deer), wide breeding seasons (i.e. calving mostly confined to 3-6 months of the year; e.g. chital deer in Australia) or complete aseasonality (i.e. calving year round; e.g. Moluccan rusa deer, Reeve's muntjac) (Chapman *et al.*, 1984; McKenzie, 1985; van Mourik, 1986; Loudon & Curlewis, 1988; Monfort *et al.*, 1991; English, 1992; Mylrea, 1992; Woodford & Dunning, 1992). It should be noted, however, that there is a general paucity of information on the birth season of tropical species in their native tropical environment (Lincoln, 1985).

It is generally accepted that entrainment of seasonal reproductive cycles is effected by endogenous recognition of photoperiodic changes, with the majority of temperate species

initiating mating activity during decreasing daylength of late summer and autumn (Lincoln & Short, 1980). Variations in the actual mating season between such species of up to eight weeks usually offsets genetically determined species differences in gestation length, such that parturition generally occurs in mid-summer (Lincoln, 1985). A notable exception amongst temperate species is the Pere David's deer, which initiates mating activity in early summer and calves in late spring despite an unusually long gestation of ~ 280 days (Wemmer *et al.*, 1989; Fennessy & Mackintosh, 1992). There is growing evidence that some tropical species may also perceive, and respond to, changes in photoperiod, although in a markedly different manner than temperate species. For example, brow-antlered Eld's deer exhibit pronounced seasonal changes in prolactin secretion that correlate closely with photoperiodic changes (Monfort *et al.*, 1993a). However, this species, as with Javan rusa deer, initiates mating activity coincidental with increasing daylength in spring, thus calving in autumn/winter (Monfort *et al.*, 1991; 1993a; van Mourik 1986). Similarly, treatment of chital deer stags with exogenous melatonin has been shown to hasten antler casting (Mylrea, 1992), indicating possible photoperiod responsiveness in a species considered to exhibit limited seasonality in both tropical and temperate environments (Loudon & Curlewis 1988; Loudon & Brinklow 1992; English, 1992).

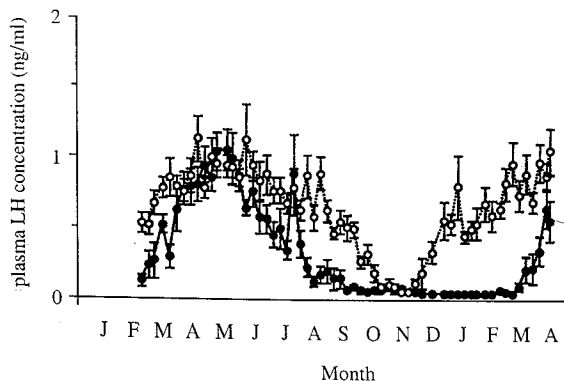
## Photoperiodism and hypothalamic regulation of reproduction

The pineal indole-amine, melatonin, is the main transducer of photic information in mammals (Reiter, 1980). Melatonin is secreted maximally during darkness, as demonstrated by recorded concentrations in the peripheral blood of fallow deer (Asher *et al.*, 1988), thus providing an endogenous measure of the relativity between day and night. Most seasonally reproducing cervids are termed "short-day breeders" (i.e. initiate mating during decreasing photoperiods). However, the assumption that seasonal reinstigation of fertility involves a direct response to decreasing daylength is an oversimplification, as males often begin the process of seasonal testicular recrudescence 4-6 weeks before the summer

solstice (Lincoln, 1971; Lincoln & Short, 1980; Asher *et al.*, 1989a; Asher & Peterson, 1991). Nevertheless, numerous studies have demonstrated convincingly that administration of exogenous melatonin prior to, and beyond, the summer solstice advances significantly the onset of reproductive cyclicity in red deer and fallow deer (Loudon & Brinklow, 1992; Asher *et al.*, 1993). While there is little doubt that melatonin plays a major role in seasonal reproduction of temperate cervid species, its role in tropical species remains to be elucidated with any certainty.

The synthesis and release of the gonadotrophins, luteinizing hormone (LH) and follicle-stimulating hormone (FSH), by the anterior pituitary gland are regulated by gonadotrophin-releasing hormone (GnRH) secreted by the hypothalamus. Studies with sheep have shown that the release of GnRH is episodic or pulsatile, and there is a direct temporal relationship between the episodic peaks in the concentration of GnRH in the hypothalamic-pituitary portal blood and episodic peaks in the concentrations of LH in the peripheral blood (Clarke & Cummins, 1982; Levine *et al.*, 1982). Recent studies have since shown that this also occurs in red deer (J.R. Webster, F.J. Karsch & J.M. Suttie, unpublished data) (Fig. 1). Furthermore, numerous studies have demonstrated pituitary responsiveness (in terms of LH secretion) to exogenous GnRH in temperate (red deer, fallow deer, Pere David's deer) and tropical (Javan rusa deer, brow-antlered Eld's deer) cervids (Lincoln & Kay, 1979; Suttie *et*

*al.*, 1984; Fennessy *et al.*, 1988; Asher *et al.*, 1989b; van Mourik *et al.*, 1986; Monfort *et al.* 1993b). It is therefore likely that seasonal reproductive changes in deer are mediated through circannual variation in endogenous GnRH release effecting corresponding circannual changes in pituitary gonadotrophin release. However, there is considerable evidence that deer exhibit seasonal variation in pituitary responsiveness to GnRH. By administering a standard dose of exogenous GnRH at different times of the year, it has been possible to test the responsiveness of the pituitary-testis axis in a number of species. Such changes in responsiveness has been reported for red deer following challenge with a wide range of GnRH doses (Lincoln & Kay, 1979; Suttie *et al.*, 1984; Fennessy *et al.*, 1988). For males of this species, pituitary responsiveness is generally greatest when endogenous LH secretion is at its nadir in late summer/early autumn, diminished during the autumn rut (possibly due to high levels of testosterone secretion exerting negative feedback) and minimal at the time of antler casting/testicular regression in spring. Seasonal variation in response to GnRH challenge has also been observed for tropical Javan rusa deer, with a similar pattern evident relative to their reproductive cycle (which is phase-shifted 5-6 months from that of red deer: van Mourik *et al.*, 1986). However, such variation was not apparent for brow-antlered Eld's deer, a species exhibiting similar seasonality to Javan rusa deer (Monfort *et al.*, 1993b).



**Figure 1.** Mean ( $\pm$  sem) plasma LH concentrations determined weekly in ovariectomised ( $\circ$ ) and ovariectomised-oestradiol treated ( $\bullet$ ) red deer hinds during the year (Meikle & Fisher, 1994).

### Prolactin secretion

Prolactin secretion from the anterior pituitary gland is correlated closely with photoperiod in mammals (Bittman, 1984), with maximal and minimal peripheral blood concentrations occurring during long and short days respectively. This pattern of secretion is apparent in red deer (Kelly *et al.*, 1982; Adam *et al.*, 1989; Suttie *et al.*, 1984; Suttie & Kay, 1985; Loudon *et al.*, 1989), white-tailed deer (Mirarchi *et al.*, 1978; Shulte *et al.*, 1981; Bubenik *et al.*, 1990), reindeer (Ryg & Jacobson, 1982), roe deer (Schams & Barth, 1982), Javan rusa deer (van Mourik & Stelmasiak, 1985) and brow-antlered Eld's deer (Monfort *et al.*, 1993a). In contrast, peak concentrations of prolactin in Pere David's deer occur about six weeks before the summer solstice, and it has been suggested that this shift is related to an early calving season relative to other temperate species (Loudon *et al.*, 1989).

The significance of prolactin as a modulator of the reproductive axis in cervids remains controversial. The temporal association between prolactin and gonadotrophin secretion in white-tailed deer prompted Bubenik *et al.*, (1990) to suggest that prolactin modulates the sensitivity of the testes to LH via receptor-mediated mechanisms and acts as a secondary messenger of photoperiodically-dependent seasonality. However, it is also possible that the prolactin secretory rhythm simply reflects changing photoperiod and is unimportant in regulating seasonal reproduction. Evaluation of a growing database for temperate and tropical cervids reveals that mating activity in separate species can occur during either the upstroke or downstroke of the circannual prolactin rhythm.

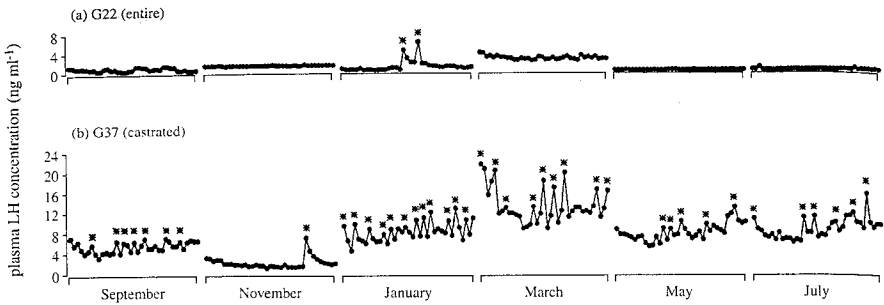
Since the temporal relationship between the seasonal changes in prolactin and gonadotrophin secretion varies between cervid species, it is probable that the two hypothalamic-pituitary control systems function independently (Lincoln 1985). The function of the circannual changes in prolactin secretion remains to be elucidated, but prolactin appears to play a role in influencing seasonal changes in pelage and appetite (Ryg & Jacobsen 1982; Milne *et al.*, 1990) and increased secretion over spring-summer may be necessary for normal lactogenesis in red deer and fallow

deer (Asher *et al.*, 1994). It is interesting that a number of tropical species residing in temperate environments express patterns of prolactin secretion correlated with the photoperiod cycle. This suggests that these species, which include Javan rusa deer and brow-antlered Eld's deer (van Mourik & Stelmasiak, 1985; Monfort *et al.*, 1993a), are responsive to daylength changes. It is also noteworthy that both these species exhibit a high degree of reproductive seasonality in temperate environments, although considerably out-of-phase with temperate species. To our knowledge, there are no data on prolactin secretion in either aseasonally breeding tropical species in temperate environments or tropical species in equatorial zones. Such studies may provide some clues as to enigmas of out-of-phase breeding in some species, and help resolve issues of control of reproductive patterns in equatorial environments.

### Gonadal and non-gonadal control of LH secretion

Two underlying hypothalamic mechanisms may be involved in controlling the breeding and non-breeding seasons in temperate cervid species, as in sheep (Lincoln & Short 1980; Karsch *et al.*, 1984). The first mechanism is dependent on the gonads, whereby gonadectomy releases the pituitary from the negative feedback regulation of gonadal steroids. For example, castrated fallow deer bucks and ovariectomised fallow deer does have two- to five-fold higher LH concentrations than do entire animals (Asher *et al.*, 1989a; 1989b). However, the sensitivity of the hypothalamus-pituitary changes seasonally. In ovariectomized and oestradiol-treated red deer hinds, LH concentrations are highest during the breeding season and lowest during anoestrus, indicating that oestradiol inhibits LH secretion only during anoestrus (Fig. 1; Meikle & Fisher, 1996). It is these changes in the sensitivity of the hypothalamic-steroid feedback mechanism, concomitant with the onset and cessation of the breeding season, which are thought to determine reproductive seasonality (Karsch *et al.*, 1984).

A second mechanism revealed by gonadectomy is a steroid-independent or direct photoperiodic-driven one. This is evident as a



**Figure 2.** Seasonal changes in plasma LH concentration in (a) a mature, entire fallow deer buck, and (b) a mature, prepubertally-castrated fallow deer buck. Asterisks indicate secretory pulses (data from Asher *et al.*, 1989a).

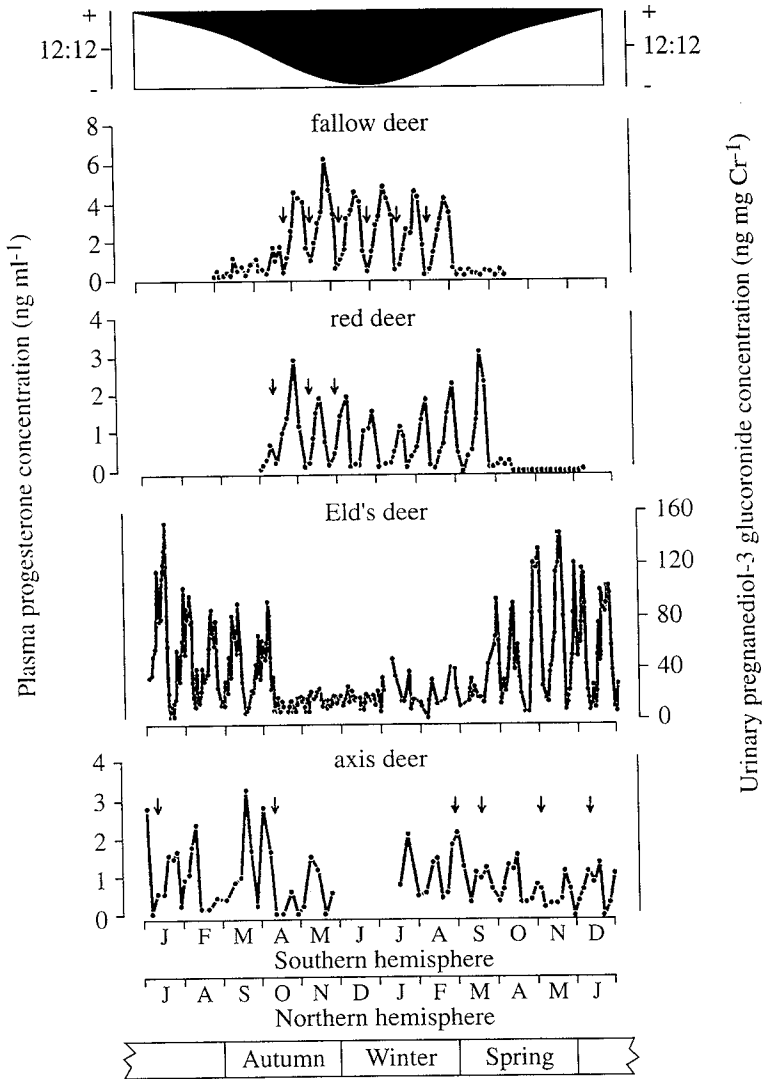
very pronounced seasonal variation in endogenous LH in long-term castrated male fallow deer (Fig. 2; Asher *et al.*, 1989a) and white-tailed deer (Bubenik *et al.* 1982), and ovariectomised female red deer (Fig. 1; Meikle & Fisher, 1994). However, such a pattern is more equivocal in the castrated red deer stag (Lincoln & Kay, 1979; McMahon, 1994) and is relatively absent, or at least more difficult to detect, in ovariectomised ewes (Robinson *et al.*, 1985). Further studies in red deer hinds have indicated that this steroid-independent pattern of LH secretion is inversely proportional to the prevailing photoperiod and is disrupted by reversing the photoperiod cycle (L.M. Meikle & M.W. Fisher, unpublished data).

The extent to which either or both of these mechanisms, and other mechanisms such as the pronounced seasonal variation in pituitary responsiveness to exogenous GnRH (Meikle & Fisher, 1994) and positive oestradiol feedback (Meikle & Fisher, 1990; Jabbour *et al.*, 1992), contribute to, or are resultant of, the control of seasonality is unknown. Seasonal patterns of LH secretion were evident for one tropical species, the brow-antlered Eld's deer (Monfort *et al.*, 1993a) although no seasonal variation was observed in the pituitary response to exogenous GnRH (Monfort *et al.*, 1993b). The species does breed seasonally, whereas a number of tropical species are aseasonal within temperate and equatorial zones (Chapman *et al.*, 1984; Loudon & Brinklow, 1992). Unfortunately, to our knowledge there are no data published on

endogenous rhythms of gonadotrophin secretion in aseasonal species. Likewise, there is a paucity of information on the effect of gonadectomy on pituitary function in any tropical cervid species. Such studies would provide interesting information on circannual reproductive cycles in both photoperiodically-entrained and non-photoperiodically-entrained species.

### Ovulatory cycle

With the exception of roe deer (see later) female cervids are polyoestrous, with non-pregnant females exhibiting either continuous oestrous/luteal cycles (e.g. some tropical species) or, more commonly, alternating periods of oestrous cyclicality and anoestrus. Oestrous cycles are characterised by luteal secretion of progesterone, either detected in peripheral blood or as a urinary metabolite (Fig. 3). In non-pregnant females of temperate species such as red deer and fallow deer, the onset and termination of oestrous cyclicality occur in autumn and spring respectively, with 5-8 oestrous cycles expressed. Anoestrus is characterised by low levels of progesterone secretion, indicating complete ovulatory arrest, and may persist for 4-6 months from spring to early autumn (Fig. 3). In contrast, brow-antlered Eld's deer (a tropical species) initiate oestrous cyclicality in spring and enter anoestrus in the following autumn in temperate regions (Fig. 3), representing a 6-month phase shift from temperate species. Recent studies on tropical axis deer in temperate regions of Australia indicate year-round oestrous



**Figure 3.** Oestrous/luteal cycles in temperate (fallow, red) and tropical (Eld's, axis) species of deer in temperate environments, as defined by peripheral plasma progesterone concentrations or urinary pregnanediol metabolite concentrations during the annual cycle of non-pregnant females. The data have been normalised about common hemispheres and placed in relation to relative annual changes in photoperiod. Arrows indicate overt oestrous behaviour (data from Asher, 1985; Asher & Fisher, 1991; Monfort *et al.*, 1991; Mylrea, 1992).

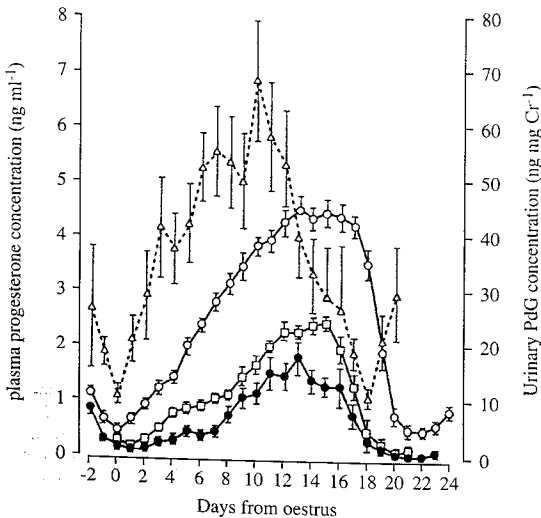
cyclicality (Fig. 3), although success of artificial oestrous synchronisation techniques appears to vary with season (Mylrea, 1992).

The transition into the breeding season is characterised by "silent ovulations" (i.e. ovulations not preceded by overt oestrus) and short-lived (8-10 days) corpora lutea in most cervid species studied (Thomas & Cowan, 1975; Harder & Moorhead, 1980; Asher, 1985; Curlewis *et al.*, 1988; Jopson *et al.*, 1990; Monfort *et al.*, 1991). The transient nature of these preliminary corpora lutea may actually serve to promote within-herd synchrony of first overt oestrus of the season (Asher, 1985). Subsequent luteal cycles ("oestrous cycles" if bounded by overt oestrus) are generally of normal duration, as determined genetically for each species, although occasional "long cycles" (2-3 times the normal duration of oestrous cycles) have been observed in some Pere David's deer and Eld's deer (Curlewis *et al.*, 1988; Monfort *et al.*, 1991). Average lengths of the oestrous cycle range from 18-20 days for red deer, 21-23 days for fallow deer and North American wapiti or elk, and 24-27 days for moose (*Alces alces*), black-tailed deer (*Odocoileus hemionus*) and white-tailed deer (Guinness *et al.*, 1971; Curlewis *et al.*, 1988b;

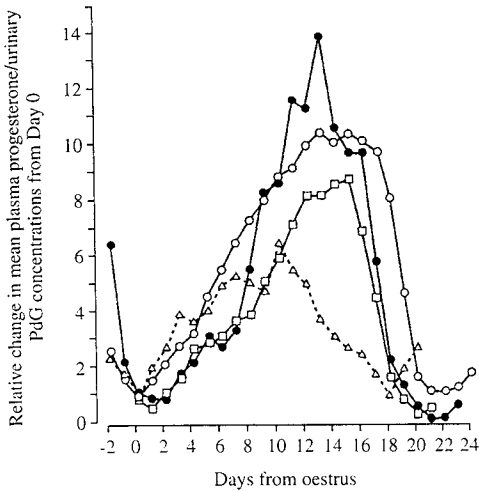
Monfort *et al.*, 1991; Chapple *et al.*, 1993; Asher, 1985; Morrison, 1960; Schwartz & Hundertmark, 1993; Wong & Parker, 1993; Knox *et al.*, 1988). The mean length of the oestrous cycle tends to increase progressively during the breeding season in red deer, fallow deer, black-tailed deer and white-tailed deer.

Luteal events during the cervid oestrous cycle are similar between species (Fig. 4) and to those occurring in other domestic ruminants. Luteinisation of ovulatory follicles is associated with increased secretion of progesterone, with maximal peripheral blood or urinary metabolite concentrations occurring between days 10 and 16 of the oestrous cycle (day 0 = oestrus). While absolute plasma concentrations vary between species (Fig. 4a), the relative changes from day 0 are remarkably similar between species (Figure 4b). Variations in absolute and relative concentrations between individuals of the same species may reflect to some extent variation in luteal mass, as animals with higher ovulation rates (e.g. as a result of induction of superovulation) exhibit higher concentrations of plasma progesterone (Kelly *et al.*, 1982; Asher *et al.*, 1992).

Clearly, the luteal cycle of cervids differs little between temperate and tropical species and between other ruminant species, all exhibiting



**Figure 4a.** Profiles of peripheral plasma concentrations of progesterone (solid line) or urinary concentrations of PdG (dashed line) during the cervid oestrus, for fallow deer (○), red deer (□), axis deer (●) and Eld's deer (△) (data from Asher, 1985; Asher & Fisher, 1991; Monfort *et al.*, 1991; Mylrea, 1992).



**Figure 4b.** Profiles of peripheral plasma concentrations of progesterone (solid line) or urinary concentrations of PdG (dashed line) during the cervid oestrus, for fallow deer (○), red deer (□), axis deer (●) and Eld's deer (△). The data is presented as relative change in mean concentrations from day 0 (data from Asher, 1985; Asher & Fisher, 1991; Monfort *et al.*, 1991; Mylrea, 1992).

cycle lengths of 18-25 days. However, the seasonal pattern of luteal cyclicity varies dramatically between taxa, demonstrating typical temperate patterns of "short-day" species, "reverse seasonality" of some apparently photoperiod-responsive tropical species, and complete aseasonality of other tropical species. However, these patterns all relate to cervids in temperate environments irrespective of their origins. It would be interesting and informative to observe oestrous cyclicity of these same species in equatorial zones. Recent transfer of European fallow deer to the tropics has been associated with apparent de-synchronisation of the female breeding season, necessitating the use of melatonin implants to reinstate a synchronous annual breeding pattern (B. Duirs, pers. comm). Unfortunately, we have no information on patterns of luteal cyclicity of tropical species in their natural environment.

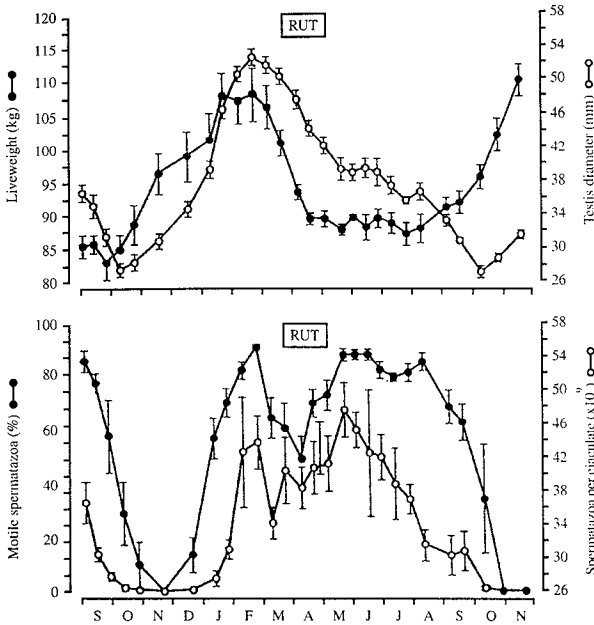
### Reproduction cycles of male cervids

Adult male deer of temperate species exhibit marked circannual fluctuations in body weight that reflect seasonal changes in voluntary feed intake (Kay, 1979; Fennessy *et al.*, 1981; Suttie & Simpson, 1985) and intense rutting activity (Lincoln, 1971; Asher *et al.*, 1989a). The annual liveweight profile of fallow deer bucks (Fig. 5) is

typical of a number of temperate cervid species. Rapid liveweight gains occur during spring and summer months, with attainment of peak annual live weight occurring immediately prior to the rut in autumn. These changes represent deposition of subcutaneous and depot fat, as well as increased neck muscle mass (Asher *et al.*, 1989a). However, during the rut males reduce their levels of feeding and exhibit intense sexual activity, with the resultant negative energy balance leading to very rapid mobilisation of fat reserves, some catabolism of muscle and changes in protein : water ratios in muscles (Jopson, 1993). Individual fallow deer bucks may lose up to 30% of total live weight, at a rate of 450 g per day<sup>-1</sup>, in 3-4 weeks (Mulley, 1989). Bucks regain very little of this lost live weight over the 3-4 month winter period following the rut, even though they may reinstate normal levels of feeding activity (Asher, 1986). It is not until the onset of spring that the growth/fat deposition cycle starts over again (Fig. 5).

Adult male deer of tropical species also exhibit cyclical changes in body mass. In the case of the brow-antlered Eld's deer a marked liveweight cycle is evident that closely resembles that occurring in fallow and red deer, albeit 6-month phase-shifted relative to the photoperiod cycle to match the different rutting season (Monfort *et al.*, 1993a). Body mass changes in individual male





**Figure 5.** Seasonal profiles of mean ( $\pm$  sem) live weight, testicular diameter, motile spermatozoa and spermatozoa per ejaculate for F<sub>1</sub> hybrid Mesopotamian x European fallow deer (G.W. Asher, unpublished data).

axis deer are associated with their cyclical reproductive patterns (e.g. testis growth and regression) but tend not to be synchronised between individuals within a population (Loudon & Curlewis, 1988). Furthermore, the magnitude of liveweight change is considerably less than observed for temperate species, perhaps indicative of less intensive rutting activity (Mylrea, 1992)

Circannual variation in testicular function is evident in most deer species, reflecting changes in fertility, gross morphometry and behaviour. Of the temperate species, these changes have been best described for red deer (Lincoln, 1971; 1985; Suttie *et al.*, 1984) and fallow deer (Asher *et al.*, 1989a; Schnare & Fischer, 1987). In the adult fallow deer buck, marked annual changes in testicular function (Fig. 5) are controlled primarily by dynamic changes in pituitary secretion of LH (Fig. 6). LH is secreted in pulses which alter in amplitude and frequency during the year, being of low amplitude and frequency during the non-breeding season (early summer) and of high amplitude and frequency leading up to the onset

of the breeding season in autumn. A similar pattern of secretion has been observed for Eld's deer, a tropical but seasonally breeding species (Monfort *et al.*, 1993b).

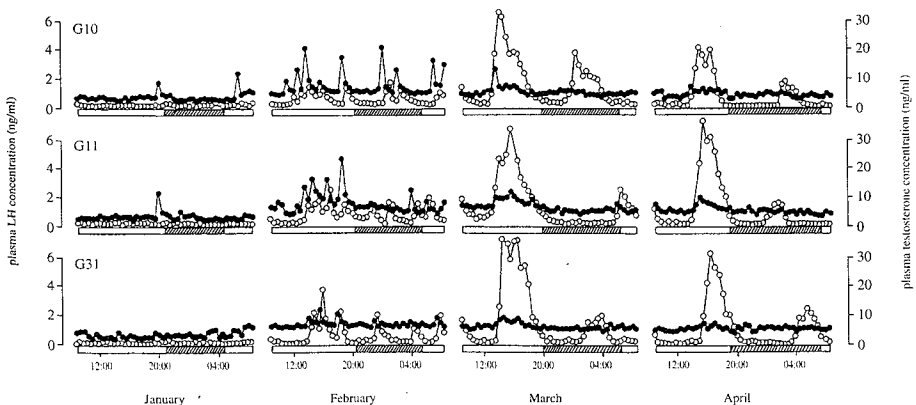
Occasional (one per 12 hours) low-amplitude pulses of LH during the non-breeding season seldom elicit any demonstrable change in testosterone secretion during times of minimal testis mass (Fig. 6). However, increased frequency of pulses (6-10 per 12 hours) 2-3 months prior to the rutting season, at a time when testis mass is increasing rapidly, is associated temporally with pulsatile secretion of testosterone, with individual LH pulses eliciting a corresponding pulse of testosterone secretion after a 20-30 minute lag phase (Asher *et al.*, 1989a; Asher & Peterson, 1991; Monfort *et al.*, 1993b). By the onset of the rut in both fallow deer and Eld's deer, basal plasma LH concentrations appear to be elevated but demonstrable LH pulsatility is not evident. However, plasma testosterone concentrations fluctuate markedly in a manner described as "surges" (Asher *et al.*, 1989a), characterised

by 50-100 fold variation between basal and peak values. Interestingly, fallow deer bucks appear to exhibit considerable synchrony in the timing of such "surges", indicating perhaps a circadian rhythm operating independently from endogenous LH pulses (Asher *et al.*, 1989a; Asher & Peterson, 1991). Recent data on Eld's deer indicate similar patterns of testosterone and LH secretion during their spring rut, although GnRH injections will elicit correlated short-term LH and testosterone responses (Monfort *et al.*, 1993b).

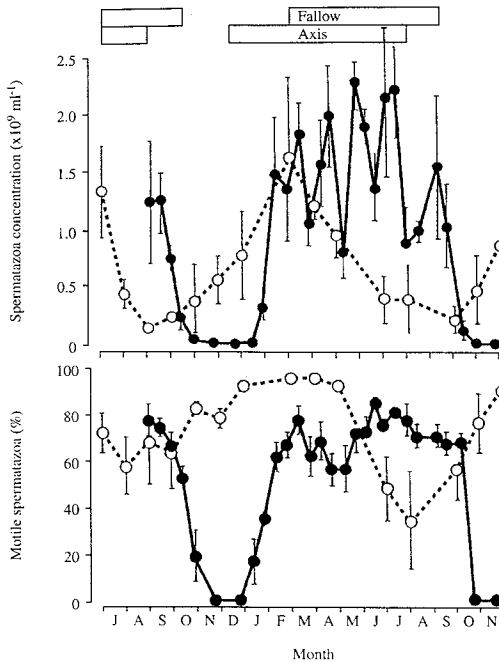
Circannual patterns of testicular regression and recrudescence occurring in temperate cervid species relate to annual cycles of sperm production. Unlike most seasonally breeding domestic ruminants which show moderate fluctuations in testicular activity (e.g. sheep), temperate cervids exhibit alternating periods of sperm production and complete spermatogenic arrest that reflect ~5-fold changes in seasonal testicular volume (Lincoln, 1971; Haigh *et al.*, 1984; Asher *et al.*, 1987; Gosch & Fischer, 1989). In fallow deer, for example, as testicular size increases towards the rut there is a concomitant increase in spermatogenic activity, such that by the onset of the rut large numbers of viable spermatozoa are present in ejaculates (Fig. 5). The testes remain active

throughout winter, secreting modest levels of testosterone and producing large numbers of spermatozoa. However, towards the onset of spring, LH and testosterone secretion diminish and the testes regress in size. Spermatogenesis is completely arrested by early summer, the bucks becoming infertile. They remain in this condition for about two months, gradually regaining fertility towards the end of summer (Fig. 5).

Although tropical cervid species often exhibit circannual cycles of reproductive development, either in a synchronous manner (e.g. Eld's deer, axis deer in Australia, Reeve's muntjac) or non-synchronous manner (e.g. axis deer in UK), males appear to remain fertile throughout the year (Loudon & Curlewis, 1988; Chapman & Harris, 1991; Mylrea, 1992; Monfort *et al.*, 1993a). Recent data on sperm production in tropical species indicate fluctuations in spermatogenesis related to the stage of the antler cycle, with reduced levels of production and minimal testis size during velvet antler growth (Fig. 7). At no stage is there complete arrest in spermatogenesis. This presumably relates to less well-defined breeding and climatic seasons within tropical environments. It remains to be seen whether males in the antler growth phase sire many offspring.



**Figure 6.** Profiles over 24 h of plasma LH (●) and testosterone (○) concentrations of three mature entire fallow deer bucks during the transition from the non-breeding seasons. The shade portion of the abscissa axis indicates night time (Asher & Peterson, 1991)



**Figure 7.** Seasonal profiles of mean ( $\pm$  sem) spermatozoa concentration and % motile spermatozoa for European fallow deer ( $\bullet$ ) (temperate species) and axis deer ( $\circ$ ) (tropical species) in the southern hemisphere. Hard antler status is indicated by the unshaded bars (G.W. Asher, unpublished data; Mylrea, 1992).

Testosterone-mediated changes in secondary sexual characteristics are very pronounced in both temperate and tropical cervid species. The antler cycle is linked closely to the testis cycle, with antlers cast annually when testes regress to their minimal dimensions. Casting is in response to a marked decline in testosterone secretion and can be induced by castration (Goss, 1983). New antler growth occurs during the quiescent phase of the testes, in the relative absence of testosterone secretion. Mineralisation of antlers coincides with increasing testicular activity and increasing testosterone secretion, and hard antlers are generally retained while testicular tissue is actively secreting modest-high levels of testosterone. This relationship holds for most antlered species studied (Goss, 1983) although the actual seasonal patterns vary between species and antler/testis cycles may not be synchronised amongst individuals of some tropical species (Loudon & Curlewis, 1988; Loudon & Brinklow, 1992).

Annual changes in testosterone secretion also

have marked effects on some muscles. In particular, increasing levels of secretion of testosterone in late summer/early autumn are associated with hypertrophy of the neck muscles of red deer, fallow deer and reindeer (Lincoln, 1971; Field *et al.*, 1985; Asher *et al.*, 1987; Kiessling *et al.*, 1987). Regression of neck muscle mass coincides with testicular regression and antler casting (Asher *et al.*, 1987). This phenomenon is common to many cervid species of both temperate and tropical origin. Behavioural changes, vocalisations and distinctive odours related to rutting activity are also associated with the annual changes in testosterone secretion, and can be modified by castration (Lincoln *et al.*, 1972; Asher *et al.*, 1987) or immunosuppression of LH and testosterone secretion (Lincoln *et al.*, 1984).

## Conclusions

There has been considerable advancement in our understanding of control of reproduction in cervids over the last 10 years and it has not been possible to cover all of this recent research in this

review. Perhaps the most interesting developments relate to observed differences between species of temperate and tropical origin. Evaluation of recent data highlight some enigmas between and within the two broad categories of cervids, although it is perhaps unfortunate that all the studies of which we are aware relate only to cervids in the temperate environment (i.e. tropical species relocated outside their natural range). It is apparent that some tropical cervids have retained vestiges of photoperiod responsiveness, as evinced by circannual patterns of prolactin secretion (van Mourik & Stelmasiak, 1985; Montfort *et al.*, 1993a). However, it is curious that some of these species (e.g. Javan rusa deer, brow-antlered Eld's deer) appear to be cued to different parts of the photoperiod signal and have effectively become phase-shifted in their reproductive patterns. The net effect of this is the occurrence of births in autumn/winter, a pattern often detrimental to the species in temperate environments (Woodford & Dunning, 1992). Other tropical species (e.g. axis deer) appear to exhibit either weak photoperiodism (Mylrea, 1992) or no apparent photoperiodic responses (Loudon & Curlewis, 1988) in temperate environments. Unfortunately, there is a profound paucity of information on endogenous pituitary function and the effects of gonadectomy and light control on pituitary function of tropical species. Such studies may answer many questions on exogenous cues that regulate reproductive patterns.

Complete testicular regression to the point of spermatogenic arrest is rare in mammals, but a feature common in the annual reproductive cycle of many temperate cervid species. This phenomenon is temporally, and probably causally, related to the annual cycle of antler casting and regrowth through a dramatic reduction in testosterone secretion (Lincoln, 1971; Chapman, 1975; Suttie *et al.*, 1992). However, tropical cervid species appear quite capable of exhibiting circannual antler cycles even though cycles of testis regression and recrudescence (and hence androgenesis?) are of reduced amplitude and there is evidence of continuous spermatogenesis, albeit seasonally fluctuating (Loudon & Curlewis, 1988; Chapman & Harris, 1991; Monfort *et al.*, 1993a). Resolution

of this apparent enigma will require further endocrine studies on tropical species, but may shed new light on endogenous control of antler growth.

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