REPRODUCTIVE PHYSIOLOGY OF CERVIDS : A REVIEW

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INTRODUCTION

Implementation of intensive husbanding 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 fallow deer (*Dama dama dama*) have been studied in detail However, research on other farmed or captive species has contributed greatly to our insights into reproductive processes of both temperate and tropical species, including North American wapiti or elk (*Cervus elaphus nelsoni/manatobensis/roosevelti*), axis (chital) deer (*Axis axis*), Pere David's deer (*Elaphurus davidianus*), Mesopotamian fallow deer (*Dama dama mesopotamica*), brow-antlered Eld's deer (*Cervus eldi thamin*), rusa deer (*Cervus timorensis*), sambar deer (*Cervus unicolor*) and white-tailed deer (*Odocoileus virginianus*). This paper aims to review current knowledge of cervid reproductive physiology, effectively updating previous reviews (16, 17, 36, 102)

SEASONALITY OF REPRODUCTION

(1)   Birth season

The necessity of most cervid species to give birth at an appropriate time of year for optimal survival and growth of offspring has exerted considerable influence on their reproductive physiology. Species of northern temperate origin (e g red, fallow, elk, white-tailed) typically conceive in autumn and calve in summer, while species of tropical origin (e g axis, rusa, sambar, Eld's) often exhibit limited seasonality or are completely non-seasonal (66). The endogenous mechanisms controlling seasonal reproductive patterns in temperate species are robust, and are manifest rigorously when animals are transferred between localities despite subtle regional variations in seasonal feed supply. Thus, transference across the equator results in an exact 6-month phase change (66, 73) even though the relationship between season and feed production differs considerably between continental northern hemisphere and insular southern hemisphere environments Interestingly, tropical species transferred from equatorial (0-15°) zones may exhibit either pronounced "reverse" seasonality (i.e. spring mating 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. axis deer) or complete aseasonality (i e calving year round e.g Moluccan rusa deer) (32, 70, 76, 81, 89, 104, 111).

It is generally recognised 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 (68) and that variations in the actual mating season between such species of up to eight weeks usually offsets genetically determined species variation in gestation length, such that calving generally

occurs in mid-summer (66). A notable exception amongst temperate species is the Pere David's deer, which initiates mating in early summer and calves in late spring despite an unusually long gestation of 280 days (34, 105). There is strong evidence that 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 with photoperiodic changes (82). However, this species, as with Javan rusa deer, appears to initiate mating activity in response to increasing daylength in spring, thus calving in autumn/winter (81, 82, 104). Similarly, treatment of axis deer stags with exogenous melatonin has been shown to hasten antler casting, indicating photoperiod responsiveness in a species considered to exhibit limited seasonality in both tropical and temperate environments (89).

(2) Endogenous recognition of photoperiod changes

Role of melatonin and photoperiod: The pineal indole-amine, melatonin, is the main transducer of photic information in mammals (92). Melatonin is secreted maximally during darkness, as demonstrated by concentrations in the peripheral blood of fallow deer (10), thus providing an endogenous measure of the relativity between day and night. Most seasonally reproducing cervids are termed "short-day breeders" (i.e initiate breeding during decreasing photoperiods), although the assumption that seasonal reinstigation of fertility involves a direct response to decreasing day-length may be an oversimplification, as males often begin the processes of testicular recrudescence 4-6 weeks before the summer solstice (i.e., during long photoperiods) (13, 68). 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 (19, 69 · see current review in these proceedings) There is little doubt that melatonin plays a major role in seasonal reproduction of temperate cervid species. However, its role in tropical species remains to be elucidated

For temperate cervid species, the long daily photoperiods of summer are probably permissive for the subsequent autumnal onset of the breeding season, while the decreasing photoperiod through summer and autumn is possibly involved in its timing. Interestingly, the timing of the breeding season may also be influenced slightly by temperature, the mean date of calving in first calving red deer hinds being approximately 3 days earlier for every 1°C cooler the mean minimum March temperature was during the previous rut (41)

Effects of photoperiod on pituitary function: A component of the underlying mechanism controlling the breeding and non-breeding seasons in the red deer hind, as in the ewe (58), is a change in the sensitivity of pituitary LH secretion to the negative feedback effects of ovarian oestradiol (78). As shown in Figure 1, implanted oestradiol is unable to suppress LH secretion in ovariectomized hind during the breeding season, whilst during the non-breeding season LH secretion is minimal, probably due to both the suppressive effects of oestradiol and photoperiod (in the absence of oestradiol, LH secretion is inversely proportional to the number of daylight hours) Further studies have demonstrated that LH secretion in ovariectomized hinds can indeed be modified by altering photoperiod (L. M. Meikle and M. W Fisher, unpublished data). These and other results, for example, the induction of behavioural oestrus with progesterone and oestradiol (54, 77), suggest that photoperiod probably acts on several components of the reproductive system to regulate reproductive seasonality.
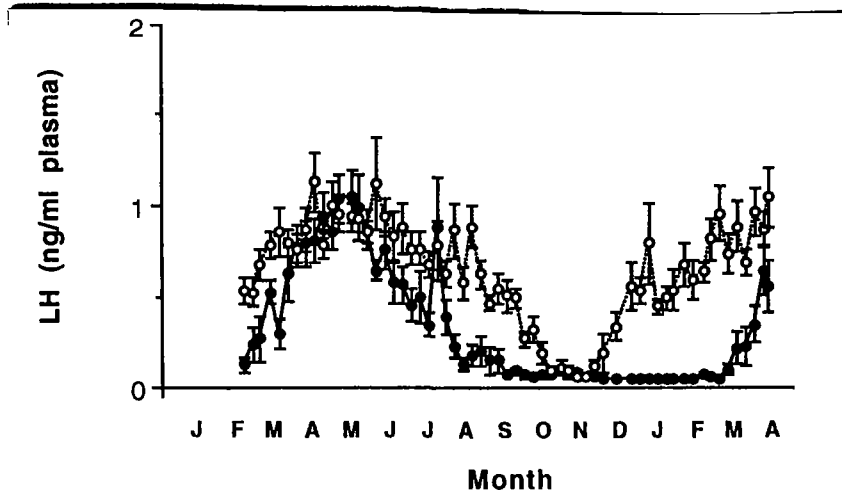
Figure 1: Mean (±sem) plasma LH concentrations determined weekly in ovariectomized (O) and ovariectomized-oestradiol treated (●) red deer hinds during the year (78)
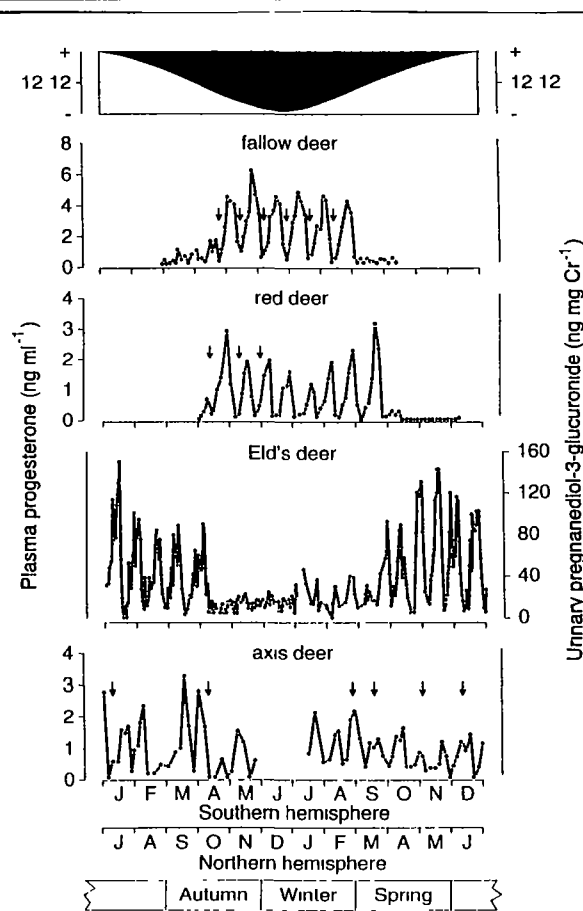

Figure 2: Oestrous/luteal cyclicity in temperate (fallow, red) and tropical (Eld's, axis) species of deer in temperate environments, as defined by peripheral plasma progesterone concentrations or urinary pregnanediol metabolite concentrations during the annual cycle of non-pregnant females. The data have been normalised about common hemispheres and placed in relation to relative annual changes in photoperiod (6, 17, 81, 89)

(3) Social facilitation

Social effects: Reproduction is regulated by social cues in many species (27) and deer are no exception. For example, the timing of the onset of the breeding season in red deer in the wild may be determined by the complex of behavioural or social interactions characteristic of the rut. Stags become reproductively active first, promoting the onset of the breeding season in the hinds. The hinds thus stimulated, may further stimulate the stag(s) resulting in the rut quickly gaining momentum (65). The calving patterns evident in both wild and farmed red deer herds also suggests that behavioural or social interactions are important in promoting a synchronous calving pattern (26, 53, 65). Evidence for these effects in farmed red deer include an advanced onset of the breeding season when adult hinds are exposed to untreated (74, 83) or seasonally-advanced (38, 108) stags. Conversely, puberty is slightly delayed when young hinds are kept isolated from stags (41).

The role of social facilitation in tropical species has received little attention. However, antler status in rusa deer stags appears to be modified by female cues Casting may be delayed by several months by the presence of oestrous hinds, whilst hardening occurs more rapidly in the presence of oestrous hinds (110). This observation suggest very powerful social effects on reproduction in some tropical species.

To what extent farm management practices can utilize social facilitation or conversely whether social interactions compromised by farm practices (e.g the removal of aggressive competition between stags by utilizing single-sire mating groups) affect reproduction remain to be determined.

FEMALE REPRODUCTION

(1) Ovulatory cycle

Seasonality: With the exception of roe deer (*Capreolus capreolus*), which are monoestrous (and undergo delayed embryonic implantation, 98), cervid species are polyoestrous, with non-pregnant females exhibiting either continuous oestrous/luteal cycles (e.g some tropical species) or, more commonly, alternating periods of oestrous cyclicity and anoestrum. Such patterns are characterised by luteal secretion of progesterone, either detected in peripheral blood or as urinary metabolite (Figure 2). In temperate species such as red deer and fallow deer, the onset of oestrous/luteal cyclicity occurs in autumn and terminates in spring, with up to 5-8 oestrous cycles expressed. Anoestrum is characterised by low progesterone secretion, indicating complete ovulatory arrest, and may persist for 4-6 months from spring to early autumn (6, 17). In contrast, brow-antlered Eld's deer, a tropical species that exhibits seasonal patterns of reproduction in temperate environments, initiate oestrous/luteal cyclicity in spring and enter anoestrum in the following autumn (81 : Figure 2), effectively representing a 6-month phase shift from temperate species Recent studies on tropical axis deer in temperate regions of Australia indicate year-round cyclicity (Figure 2), although success of artificial synchronisation of females appears to vary with season (89).

Oestrus and ovulation: The periodic display of oestrus is a feature of most mammalian species (humans are a notable exception). In general, behavioural components of oestrus in cervids are similar to those observed in other ruminants and have been described in detail for red deer and fallow deer (107) In these two species the temporal relationships between

preovulatory endocrine changes, the onset of oestrus and ovulation have been studied (8, 15, 17, 18). It has been shown that in the relative absence of progesterone secretion following the luteolytic demise of the preceding corpus luteum (or removal of an intravaginal CIDR device), there is an increase in pulse frequency and amplitude of the pituitary secretion of luteinizing hormone (LH) in red deer (17) and fallow deer (86) This is associated with, and probably causal of, increasing peripheral blood concentrations of oestradiol (21) and androstenedione (8) derived from the recently recruited preovulatory follicle. The follicular source of these steroids was confirmed by an observed correlation between the number of preovulatory follicles recruited and the mean concentration of each hormone following induction of superovulation in red deer and fallow deer (21). It is presumed that the classical "oestradiol feedback switch" (62) occurs in deer, whereby increasing blood concentrations of oestradiol elicit a change from negative feedback on LH secretion to one of positive feedback and induction of the preovulatory LH surge at the onset of oestrus (17). As with other ruminant species, the preovulatory LH surge involves a massive elevation in circulating plasma LH concentrations (30-40 times basal concentrations) for periods of 16-20 hours (8, 12, 15, 18) and heralds the final stages of follicular maturation leading to ovulation at a mean interval of 24 hours after the onset of oestrus in both red deer and fallow deer (15, 18)

Oestrous cycle: While most individuals conceive early in the breeding season, effectively terminating ovulatory activity for the season, recurrent oestrous/ovulatory cyclicity will occur in the absence of pregnancy. The transition into the breeding season is characterised by "silent ovulations" (i.e. ovulation not preceded by overt oestrus) and short-lived (8-10 days) corpora lutea in most cervid species studied (6, 31, 49, 56, 103). The transient nature of these preliminary corpora lutea (Figure 3) may actually serve to promote within-herd synchrony of first overt oestrus of the season (6). Subsequent luteal cycles ("oestrous cycles" if bounded by overt oestrus) are generally of normal duration, as determined genetically for individual 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 (31, 81). Average lengths of the oestrous cycle range from 18-20 days for red deer, Pere David's deer, eld's deer and axis deer (30, 31, 47, 56, 81), 21-23 days for fallow deer and North American elk (6, 84) and 24-27 days in moose (*Alces alces*), black-tailed deer (*Odocoileus hemionus*) and white-tailed deer (61, 96, 109). In red deer, fallow deer, black-tailed deer and white-tailed deer, the mean length of the oestrous cycle tends to increase progressively during the breeding season (6, 47, 61, 109) but this phenomenon was not observed in moose (96).

Luteal events during the cervid oestrous cycle are similar between species (Figure 4) and to other domestic ruminants. Luteinization of the ovulatory follicle 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. While absolute plasma concentrations vary between species (e g. fallow, red and axis deer; Figure 4a), the relative changes from Day 0 (oestrus) 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 concentration of plasma progesterone (18, 21).
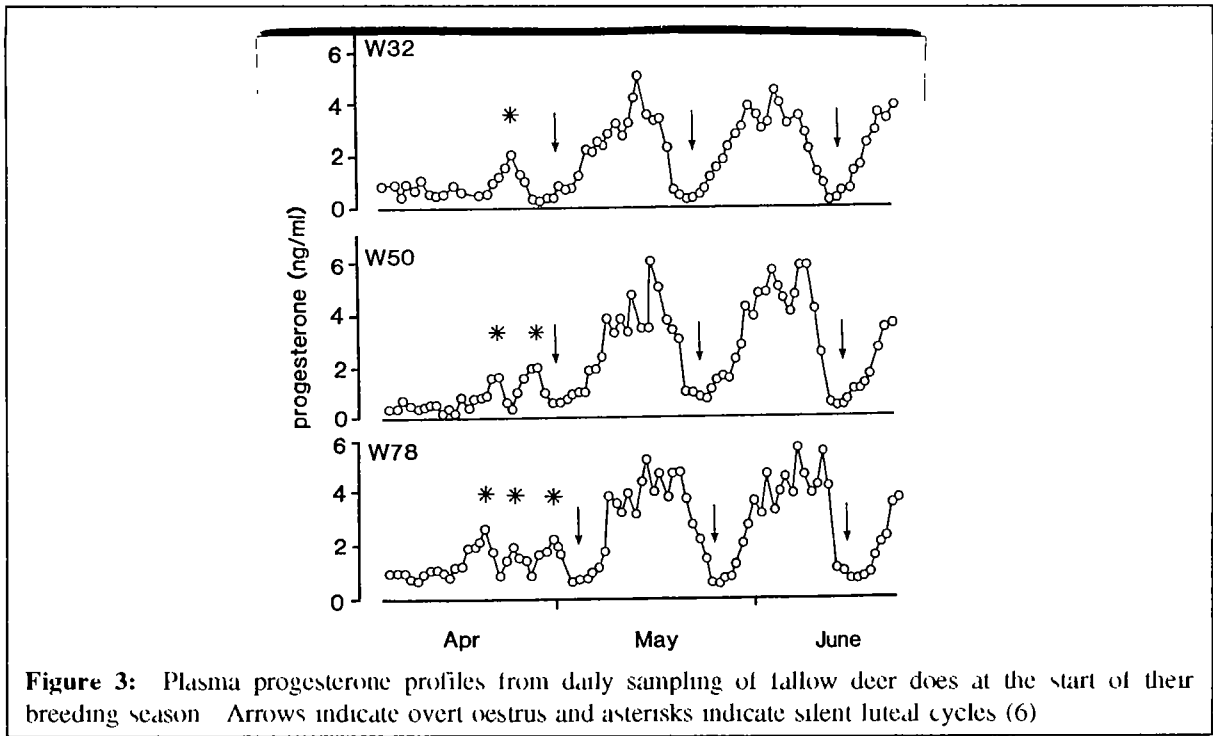
Figure 3: Plasma progesterone profiles from daily sampling of fallow deer does at the start of their breeding season Arrows indicate overt oestrus and asterisks indicate silent luteal cycles (6)
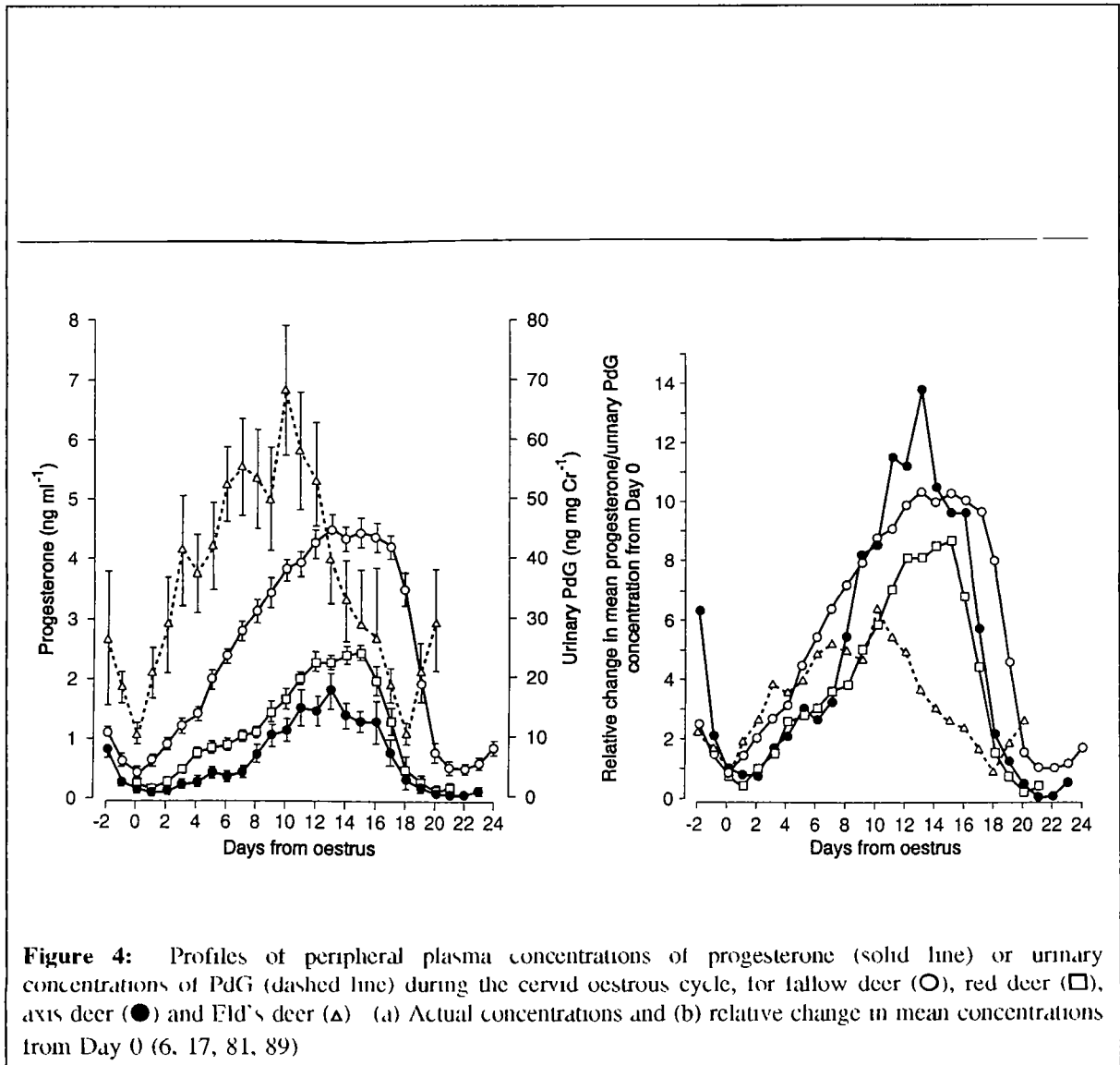

Figure 4: Profiles of peripheral plasma concentrations of progesterone (solid line) or urinary concentrations of PdG (dashed line) during the cervid oestrous cycle, for fallow deer (O), red deer (□), axis deer (●) and Eld's deer (Δ) (a) Actual concentrations and (b) relative change in mean concentrations from Day 0 (6, 17, 81, 89)

Pulsatile release of both LH and progesterone occurs during the oestrous cycle (Figure 5). LH pulsatility is greatest during the oestrous/preovulatory period in the relative absence of luteal tissue in both red and fallow deer (17, 86). Conversely, marked pulsatility of progesterone in fallow deer occurs during the late luteal phase and probably represents the initiation of luteolysis (86) It is notable that such pulses often exceed 2-5 times base progesterone concentration (Figure 5)

Luteolysis generally occurs only 4-5 days prior to next overt oestrus, and is characterised in all species studied by a rapid overall decline in plasma progesterone or urinary metabolite concentrations over a 3-4 day period (6, 56, 81, 89). As with other domestic ruminants, luteolysis appears to involve a dynamic interaction between uterine secretion of prostaglandin-F2α (PGFα) and luteal/pituitary secretion of oxytocin towards the end of the oestrous cycle, as demonstrated in fallow deer (11) Induction of luteolysis during the oestrous cycle by injection of prostaglandin analogues promotes a synchronous return oestrus. Early studies on fallow deer indicated a high level of efficacy when cloprostenol was delivered on Day 13 of the oestrous cycle (12). However, a more recent study on red deer has shown that the level of efficacy was high on Days 13-14 (100% of hinds treated) but low on Days 9-10 (50%), with non-responsive hinds exhibiting only transient reductions in progesterone secretion in response to cloprostenol (40) This suggests that the corpus luteum is refractory to the luteolytic effects of prostaglandin early in the oestrous cycle These data contrast with more recent studies whereby delivery of cloprostenol to red deer hinds on Days 4, 6, 8, 10, 12, 14 or 16 of the oestrous cycle indicated refractoriness on Day 4 only, thereafter most hinds exhibited complete luteolysis and subsequent ovulation. However, a high proportion of hinds on Day 6-10 experienced a short luteal cycle following induced ovulation. Furthermore, the interval from cloprostenol delivery to the onset of oestrus was shorter on Days 6 and 8 (46-50 h) than for hinds at later stages of the oestrous cycle (61-66 h) (G W Asher & M W Fisher, unpublished data).

Ovarian follicle emergence: During each oestrous cycle, a small number of growing follicles are selected to undergo a further period of rapid growth and development and 1 or 2 of these follicles will eventually ovulate. Patterns of follicle growth and the period of preovulatory development that culminates in ovulation have been studied extensively in other species, but little is known about the growth and development of ovarian follicles in deer. Recently, ovarian follicle populations have been monitored in red deer (B.J. McLeod, L.M Meikle and M W. Fisher, unpublished data)

To assess preovulatory follicle development, ovaries were recovered from adult hinds at various times over the follicular phase of the oestrous cycle All follicles ≥ 2.0 mm diameter were dissected free of extraneous tissue, measured and classified as healthy or atretic on the basis of thecal vascularity, number of granulosa cells present and the integrity of the oocyte The mean number of follicles present (approximately 25 follicles/hind) did not change significantly during the follicular phase, but the proportion of follicles that were non-atretic increased from less than 40% at the end of the luteal phase to more than 80% immediately before ovulation. Surprisingly, the mean diameter of the largest follicle (about 8 mm) present (putatively, but not necessarily the follicle that would ovulate), did not increase over the follicular phase of the cycle The most obvious change noted was that whereas there were usually two large antral follicles present at the beginning of the follicular phase, 40 h later there was only one. When hinds were treated with a low dose of PMSG to promote superovulation, this decrease in the number of large follicles did not occur
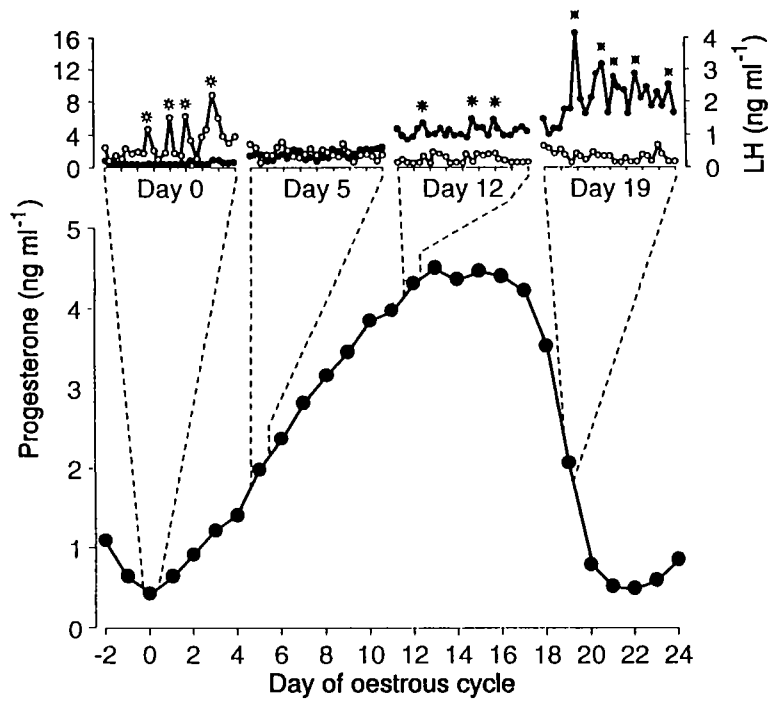
Figure 5: Pulsatile secretion of LH (O) and progesterone (●) during the oestrous cycle of a fallow doe (W40) superimposed on the mean plasma progesterone profile for cyclic does. Blood samples were collected every 20 minutes for 8-hour periods on Days 0, 5, 12 and 19 of the cycle. Asterisks denote secretory pulses detected by the PULSAR algorithm (86).
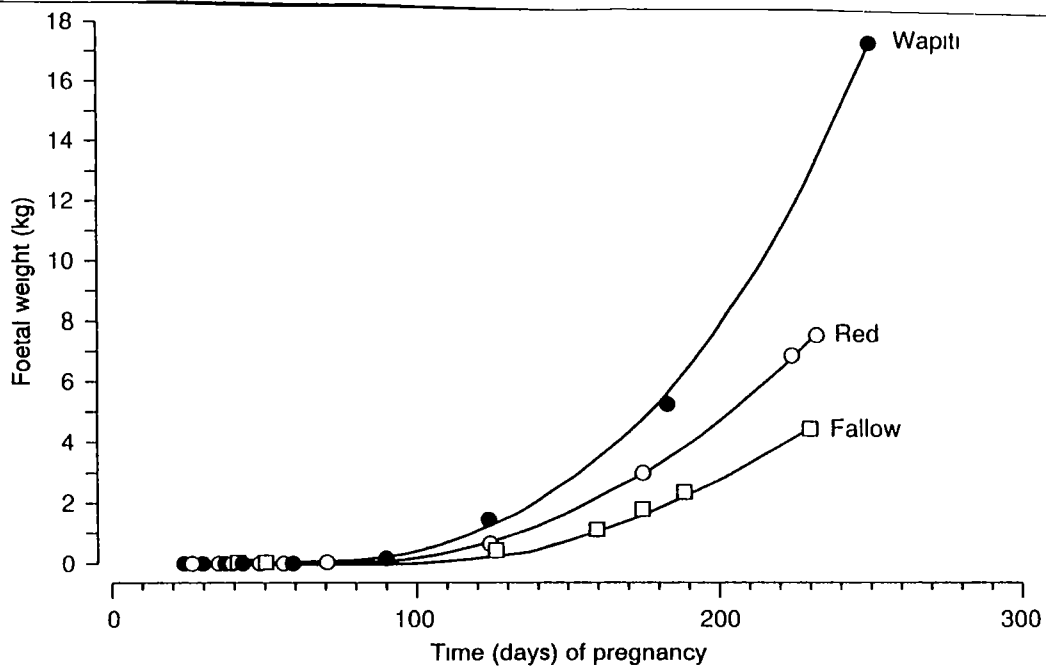

Figure 6: Mean foetal weights in wapiti, red and fallow deer throughout gestation (1, 28, 85, C D McMahon and M W Fisher, unpublished)

In other seasonally breeding species (sheep and goats), administration of GnRH during seasonal anoestrus stimulates follicle development and induces ovulation in a high proportion of animals, irrespective of the stage of the anoestrous period. In contrast, it has been shown for both red deer (37) and for Pere David's deer (35) that although a high proportion of hinds will ovulate when treated with GnRH in late anoestrus, few respond if treated in mid-anoestrus. It was suggested that this may have been indicative of a period of deep seasonal quiescence during which there is little ovarian activity. To assess this, ovaries were recovered from adult hinds during mid-anoestrus (January) The mean number of antral follicles > 2 mm diameter of the largest healthy follicle (8 mm) was the same as that previously recorded during the breeding season.

These results indicate that 1 or 2 large antral follicles are present throughout the oestrous cycle and during anoestrus With the exception of preovulatory development, gross morphology of follicle populations differs little between the breeding season and anoestrus, indicating that seasonal anoestrus in deer is unlikely to be due to a gonadal block.

(2) Pregnancy

Pregnancy recognition: The maternal recognition of pregnancy, in part, involves the protection of the corpus luteum from the normal luteolytic mechanisms which begin to develop near the end of the period of the normal oestrous cycle The embryo and its associated membranes produce proteins or agents which modify or inhibit the development of the luteolytic oxytocin/PGF$_{2\alpha}$ interaction, resulting in continued luteal progesterone secretion, essential for the maintenance of pregnancy. Embryo-derived factors in ruminants include the antiluteolytic trophoblast proteins (which share structural similarity with the α interferons) and luteal protective agents such as PGE$_2$ (23).

Products derived from the embryo and its membranes and specific for pregnancy, can be used to detect pregnancy in many species, including deer. For example, pregnancy-specific protein B (94, 106) and early pregnancy factor (87; G E. Lash and M Legge, unpublished data)

Preimplantation embryonic development: The site of fertilisation in mammals is the ampullary-isthmic junction. The egg, by means of ciliary action, is moved to the site of fertilisation within 15-30 minutes of ovulation. There it remains for many hours awaiting penetration by sperm (52). After fertilisation, the embryo moves down to the isthmus portion of the oviduct where it develops to the appropriate stage and enter the uterus. The stage of development and numbers of days spent in the oviduct varies between species.

There is little information concerning the fertilisation and early embryo development for deer. One study, using synchronised red deer hinds, has demonstrated that fertilisation is completed by 36 hours after mating (24). The rate of embryo transport into the uterus appears to be slower in cervids than other ruminants Day 6 (Day 0 = onset of oestrus) morula were located in the oviduct and tight morula and blastocytes were recovered from the utero-tubal junction (UTJ) region of synchronised red deer hinds. Blastocysts were not recovered from the upper uterine horns until Day 7 5 (25) Results from superovulated fallow deer demonstrated that the majority of embryos (87%) recovered on or before Day 7 are located in the oviduct or UTJ region (D.K. Berg, unpublished data).

Implantation and foetal development: Attachment of the embryo and membranes (placentome formation) to the uterine surface occurs at the uterine caruncles (usually 4 or more in each horn) from about day 34 - 41 onwards in red deer and probably at a similar time in fallow deer (C.D. McMahon and M.W Fisher, unpublished data) There may also be some accessory placentome formation between the main placentomes, at least in red deer in later gestation. The placenta is described as syndesmochorial, the embryonic chorionic epithelium being in contact with the maternal endometrial connective tissue. Hamilton *et al* (48) have described placentation in deer in detail, whilst aspects of foetal growth in red deer have been reported (1, 93). The comparative weights of red, elk and fallow foetuses during gestation are presented in Figure 6.

Endocrine support of pregnancy: As with other ruminant species, a functional corpus luteum is required for maintenance of normal pregnancy in deer, at least for part of the first trimester of pregnancy. Lutectomy (ablation of the corpus luteum) or ovariectomy before Day 70 results in foetal loss in red deer (M.W. Fisher & G.W. Asher: unpublished data) However, ovariectomy before Day 70 in reindeer (*Rangifer tarandus*) does not always terminate pregnancy, indicating that, for this species at least, the foeto-placental unit is an additional source of progesterone production (99). For red deer and fallow deer, plasma progesterone concentrations remain elevated between 2 and 8 ng ml⁻¹ throughout the 234 days of gestation, with a dramatic decline to <0.05 ng ml⁻¹ occurring around the time of parturition (17, 60). However, the relative contributions of luteal and placental tissues to progesterone secretion have not been elucidated.

Plasma oestradiol and serum oestrone sulphate concentrations are elevated in red deer hinds during the first and second trimesters of pregnancy (22, 60). While high concentrations of oestrone sulphate (>1 0 ng ml⁻¹) before Day 100 may be diagnostic of pregnancy (22), there was no apparent difference in oestradiol secretion between pregnant and non-pregnant hinds during this period (60) However, plasma oestradiol concentrations were significantly elevated in pregnant hinds 20 days prior to parturition (60).

(3) Lactation

Lactogenesis: The induction of lactation in cervids occurs during the late stages of pregnancy, with initial mammary tissue development being palpable in red deer hinds about six weeks before parturition and maximum mammary extension occurring at parturition (20). The hormonal regulation of lactogenesis is not well studied in cervids but is assumed to be similar to that of other ruminant species. Prolactin is considered to be essential for normal initiation of lactation (42, 46, 50, 57). As temperate species of cervids generally calve in summer months, lactogenesis coincides with high endogenous secretion of prolactin induced by increasing photoperiods (5) A chance observation on fallow deer indicated that delivery of exogenous melatonin starting ~ 40 days before parturition suppressed lactogenesis in some does (10), this being possibly due to a dramatic suppression of prolactin secretion. This observation was extended to a recent study on pregnant red deer hinds, whereby melatonin implants were administered from either 80, 40 or 0 days prior to parturition. Hinds in the earliest treatment group all failed to initiate lactogenesis but hinds in all other treatment groups initiated normal lactation relative to untreated controls (20). It is also noteworthy that fetal development appeared also to be compromised by melatonin treatment, with a significant reduction in mean birthweight noted for calves born in the early treatment regimen (20). Data on plasma prolactin concentrations did not provide unequivocal evidence for a role of this

hormone in lactogenesis. Interestingly, experimental reversal of photoperiod did not inhibit lactogenesis in red deer hinds (2), indicating that pharmacological delivery of melatonin via implants is not necessarily mimicking reversal to short photoperiods, and that exogenous melatonin may exert a more direct suppressive effect on lactogenesis and fetal development.

Maintenance of lactation: Again, little is known about the hormonal maintenance of lactation in cervids. It is noteworthy, however, that once established, lactation does not appear to be affected by exogenous melatonin treatment in red deer (4, 20, 39), indicating that suppression of prolactin secretion does not impact negatively on milk yields

Effects of lactation on ovulation: Lactation may, as in many species, impose a constraint on reproductive performance, an effect best described in red deer. The existence of a post-partum or lactational anoestrus was suggested by a study where matings in red hinds were timed to occur from the beginning of the breeding season until the end of winter (47). Whilst the shortest interval between calving and the onset of breeding in a lactating hind was 10 weeks, if the calf was lost at birth so that the hind stopped lactating, this interval was as short as 20 days. In poor conditions such as in the wild in the Scottish Isles, where puberty is normally reached a year later than in farmed animals, red hinds lactating during the autumn may fail to conceive until the following breeding season, thereby producing a calf in alternate seasons only (79).

The importance of the relationship between nutrition, lactation and fertility was highlighted in a study reported by Loudon *et al.* (71). Hinds on a lower plane of nutrition (Scottish hill pasture) produced less milk and smaller calves, and returned to breeding 6 2 days later than those on better nutrition (permanent pasture) They suggested that the decrease in milk production, associated with poorer nutrition, resulted in the calves sucking and attempting to suck more frequently This may have resulted in the higher plasma prolactin levels observed, and the reduced reproductive efficiency Although calves with hinds on better nutrition, sucked less frequently, it was of a considerably longer duration However, perhaps indicative of the complexity of the relationship, in another study, Heydon *et al.* (51) found no effect of nutrition and lactation on the onset of oestrous cyclicity.

In farmed red deer, weaning immediately prior to stag introduction for mating had no influence on hind fertility, when compared with hinds lactating (calves at foot). However, there was a small, but significant, tendency for a greater calving spread in those hinds which had had their calves weaned (48) In apparent contrast, Adam *et al.* (3) found that hinds weaned about a month prior to the onset of the breeding season, started ovarian cycles 10 days earlier than did hinds with calves at foot Furthermore, all 13 weaned hinds conceived at their first oestrus compared with 14/19 unweaned hinds, resulting in a 16 day earlier mean conception date. Interestingly, Margulis (72) suggests that the apparent preference that mule deer (*Odocoileus hemionus*) bucks show for mating with nonlactating, rather than lactating females, may reflect the latters reduced reproductive fitness.

Methods of inducing early season breeding, would appear to be similarly effective in both lactating and non-lactating hinds, although few direct experimental comparisons have been undertaken on large numbers of animals (3, 4, 5, 51) Thus it would appear that lactation, at least in red deer, has the potential to modify reproductive performance, particularly if the animals are nutritionally compromised

MALE REPRODUCTION

(1) Male reproductive physiology

Adult male deer of temperate species exhibit marked annual fluctuations in liveweight that reflect seasonal changes in voluntary feed intake (33, 59, 100) and rutting activity (9, 13, 64, 65). The annual liveweight profile of fallow deer bucks (Figure 7) is typical of a number of temperate cervid species. Rapid liveweight gains occur during spring and summer months, with attainment of peak annual liveweight occurring immediately prior to the rut in autumn. The increases in liveweight represent increased deposition of subcutaneous and depot fat, as well as increased neck muscle mass (13). However, during the rut male deer reduce feed intakes and increase rutting activities, with the resultant negative energy balance leading to very rapid mobilisation of fat reserves, some catabolisation of muscle and changes in protein : water ratios in muscle (55) Individual fallow deer bucks may lose up to 30% of total body weight, at a rate of 450 g day⁻¹, in 3-4 weeks (7, 88). Bucks regain very little of this lost weight for the 3-4 month winter period after the rut, even though they may reinstate normal levels of grazing activity (7). It is not until the onset of spring that the growth/fat deposition cycle starts over again.

While the liveweight cycles of stags/bucks are related to seasonal reproduction, there are other annual reproductive changes more directly associated with the annual rut. These include marked endocrine changes linked to photoperiodic cues and associated changes in testicular development, spermatogenesis, androgenesis, and the development of secondary sexual characteristics (e g. antlers, neck muscle hypertrophy) These annual changes have been described for red deer stags (64, 66, 101) and fallow deer bucks (9, 13, 95), and are essentially similar for the two species In the adult fallow buck, for example, testicular development undergoes marked annual cyclic changes (Figure 7) This is primarily controlled by marked changes in secretion of luteinizing hormone (LH) from the pituitary gland 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. These changes in LH secretion in late summer and autumn directly influence testicular activity by promoting testis growth and increasing testosterone secretion 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 (45, 88) The testes remain active throughout winter, secreting modest levels of testosterone and producing large numbers of spermatozoa (9, 13) However, towards the start of spring, LH secretion diminishes and the testes regress in size and secrete only very low levels of testosterone Spermatogenesis is completely arrested by early summer, the bucks becoming effectively infertile. The animals remain infertile for about two months, gradually regaining fertility towards the end of summer (45)

The antler cycle of bucks is closely linked to the testosterone cycle Antlers are cast during spring when the testes regress Casting is in response to a marked decline in testosterone secretion. The new antler grows during the following period of minimal testosterone secretion through spring and early summer As blood testosterone concentrations increase in late summer and early autumn, the antler mineralizes rapidly and eventually the soft velvet layer is stripped off. The hard antlers are retained through autumn and winter. Annual changes in testosterone secretion also have marked effects on some muscles (35, 64) in particular,
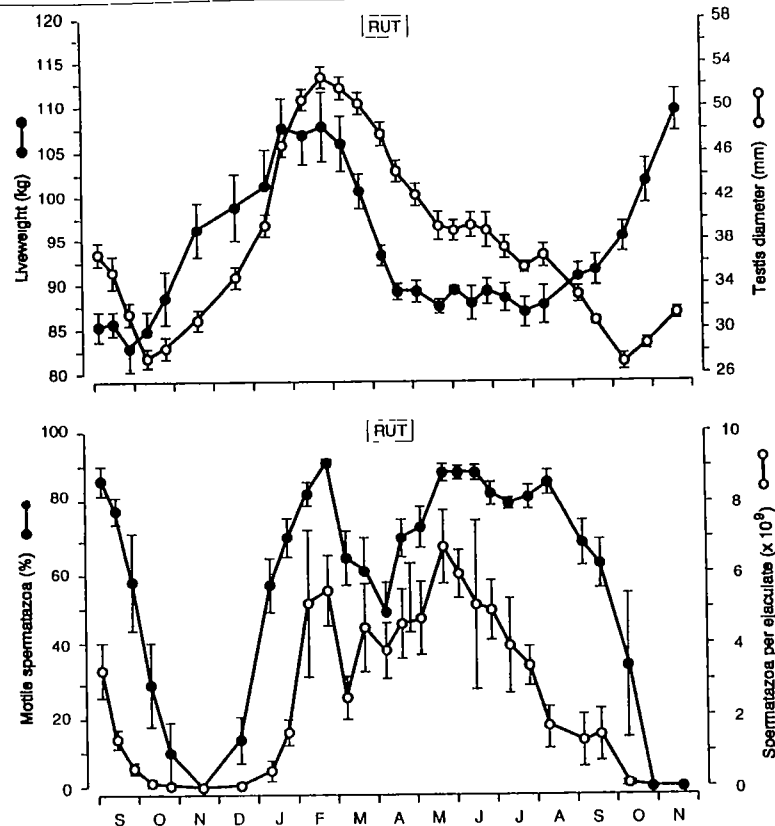
Figure 7: Mean (±sem) profiles of liveweight, testicular diameter, motile spermatozoa and spermatozoa per ejaculate for F1 Mesopotamian x European fallow deer (G W Asher, unpublished data)
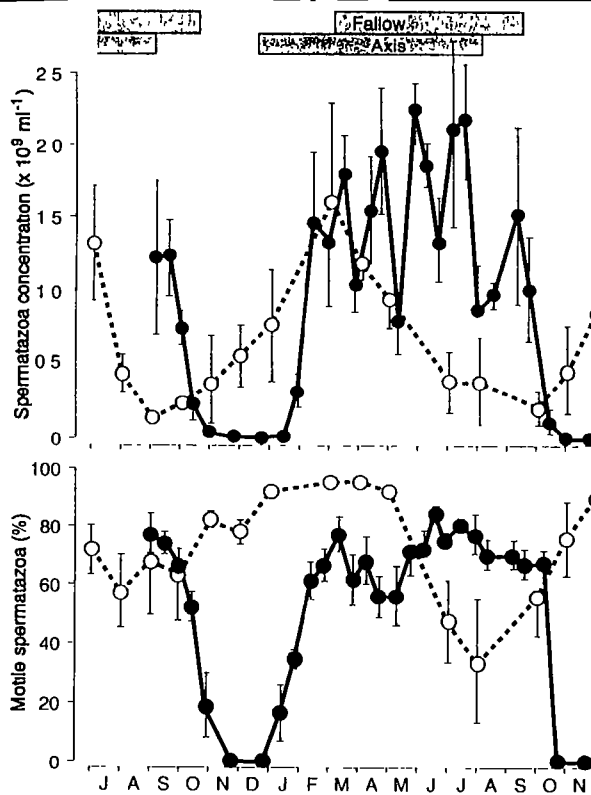

Figure 8: Mean (±sem) profiles of spermatozoa concentration and % motile spermatozoa for European fallow deer (●) (temperate species) and axis deer (O) (tropical species) in the southern hemisphere Hard antler status is indicated by the shaded bar (89, G W Asher, unpublished data)

rising testosterone concentrations in late summer/early autumn cause hypertrophy of the neck muscles This results in a massive increase in neck muscle mass by the start of the rut Loss of liveweight over the rut results in a decrease in neck girth However, when the testes fully regress and liveweights begin to increase in spring, neck girth decreases further in the relative absence of testosterone (9, 13, 95).

Adult male deer of tropical origin (e.g axis deer, rusa deer) generally exhibit individual cirannual cycles of sexual development, although these cycles may lack synchrony between individuals within a population. Such is the case for axis deer stags studied at Whipsnade Park, UK (70). Interestingly, axis deer stags studied near Sydney, Australia, exhibited marked within-herd synchrony of annual reproductive cycles (89). The difference between the two populations may reflect variation in overall management or genetic differences between founder stock. Other tropical species generally exhibit within-herd synchrony between males, including brow-antlered Eld's deer (82,) and Reeves' muntjac (Muntiacus reevsi, 29). However, whereas temperate species exhibit spermatogenic arrest during the velvet antler growth phase, tropical species exhibit reduced levels of spermatogenesis only. Tropical species are effectively fertile throughout the year (Figure 8) (29, 70, 82, 89), although it remains to be seen whether males in the antler-growth phase sire many offspring

INFLUENCE OF OTHER ENDOCRINE GLANDS

(1) Adrenal glands

The hypothalamic-pituitary-adrenal (HPA) axis has long been considered to have a major influence on reproductive function in mammals (80), primarily through mediation of the effects of chronic and acute stress on gonadal function. Much has been written on the role of adrenal corticosteroid secretion on ovarian function and pregnancy, and it is generally acknowledged that these hormones (e.g cortisol) can cause perturbation of reproductive processes. particularly at ovulation and embryonic implantation (80) Cervids appear to differ from conventional domestic ruminants in their ability to secrete physiologically significant levels of adrenal progesterone (i.e. 2-5 times maximum luteal output) under acute ACTH stimulation or high levels of acute stress, as demonstrated for white-tailed deer (91), fallow deer (14) and red deer (56). As progestagens exert profound negative feedback on pituitary LH secretion, it is reasonable to assume that adrenal progesterone could act to disrupt the ovulatory process if stress is applied during the preovulatory period (8) This could result in failure to establish pregnancy. and may in fact account for a significant proportion of reproductive failures observed occasionally in artificial breeding programmes. For example, overnight fasting of fallow deer prior to laparoscopic insemination induces stress responses during the preovulatory period, and seems to depress conception rates (G.W. Asher; unpublished data). Conversely. secretion of adrenal progesterone during established pregnancy may serve to support progesterone-secreting luteal/placental tissues during times of acute stress. thus protecting the foetus from abortion in the face of high levels of circulating corticosteroids

The actual role of adrenal progesterone secretion in cervid reproduction has yet to be evaluated and is certainly worthy of further research

(2) Thyroid gland

Seasonal breeding is a manifestation of changes in release of LH and FSH arising from changes in secretion of hypothalamic GnRH, and changes in the sensitivity of these hormones to negative feedback by gonadal steroids (44, 63) In recent years there has been growing acknowledgement as to the contributory role of the thyroid hormones in reproductive seasonality of birds and mammals (43, 90) Studies involving thyroidectomy have indicated that thyroid function may be required for termination of the annual breeding season In this respect, Shi & Barrell (97) demonstrated convincingly that thyroidectomy of red deer stags blocked the seasonal transition from the breeding to the nonbreeding season. There was no effect of thyroidectomy on prolactin secretion, indicating that thyroid hormones are not involved in the regulation of seasonal patterns of prolactin release. The physiological level of action of the thyroid has yet to be elucidated

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