REPRODUCTIVE PHYSIOLOGY OF FARMED RED DEER (*CERVUS ELAPHUS*) AND FALLOW DEER (*DAMA DAMA*)

GEOFFREY W. ASHER, Ruakura Agricultural Centre, Ministry of Agriculture and Fisheries, Private Bag, Hamilton, New Zealand.
MARK W. FISHER, Invermay Agricultural Centre, Ministry of Agriculture and Fisheries, Private Bag, Mosgiel, New Zealand

Abstract: Red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) exhibit highly seasonal patterns of reproduction, with mating/conceptions occurring in autumn and parturition occurring in summer. The reproductive cycles are entrained by prevailing photoperiodic regimens. The occurrence of first estrus in hinds/does in autumn is preceded by one or more silent ovulations that may facilitate synchronisation of mating activity (rut). The estrous cycle (18-19 days for red deer; 21-22 days for fallow deer) is characterized by a 10- to 14-day luteal phase and a 2- to 3-day luteolytic phase, being similar to other domestic ruminants. In the absence of conception, the duration of estrous cyclicity is 4-6 months, followed by deep anestrum. However, most hinds/does conceive to their first or second estrus and exhibit continuously elevated plasma progesterone concentrations throughout the gestating period (233 days). Parturition is associated with a marked decline in progesterone secretion. The two species have similar mean calving/fawning dates but the fallow deer birth pattern is more concise. Red deer stags and fallow deer bucks exhibit pronounced annual liveweight and reproductive cycles. Testicular, spermatogenic, antler and neck girth cycles are associated with pronounced changes in testosterone secretion which are influenced by the seasonal secretory pattern of luteinizing hormone (LH) from the pituitary gland.

Key Words: red deer, *Cervus elaphus*, fallow deer, *Dama dama*, reproduction, hormones

Résumé: Le cerf rouge (*Cervus elaphus*) et le daim (*Dama dama*) suivent un cycle de reproduction très marqué par les saisons, avec l'accouplement et la conception en automne et la parturition en été. Les cycles reproducteurs répondent aux régimes photopériodiques. Le premier oestrus des biches en automne est précédé par une ovulation muette ou plus, ce qui peut faciliter la synchronisation de l'accouplement (le rut). Le cycle oestral (18-19 jours pour le cerf rouge; 21-22 jours pour le daim) se caractérise par une phase de lutéine de 12-14 jours et une phase sans lutéine de 2-3 jours, comme d'autres ruminants domestiqués. Sans conception, la durée du cycle oestral est de 4-6 mois, suivi par l'anoestrus profond. Cependant, la plupart des biches conçoivent au premier ou au deuxième oestrus et elles montrent des concentrations élevées de progestérone dans le sang pendant toute la gestation (233 jours). La parturition est associée à un déclin net de progestérone. Les deux espèces ont des dates de mise bas similaires, mais le cycle natal des daims est plus concis. Les mâles des cerfs rouges et des daims ont des cycles annuels marqués pour la pesanteur et pour la reproduction. Des cycles testiculaires et spermatogéniques, et des cycles des bois et de la circonférence du cou sont associés aux changements marqués de l'excrétion de testotérone qui sont influencés par le cycle saisonnier de l'excrétion de lutéine (LH) de la glande pituitaire.

Mots-Clés: cerf rouge, *Cervus elaphus*, daim, *Dama dama*, hormones, reproduction

Red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) are the two most commonly farmed cervid species within temperate climatic zones. Although they do not interbreed, they are closely related and exhibit similar breeding patterns. Reproductive productivity is one of the main criteria affecting on-farm economic efficiency. Therefore, reproductive management of the herd is of prime importance to the farmer and requires a thorough knowledge of cervid breeding patterns. This is particularly so if artificial breeding technologies are to be applied effectively for genetic improvement. This paper reviews and summarizes recent studies on reproductive physiology of farmed red and fallow deer.

Seasonality of Reproduction

Photoperiod induction of reproductive cycles

Reproduction in cervids of temperate origin is characterised by the high degree of seasonality. All subspecies of fallow deer and red deer exhibit seasonal breeding patterns, with mating/conception occurring in autumn and parturition occurring in summer. Clearly, these patterns have evolved in regions of marked climatic seasonality to ensure that offspring are born at a time of year most conducive to their survival (Lincoln and Short, 1980). The importance of the seasonal variation of the daily light:dark ratio (photoperiod) in mediating the timing of

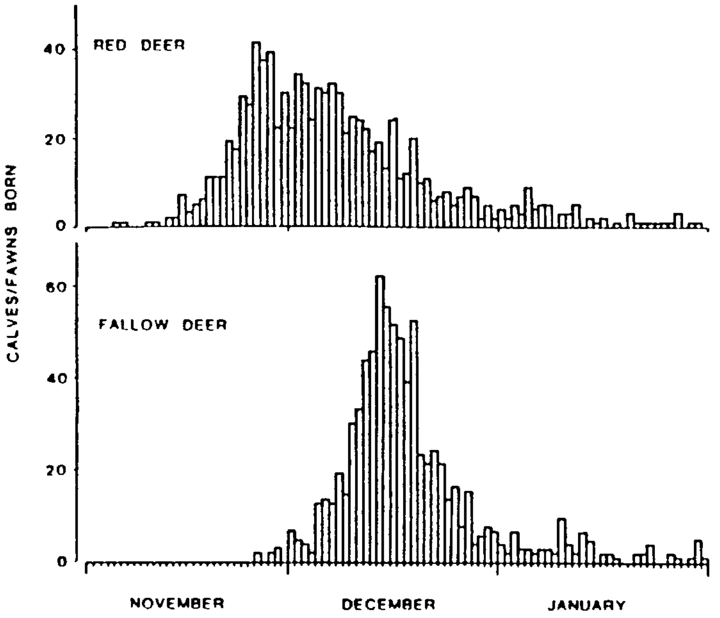

Fig. 1. Frequency distributions of birth dates for red and fallow deer on some commercial farms in northern regions of New Zealand between 1980 and 1984.

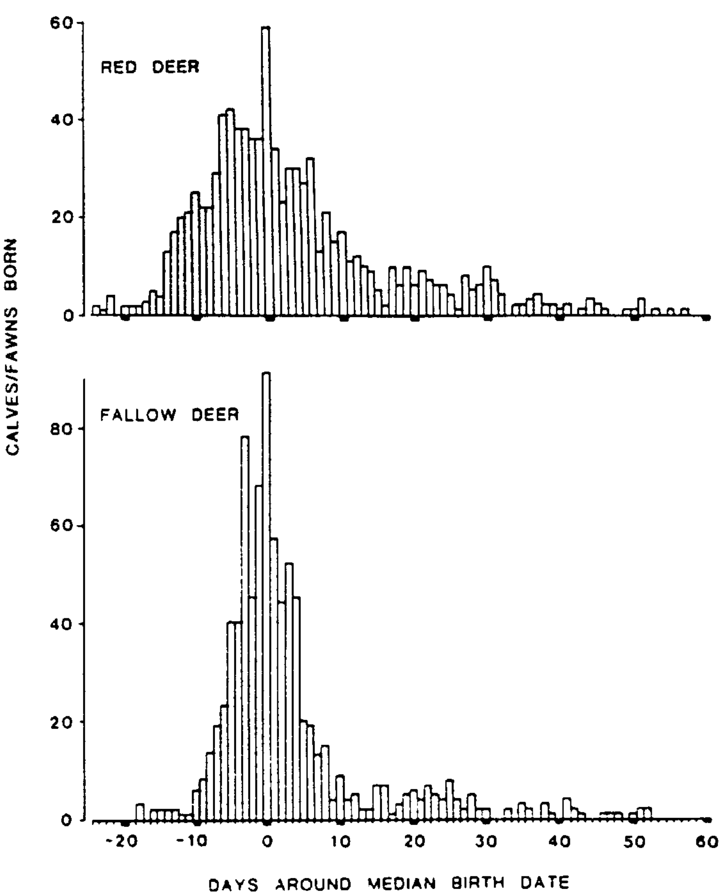

Fig. 2. Frequency distributions of birth dates of red and fallow deer normalized around within-farm and within-year median birth dates (data from Fig. 1).

annual reproductive cycles of many non-equatorial mammalian species has long been recognized, either from the relationship observed between photoperiod and sexual activity or by the results of experimental photoperiodic manipulation (Thibault et al., 1966). The generally accepted role of photoperiod in mediating seasonality in temperate cervids has been inferred largely from photoperiod manipulation studies on red deer (Jaczewski, 1954; Suttie and Simpson, 1985; Webster and Barrell, 1985), fallow deer (Schnare and Ficsher, 1987), and sika deer (*Cervus nippon*) (Goss, 1983), from experiments involving strategic administration of exogenous melatonin in red deer (Adam and Atkinson, 1984; Adam et al., 1985, 1986, 1989; Webster and Barrell, 1985; Fischer et al., 1988; Asher, 1990), fallow deer (Asher et al. 1987, 1988a, Mulley 1989) and white-tailed deer (*Odocoileus virginanus*) (Bubenik, 1983), or from studies on pinealectomy/cranial cervical ganglionectomy of red deer (Lincoln, 1985) and white-tailed deer (Brown et al., 1978; Plotka et al., 1979; Schulte et al., 1981; Snyder et al., 1983).

Season of parturition

While photoperiodic entrainment of reproductive cycles is directed primarily at seasonal synchronisation of conceptions, the ultimate outcome is a concise fawning (fallow deer) or calving (red deer) season, given that gestation length is genetically determined and relatively invariable. The birth seasons of farmed fallow deer and red deer in northern regions of New Zealand (latitudes 36°-40° south) are presented in Fig. 1. The fawning season of fallow deer generally starts later than that of red deer, but tends to be more condensed (Asher and Adam 1985). The first fallow births usually occur in early December, whereas red deer births may commence in early-mid November. However, because of the higher degree of birth synchrony among fallow deer (Fig. 2), medium calving dates are very closely aligned between the two species (i.e. 8-14 December). Latitudinal effects on birth seasons do not seem to be particularly pronounced in New Zealand (latitudes 34°-45° south). Hybridization of red deer (*Cervus elaphus scoticus*) with North American wapiti (*Cervus elaphus nelsoni*) or Père David's deer (*Elaphurus davidianus*) may result in a later seasonal pattern of hybrid births due to fetal genotype effects on increasing gestation length in red deer dams (Moore and Littlejohn, 1989; Asher et al., 1988b). It has yet to be determined if hybridization of European fallow deer (*Dama dama dama*) with Mesopotamian fallow deer (*Dama dama mesopotamica*) will alter genetically the fawning season of the species.

Although data are presently limited, there are indications that the seasonal birth patterns of farmed red deer and fallow deer on the North American continent are essentially similar to those in New Zealand, albeit 6 months out-of-phase due to the reverse photoperiod cycles.

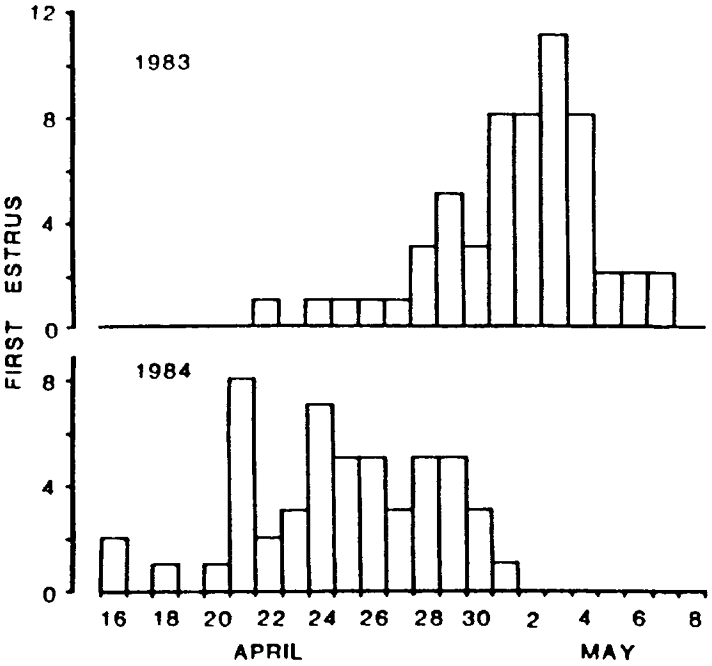

Fig. 3. Occurrence of first estrus of the breeding season among fallow deer does on the Ruakura Agricultural Centre, New Zealand during 1983 and 1984 (Asher, 1986).

Female Reproductive Physiology

Estrous cyclicity

The onset of the breeding season of female red and fallow deer is determined largely by the occurrence of first overt estrus within each herd. Estrus/mating in red deer hinds in New Zealand is generally first observed in mid-late March, whereas it is seldom observed in fallow does until mid April (Asher, 1985a; Moore and Cowie, 1986). In fallow deer, the occurrence of first estrus within a herd appears to be confined to within a 12- to 14-day period (Fig. 3). While such data on red deer are limited, it would appear that hinds do not exhibit quite the same degree of estrous synchrony, as indicated by their less synchronous calving pattern (Fig. 2).

There is strong evidence that in both species first overt estrus of the breeding season is preceded by one or more silent ovulations associated with short-lived (8- to 10-day) corpora lutea (Fig. 4) (Asher, 1985a; Mulley, 1989; Jopson et al., 1990). These ovulations may be a necessary prelude to the expression of behavioral estrus at the start of the breeding season and may, by virtue of the transient nature of the resultant corpora lutea, play a role in within-herd synchrony of first estrus (Asher, 1985a).

While under normal farm management practices it is usual for about 85% of fallow deer does (Asher, 1987), and probably the majority of red deer hinds, to conceive to first estrus matings, in the absence of conception/pregnancy females of both species will exhibit regular estrous/luteal cycles for periods of 4-6 months (Guinness et al., 1971; Asher, 1985a). The duration of the estrous cycle differs between the two species and generally becomes more variable towards the end of the potential breeding season (Table 1). The remarkable uniformity of the first estrous cycle in fallow deer (21.0 + 0.65 days; Asher, 1985a) has been confirmed in a number of subsequent studies (Asher et al., 1986; Asher and Thompson, 1989; Mulley, 1989). By contrast, the first estrous cycle of red deer hinds is shorter (about 18 days) but somewhat more variable in length (Guinness et al., 1971; Adam et al., 1985; Asher et al., 1988b).

In fallow deer, the onset of estrus precedes ovulation by 24 hr (Asher et al., 1990). As yet there are no similar data for red deer. However, in both species, luteal development following estrus/ovulation is associated with a progesterone secretory pattern that has been well documented for other domestic ruminant species (Fig. 4). The luteal phase of the estrous cycle, which is associated with increasing secretory output of progesterone by the developing corpus luteum, lasts for 10-14

Table 1. Observed length and variance of the estrous cycle for red deer in Britain (Guinness et al. 1971) and fallow deer in New Zealand (Asher, 1985a).

Cycle no.	Red deer			Fallow deer		
	No observations	Mean cycle length (days)	S.D. (days)	No observations	Mean cycle length (days)	S.D. (days)
1	29	17.8	1.7	33	21.0	0.64
2	21	18.2	1.7	33	22.0	0.66
3	14	18.8	1.7	33	22.9	0.97
4	7	19.1	1.1	28	23.0	1.11
5	4	18.3	-	12	23.5	1.45
6	2	19.0	-	3	25.7	1.53
Total	77	18.3	1.7	142	22.4	1.30

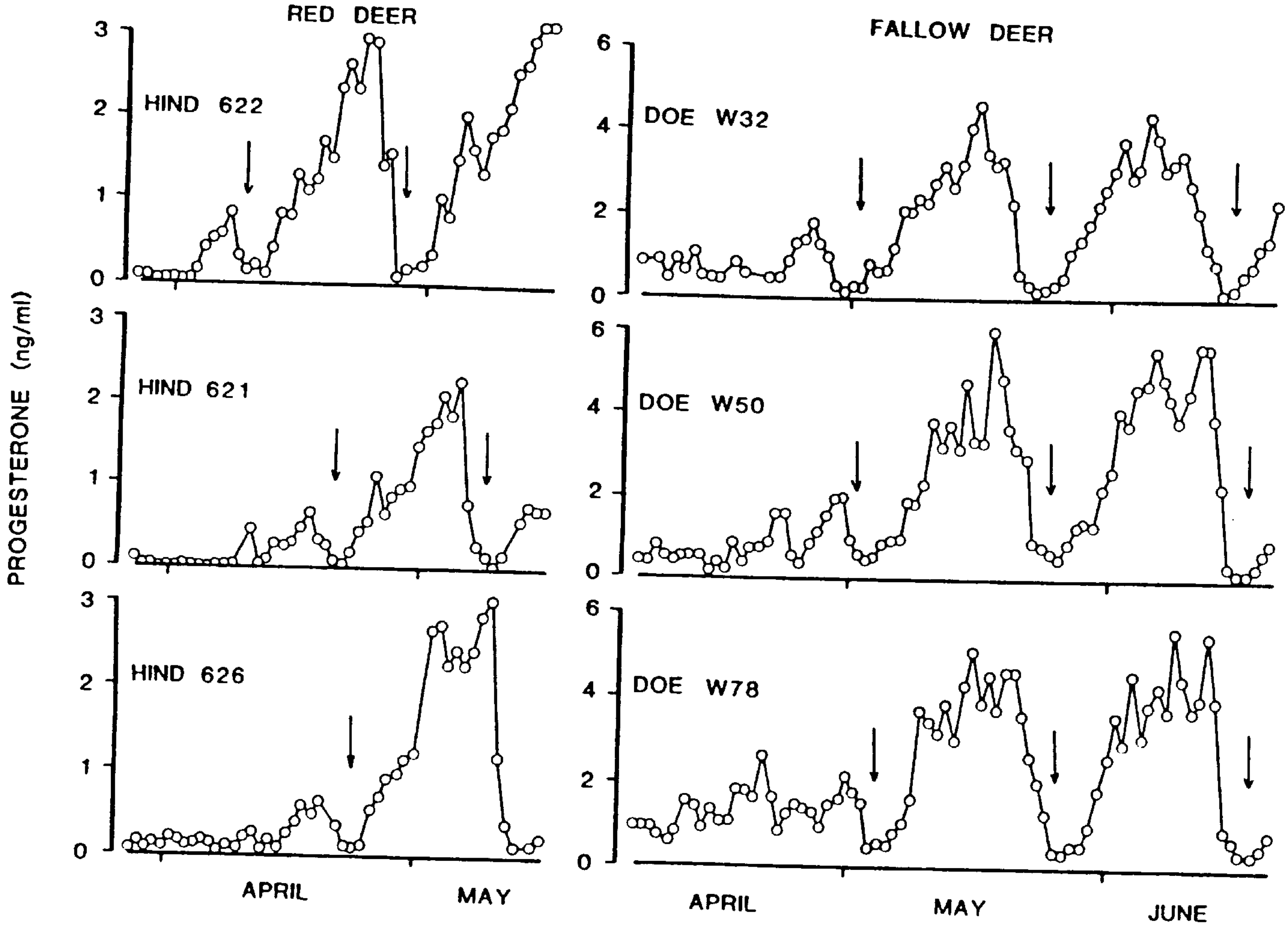

Fig. 4. Plasma progesterone profiles from daily sampling of red deer hinds and fallow deer does at the start of their respective breeding seasons. Arrows indicate overt estrus (Asher, 1985a; Jopson et al,. 1990).

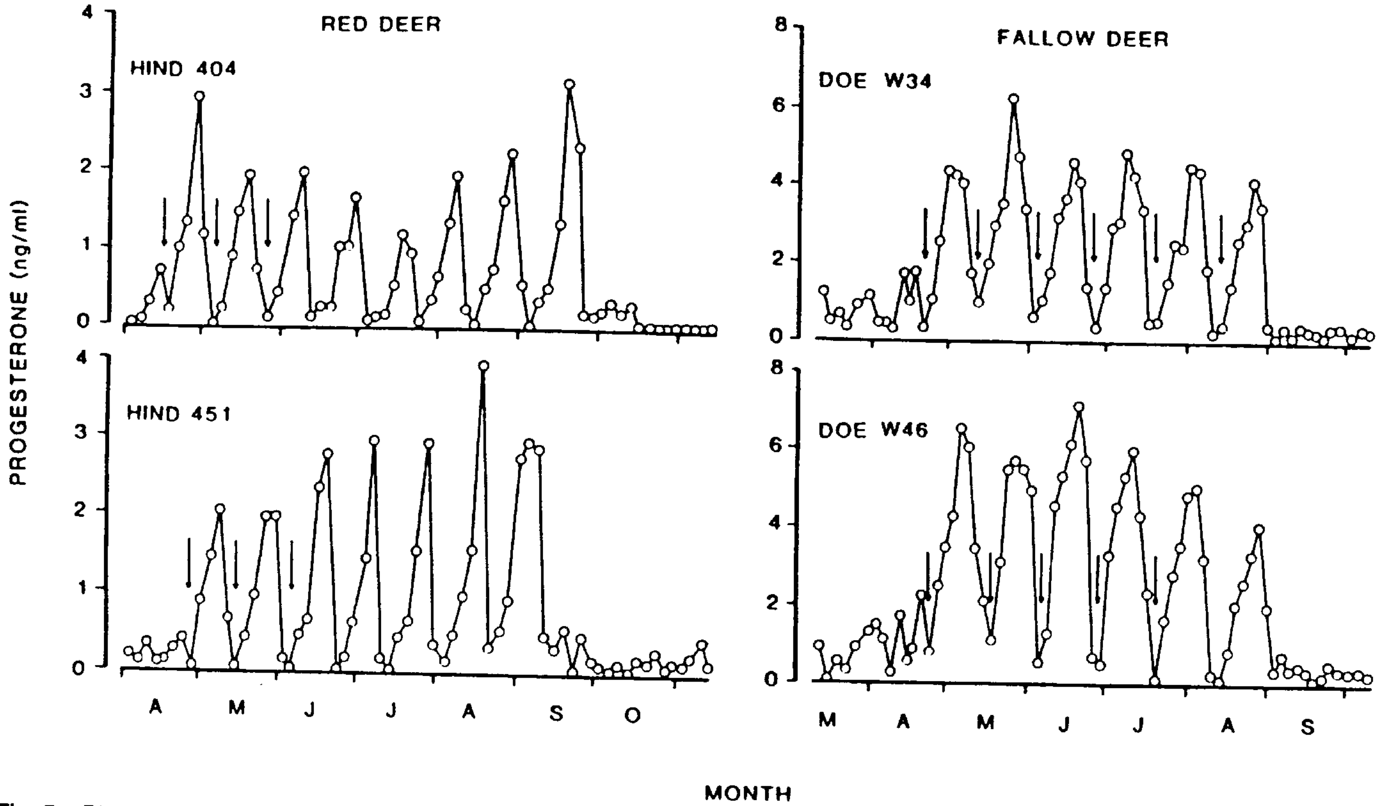

Fig. 5. Plasma progesterone profiles of red deer hinds and fallow deer does run continuously with vasectomized males. Arrows indicate overt estrus (Asher, 1985a; M.W. Fisher, J.M. Suttie and I.D. Corson, pers. commun.).

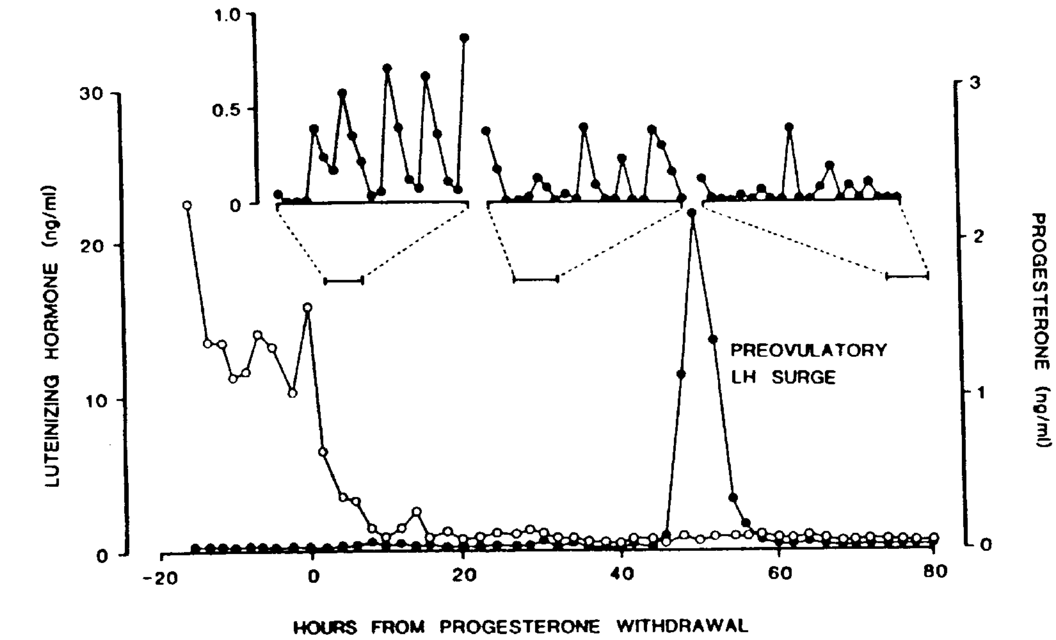

Fig. 6. Plasma luteinizing hormone (●) and progesterone (o) profiles from intensive blood sampling regimens for a red deer hind (R402) during the follicular phase of the peri-ovulatory period (M.W. Fisher, I.D. Corson, and J.M. Suttie, pers. commun.).

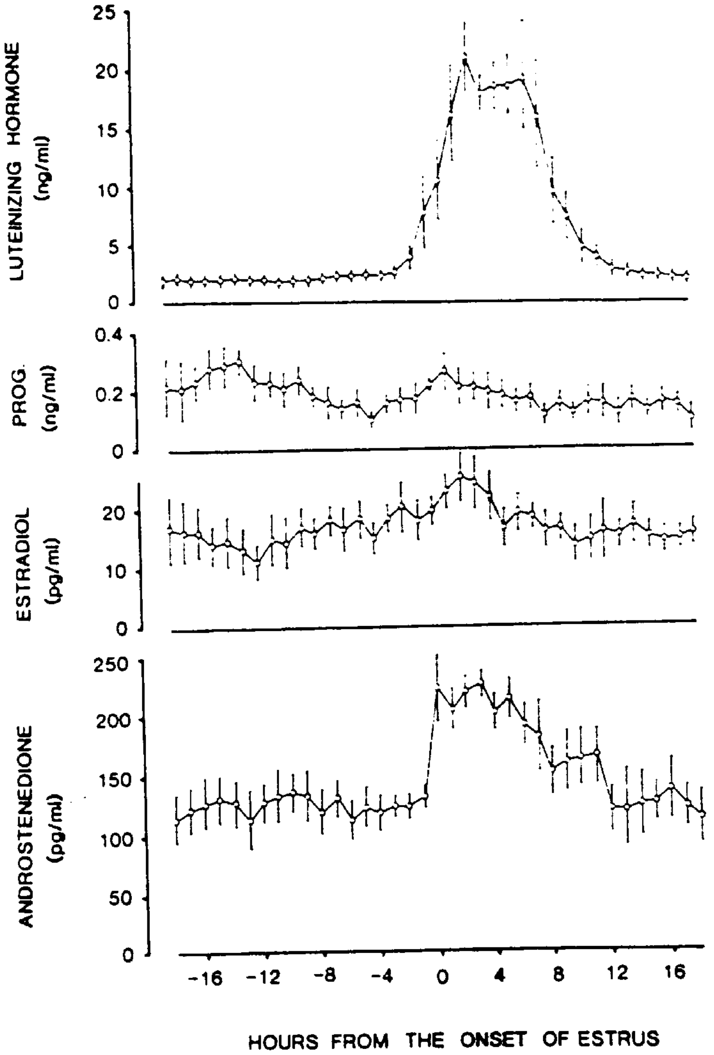

Fig. 7. Mean (± S.E.) serum concentrations of luteinizing hormone, progesterone, estradiol-17b and androstenedione recorded hourly about estrus of four fallow deer does (Asher et al., 1986).

days according to species. Luteal regression (luteolysis) is associated with luteal oxytocin and uterine prostaglandin secretion (Asher et al., 1988c; G. Asher and M. Fisher, pers. commun.) and occurs within the last three days of the estrous cycle 3(Fig. 4).

The potential breeding season of red and fallow deer is 4-6 months (Guinness et al., 1971; Asher, 1985a). During this time the non-pregnant female exhibits continuous estrous/luteal cycles that are characterised by sequential cycles of luteal progesterone secretions (Fig. 5). There are significant age effects on the duration of the potential breeding season with fallow deer. Generally, younger does exhibit fewer estrous cycles than older does (Asher, 1985a). For both species, termination of all cyclic activity occurs in early-mid spring. Thereafter, the hinds/does are deeply anovulatory/anestrous until the following autumn.

Hormonal control of estrus/ovulation

Red deer hinds and fallow deer does are almost invariably monovulators (Chapman and Chapman, 1975). The natural endocrine regulation of estrus/ovulation in hinds/does has many similarities with other domestic ruminants. Recent studies have characterised the changing secretory pattern of luteinizing hormone (LH) during the estrous cycle of red and fallow deer (G.W. Asher and M.W. Fisher, pers. commun.). There are clearly marked changes in the pulsatile release of LH from the pituitary gland towards the onset of estrus (Fig. 6). In most cases, the preovulatory LH surge is initiated at the onset of estrus and has a duration of 13-14 hr (Fig. 7). Its initiation is probably triggered by decreasing secretion of progesterone during luteolysis and increased secretion of follicular estradiol-17b and androstenedione. The relative roles of preovulatory increases in estradiol-17b and androstenedione secretion in inducing estrous

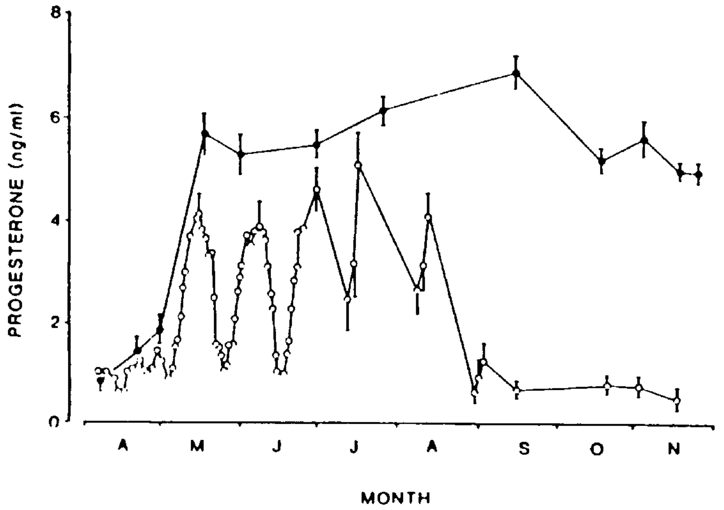

Fig. 8. Mean (± S.E.) plasma progesterone profiles of cyclic non-pregnant (●) and pregnant (o) fallow does (Asher, 1987).

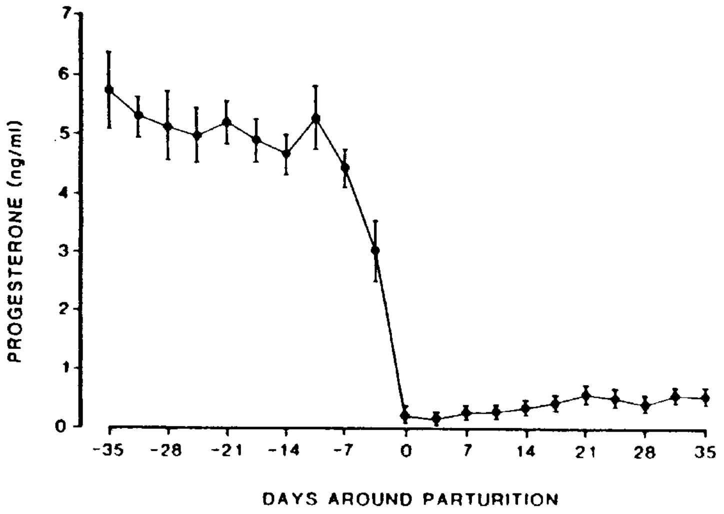

Fig. 9. Mean (± S.E.) plasma progesterone concentrations during the parturient period of fallow does (Asher et al., 1988a)

behaviour have yet to be evaluated (Asher et al., 1986).

Pregnancy and parturition

Following fertilisation the egg divides or cleaves into many cells and passes down the oviduct into the uterus by about 3-4 days after ovulation and eventually forms the blastocyst (Boyd and Hamilton, 1952). The blastocyst then goes through a period of rapid development with gastrulation (establishment of the germ layers) complete by day 27 in red deer, by which time the trophoblast had elongated and extended through both uterine horns (McMahon and Fisher, 1990). Attachment of the embryonic and maternal membranes (implantation) occurs at the uterine caruncles (usually 4 or more in each uterine horn; Harrison and Hyett, 1954, Thorne 1980) from about day 34-41 onwards in red deer (McMahon and Fisher, 1990) and probably at a similar time in fallow deer (Harrison and Hyett 1954).

The placenta is syndesmochorial (the chorionic epithelium is in contact with the endometrial connective tissue) and has been described in detail in deer by Hamilton et al. (1960). The red deer embryo displays a typical mammalian growth pattern (Adam et al., 1988; Wenham et al., 1986; McMahon and Fisher, 1990), weighing about 3 g at day 48 of pregnancy, 660 g at day 125 and 6.8 kg at day 225. Birth weights average about 9 kg in red deer (Moore et al., 1988) and 4 kg in fallow deer (Asher and Adam, 1985).

The gestation length of red and fallow deer is around 233-234 days (Guinness et al., 1971; Kelly and Moore, 1977; Clutton-Brock et al., 1982; Asher, 1987). In contrast to the non-pregnant cyclic female, pregnant hinds/does exhibit continuously elevated plasma progesterone concentrations (4-10 ng/ml) until the initiation of parturition (Fig. 8 and 9). The relative secretory contributions of the corpus luteum of pregnancy and the placenta have yet to be determined for deer.

Progesterone as an indicator of pregnancy status

The corpus luteum appears to be the principal source of progesterone in female red deer (Adam et al., 1985) and fallow deer (Asher, 1985a, 1987). Clearly, plasma progesterone analysis of sequential blood samples collected over periods longer than the duration of the estrous cycle may differentiate between cyclic and pregnant hinds/does. Similarly, single samples collected after the potential period of cyclic activity and before parturition (i.e. between late spring and summer) may also differentiate pregnant and non-pregnant females. However, recent studies on ovariectomised red deer hinds (Jopson et al., 1990) and fallow deer does (Asher et al., 1989a) challenged with ACTH provided strong evidence that the adrenal glands are secondary and major sources of progesterone in these species. It is concluded that progesterone of adrenal origin, secreted in response to stress stimuli, may occasionally confound interpretation of plasma progesterone profiles as indicators of ovarian/pregnancy status if animals are not habituated to the handling/sampling procedures. This may limit the usefulness of progesterone analysis for pregnancy diagnosis.

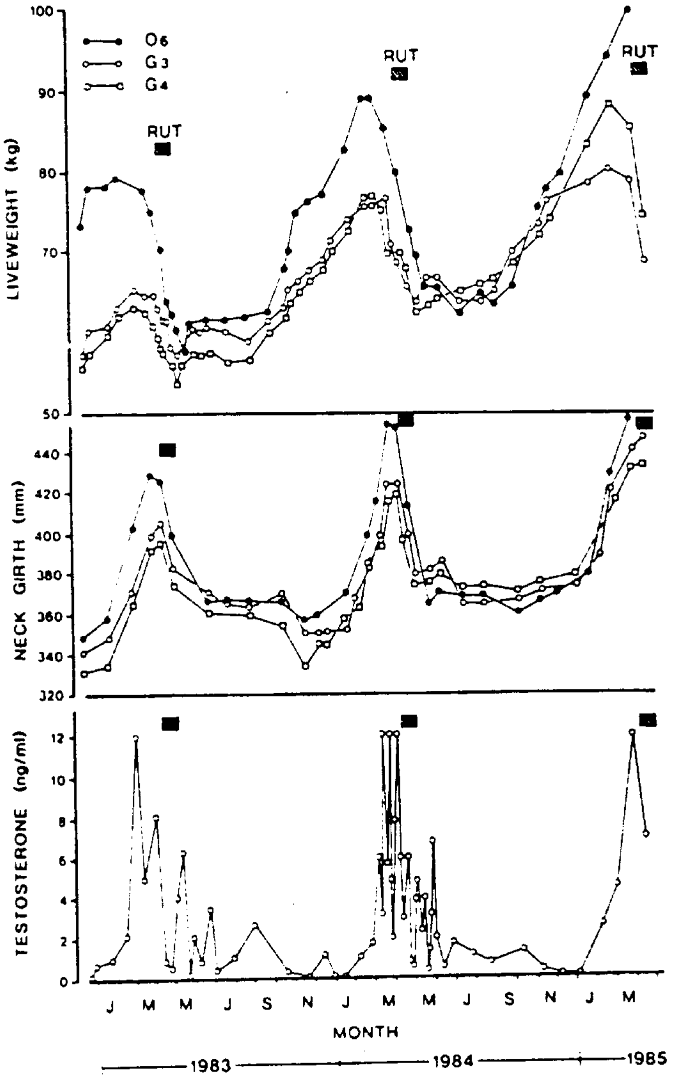

Fig. 10. Seasonal liveweight, neck girth, and serum testosterone profiles of three mature fallow bucks over a 2.5-year period (Asher, 1986).

Male reproductive physiology

Growth and reproductive cycles

Adult red deer stags and fallow deer bucks exhibit marked annual fluctuations in liveweight that reflect seasonal changes in voluntary feed intake (Kay, 1979; Suttie and Simpson, 1985; Fennessy et al., 1981) and mobile activity (Lincoln, 1971; Lincoln and Guinness, 1973; Asher et al., 1987, 1989b). The annual liveweight profile of fallow bucks (Fig. 10) is typical for a number of temperate cervid species. Rapid liveweight gains occur during spring and summer months and bucks attain their peak annual liveweight immediately prior to the rut in autumn. The increases in liveweight mostly represent increased deposition of subcutaneous and depot fat, as well as increased neck muscle mass (Asher, 1985b). However, during the rut bucks reduce feed intakes drastically and increase rutting activity. The resultant negative energy balance leads to very rapid mobilisation of fat reserves and some catabolisation of muscle, such that individual bucks may lose up to 30% of total body weight, at a rate of 450 g/day, in 3-4 weeks (Asher, 1986; Mulley, 1989). Bucks regain very little of this lost weight for the 3- to 4-month winter period after the rut, even though they reinstate normal levels of grazing activity (Asher, 1986). Bucks, therefore, overwinter in very poor body condition. 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 (Lincoln, 1971, 1985; Suttie et al., 1984) and fallow deer bucks (Asher et al., 1987, 1989b; Schnare and Fischer, 1987), and are essentially similar for the two species. In the adult fallow buck, for example, testicular development undergoes marked annual cyclic changes (Fig. 12). This is primarily controlled by marked changes in secretion of luteinizing hormone (LH) from the pituitary gland (Fig. 11). 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 (Gosch and Fischer 1989, Mulley 1989). The testes remain active throughout winter, secreting modest levels of testosterone and producing large numbers of spermatozoa (Asher et al. 1987, 1989b). 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 (Gosch and Fischer, 1989).

The antler cycle of bucks is closely linked to the testosterone cycle (Fig. 12). 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. (Fig. 12). Annual changes in testosterone secretion also have marked effects on some muscles (Lincoln, 1971; Field et al., 1985). In particular, 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 (Fig. 10). 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 (Asher et al., 1987, 1989b; Schnare and Fisher, 1987).

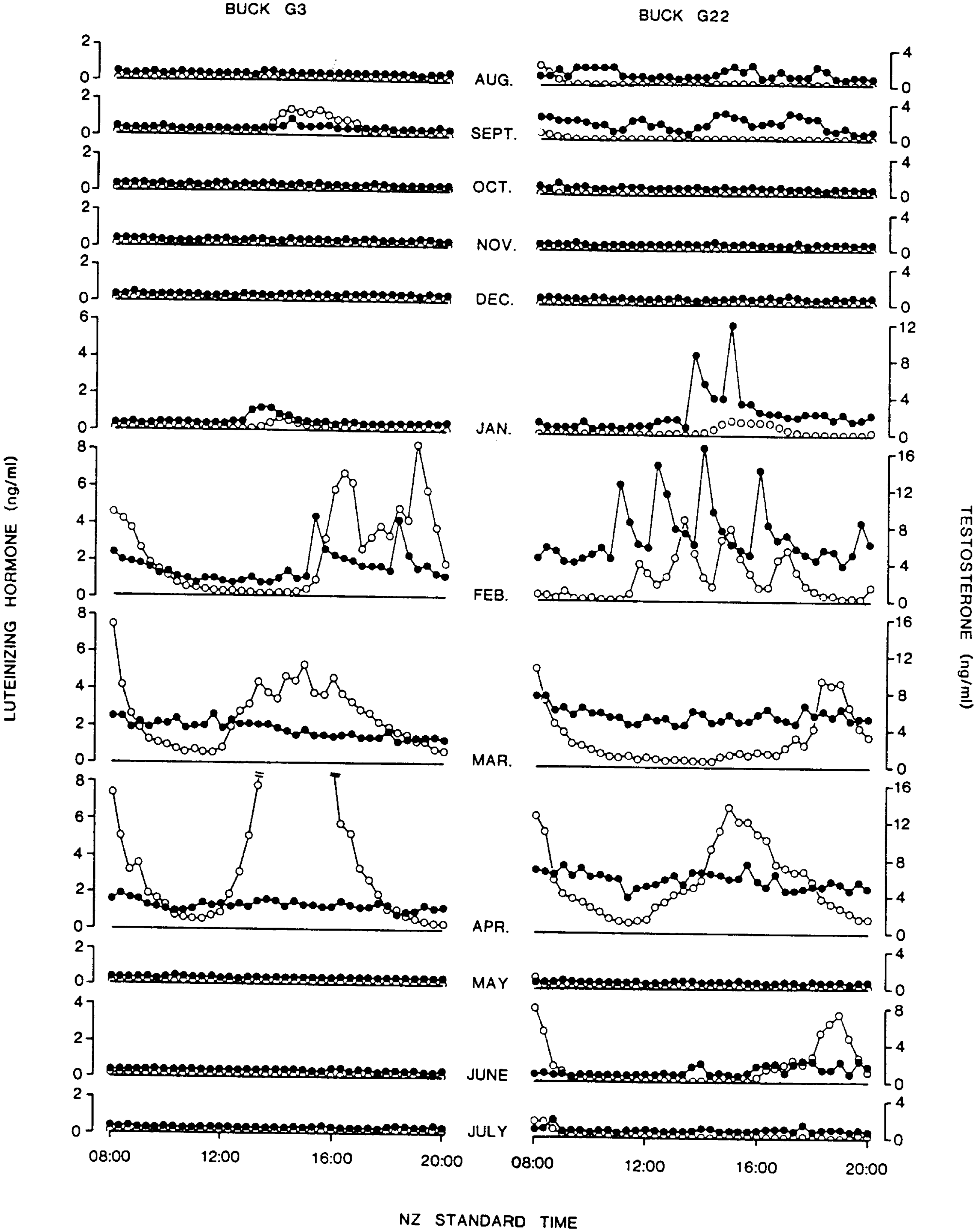

Fig. 11. Twelve-hour profiles of plasma luteinizing hormone (●) and testosterone (o) concentrations for two mature fallow bucks recorded monthly for one year (Asher et al., 1989b).

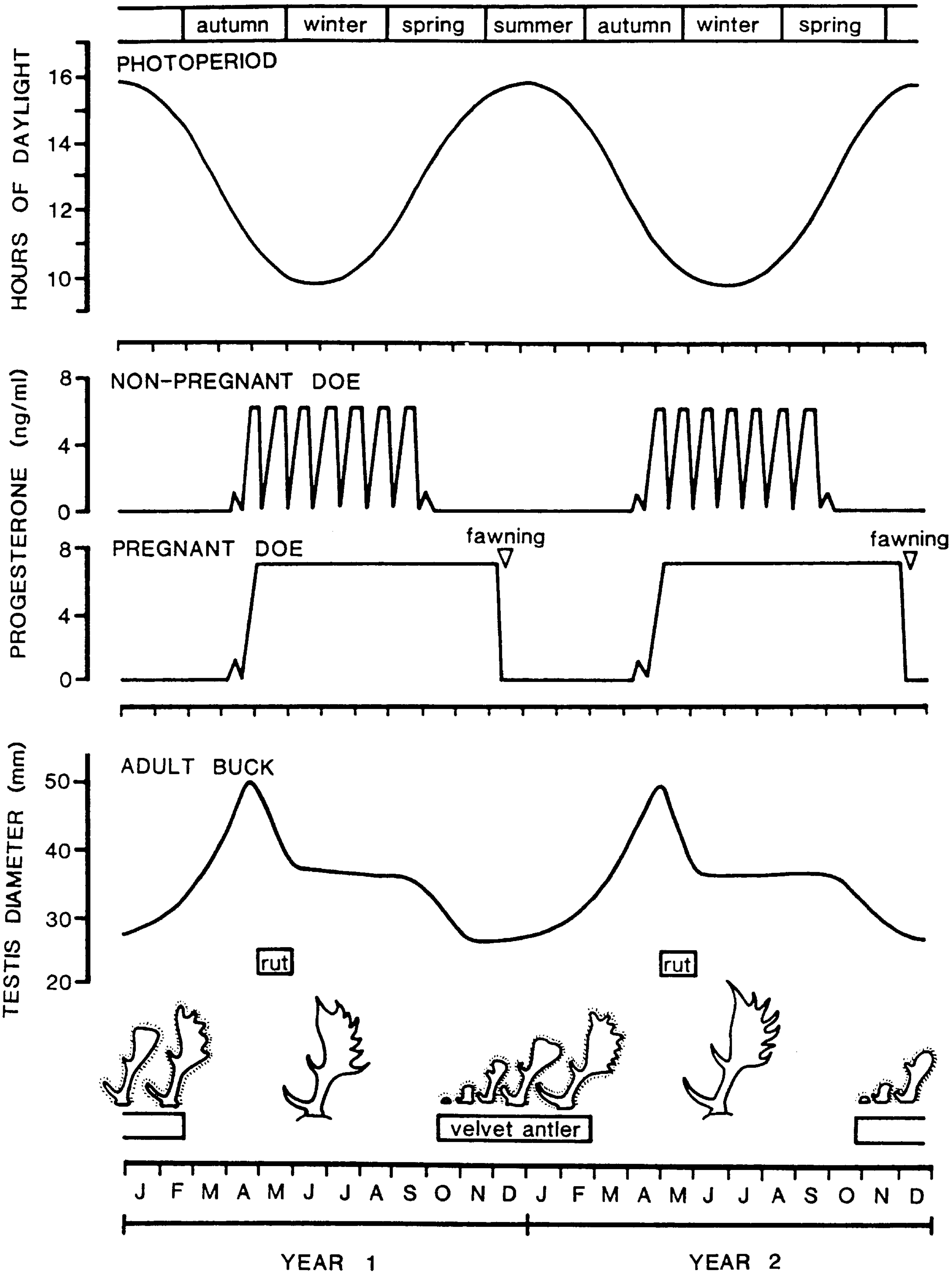

Fig. 12. Schematic summary of the annual cyclic reproductive changes that occur for fallow does and bucks in relation to photoperiod and season (southern hemisphere).

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