REPRODUCTIVE PHYSIOLOGY OF FEMALE RED DEER AND WAPITI

M.W. Fisher* and P.F. Fennessy
Invermay Agricultural Research Centre
Private Bag
Mosgiel

*Alpine Helicopters Fellow

SUMMARY

Female red deer and wapiti breed first as yearlings and high pregnancy rates can be expected provided mating weights are over about 65-70% of mature bodyweight. The onset of the breeding season is under photoperiodic control and occurs in the autumn, and is often characterised by short ovarian cycles and silent heats. An earlier breeding season can be induced with photoperiodic or hormonal stimulation. Oestrus lasts 12-24 hours and may recur at 18 and 21 day intervals in red and wapiti, respectively. Implantation of the foetus occurs by 5-6 weeks of a 231 (red) or 250 (wapiti) day gestation period. Accessory corpora lutea have been noted in some pregnant animals. Oestrus synchronisation and superovulation have been achieved using methods developed in other domestic species.

INTRODUCTION

Generally, and from the point of reproductive physiology, red deer and wapiti represent different subspecies of *Cervus elaphus* and for all practical purposes the various sika deer strains (*Cervus nippon*) can also be regarded as further subspecies. Therefore, the 'red deer' cover a very wide range in both bodyweight and geographical origin.

ANATOMY

The gross anatomy of the genital tract of the non-pregnant female red deer is shown in Fig. 1. The points to note are the small number of caruncles (6-14), the cervical rings (about 4-6), and the very small junction between the two uterine horns (approximately 1 cm in diameter).

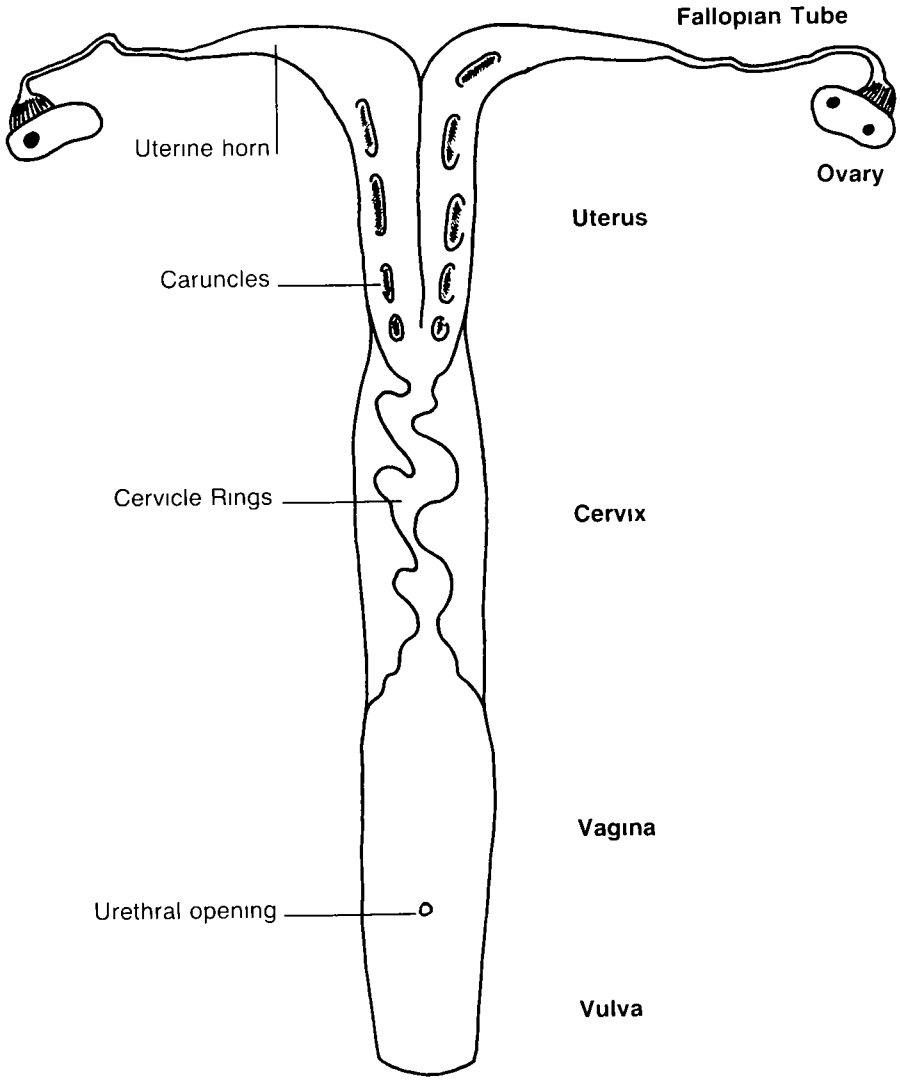

Fig. 1: Gross anatomy of the reproductive tract of a non-pregnant red hind.

CONTROL OF OVULATION

A simplified scheme of the hypothalmic-pituitary-ovarian regulation of ovulation and oestrus is shown in Fig.2. An understanding of the

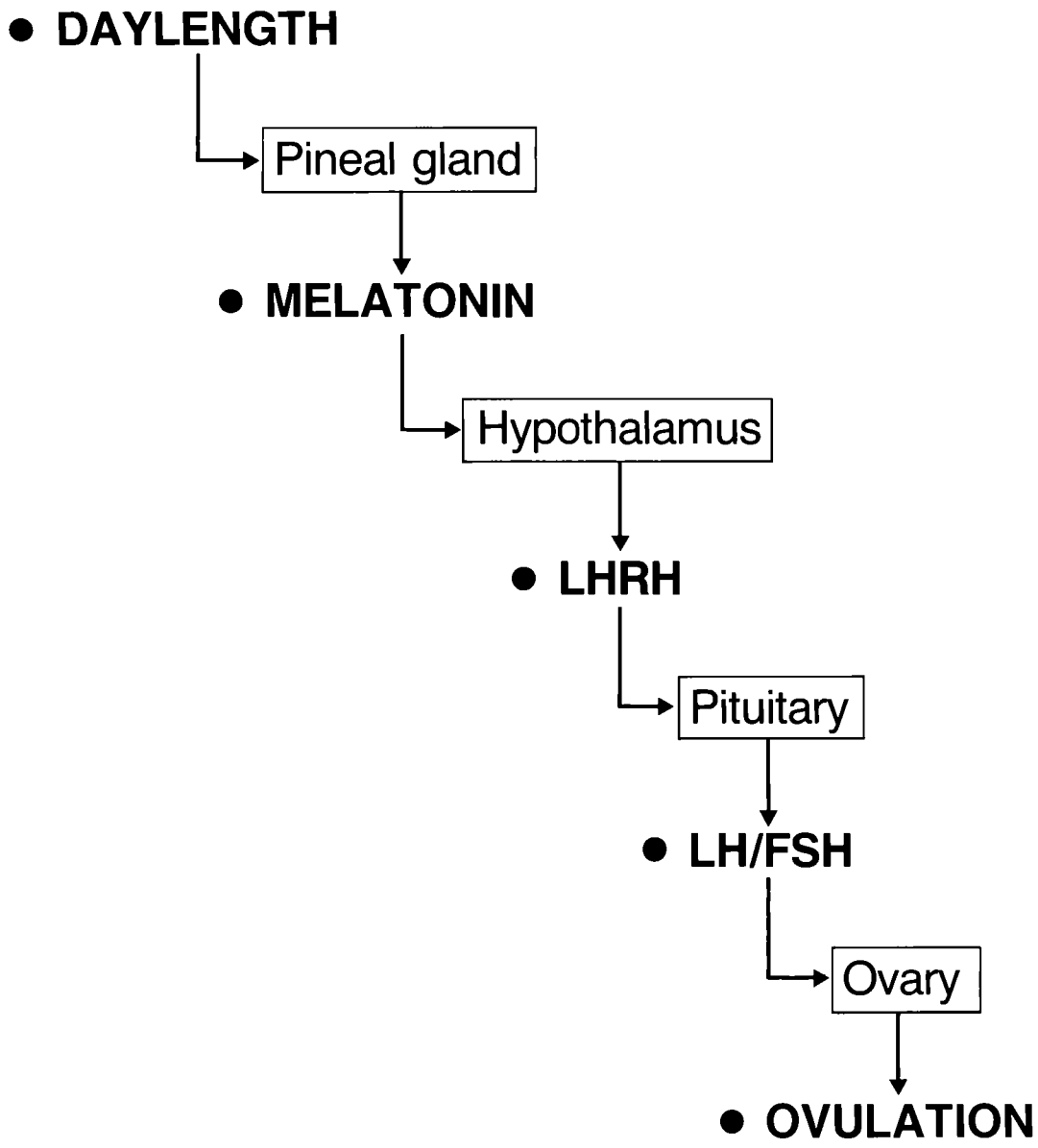

Figure 2: Simplified representation of the regulation of oestrus and ovulation in the female deer.

regulation of ovulation and oestrus indicates the possibilities for controlling reproduction in female deer. Where the aim is to advance the breeding season, induce superovulation or manipulate the oestrous cycle, the possibilities may involve:

(i) reducing daylength
(ii) treatment with melatonin
(iii) treatment with gonadotrophin releasing hormone (GnRH)
(iv) treatment with luteinising hormone (LH) or follicle stimulating hormone (FSH)

and/or

(v) treatment with progesterone.

PUBERTY AND SEASONALITY

Generally, puberty in red deer (defined as the onset of oestrus and ovulation) occurs at about 16 months of age and is related to the nutritional status of the animal as reflected in body condition and weight. For red deer at Invermay the threshold weight for attainment of puberty, ascertained from calving data, is in the range of 65-75 kg

(Table 1). Red deer may be capable of breeding in their first year i.e. around 3-5 months of age, given exceptional nutritional conditions (Daniel, 1963). Alternatively, given poor nutritional conditions reflected in low weights and poor condition at 15 months of age, puberty can be delayed until the following year. It would appear that puberty in female deer occurs at a threshold weight of about 70% of the mature body weight.

Table 1: Relationship between mating weight as yearlings and calving success in 2-year-old red hinds. % Calving.

Liveweight (kg)	Invermay[1] 1975-80 (n = 130)	Invermay[2] 1984 (n = 43)	Scotland[3] 1971-75 (n = 182)
<49			0
49-53			0
54-57			19
58-61			48
62-65	51	0	76
66-69	81	0	75
70-73	78	66	96
74-77	91	78	100
78-81	97	71	100
82-85	73	89	
>85	85	92	

[1] Kelly *et al.*, 1982b

[2] Early induction of oestrus and ovulation experiment, unpublished data

[3] Hamilton and Blaxter, 1980

Red deer and wapiti are seasonal breeders, the mating season starting in autumn (i.e. "short-day" breeders) to give calving in late spring-early summer. Seasonality has been likened to a yearly puberty, and photoperiodic changes have been implicated in the control of both events. Hinds subjected to earlier seasonal photoperiods by shortening daylength or treatment with melatonin designed to mimic photoperiodic changes, may ovulate and calve earlier in the season (Adam and Atkinson, 1984; Webster and Barrell, 1985).

In our work, Controlled Internal Drug Releasing devices (CIDR's) containing progesterone are inserted into the vagina of the hind for 12-15 days (a period of progesterone priming is required to ensure that oestrogen produced by the developing follicle induces oestrus). At the time of CIDR withdrawal the hind is treated with GnRH or pregnant mare's serum gonadotrophin (PMS) which has both LH- and FSH-like activity. The use of progesterone alone will cause ovulation and oestrus in a small proportion of hinds. Some of the Invermay work with yearling hinds is

summarised in Table 2. Similar results (resulting in calving in October) have been recorded in non-lactating adult hinds (Moore *et al.*, unpublished data).

Table 2: Induction of ovulation prior to the breeding season in yearling red hinds.[1]

Treatment			n	Hinds ovulating
Controls		1984	10	0
		1985	9	1
CIDR[2]		1984	9	1
		1985	8	2
CIDR + PMS[3] (IU)	125	1984	4	1
	250		4	2
	500		4	4
CIDR + PMS[4] (IU)	250	1985	8	7
CIDR + GnRH[5] (ng/h)	63	1984	4	1
	125		4	0
	250		4	2
	200	1985	7	4
	400		8	3
	800		7	3

1 Of 13 hinds induced to ovulate in 1984, 7 calved prior to the beginning of the normal calving season. In 1985, ovulations were induced in 19 hinds.

2 14 days treatment with CIDR containing 12% progesterone (Alex Harvey Industries, Hamilton)

3 *Pregnecol* (Commonwealth Serum Laboratories, Australia) given at CIDR withdrawal

4 *Folligon* (Intervet, Australia) given at CIDR withdrawal

5 Sigma Chemicals (U.S.A.) delivered in a 7-day osmotic minipump (Alza, U.S.A.) inserted at CIDR withdrawal.

The onset of the breeding season in hinds may also be modified by body condition in that those hinds in poorer condition often conceived later than those in good condition (Mitchell and Lincoln, 1973; Clutton-Brock *et al.*, 1982).

OESTROUS CYCLE

Red deer and wapiti are seasonally polyoestrous, with oestrus and ovulation occurring regularly in some unmated hinds for up to 3-5 months from the onset of the breeding season (Guinness *et al.*, 1971; Invermay, unpublished data).

The oestrous cycle lasts about 18 days in red deer and 21 days in wapiti (Table 3), and oestrus generally about 12-24 hours (Morrison, 1960; Clutton-Brock *et al.*, 1982).

Table 3: Duration of the oestrous cycle in *Cervus elaphus* females.

Species	Location	n	Oestrous cycle duration (days) mean	mode	range	Reference
Red	N.Z.	17	18.2			Kelly & Moore, 1977
	Scotland	12	18.3	18	14-22	Guinness *et al.*, 1971
	Poland	12	18.8			Krzywinski & Jaczewski, 1978
Wapiti	Canada	14			19-21	Glover, 1985
	U.S.A.	7	21.2		19-25	Morrison, 1960

At the beginning of the breeding season, in some animals ovarian cycles may be short, and the first ovulation may occur without oestrus, i.e. a silent heat (Morrison, 1960; Webster and Barrell, 1985).

Hormonal patterns

There have been very limited studies of hormonal patterns during the oestrous cycle in red deer. In one such study (Kelly *et al.*, 1985) when hinds were sampled daily, peak LH concentrations were recorded within a day of oestrus, with maximal oestradiol concentrations on the day prior to or the day of oestrus. A second peak of oestradiol was recorded 3-7 days after oestrus. Highest plasma progesterone levels were recorded during the luteal phase, although on the day of oestrus some hinds had very high concentrations of unknown origin or significance. Another limited study did not confirm the presence of high progesterone concentrations at oestrus (Adam and Atkinson, 1984).

Synchrony of oestrus

Several studies have implied that mating/conception within a population is highly synchronous as calving is frequently concentrated over a short time (Lincoln and Guinness, 1973; Kelly and Whateley, 1975; Clutton-Brock *et al.*, 1982), despite both the stag and hind being capable of breeding over an extended period. More recently, studies have shown that synchrony can be induced. In this work some hinds at Invermay were treated with progesterone and PMS to advance the breeding season. This had the effect of synchronising oestrus and subsequent calving date in untreated control hinds run with the progesterone-PMS treated hinds (Moore *et al.*, unpublished data). The exact mechanism is unknown but may involve either a "hind effect" (an oestrus hind may stimulate other hinds to ovulate) or a "stag effect" possibly mediated via pheromonal influences.

Accessory corpora lutea

A feature of the reproductive physiology of many species of deer, including both red deer and wapiti, is the occurrence of accessory corpora lutea (Halazon and Buechner, 1956; Kelly and Challies, 1978). The accessory corpus luteum which is present in addition to, and about half the size of, the primary corpus luteum of pregnancy, has been recorded in up to 65% of pregnant females. The accessory corpus luteum may be present prior to pregnancy and possibly represents an earlier corpus luteum which has failed to regress completely. Alternatively, it may form during pregnancy following an actual ovulation.

Synchronisation of oestrus

The oestrous cycle has been artificially synchronised in both red and wapiti females using a 14 day progesterone treatment. When progesterone-containing CIDR's were used, oestrus usually occurred 48-96 hours after CIDR withdrawal (Table 4). Intravaginal sponges containing progesterone have also been used, though their retention rate may be poorer than CIDR's (Kelly *et al.*, 1982a; T.E. Dixon, *pers.comm.*). Prostaglandin treatment has also been used to synchronise oestrus in wapiti females; Glover (1985) found that a prostaglandin $F2\alpha$ analogue was luteolytic when administered 11 or more days after ovulation. Treatment prior to day 9 post-ovulation usually resulted in a transient decline in serum progesterone concentrations which recovered rapidly to luteal phase levels, suggesting that the early corpus luteum is refractory to prostaglandin-induced luteolysis. This would necessitate a double prostaglandin treatment with injections given 10 days apart, to induce oestrus in all hinds in a herd.

Table 4: Occurrence of oestrus[1] following progesterone[2] withdrawal in mixed age red hinds.

Hours following progesterone withdrawal		0-24	24-48	48-72	72-96	96-120	Not detected
	n						
Untreated	63	0	15	20	10	4	14
%	100	0	24	32	16	6	22
Treated[3]	54	11	15	9	3	1	15
%	100	20	28	17	6	2	27
Total	117	11	30	29	13	5	29
%	100	9	26	25	11	4	25

[1] Oestrus was detected by using a greased stag and checking daily for mating marks.

[2] CIDR (Alex Harvey Industries, Hamilton).

[3] Includes hinds treated with PMS, FSH and GnRH as part of superovulation and early induction of oestrus experiments.

Stress and ovulation

Much has been written concerning the influence of stress on reproduction in many species (see Dunbar, 1985). In red hinds, we observed the apparent effects of stress in a recent experiment where a group of hinds was brought onto Invermay in March. The hinds were synchronised and ovulation recorded by laparoscopy at about day 7 after the expected oestrus. Of the 50 hinds, only 25 had ovulated compared with 64 of a group of 67 Invermay hinds. The low incidence of ovulation may have been due to a number of factors including transportation, changes in nutrition, yarding and handling or the new environment imposed.

Superovulation

Both PMS and FSH have been used to induce superovulation in synchronised hinds. The results of Invermay studies are summarised in Table 5. Although some very high ovulation rates have been recorded, fertilisation rates and embryo recovery rates at surgery have been variable. In 1984, all 12 out of a total of 12 expected embryos were recovered from 6 hinds and of these 11 were fertilised. However, in 1985 26 of a possible 61 embryos were recovered from 5 hinds, of which 9 were assessed as viable on microscopic examination.

Table 5: The ovulatory responses of adult red deer to PMS and FSH. Treatments were administered at or around CIDR[1] withdrawal or several days prior to the day of expected oestrus.

Treatment		Year	n	Number ovulated	Range of ovulations	Number with >1 ovulation
Controls		1984	4	4	1	0
		1985	10	10	1	0
PMS (IU)	*Pregnecol*[2] 500	1984	4	2	0-1	0
	1000		10	9	0-5	7
	1500		3	3	1-2	1
	Folligon[3] 400	1985	5	4	0-3	2
	800		8	8	1-4	3
	1600		5	5	1-3	2
FSH[3] (mg)	Single injection	1984				
	15		4	4	1	0
	30		4	2	0-1	0
	60		4	3	0-2	1
2 x daily injection over 4 days		1985				
	4		4	4	1	0
	8		3	3	1	0
	15		8	8	1-28	6
	30		5	4	0-10	3
	60		5	5	1-5	2

[1] Alex Harvey Industries, Hamilton

[2] Commonwealth Serum Laboratories, Australia. In 1984, PMS treatment resulted in the birth of one set of viable twins.

[3] Intervet, Australia

PREGNANCY

Gestation is about 233 days in the red hind and may be up to 30 days longer in the wapiti (Table 6).

Table 6: Length of gestation in *Cervus elaphus* females.

Species	Location	n	Length of gestation (days) Mean	Range	Reference
Red	N.Z.	38	233		Kelly & Moore, 1977
	Scotland	13	231	226-238	Guinness *et al.*, 1971
Wapiti	U.S.A.			249-262	Asdell, 1964

The actual source of progesterone throughout pregnancy has not been ascertained although in the wapiti the corpus luteum appeared to be the main source, at least until 180 days (Greer *et al.*, 1968).

Deer have an epitheliochorial placenta with about 6-14 placentomes. Even though the single foetus is located in only one horn the placenta extends through both sides of the uterus. Implantation is apparently complete by 6 weeks post-conception (Morrison *et al.*, 1959; Thome, 1980). Of the four foetal membranes (amnion, chorion, yolk sac and allantois) the yolk sac, usually only transitory in ruminants, has apparently disappeared by this stage (Morrison *et al.*, 1959).

LACTATION

Milk production in the hind reaches an early peak and in red hinds daily milk yield may exceed 2 kilograms. Lactations of up to 9 months have also been recorded (Arman *et al.*, 1974; Loudon *et al.*, 1983). It is also worth noting that red deer milk is a relatively high energy feed, containing about 22% solids of which about 40% is fat, 33% protein and 22% lactose giving an energy value of about 27 MJ gross energy/kg DM.

In many species, including deer, lactation may have a depressive effect on reproductive efficiency. Under conditions of poor nutrition, such as on the Scottish Isles, lactating hinds either do not get pregnant or alternatively get pregnant late in the season (Clutton-Brock *et al.*, 1982). No such effects have been reported for farmed red deer in Scotland (Hamilton and Blaxter, 1980) or New Zealand. However, there is some aprocryphal evidence that lower calving percentages were experienced on some Canterbury farms following a recent drought when weaning occurred post-rut.

Removing calves from farmed hinds immediately prior to joining with the stag had no effect on subsequent fertility (Hamilton and Blaxter, 1980), but in hinds mated at different times of the year, calf removal markedly

reduced the calving to first oestrus interval (Guinness *et al.*, 1971). Certainly when feed supplies are short it would seem advisable to wean pre-rut and allow the hinds some time to recover body condition prior to mating.

Lactation may also affect the induction of oestrus and ovulation. Melatonin treatment was unable to induce early oestrus and ovulation in the lactating hind (Nowak *et al.*, 1983) unlike the situation in the non-lactating hind. However, PMS or GnRH administration following progesterone treatment did induce ovulation in lactating hinds (Adam, 1983) and our work at Invermay is summarised in Table 7.

Table 7: Induction of ovulation prior to the breeding season in lactating 3-year-old red hinds.

Treatment	n	Number ovulated
CIDR[1]	6	0
CIDR + 300 IU PMS[2]	7	6
CIDR + 500 ng/h GnRH[3]	6	3

[1] 14 days treatment with CIDR containing 9% progesterone (Alex Harvey Industries, Hamilton).

[2] *Folligon* (Intervet, Australia) given at CIDR withdrawal.

[3] Sigma Chemicals (U.S.A.) delivered in a 7-day osmotic minipump (Alza, U.S.A.) implanted at CIDR withdrawal.

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