Reproductive physiology of deer in relation to management : implications of current research
G.W. Asher and M.W. Fisher

Abstract

This paper provides an update of some present and intended research into deer reproduction, placing the research in context with improving practical management and/or development of more effective reproductive technologies. While the topics discussed appear somewhat disjointed from each other, their central theme is reproductive productivity, and they are generally subset studies of larger programmes on seasonality, ovarian control, stress physiology and breeding management.

Introduction

There have been a number of reviews of deer reproductive physiology and artificial breeding technologies at previous Deer Branch NZVA conferences (Asher 1985, Asher *et al.*, 1990, 1991, 1994a, 1994b, Hunter 1997). It is not our intention to simply repeat and extend these reviews. Rather, we propose to focus on a few current research topics that have implications for farmed deer management. For example, studies on genetic influences on reproductive seasonality, ultrasonographic monitoring of ovarian function, nutrition of the pregnant hind, adrenal gland influences on reproduction and calving behaviour of hinds, all open up a range of possibilities for improving, in some way, reproductive management and for improving techniques of artificial breeding.

Genetic influences on seasonal breeding

Few aspects of cervid physiology have greater impact on overall management than their highly seasonal patterns of growth, feed utilisation and reproduction. The relative inflexibility of these photoperiod-mediated rhythms places a number of constraints on on-farm productivity within the New Zealand pastoral environment. In particular, autumn mating/summer calving patterns inherent in red deer/wapiti (*Cervus elaphus* spp) and fallow deer (*Dama dama* spp) often lead to misalignments between the high energy demands of lactation over summer and peak pasture production/quality occurring normally in spring.

There is considerable incentive for at least a proportion of deer farmers to create improved synchrony between animal and pasture production. Options include: (1) shifting the seasonal peak of pasture growth by utilising different pasture cultivars, applying chemical treatments, or judiciously using other animal species to harvest early pasture surpluses in order to prevent reproductive senescence of grasses, (2) selecting deer genotypes with genetic propensity to calve earlier (Fennessy, 1993); and (3) artificially manipulating the reproductive seasonality of the breeding herd (see Asher *et al*, 1993).

The first series of options are, in various guises, used frequently by deer farmers, but are outside the scope of this review. Genetic selection of deer for improved alignment with regional pasture production patterns holds long-term promise, but there are some difficulties associated with selection of appropriate animals. For example, while population variation for seasonality traits may exist, it is often not expressed due to biological or management constraints. This may be the case for females that initiate early ovulatory activity, but fail to conceive early in their breeding season due to sexually inactive males or late joining practices. As calving date is often the only obvious indicator of the female's reproductive seasonality, essential information on within-herd variance is unavailable for selection practice. In contrast, male deer exhibit obvious signs of their reproductive seasonality in the form of antlers and behaviour. It may be possible, therefore, to select sires on the basis of measurable asynchrony of such traits (e.g. antler velvet stripping) within the herd (Fennessy, 1993). Indeed, individual red deer stags that deviate markedly from the herd (i.e. by up to 2 months) in antler growth and rutting behaviour have been observed occasionally in New Zealand (G.W. Asher, personal communication, 1985). However, such outliers have yet to be progeny-tested for genetic correlates in reproductive seasonality. Red deer of eastern European origin (e.g. Hungary) can exhibit more advanced calving patterns than is usual in NZ red deer (descended from deer of mainly English and Scottish origin) under New Zealand farmed conditions (N. Beatson, personal communication, 1996), indicating pronounced genotype differences within a species.

A practical approach to selecting deer for early breeding characteristics would involve screening of the national red deer population (Fennessy, 1993). The aim would be to identify outlier animals and then to evaluate them to ascertain whether the observed variation had a genetic basis (e.g. alternative causes of abnormal seasonality could include pituitary tumours). One approach to selection for early breeding could involve running yearling hinds with a melatonin-treated (i.e. seasonally advanced) stag and then identifying those which have become pregnant prior to the normal breeding season. Alternatively, screening of stags is a possibility. This makes the highly tenable assumption that since the onset of the breeding season is a daylength-entrained phenomenon in both sexes, the trait is highly correlated (in a genetic sense) in both sexes. Thus, the essential hypothesis is that the basis of any genetic variation is an altered response to photoperiod. In stags, selection for those which clean their antlers of velvet early (reflecting an early rise in the levels of circulating testosterone) would offer the most scope. However, this is difficult in practice, and it may be necessary to use other approaches such as selecting stags which cast their old antlers earlier in the spring, since this reflects an earlier decline in levels of circulating testosterone.

There is considerable scope for hybridisation between cervid taxa, with some genetically compatible species exhibiting different patterns of reproductive seasonality. Thus, it may be possible to create synthetic breeds, whose reproductive repertoire more closely matches the pattern of pasture production in a agricultural environment, by selecting in certain directions from amongst the F_2 or backcross population. Three notable examples that have been investigated over the last 2-3 years are: (1) Red deer x Père David's deer (*Elaphurus davidianus*), (2) Red deer x North American wapiti, and (3) Fallow deer x Mesopotamian fallow deer. In the case of the former hybrid, the parental species exhibit a 2-3 month difference in reproductive patterns (Loudon *et al*, 1989). Summer rutting patterns that characterise the Père David's (PD) deer have strongly influenced early rutting (relative to red deer) behaviour of F_1 hybrid males (G.W. Asher, unpublished results). However, ¼ PD/¾ red

deer (ie. maternal backcross with red deer) females fail to express a significantly earlier onset of first oestrus/ovulation of the breeding season when compared to red deer (Table 1). Studies are underway to compare F₁ female hybrids with pure red deer, although anecdotal information suggests that these animals may also not differ significantly from red deer. This result would be very surprising given the intermediate seasonality of male hybrids.

Interestingly, F₁ wapiti x red deer hybrid females were shown to initiate oestrous/luteal cyclicity significantly earlier (~ 9 days) than red deer (Table 1). This has been suspected for some time (A.J. Pearse; personal communication) but has been largely masked by the similarity in calving dates due to a significantly longer gestation of the wapiti-type animal.

Table 1 : Mean parameters of reproductive seasonality of non-pregnant female red deer, F₁ wapiti x red deer and maternal backcross PD x red deer hybrids run continuously with vasectomised red deer stags in 1995 (Asher et al., 1998)

Genotype	Day of first oestrus (date)	Number of full oestrus/luteal cycles	Day of last oestrus (date)	Duration, in days, of breeding season
Red (n=9)	101 7 (12 April)	7 7	231 2 (19 August)	129 6
Wapiti hybrids (n=6)	93 2 (3 April)	8 3	236 3 (24 August)	143 2
PD hybrids (n=9)	97 4 (7 April)	7 9	229 9 (18 August)	132 4
SED¹	2 8	0 5	7 8	8 6
SED²	2 5	0 4	6 9	7 7
Genotype effect	*	NS	NS	*

¹ For contrasts between (1) red deer and wapiti hybrid, (2) wapiti hybrid and PD deer hybrid
² For contrasts between red deer and PD hybrid; * P,0.05; NS non significant

Attempted hybridisation of red deer with aseasonal species of *Cervus*, with the aim of influencing seasonality of a synthetic "red deer" breed, holds some small promise. However, marked karyotypic and physiological differences between species have hindered progress in obtaining viable hybrids. For example, attempts to obtain F₁ hybrids between red deer (2n=68) and sambar deer (*Cervus unicolor*; 2n=56) have yielded only one live hybrid female (2n=62) from 400 AI attempts (Muir et al, 1997). Furthermore, the fertility of this hybrid has yet to be assessed. The same considerations apply to the production of red deer x rusa deer (*Cervus timorensis*; 2n=60) hybrid in Australia (P.F. Fennessy, personal communication).

Recent hybridisation of European fallow deer with the very rare Mesopotamian fallow subspecies has yielded a very large number of F₁ hybrids (>2000 individuals) and an even greater number of backcross individuals. While such hybridisation was aimed primarily at increasing growth rates, recent studies have demonstrated a 2-3 week advancement in reproductive seasonality of F1 hybrids relative to European fallow deer (Asher et al., 1996).

Within-breed or cross-breed selection for altered seasonality does hold some promise. However, even with hybridisation to increase genetic variability, progress towards a desired

goal is likely to be slow and will require considerable dedication by the breeder. The hybridisation approach may additionally be hindered by reduced fertility in the hybrid, particularly when parental "species" are widely separated genetically. Subspecies hybridisation (eg. red/wapiti; European x Mesopotamian fallow) is generally not subjected to major reductions in fertility.

Ovarian follicular dynamics

Strategic control of ovarian function is a key feature of all artificial breeding technologies including AI, ET and in vitro embryo production (IVP). While it is true to say that most of these technologies, adapted from those developed for more traditional livestock species, are applied successfully in red deer and fallow deer (Asher *et al.*, 1993), there is little doubting that there is room for improvement. In particular, oestrous synchronisation in red deer is an area of concern. Present techniques using intravaginal CIDR devices (with or without PMSG) within the breeding season are associated with a spread of oestrus onset of > 30 hours (ie. 95% of treated hinds initiate oestrous behaviour between 32 and 62 hours from device removal/PMSG injection (G.W. Asher unpublished results from Ruakura and Invermay). If this reflects the range of times to ovulation (see Asher *et al.*, 1992) then, clearly, a significant proportion of conception failures to fixed-time AI represents mistimed insemination relative to timing of oocyte presence in the oviduct. While it can be argued that modification of the CIDR device to better suit the morphology and physiology of red deer would enhance oestrous synchrony, in reality we know very little about cervid ovarian function in relation to the oestrous/ovulatory cycle. A better understanding would facilitate improvements in treatment protocols.

Within the last decade, real-time ultrasonography has been used to track ovarian follicular development in the mare, ewe and cow. From these studies has emerged clear temporal profiles of "wave-like" patterns of follicle recruitment, growth and atresia/ovulation. In monovulatory cattle, in particular, these "waves" are associated with strong "dominance" effects by a single large follicle that effectively limits development of all other follicles for a defined period of time. In the bovine oestrous cycle, at least 2 or 3 dominant follicle "waves" occur, with the last one attaining ovulatory status. These waves, in effect, control the age of the ovulatory follicle by the time luteolysis occurs, ensuring a healthy oocyte is released at time of ovulation.

Exogenous progestagens (eg. CIDR devices), although acting as artificial corpora lutea, often lead to perturbation of follicular waves and inappropriately aged oocytes at ovulation. Recent developments in oestrous synchronisation in cattle include ablation/removal of the existing dominant follicle (eg. with oestradiol) at a key time relative to progestagen withdrawal in order to ensure a new, healthy dominant follicle will achieve ovulatory status.

Recently we have monitored follicular patterns in the ovaries of red deer and fallow deer (Figure 1). Either transvaginal imaging of intact ovaries surgically aligned to the vaginal wall (red deer : Asher *et al*, 1997) or transrectal imaging of unmodified tracts (fallow deer ; G.W. Asher, unpublished results) provided repeatable visualisation of ovarian follicles ≥ 3 mm diameter. Scanning daily or every second day during the oestrous cycle revealed a dominant follicle wave pattern similar to that seen in cattle (Figure 1).

The number and longevity of follicular waves was more consistent for fallow deer than red deer. This may reflect some artefacts of surgical relocation of ovaries in the latter species. although it should be noted that fallow deer generally exhibit more consistency (ie. less variation) in most reproductive parameters.

Future studies will likely focus on ways to control the lifespan of dominant follicles in deer. thus providing means of recruiting new ovulatory follicles just prior to progestagen withdrawal. Initial studies of the use of oestradiol injection did not show on improvement in synchrony and, if anything. resulted in reduced fertility. Observations that some treated hinds exhibited oestrus soon after injection, while CIDR devices were still in place. indicate an acute sensitivity of deer to oestradiol and highlight the need to investigate other avenues (eg. prostaglandins, GnRH, etc.).
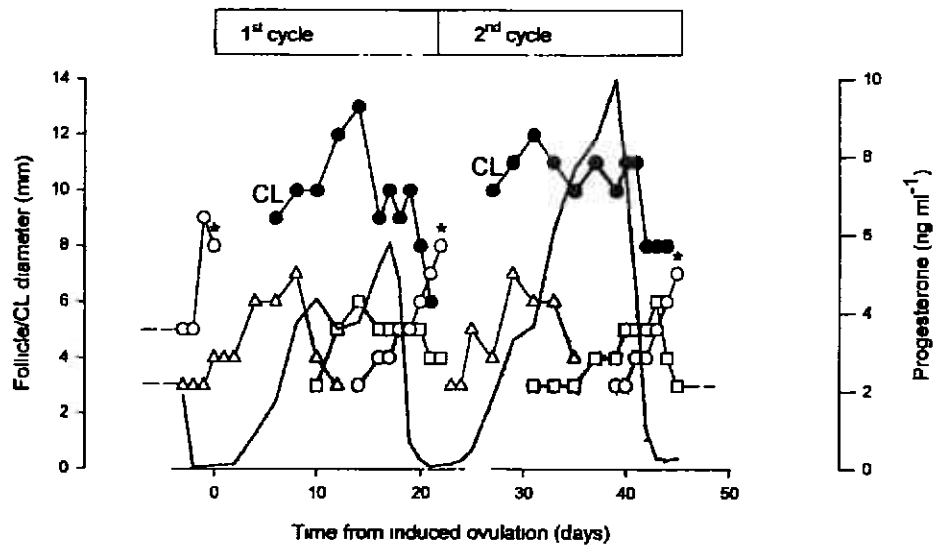

Figure 1 : Profile of the diameters of dominant follicles (O| |□△) and corpora lutea (●) plotted relative to concentrations of plasma progesterone (shaded profiles) during two consecutive oestrous cycles of a fallow deer doe

Nutrition of the pregnant hind

Some differences of opinion exists within the deer farming industry as to the appropriate level of nutrition offered to pregnant hinds ; particularly during the last 3-4 months of gestation. One school of thought. focused largely on preventing calving problems (dystocia), aims to restrict feed intake over spring/early summer in order to reduce overall hind fatness and, perhaps, prevent excessive calf birthweights. On the other end of the scale. the other school aims to feed hinds to appetite, perhaps so as to not compromise fetal development. Although these are extreme ends of a continuous scale. they do highlight a paucity of knowledge on the

interaction between nutrition and reproduction. Earlier studies on fallow deer in Australia (R. Mulley : unpublished data) showed that undernutrition of does severely compromised fetal development, leading to a high incidence of non-viable (underweight) neonates, a feature that was reasonably common on some fallow deer farms in New Zealand (Asher and Adam 1985). However, less is known about the influence of nutrition in pregnancy and subsequent neonate viability in the red deer species. Anecdotal information suggests that restrictive feeding of red deer hinds reduces the incidence of dystocia but may increase the incidence of calf non-viability.

We have initiated a trial at Invermay that aims to determine the influence of level of nutrition to hinds within the last 3-4 months of pregnancy on dam body composition (as determined by computer-assisted tomography or CAI Scan), fetal development (CATScan), mammary development (palpation scoring), parturient and maternal behaviour and calf growth, hopefully, this will go some way toward improving management regimens during pregnancy.

Adrenal gland influences on reproductive

Intensification of the farming of red deer in New Zealand has progressed rapidly since its inception in the 1970s. While most of the present farmed stock have been born and raised in the pastoral environment, only 2-3 generations separate them from their wild, forest-dwelling progenitors. The farm environment clearly differs in many aspects from the free-ranging habitat of wild red deer, and the consequences of established pastoral management practices on the well-being of farmed red deer are the focus of considerable attention. In particular, when compared with traditional domestic ruminants such as sheep and cattle, red deer are generally more reactionary to adverse stimuli and have complex social structures (particularly during mating and calving). Therefore, their welfare is often perceived to be comprised by stressful conditions. However, little is understood about the impact of stressors on red deer performance. For example, it is a commonly held belief that "severely stressed" red deer exhibit poor reproductive performance, perhaps best exemplified by low calving percentages of newly captured wild stock (Yerex and Spiers 1987). However, links between stress and reproduction have generally been derived by conjecture rather than having been demonstrated conclusively.

Fundamental to the understanding of the interaction between stress and reproductive performance is a detailed knowledge of adrenal function and the impact of acute and chronic adrenal stimulation on other endocrine systems. One unique feature of the cervid adrenal gland is its ability to secrete high concentrations of progesterone under acute stimulation, as demonstrated for white-tailed deer *(Odocoileus virginianus*; Plotka *et al.* 1983), fallow deer (Asher *et al.* 1989) and red deer (Jopson *et al.* 1990). Acute ACTH challenge and high levels of duress will elicit plasma peaks in progesterone equivalent to, or greater than, those observed during the luteal phase of the oestrous cycle. As progesterone is a potent modifier of hypothalamic and pituitary function, it is possible that stress-induced adrenal secretion of this hormone, as well as that of cortisol, could influence reproductive function.

In a recent study, we investigated the effects of either single ACTH injection (125 μg tetracosactrin) or multiple injection (125 μg every 30 min. for 4 hours) to ovariectomised red deer hinds (ie. hinds with elevate LH secretion) on peripherally circulating concentrations of progesterone, cortisol and LH (Figure 2).
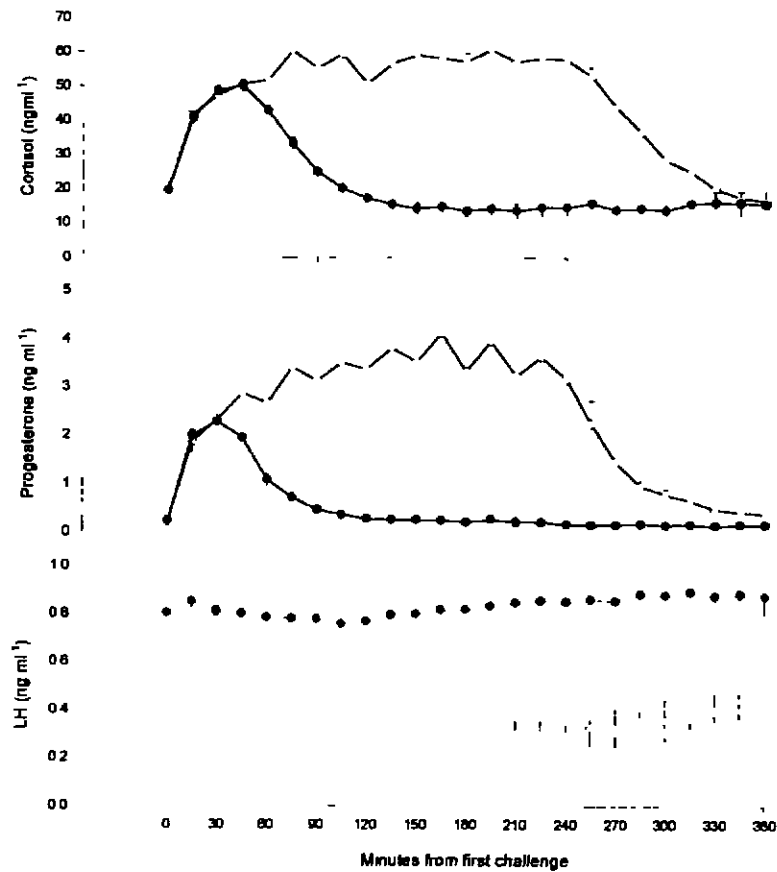

Figure 2 : Profiles of adjusted mean (+ sem) concentrations of plasma cortisol, progesterone and LH for single (●) and multiple (O) ACTH challenge hinds (n=12-16 per treatment). The treatment means, synchronised around first challenge, are adjusted to a constant (horizontal line) which is the mean of pre-challenge and control hind (n=10) data.

Single challenge regimens elicited transient elevations (ie. 60-90 minutes) of cortisol (2-2.5 times basal) and progesterone (10 times basal), but had little impact of pituitary LH secretion. By contrast, multiple challenge regimens not only sustained cortisol and progesterone secretory output for the 4-hour challenge period, they also resulted in a significant depression in pituitary LH secretion.

This study confirms a possible link between chronic adrenal stimulation and perturbation of pituitary LH secretion in red deer, arguably as a consequence of adrenal progesterone and cortisol secretion. The precise nature of the mechanisms involved have yet to be elucidated, as other hormonal pathways may also be implicated (eg. direct action of ACTH on pituitary function). The question remains as to the overall impact of adrenal stimulation/stress on reproductive function. In reality, the model of multiple ACTH challenge over a 4-hour period may have little overall consequence on reproductive function, except perhaps at critical discrete events (eg. initiation of the preovulatory LH surge), and is still essentially an "acute" stimulation model. The consequences of truly "chronic" stimulation (measured in days rather than hours) of adrenal function have yet to be evaluated but are the focus of some on-going research. Intuitively, such long-term infusion of ACTH might be expected to lead to equally long-term reductions in LH secretion leading to reproductive perturbation. However, this hypothesis ignores the animals potential ability to habituate (ie. become refractory) to continual challenge/stress ..... a fertile area of research [sic].

Calving behaviour in the pastoral environment

While red deer appear to have, generally, habituated well to the New Zealand pastoral environment, it is important to recognise that their behavioural repertoire has evolved for life on the forest fringe. It is not surprising, therefore, that certain components of the farmed environment compromise their ability to express certain types of behaviour. The most notable example is the natural propensity of hinds to seek isolation and seclusion for the birthing process (Clutton-Brock & Guinness, 1975). Close confinement of herds in small paddocks devoid of any forest cover is probably the most common calving environment offered on deer farms.

The consequences of inhibiting full expression of natural calving behaviours may include disruption of dam : calf bonding leading to calf desertion, cross-fostering and pirating. This is perhaps most noticeable in herds with highly synchronised calving patterns. Evidence that perturbation of the bonding process does occur on New Zealand deer farms was presented by Fisher *et al.* (1997). Biochemical testing of over 1000 farmed pedigrees showed significant (19 %) hind-calf mismatching, a component of which undoubtedly involves hinds raising calves other than their own. In contrast, similar tests on wild or natural populations in the UK did not detect mismatching.

The motivation for isolation is thought to be reflected in the presence of fence pacing in the days leading up to parturition. Generally, two sorts of fence pacing can be seen (Cowie *et al*, 1985). The first is characterised by relatively mild periods of walking and can begin up to 7-10 days prior to calving. The second, beginning up to 1-2 days before calving, is more intense with the hind determinedly pacing, often galloping and sometimes appearing slightly stressed. In an earlier experiment (Endicott-Davies *et al*, 1996) all hinds were observed fence pacing on the day prior to birth (Figure 3).
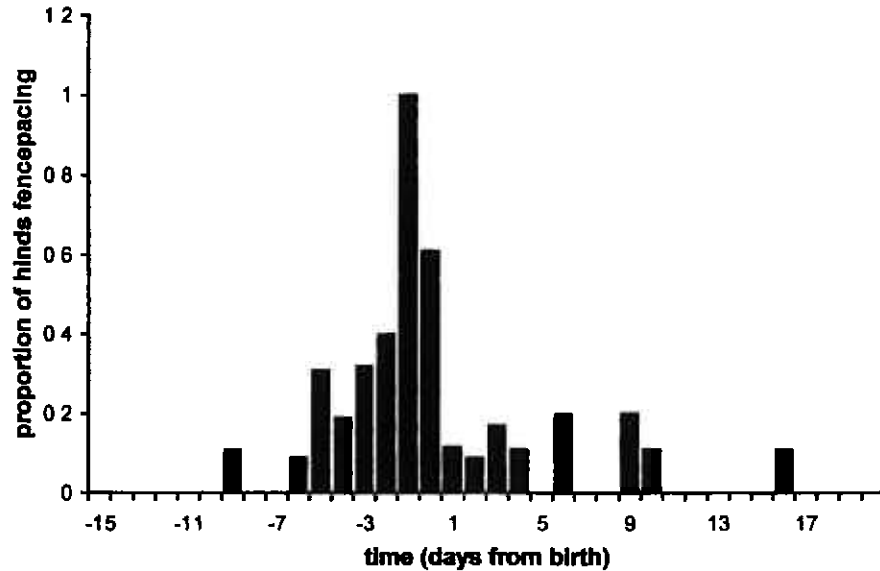
Figure 3 : Incidence of fence pacing amongst red deer hinds during the periparturient period (M.W. Fisher, unpublished data).

Interestingly, fence pacing has also been described in sheep from wild populations held in enclosures during lambing time (Shackelton and Haywood, 1985). If regarded as a stereotypic behaviour, it could be indicative of poor welfare (Broom and Johnston, 1993).

Studies performed at Invermay during the latest calving season (1997/98) investigated the effects of paddock size on the incidence of various behaviours and the relative spatial positioning of hinds. Groups of 12 hinds of known calving date (± 5 days) were set-stocked over the calving period in either a small paddock (1.8 ha : "Tower paddock") or a large paddock (4.2 ha : "Thistle paddock") situation. There were significant effects of paddock size on the incidence of fence pacing, with considerably less fence pacing occurring in the larger paddock. Grazing and resting behaviours were affected by fence pacing activity, with the "Tower" group exhibiting a greater decline in these activities around the calving period. Spatial separation of hinds was clearly greater over the calving period for the "Thistle" group. In reality, the "Tower" group showed less variation in separation as all hinds tended to utilise the maximum distances (~ 190 metres) available to them, whereas the "Thistle" group were generally able to achieve a desired separation within the large paddock confines (eg. within 340 metres).
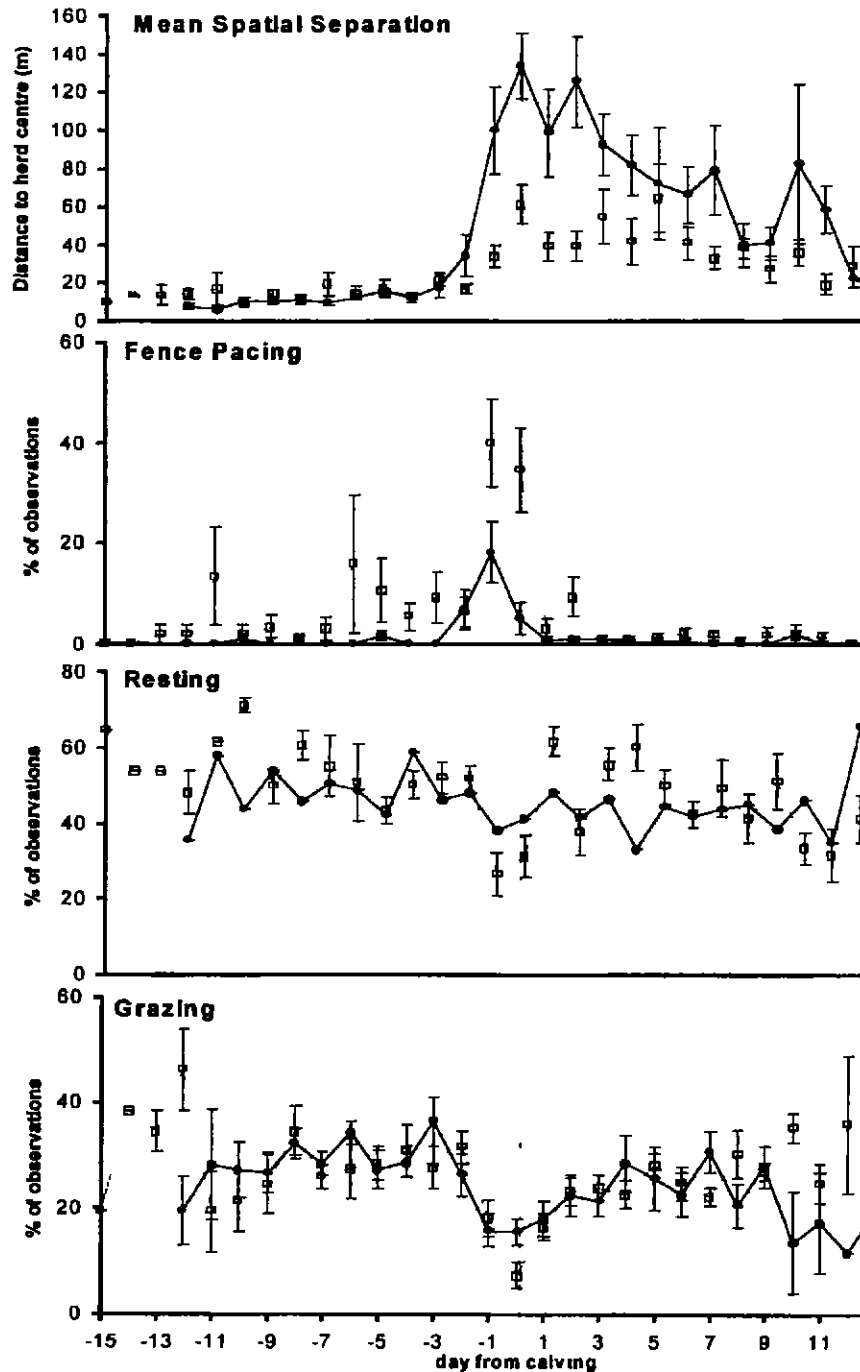
Figure 4. Behaviours (means ± 1) around the calving date in red deer hinds for large (●) and small (I) paddock situations

While there were no marked effects of paddock size on calf mortality, it is important to remember the high level of habituation of Invermay hinds. Despite such habituation to intensive farming practices, major behavioural difference in response to paddock size were observed. Populations of deer less habituated to high levels of confinement during calving may well exhibit greater levels of perturbation of normal calving behaviour.

This research highlights that more consideration should be given to designing calving environments that promote improved dam:calf bonding. This will likely have the overall impact of reducing perinatal calf mortality. Consideration of the impact of human activity at and around calving is also planned as part of our ongoing research in this area.

References

Asher, G W. (1985). Deer Branch NZVA Course Proceedings No 2 107-125.

Asher, G.W and Adam, J L (1985). Biology of Deer Production ; Royal Society Bulletin No 22 ; 217-224.

Asher., G.W. *et al* (1989). J. Reprod. Fert. 85 , 667-675

Asher., G.W. *et al.* (1990). Deer Branch NZVA Course Proceedings No. 7 ; 93-115.

Asher , G.W et al (1991). Deer Branch NZVA Course Proceedings No. 8 ; 275-306.

Asher., G.W et al (1992 J. Reprod. Fert. 96 ; 261-273

Asher., G.W. et al. (1993a). Anim. Reprod. Sci. 33 ; 241-265.

Asher., G.W et al (1993b). Anim. Reprod. Sci. 33 , 267-287.

Asher., G.W. et al. (1994a). Deer Branch NZVA Course Proceedings No. 11 ; 294-317.

Asher., G.W. et al. (1994b). Deer Branch NZVA Course Proceedings No. 11 ; 257-277.

Asher., G.W. et al. (1996). Anim. Reprod. Sci. 45 , 201-216.

Asher., G.W. et al. (1997). J. Reprod. Fert. 111 , 91-99

Asher., G.W. et al. (1998). Anim Reprod. Sci (in press).

Broom, D.M. and Johnston, K.G. (1993). *Stress and Animal Welfare*. Chapman & Hall, London

Clutton-Brock, T.J. and Guinness, F E (1974) Behaviour 55 ; 287-300

Cowie, G.M. *et al* (1985). Deer Branch NZVA Course Proceedings No. 2 ; 143-154

Endicott-Davies, D.R. *et al* (1996). Animal Science 62 , 363-367

Fennessy, P.R. (1993). Proc. Symp Animal Breeding & Genetics, Massey University ; 132-141

Fisher, M.W. *et al* (1997). Biology of Deer Congress Proceedings, Edinburgh (in press).

Hunter, J.W. (1997). Deer Branch NZVA Course Proceedings No. 14 ; 179-195.

Jopson. N.V *et al* (1990) Anim. Reprod Sci 23 ; 61-73

Loudon, A.S.I. *et al* (1989). J. Endocr 122 ; 733-745.

Muir, P.D. *et al* (1997) J. Hered 88 ; 366-372.

Plotka, E D *et al* (1983). J Wildl Manage 47 , 38-44

Shackelton, D.M. and Haywood, J. (1985). Can. Jl. Zool. 63 , 868-875.

Yerex, D. and Spiers, I. (1987). *Modern Deer Farm Management* Ampersand Publishing Associates Ltd., Carterton, NZ.