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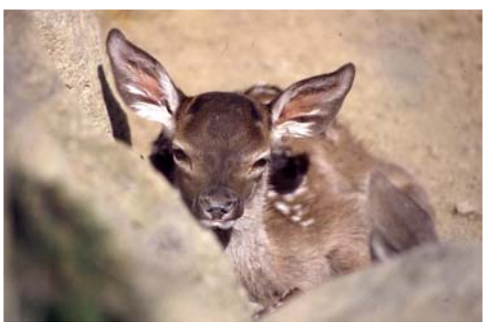
# The effect of conception date on gestation length of red deer (*Cervus elaphus*)

June 2007



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# Client Report

**Report prepared for DEEResearch**

**Contract 5.04**

## The effect of conception date on gestation length of red deer (*Cervus elaphus*)

**June 2007**

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## For DEEResearch Ltd

**June 2007**

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# 1 Summary


- Red deer exhibit a highly seasonal pattern of autumn conception and summer calving that has evolved to optimise reproductive capacity within cool-temperate northern hemisphere environments. Such rigorous entrainment of seasonality presents productive constraints for red deer farmed in the milder, more equable climates of many of New Zealand's pastoral environments. Considerable emphasis has been placed on advancing the average calving date of farmed red deer to better align the high energy demands of lactation with optimal feed production in spring, and thus enhance reproductive capacity within that specific environment.
- It is generally considered that gestation length is genetically fixed at around 233 days and, therefore, time of calving is determined solely by date of conception. It is not surprising, therefore, that all efforts-to-date to advance average calving dates of farmed red deer have involved management regimens designed to advance average mating and conception dates.
- However, there is emerging evidence that gestation length in red deer is not as predictable as previously thought. Precise conception and calving date data for red deer hinds that have been synchronised for artificial insemination have indicated that there is substantially greater variation in gestation length than shown in previous studies of the species.
- Recent research at the Invermay Agricultural Centre has shown that level of nutrition over the last third of pregnancy influences fetal growth trajectory and gestation length, providing convincing evidence for a degree of environmental control over the duration of pregnancy in red deer.
- There has also been an indication from an overseas study that the date of conception may, in itself, influence gestation length, with hinds compensating for variation in conception date in order to achieve a more defined or synchronised calving period. The study indicated that hinds induced to conceive earlier than normal tended to exhibit extended pregnancy durations, thus calving closer to the birthing period of normally conceiving herd-mates. However, the study was confounded by variable nutritional influences manifesting as between-group differences in live weight changes during pregnancy.
- The present study was designed principally to investigate this putative relationship between conception date and gestation length in red deer, but also sought to evaluate possible differences in gestation length between pubertal ('yearling') hinds undergoing their first pregnancy (i.e. primiparous) and adult hinds (i.e. multiparous). The following hypotheses were tested:

1. Hinds that conceive early or late in the breeding season will exhibit longer or shorter gestation lengths, respectively, than those hinds that conceive around the median date.
2. Yearling hinds invest more energy into their own growth while pregnant, leading to a longer gestation length than for adult hinds.

- The study was carried out over two years. In Year 1, yearling and adult hinds were naturally mated to provide a range of conception dates. In Year 2, yearling and adult hinds were treated with progesterone CIDR devices to provide synchronised matings in early-April, mid-April and early-May. In both years conception date was determined by ultrasound fetal aging and individual calving dates were recorded. Hinds were weighed regularly.
- Both yearling and adult hinds varied greatly in their gestation length. Yearling hinds ranged from 221-243 days and adults 218-257 days.
- There was a significant negative correlation between conception date and gestation length: the early conceiving hinds exhibited longer gestations, while late conceiving hinds exhibited shorter gestation. This supports the first hypothesis of a "push-pull"

environmental effect on the control of pregnancy duration in order to facilitate an optimum birth season.

- After correction for any variation in conception date, yearling hinds exhibited shorter gestations than adult hinds by 2.2 days. There was no significant effect of yearling hind live weight on gestation length. This collectively does not support the second hypothesis.
- In summary, our results show that gestation length is influenced markedly by conception date. This appears to be another compensatory mechanism by which red deer attempt to optimise calving seasonality in the face of variation in conception date. It will have an obvious impact on attempts to advance calving date in farmed populations but does not completely negate such attempts. The regression coefficients indicates that for every 10 days of advancement in conception date there will still be between 6-8 days advancement in calving date.

# 2 Introduction

Seasonal changes in climate and food availability are the environmental factors that most influence animal survival and, thus, timing of birth (Lincoln and Short, 1980). In this respect, seasonal breeding has evolved as a means of maximising reproduction efficiency. Red deer (*Cervus elaphus*) evolved in northern cool-temperate regions and exhibit a highly seasonal pattern of autumn conceptions and summer calving (Lincoln and Guinness, 1973). Calves that are born very early or late in the season are less likely to survive their first summer as neonates than those born at the peak of calving. Also, late-born calves are less likely to survive their first winter because they have insufficient time to lay down the body reserves necessary for survival (Clutton-Brock *et al.*, 1982).

Hinds are polyoestrus and may have from six to nine oestrous cycles over the breeding season (Guinness *et al.*, 1971; Asher *et al.*, 2000). However, in the wild, red deer have a very restricted mating season (the rut) lasting little more than a month, with most hinds conceiving at the first oestrus of the season (Guinness *et al.*, 1971). Because about two-thirds of calves are born over a three week period, any variance from this calving time is considered to be due to hinds failing to conceive at first oestrus (Guinness *et al.*, 1978). Gestation length is generally considered to be genetically fixed at around a mean of 233 ± 3-4 days (e.g. Guinness *et al.*, 1971; Kelly and Moore 1977; Clutton-Brock *et al.*, 1982; Adam *et al.*, 1985) and thus, timing of parturition is regarded as being determined by date of conception, with little consideration being given to possible environmental effects of variance in gestation length.

With the adoption of artificial insemination of synchronised hinds and the use of DNA methodology for parentage testing, it has recently become apparent that gestation length of red deer is much more variable than previously thought (Asher, 2007). Guinness *et al.* (1978) noted a five-day difference in gestation length between hinds that were in an enclosed area and those that were free-range. Hinds in the enclosure had been offered supplementary feed during winter and they hypothesised that differences in nutrition may have accounted for the variation in gestation length. More recently, Asher *et al.* (2005a) observed marked variation in gestation length between hinds that were fed either high or low levels of nutrition during the third trimester of pregnancy. In that study gestation length was negatively correlated with change in hind live weight and the authors considered that, under conditions of modest feed imbalance that appeared to influence fetal growth trajectory, a gestation length compensatory mechanism ensured optimal birth weight. In effect, gestation length matched fetal growth rate to ensure optimum birth weight (possibly at the expense of optimal calving date).

In a more recent study, Garcia *et al.* (2006) observed that red deer hinds artificially induced to conceive up to 68 days before the standard mating date exhibited longer gestation lengths than those conceiving later in the breeding season. They postulated that the hinds were able to modify gestation length to counteract out-of-season calving, thus matching parturition to time of peak plant (feed) production. However, their data was confounded by the fact that early conceiving hinds exhibited lower live weight gains over pregnancy, thereby adding some support to the observations of Asher *et al.* (2005a) that nutrition was a driver of the gestation length variation.

Further evidence of an adaptive modification of gestation length by hinds was found in a recent study (IC Scott & GW Asher, unpublished data) where a significant negative correlation between conception date and gestation length was observed in a single cohort of yearling hinds. The regression had a slope of -1.39 ( SE = 0.126 ; $R^2$ = 67.8%), indicating that for every 10 days difference in conception date there was a change in gestation length of 13.9 days. This had the effect of producing a much higher level of within-herd calving synchrony than expected from the known conception dates. Unfortunately, the validity of some of the calf/dam data could not be assured to verify the soundness of the observed relationship, but it provided an indication that early conceiving hinds had extended their pregnancy intervals (>233 days), while those that conceived late had reduced gestation length (<233 days).This introduces an intriguing concept of a “push-pull” mechanism to induce optimum birthing seasonality. Interestingly, no such effect was noted in a contemporary cohort of adult hinds, indicating that it may have been a unique feature of first pregnancy. As first pregnancy of yearling hinds coincides with continuing somatic (non-reproductive) growth, it was considered that between-animal variation in gestation length of first-calvers was possibly an effect of the conflict between energy investment into somatic and reproductive development.

On the basis of evidence for the existence of a putative adaptive modification of gestation length by hinds, we have undertaken this study to test two hypotheses:

1. Within-herd synchrony of red deer births is facilitated by a "push/pull" control over gestation length, such that hinds conceiving early and late in the breeding season have longer and shorter gestation periods, respectively.
2. Gestation length of yearling (primiparous) hinds is influenced by nutritional demands for somatic growth (i.e., requirement for investment into the dam's own body growth) during pregnancy. Reduced energy investment of yearling hinds into conceptus development relative to adult hinds will retard fetal growth rate and increase gestation length.

# 3 Materials and Methods

All animal treatments and procedures in this trial were approved by the Invermay Animal Ethics Committee.

## 3.1 Year 1: Non-synchronised hinds

- Conception and calving dates were obtained from yearling (n = 80) and mature (n = 165) hinds that were naturally mated for unrelated trials on the Invermay Agricultural Centre (Sire Referencing i.e. FoRST 100202) and Winchmore (DEEResearch Contract # 4.10) farms. Both populations were of European red deer genotypes (i.e. *scoticus* and *hippelaphus* subspecies composites) with negligible introgression of Wapiti genotypes, as assessed from prior DNA microsatellite analysis (Asher *et al.*, 2005) and detailed pedigree records.
- Hinds were weighed regularly and each scanned by rectal ultrasonography twice to determine pregnancy status and to estimate fetal age to within 5 days of actual age (estimated operator accuracy based on variance parameters for fetal growth trajectory and ultrasound resolution). Conception date was calculated from the estimated fetal age on the day of scanning.
- Calving paddocks were monitored daily and individual calving dates recorded. Calves were weighed and tagged within 24 hours of birth.
- Dam/calf pairs were matched by DNA analysis (Tate *et al.,* 1998) of hair samples from the hinds and blood samples from the calves. Gestation length was calculated for each hind as the difference between birth date of its matched calf and estimated conception date based on fetal age at scanning.

## 3.2 Year 2: Synchronised hinds

- Oestrus and ovulation were synchronised to provide a spread of known conception dates of yearling and mature red deer hinds in a 2 x 3 factorial design trial. The study was conducted on the Invermay Agricultural Centre using European subspecies composite hinds with negligible introgression of Wapiti genotypes, as assessed from detailed pedigree records.
- An equal number (n = 20) of yearling and mature hinds had CIDR devices inserted intravaginally on each of 22 March (Day 0, Group 1), 31 March (Day 0, Group 2) and 19 April (Day 0, Group 3), with CIDR device replacement on Day 9, and removal on Day 12. Hinds received an injection of 200 i.u. equine chorionic gonadotropin (eCG) at CIDR device removal (3 April, 13 April and 1 May for Groups 1, 2 & 3 respectively).
- Hinds were joined with entire stags, at a ratio of 1 stag to 10 hinds, immediately after CIDR device removal. They remained with the stags until 5 May (i.e. Group 3 hinds only had a chance to be mated at the induced oestrus). To avoid bullying, the yearling hinds were mated in separate groups to the adult hinds.
- Rectal ultrasound scanning was carried out on all hinds 45 days after CIDR device removal to determine pregnancy status and to confirm fetal age.
- Yearling and adult hinds were over-wintered in two separate groups, again to prevent bullying. Animals were weighed regularly and managed to minimise any effects of live weight change on gestation length.
- Pregnant hinds were allocated to one of five calving paddocks on 20 November. Each calving group consisted of yearling and adult hinds from each mating group. All calving paddocks were monitored daily and individual calving dates recorded. Calves were weighed and tagged within 24 hours of birth.
- Dam/calf pairs were matched by DNA analysis of hair samples from the hinds and blood samples from the calves. Gestation length was calculated for each hind as the difference between birth date of its matched calf and estimated age of the fetus at scanning.

## 3.3 Statistical analysis

Statistical analyses were carried out by linear regression, with gestation length as the response variable, and conception date and any other available covariates and factors as explanatory variables.

Gestation length was calculated via the difference between conception and birth dates. This carries the possibility of inducing a negative correlation in the regression analysis of conception date on gestation length, which may affect the Year 1 data, but not the Year 2 data, for which synchronised matings were used. Caution is therefore required in interpreting the results of this analysis because an error where fetal age has been overestimated (i.e. earlier conception) will result in a longer gestation length being calculated and vice versa.

# 4. Results

## 4.1 Year 1: Non-synchronised hinds

Conception and calving date records were available from 80 yearling hinds in the Invermay Sire Referencing herd. Mean conception date was 18 April (± 0.6 days) and ranged from 31 March to 25 April (25 days). Mean gestation length was 232.3 (± 0.5) days

The regression of gestation length against conception date showed a significant ($P < 0.01$) negative slope of -0.27 (SE = 0.085; $R^2$ = 10.1%). This means that for every 10 days difference in conception date there was a change in gestation length of 2.7 days (Fig. 1).

Other effects for hind live weight, sire breed, calf sex and birth weight were not significant ($P > 0.05$).

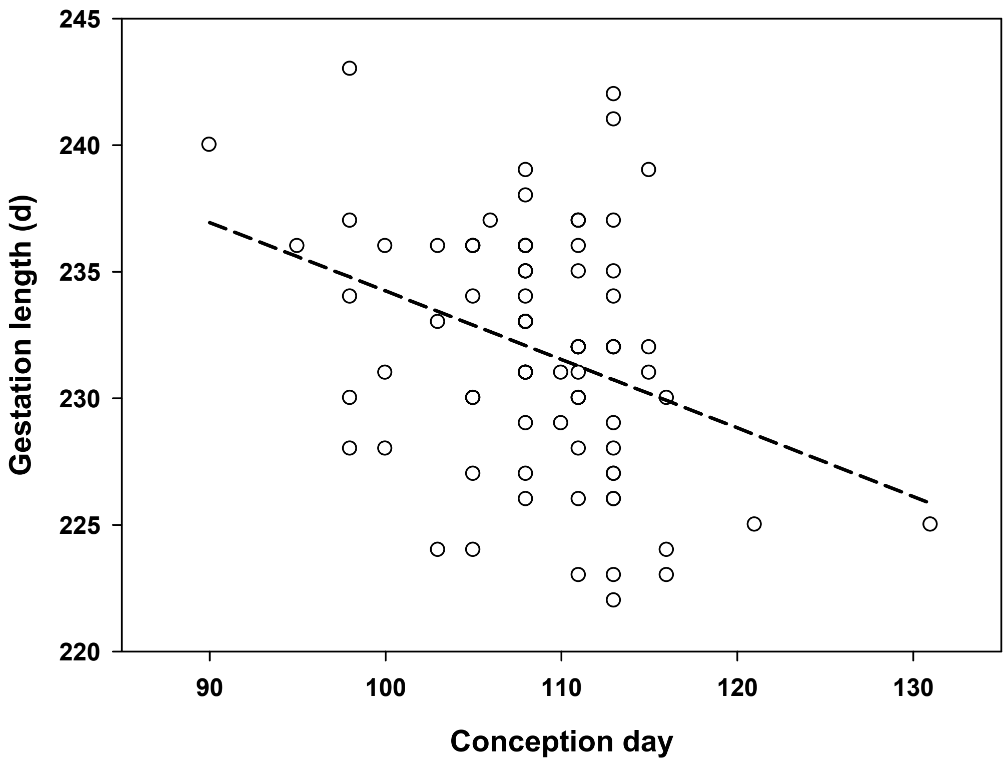


**Figure 1:** Regression of gestation length against conception date for 80 yearling red deer hinds from the Invermay Sire Reference project (Day 1 = 1 January).

Conception and calving date records were available from 165 mature hinds in the Winchmore early calving trial. Mean conception date was 25 March (± 0.7 days) and ranged from 1 March to 4 May (64 days). Mean gestation length was 238.6 (± 0.5) days

The regression of gestation length against conception date showed a highly significant ($P < 0.001$) negative slope of -0.36 (SE = 0.047; $R^2$ = 26.7%). This means that for every 10 days difference in conception date there was a change in gestation length of 3.6 days. When hind age was added to the model, it gave a non-significant effect for gestation length of 1.66 (SED = 1.47) days for 3 year-olds relative to older hinds (Fig. 2). Other effects for hind live weight were not significant $P > 0.5$).

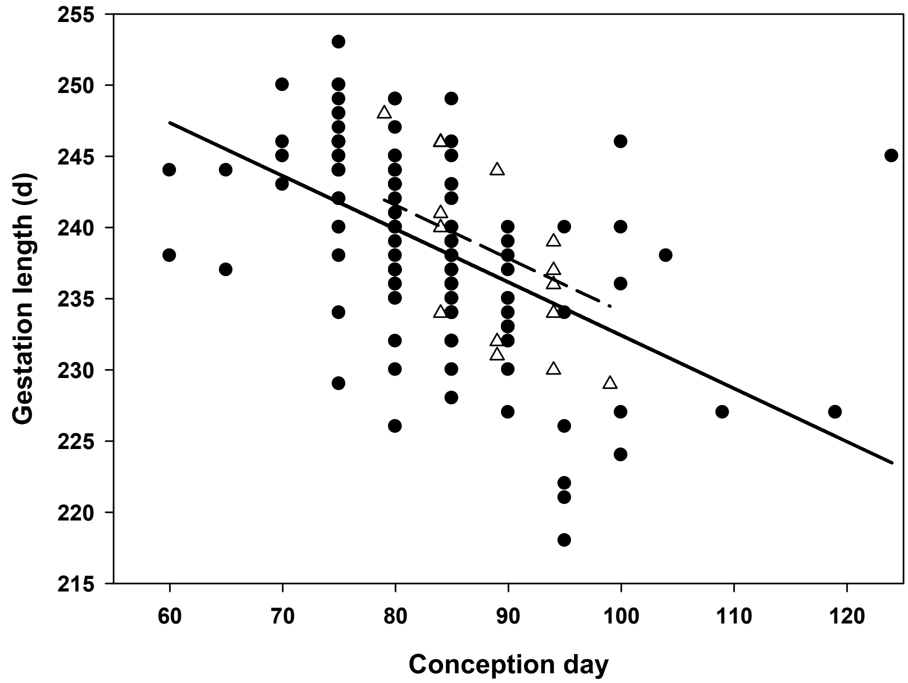


**Figure 2:** Regression of gestation length against conception date for 165 adult red deer hinds from the Winchmore study (Day 1 = 1 January); 4+ year-olds = circle, solid line; 3-year-olds = triangle, dashed line.

## 4.2 Year 2: Synchronised hinds

The number of hinds that conceived and were matched to a calf, mean conception date and mean gestation length for each mating group is shown in Table 1.

**Table 1:** Number of hinds conceived and matched to a calf, mean (± SEM) conception date and gestation length for each mating group.

| | Yearling | | | Adult | | |
|---|---|---|---|---|---|---|
| | **n** | **Conception Date** | **Gestation Length** | **n** | **Conception Date** | **Gestation Length** |
| **Group 1** | 17 | 9 April | 233.4 | 18 | 4 April | 236.6 |
| | | (2.2) | (0.9) | | (0.8) | (1.5) |
| **Group 2** | 17 | 18 April | 232.4 | 16 | 15 April | 232.9 |
| | | (1.7) | (1.1) | | (0.9) | (0.7) |
| **Group 3** | 13 | 3 May | 228.1 | 10 | 3 May | 230.9 |
| | | (0.0) | (1.0) | | (0.0) | (1.0) |

The regression of gestation length against conception date showed a highly significant ($P < 0.001$) negative slope of -0.19 (SE = 0.040; $R^2$ = 21.2%). This means for every 10 days difference in conception date there was a change in gestation length of 1.9 days. Hind age and October hind live weight were also added to the model. This showed a significant difference between adults and yearlings of 2.2 (SE 1.04) days. The effect of live weight was not in itself significant (Figure.3). Other effects for live weight, calf sex and birth weight were not significant ($P > 0.05$).

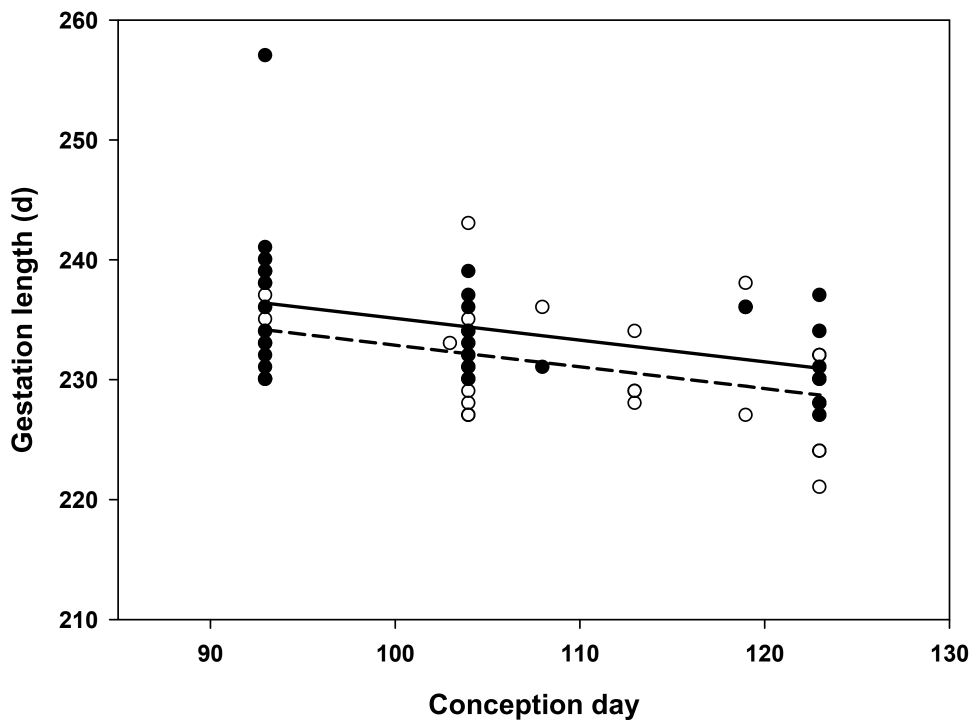


**Figure 3:** Regression of gestation length against conception date for 47 yearling and 44 adult red deer hinds from Year 2 (Day 1 = 1 January); Adults = closed circle, solid line; yearlings = open circle, dashed line.

# 5. Discussion

A species-specific gestation period (the interval from fertilisation to birth) is a profound feature of mammalian reproductive cycles. There is a general underlying acceptance that gestation length for any given species is genetically programmed and relatively robust in the face of variations in environmental conditions. Recognition is given to the influence of fetal genotype as being the single most important determinant of gestation length, this even accounting for some subspecies and breed differences (Kenneth & Richie 1953; Racey 1981). Indeed this has been well demonstrated for the red deer species (*Cervus elaphus*) in which there is considerable subspeciation and subspecies variation in observed mating-birth intervals ranging from 233 days for *C.e. scoticus* (Scottish red deer) to 247 days for *C.e. nelsoni, roosevelti, manitobensis* (North American Wapiti subspecies) (Guinness *et al* 1971; Haigh 2001). Furthermore, hinds gestating crossbred fetuses show mean gestation lengths intermediate between parental genotypes (Asher *et al* 1988; Asher *et al* 2005b).

Recently there has been a growing awareness that there is considerably greater variation in red deer gestation length than earlier indicated and that there is a significant element of environmental, and possibly even social, control over the duration of pregnancy (Asher 2007). First indication of this arose from observation of birth dates of calves conceived through artificial insemination and verified through DNA genotyping. However, the reasons behind the variation were obscure.

More recently, Asher *et al* (2005a) observed a marked effect of level of dam nutrition between days 150 and 220 of pregnancy on fetal growth and gestation length. Dams on differential regimens expressed unexpectedly wide variation (range = 27 days) in gestation length, with low nutrition hinds exhibiting longer gestations (>240 days) than high nutrition hinds (<230 days). It was concluded from this study that variations in nutrition to hinds during the last trimester of pregnancy strongly influenced fetal growth trajectory, but variation in gestation length compensated to ensure optimisation of birth weight (and maximise calf survival) (Asher *et al* 2005a). The underlying assumption of this hypothesis is that hinds may compromise an optimum calving date in order to ensure optimisation of birth weight (see later).

Also, Garcia *et al* (2006) observed that Spanish (*C.e. hispanicus*) and Scottish (*C.e. scoticus*) red deer hinds artificially induced to conceive 6-8 weeks before the natural breeding season exhibited extended gestation lengths by 8-10 days compared with later-conceiving control hinds, with no discernable effect on birth weight. They postulated that optimisation of birth date (not birth weight) was the principal driver of gestation length. However, their study was confounded by lower live weight gains over pregnancy in the early-conceiving hinds, lending possible support to the nutritional-foetal growth influence model of Asher *et al* (2005a).

Collectively, these studies debunk the commonly held notion that gestation length of red deer is genetically fixed within restricted limits, and indicates environmental modifiers act as buffers to enhance neonate survival (Asher 2007). However, the precise nature of such modifiers is only starting to be resolved, and there are conflicting hypotheses over the buffering mechanisms involved (e.g. optimisation of birth weight vs. birth date).

The present study was principally designed to investigate the hypothesis that birth date is optimised by a "push-pull" effect of gestation length control relative to conception date. That is, early-conceiving and late-conceiving hinds will exhibit longer and shorter gestation lengths, respectively, to induce a more synchronised calving pattern than would otherwise be expected from a genetically-fixed gestation interval. In all study groups, including yearling and adult hinds, there were significant negative correlations between conception date and gestation length. For every 10 days difference in conception date there was between 1.9 and 3.6 days change in gestation length for the study populations. Given that these populations were spread across regions, years and hind age groups, this effect is clearly robust and profound. It produces very strong support for the tested hypothesis and hints at the extreme evolutionary importance of optimisation of birth date in red deer.

A significant effect of conception date on gestation length has been reported in several ruminant species, including sheep (Davies *et al*, 1966), goats (Mellado *et al*, 2000), alpaca (Davis *et al*, 1997) dromedary (Elias *et al*, 1991), cattle (Piedrafita *et al* 2000), and bison (Berger 1992). These effects range from being very small (e.g. goats bred in summer showed a 1-day increase in gestation length compared with those bred in autumn) to quite large (12.5 days difference in summer vs. autumn mated alpaca). The effects observed in the current studies on red deer are profound compared to these other species, as they relate to conception date variation over periods of time that are substantially less than in studies in other ruminants. If similar regression coefficients were applied to alpaca, for example, the difference in their gestation length between autumn and summer conception would be in the order of 30-40 days.

We found evidence in the present study on red deer of a significant effect of dam age on gestation length. Yearling hinds undergoing their first pregnancy exhibited mean gestation lengths 2.2 days shorter than adult hinds. This seemingly negates the second hypothesis related to somatic growth demands of the younger hinds. We had expected that because yearling hinds seemingly invest significant resouces into somatic growth during their first pregnancy, fetal growth rates would likely lag behind those of adult hinds. If this was the case, the birth weight optimisation model of Asher et al. (2005a) would predict increased gestation length. However, it is well established in the literature that pubertal hinds (16 months old) generally conceive 2-3 weeks later than adults hinds within any given population, therefore, optimisation of birth date, rather than birth weight, may have greater impact on calf survival. It should be noted, however, more rigorous testing of the hypothesis in future needs to evaluate the effect of changes in yearling hind weight over first pregnancy (particularly, perhaps, during the first and second trimesters when foetal weight is an insignificant proportion of total live weight) on gestation length. Such weight changes between hinds may better reflect differing energy investments between individuals into somatic growth. In sheep, overfeeding of hoggets to promote rapid maternal growth throughout pregnancy is associated with, among other things, a reduction in gestation length (Wallace, 2000), and this may well also influence foetal growth and gestation length in red deer.

Clearly, red deer appear to possess various physiological mechanisms for buffering reproductive processes from the vagaries of the environment within which they live. This indicates strong evolutionary pressure to optimise reproductive capacity within highly seasonal environments. These buffering systems range from optimisation of neonate birth weight (possibly at some expense to birth date), to optimisation of birth date (possibly at the expense of birth weight but this has not been demonstrated). Although these systems appear contradictory, they are possibly subject to different environment triggers, and the animals adopt a particular set of environmental circumstances according to the “trade-offs” required. We are a long way from understanding the dynamics of such compensatory mechanisms.

Furthermore, the precise physiological mechanisms behind the environmental control of gestation length remain to the discovered. The hypothetical model of Asher *et al* (2005a), in which birth weight is optimised by fetal adrenal induction of parturition being dependant on attainment of specific size or stage of fetal development, may account for the observed effects of late pregnancy nutrition, but cannot account for the “conception date : gestation length” effect on birth date.

One possibility to be considered is that birth date is influenced directly by photoperiod, in particular, increasing day lengths of spring and summer. Davis *et* al. (1997) hypothesised that observed differences in gestation length between spring- and autumn-mated alpacas may be in response to changing day length. Although photoperiod is well established as the ultimate driver of the timing of conceptions (Lincoln and Short 1980), little consideration has been given to later direct effects of photoperiod on the reproductive processes. However, it is well established that the entire annual cycles of reproduction, growth, feed intake and pelage replacement (to name only a few) of red deer are all strongly influenced by prevailing photoperiod throughout the year. Furthermore, there is evidence that long photoperiods around the timing of calving influence the initiation of lactation. Asher *et al* (1994) found that exogenous melatonin delivery to hinds in late pregnancy (i.e. from ~80 day prior to expected calving), effectively mimicking a sudden switch to short photoperiods, resulted in hinds failing to undergo mammary development and lactogenesis. There was also a suggestion that the treatment adversely affected fetal development, leading to non-viability of the neonate. This provides strong evidence that photoperiod directly influences aspects of the parturition process of red deer. A role of photoperiod in controlling gestation length via direct influence on parturition timing is highly speculative at this stage. Further considerations include the possibility of social modifiers of gestation length, although it is difficult to identify a mechanism by which early conceiving hinds receive cues from later conceiving hinds to inhibit the parturition process.

From a more practical perspective for the deer farming industry, there are important implications of the present study for deer management. There has been a strong push within the New Zealand deer industry to advance calving dates of red deer so that the demands of hind lactation are better matched to pasture quality (Asher *et al* 1996). Management practices such as early stag introduction, early weaning and improved nutrition to the hind are all premised on advancing conception dates in order to advance calving dates. However, the results of the present study demonstrate that to a certain extent we are fighting against nature. Evolutionary selection pressures have engineered within red deer the capability of adjusting components of their reproductive processes in order to meet their needs for optimal reproductive productivity within their northern hemisphere environment. The fact that the New Zealand pastoral environment differs significantly from the northern hemisphere has little relevance to the internal mechanisms of red deer, as there has been insufficient time for selection pressures to exert favourable control over reproductive seasonality with the new environment.

However, while clearly the compensatory mechanism evolved in deer will mitigate some of our efforts to achieve early calving, the fact remains that significant gains in calving date are presently being achieved on many farms. The regressions of gestation length on conception date presented in the current study indicate that for every 10 days advancement in conception date there will likely be a 6-8 day advancement in calving date. However, while we have long pondered the management options for advancing conception dates as the key to promoting earlier calving, consideration should perhaps now also be given to genetic factors influencing reproductive seasonality. Recent studies have indicated opportunities of introgressing genes from certain red deer genotypes (e.g. Eastern European red deer (*C. e. hippelaphus*) that confer early conception traits (Scott *et al*. 2006). Subsequent studies arising from this now need to additionally address issues of gestation length as an important component of advancing calving dates.

## 6. Acknowledgements

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