Red deer as a novel ruminant model for nutritional and genetic influences on maternal expression of foetal and neonatal growth

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ABSTRACT

The red deer species (*Cervus elaphus*) is represented by morphologically disparate subspecies that freely crossbreed. All are highly seasonal breeders adapted to cold-temperate climates characterised by extreme annual oscillations in temperature and feed availability. Calves are born in summer following relatively long average gestation lengths of 234-250 days (depending on subspecies), with >70% of pregnancy mass acquired over spring/early summer.

The ability of the smaller red deer hind (100 kg) to successfully gestate, birth and rear crossbred (e.g. wapiti x red deer) progeny of 40% increased foetal and post-natal growth potential is quite remarkable, and raises numerous questions about mechanisms of maternal and foetal control of reproductive processes. Recent research on moderate variations in late gestational nutrition to red deer hinds gestating red deer foetuses has revealed an interesting phenomenon in which nutritional influences on foetal growth trajectory appears to influence gestation length to ensure optimisation of birth weight (and, hence, neonate survival). This is quite contrary to expectations for sheep and cattle, but may have parallels amongst other wild ruminant species. Interestingly, hinds gestating crossbred (wapiti x red deer) foetuses of greatly increased growth potential appear unable to adopt such compensatory mechanisms, with hind under-nutrition leading to reduced birth weight relative to *ad-libitum* fed controls. These observations hint at some interesting and useful future research on mechanisms of maternal and foetal growth control in red deer.

Keywords: Red deer, reproduction, gestation, nutrition, crossbreeding.

INTRODUCTION

The red deer (*Cervus elaphus*), which includes a wide range of morphologically different subspecies, is a newly domesticated ruminant that has been subjected to little artificial genetic selection for improved domestility within pastoral environments. Although behaviourally plastic, and capable of habituating well to this environment, their physiological and behavioural genotype and phenotype are essentially those of their wild progenitors.

In New Zealand, the subspecies composition of the national herd is largely unknown due to the widespread introgression of various genotypes. Such introgression includes the small-bodied Scottish red deer (*C.e. scoticus*), with mature hind weights ~100 kg, the Eastern European red deer (*C.e. hippelaphus*) at ~140-160kg, and the North American wapiti (*C.e. nelsoni*, *manitobensis roosevelti*) at ~210-240 kg.

Irrespective of genotype composition, all red deer subspecies are highly seasonal breeders cued by changes in local photoperiod (Lincoln and Short, 1980). The season of conceptions in autumn is characterised by the "rut", a short period of hypersexual activity in which stags complete aggressively for access to oestrous females. Hinds typically exhibit high fertility to first oestrus mating of the season, which is naturally synchronised within a 10-12 day period within the herd (Clutton-Brock *et al.*, 1982). Such synchrony of conceptions results in subsequent synchrony of calving in early-mid summer after relatively long gestation (c.f. sheep and goats) of about 234 days for the smaller-bodied sub-species and 250 days for the larger-bodied subspecies (Asher *et al.*, 2004a; Asher *et al.*, 2004b). Clearly, there has been high evolutionary pressure for high birth synchrony in northern hemisphere continental environments to ensure optimal survival and growth of calves in regions of seasonal climatic extremes (Lincoln and Short, 1980).

FOETAL DEVELOPMENT

Early embryonic and foetal development occurs over autumn and early winter, and exerts little apparent metabolic drain on the hinds. Total conceptus mass at mid-point gestation (mid/late winter) accounts for less than 1% of total dam mass (Adam *et al.*, 1988). Thus, 80-90% of conceptus mass (i.e. foetal and maternal components of pregnancy) is acquired in the latter half of gestation over spring and early summer, with ultimate conceptus mass at parturition approaching 20% of total hind mass (Adam *et al.*, 1988). Therefore, the metabolic impacts of pregnancy on the dam occur mainly during spring and summer. Feed availability in the native northern continental climes can be highly variable over this period, and hinds can be under severe nutritional constraints during late pregnancy (Albon *et al.*, 1983). However, the New Zealand climate is more amenable to improved feed supply over late gestation (Asher *et al.*, 1996). This raises questions as to the physiological adaptions of red deer to cope with nutritional vagaries (either low or high nutritional planes) during crucial phases of foetal development. Recent studies hint at some unusual adaptions (at least in respect to domesticated ruminants like sheep and cattle) to deal

with such conditions and ensure optimisation of neonatal survival.

GENOTYPIC EFFECTS ON FOETAL AND NEONATAL GROWTH

The extreme contrasts in subspecies mature bodymass (e.g. 100 kg vs 240 kg for female Scottish red deer and North American wapiti, respectively), and the fact that all subspecies freely cross-breed to produce fertile progeny, is possibly unique amongst domesticated ruminants. The red deer x wapiti crossbred has particular significance to the New Zealand deer farming industry, where it is used to increase efficiency of meat production systems (Fennessy and Thompson, 1988). The crossbred progeny from red deer dams exhibit 30-40% faster neonatal growth than red deer contemporaries (Nicol *et al.*, 2003). The mechanisms by which this is achieved are presently the subject of considerable research. The salient points in relation to the production of crossbred calves are as follows:

(1) While little is known of foetal growth trajectory of the crossbred relative to the red deer foetus, there is a 3% increase in average gestation length (i.e. 234 vs 240 days) and a 50-60% increase in average birth weight (i.e. 9 vs 14 kg) for crossbred vs red deer offspring (Asher *et al.*, 2004b; Moore and Littlejohn, 1989).

(2) The red deer hind has a remarkable ability to undergo normal, uncomplicated parturition processes with crossbred neonates, despite the birthweight increase. Birthweights in excess of 18 kg (~15% of dam pre-rut liveweight) have been occasionally observed, with no evidence of parturition difficulties (Moore and Littlejohn, 1989). In marked contrast, studies on hybridisation of red deer with Pere David's deer (*Elaphurus davidianus*), sambar deer (*Cervus unicolor*) and rusa deer (*Cervus timorensis*) have been plagued with (amongst other things) aberrant and highly variable gestation lengths, lower than expected birth weights (especially for the latter two species) and very high incidences of dystocia (Goosen, 1997; Muir *et al.*, 1997), indicating foetal genotype disruptions to normal parturition processes.

(3) Red deer hinds have the ability to sustain the growth of crossbred calves at rates 30-40% higher than for red deer calves (Moore and Littlejohn, 1989). The lactational mechanisms by which this is achieved have not yet been fully evaluated.

HIND NUTRITION DURING LATE PREGNANCY

The last trimester of pregnancy of red deer hinds, when the conceptus acquires >70% of its ultimate mass, coincides with the spring pasture "flush" on many New Zealand deer farms. While this alignment outwardly seems desirable given the increasing energy demands of the conceptus, there are often questions raised about the appropriate nutritional management during late pregnancy to optimise neonate survival and growth (i.e. balancing the putative consequences of luxury versus restrictive feeding practices during a crucial phase of foetal development).

Two opposing schools of practice have emerged on New Zealand deer farms in relation to feeding hinds in late pregnancy. The first strategy is to provide maximal nutrition to hinds on the basis that neonate viability is enhanced by increasing birth weight, and high body condition score (BCS) of dams by calving time bodes well for impending lactational energy drains. The second strategy seeks to restrict hind access to feed on the belief that unrestricted intake results in increased incidences of neonate/dam mortality due to dystocia as a result of over-developed neonates (i.e. high birth weight) and over-conditioned dams (i.e. obesity).

After 25 years of deer farming in New Zealand, the issue of optimal feeding strategies for hinds in late pregnancy has remained unresolved. This highlights a paucity of information on the relationship between nutrition and reproduction performance in red deer.

Recently completed studies (Asher *et al* 2004a) aimed to relate feed intake of hinds during late pregnancy to dam BCS, foetal development and calf growth. A total of 51 hinds gestating red deer calves of known conception date where housed indoors and individually fed a set level of concentrate ration from Days 150 – 220 of gestation. The study included multiparous hinds and primiparous hinds on either *ad libitum* intake or a reduced level of feed allowance (30-50% less than *ad-libitum*). Hinds on *ad-libitum* intake showed a substantial increase in daily dry matter intake (DDMI) from 1.8 to 3.2 kg (0.6 to 0.9 MJME/$kg^{0.75}$) between Days 150 and 220, reflecting the increasing demands of the growing conceptus. Restricted diets were associated with significant effects on liveweight gain, changes in BCS and changes in mammary development relative to hinds on *ad-libitum* intakes. Furthermore, repeated CT scanning of the conceptus indicated an effect of hind nutrition on foetal growth, with reduced foetal growth associated with lower planes of nutrition. While it was hypothesised that retarded foetal growth would lead to reduced neonatal birth weights, hinds appeared to compensate by prolonging the term of pregnancy. This was reflected in an unusually wide spread in gestation lengths during the study, with gestation length being significantly negatively correlated to change in hind liveweight between Days 150 and 220 of pregnancy (indicative of nutritional level). It was concluded from this study that while modest variation in nutrition hinds during the last trimester may influence foetal development, variation in gestation length compensates to ensure optimisation of birth weight. Such a compensatory mechanism would seem to be driven by a model of foetal induction of parturition/lactogeneses dependent on attainment of a specific size or stage of development being influenced by foetal growth trajectory (Liggins, 1979). Numerous studies on the influence of maternal nutrition on the reproductive performance of sheep and cattle are generally contradictory to this (Alexander, 1956; Alexander *et al.*, 1957; Bewg *et al.*, 1969; Tudor, 1972). However, support for the hypothesis of compensatory,

control of gestation length in response to foetal growth trajectory in red deer lies with a few studies on other non-domesticated ruminants such as white-tailed deer (*Odocoileus virginianus*), Alaskan moose (*Alces alces gigas*) and African eland (*Taurotragus oryx*) (Keech *et al.*, 2000; Skinner and van Zyle, 1969; Verme, 1965). This hints to a more widespread phenomenon of environmental control of gestation length in ruminants than may be evinced from studies on highly domesticated sheep and cattle (Racey, 1981).

PERTURBATION OF THE "COMPENSATORY GESTATION LENGTH" MODEL

More recent studies on the influence of maternal nutrition during late pregnancy on neonate performance have included the production of red deer x wapiti crossbred calves from red deer dams (Asher *et al.*, 2004b). As expected, there was a foetal genotype effect on mean gestation length (234 vs 239 days for red deer vs crossbred) and mean birth weight (10 vs 14.5 kg). However, in contrast to previous studies on red deer foetuses, regression analysis revealed weak relationships between changes in hind liveweight and gestation length, but a significant relationship with birth weight for crossbred foetuses. These results indicate that the genetically determined higher growth requirements of crossbred foetuses may override mechanisms of compensatory control of gestation length at the expense of calf birthweights (Asher *et al.*, 2004b).

IMPLICATIONS FOR FURTHER RESEARCH

The red deer clearly provides some interesting contrasts with other domesticated ruminants in the maternal and/or foetal control of gestation length and parturition processes. One might even argue that the red deer may be more representative of ruminant species in general, as they have been subjected to little artificial selection pressure that may lead to altered physiological processes affecting reproductive outcomes. Thus, the contrasting results from similar studies in sheep and cattle may be the result of genetic perturbation of "normal" processes through millennia of artificial selection. (One test of this hypothesis may be to study archaic breeds such as the Soay sheep, or progenitor species if they still exist.) Irrespective of these considerations, it would be potentially useful to further expand research into the following areas of red deer physiology in order to understand maternal and/or foetal control of reproduction and growth processes.

(1) Nutritional influences during all stages of pregnancy on foetal growth and gestation length.

(2) Maternal and foetal genetic control of conceptus growth and parturition processes, particularly in relation to crossbreeding using large sire strains (e.g. wapiti) or hybridisation with disparate genotypes (e.g. sambar deer).

(3) Lactational drivers of neonate growth, particularly in relation to crossbreeding to produce progeny of significantly greater growth potential (e.g. red x wapiti crossbreds). This should also include investigation of possible foetal genotype effects on preparturient mammary gland development.

(4) Carry-over effects of dam nutrition, foetal development and lactational energy drains on development of subsequent progeny.

REFERENCES

Adam, C.L.; McDonald, I.; Moir, C.E.; Pennie, K. 1988. Foetal development in red deer (*Cervus elaphus*) 1. Growth of the foetus and associated tissues. *Animal Production 46*: 131-138.

Albon, S.D.; Guinness, F.E.; Clutton-Brock, T.H. 1983. The influence of climatic variation on the birth weights of red deer (*Cervus elaphus*). *Journal of Zoology 200*: 295-297.

Alexander, G. 1956. Influence of nutrition upon duration of gestation in sheep. *Nature 178*:

Alexander, G.; McCance, I.; Watson, R.H. 1957. The relation of maternal nutrition to neonatal mortality in Merino lambs. Proceedings of the Third International Conference on Animal Reproduction *Section 1*: 5-7.

Asher, G.W.; Fisher, M.W.; Fennessy, P.F. 1996. Environmental constraints on reproductive performance of farmed deer. *Animal Reproduction Science 42*: 35-44.

Asher, G.W.; Mulley, R.C.; O'Neill, K.T.; Scott, I.C.; Jopson, N.B.; Littlejohn, R.P. 2004a. Influence of level of nutrition during late pregnancy on reproductive productivity of red deer (1) Adult and primiparous hinds gestating red deer calves. *Animal Reproduction Science* (in press).

Asher, G.W.; Scott, I.C.; O'Neill, K.T.; Littlejohn, R.P. 2004b. Influence of level of nutrition during late pregnancy on reproductive productivity of red deer (2) Adult hinds gestating wapiti x red deer crossbred calves. *Animal Reproduction Science* (in press).

Bewg, W.P.; Plasto, A.W.; Daly, J.J. 1969. Studies on reproductive performance of beef cattle in a sub-tropical environment. 1. Conception rate, length of oestrus cycle and length of gestation. *Queensland Journal of Agricultural Animal Science 26*: 629-637.

Clutton-Brock, T.H.; Guinness, F.E.; Albon, S.D. 1982. Red deer: Behaviour and ecology of two sexes.

Fennessy, P.F.; Thompson, J.M. 1988. Hybridisation and biological efficiency for venison production in red deer. Proceedings of the Australian Association of animal Breeding and Genetics *7*: 532-535.

Goosen, G.J.C. 1997. An interspecies hybrid in deer PhD thesis. University of New England, Armidale, NSW, Australia.

Keech, M.A.; Bowyer, R.T.; ver Hoef, J.M.; Boertje, R.D.; Dale, B.W.; Stephenson, T.R. 2000. Life-history consequences of maternal condition in Alaskan moose. *Journal of Wildlife Management 64*: 450-462.

Liggins, G.C. 1979. Initiation of parturition. *British Medical Bulletin 35*: 145-150.

Lincoln, G.A.; Short, R.V. 1980. Seasonal breeding: Nature's contraceptive. *Recent Progress in Hormone Research 36*: 1-52.

Moore, G.H.; Littlejohn, R.P. 1989. Hybridisation of farmed wapiti (*Cervus elaphus manitobensis*) and red deer (*Cervus elaphus*). *New Zealand Journal of Zoology 16*: 191-198.

Muir, P.D.; Semiadi, G.; Asher, G.W.; Broad, T.E.; Tate, M.L.; Barry, T.N. 1997. Sambar deer (*Cervus unicolor*) x red

deer (*C. elaphus*) interspecies hybrid. *Journal of Heredity 88*: 366-372.

Nicol, A.M.; Judson, H.G.; Taylor, A.W. 2003. The effect of hybridisation on venison production. Proceedings of the New Zealand Society of Animal Production *63*: 222-228.

Racey, P.A. 1981. Environmental factors affecting the length of gestation in mammals. Pp. 199-213 *In:* Environmental factors in mammal reproduction., G. Cook; D.P. Gilmore (eds.). Macmillan, London.

Skinner, J.D.; van Zyle, J.M.H. 1969. Reproductive performance of the common eland, *Taurotragus oryx*, in two environments. *Journal of Reproduction and Fertility* 319-322.

Tudor, G.D. 1972. The effect of pre- and post-natal nutrition on the growth of beef cattle. 1. The effect of nutrition and parity of the dam on calf birth weight. *Australian Journal of Agricultural Research 23*: 389-395.

Verme, L.J. 1965. Reproduction studies on penned white-tailed deer. *Journal of Wildlife Management 29*: 74-79.