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Gestation length in Père David's x red deer hybrids

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ABSTRACT

Père David's deer (PD) have a 49 day longer gestation than red deer (283.4 ± 6.1 (SD) and 234.4 ± 3.4 days). In F₁ hybrids (PD sire), male progeny had a longer gestation than females (268.8 ± 6.4 , n=10 and 262.0 ± 4.5 , n=10, P<0.01), both greater than the mid-parent mean of 259 days. The male and female progeny of F₁ sires and red dams had a gestation length of 249 ± 5.5 (n=275). Segregation analysis suggests two normal distributions with a difference in means of 7 days. In the reverse hybrid (F₁ dams), the gestation length of 242.5 ± 3.3 days (n=19) was significantly shorter than the backcross hybrid progeny of F₁ stags. The control of gestation length in PD hybrids is clearly very complex although we have found evidence of two linked markers which individually account for 2.4 and 2.7 days of the difference in gestation length.

Keywords: Père David's deer; red deer; gestation length; hybrid.

INTRODUCTION

Père David's deer (PD, *Elaphurus davidianus*) were originally imported to New Zealand for several reasons, the major one being the possibility of hybridisation with red deer (R) to advance the time of calving in farmed deer species. PD are long day breeders typically mating in December and calving around 9 months later. In contrast red deer are short day breeders mating in March/April and calving after a gestation which is around 7 weeks shorter than PD (Table 1). In 1983 interest in hybridisation was stimulated by a recent report of a fertile hybrid at Woburn Abbey supplementing a report earlier this century (Beck and Wemmer, 1983). This resulted in a number of importations of PD and several attempts at natural and artificial hybridisation (Asher *et al.*, 1988; Fennessy and Mackintosh, 1992). This paper summarises the results of these studies with special emphasis on gestation length.

TABLE 1: Gestation lengths in the parental species

	Gestation length	Mating	Calving	Reference
Red	234.4 ± 3.4	Mar/Apr	Nov/Dec	Fennessy <i>et al.</i> (1991)
Père David's	283.4 ± 6.1	Dec/Jan	Oct/Nov	Wemmer <i>et al.</i> (1989)

MATERIALS & METHODS

All F₁ hybrids were generated by artificial insemination (AI) of R hinds with PD semen. Backcross hybrid progeny ($1/4$ PD x $3/4$ R) were generated over a period of four years using AI of R hinds with F₁ hybrid (PDxR) semen or multiple ovulation and embryo transfer (MOET) using F₁ hinds (PDxR) as donors (R sire) and R hinds as recipients.

Semen from 5 F₁ stags was used in a total of 841 laparoscopic intrauterine inseminations (Fennessy *et al.*, 1991; Asher *et al.*, 1993). Semen was collected on the day of AI by electroejaculation (Asher *et al.*, 1993) and hinds were each inseminated with 3 to 30 million live sperm. For MOET, embryos obtained from the synchronised natural matings of five superovulated F₁ hinds were transferred to R recipients (Fennessy *et al.*, 1994). For a more detailed description of the methods used see (Tate *et al.*, 1997).

Hinds in the AI and MOET programs were examined by rectal ultrasonography (Wilson and Bingham, 1990), 32 to 42 days after insemination or transfer, to assess pregnancy status. During the calving season hinds were monitored daily, newborn calves tagged and birth weight, sex and dam recorded. For hinds conceiving to AI, conception was taken as the AI date, while for hinds conceiving to ET, it was taken as 72 hours after withdrawal of progesterone treatment. Each cohort of backcross hybrid animals was raised on pasture with a comparison group of at least 30 red deer.

The hybrid status of all backcross hybrids was confirmed by DNA typing and that of F₁ hybrids by DNA and/or protein testing (Tate *et al.*, 1995). All backcross hybrids were genotyped using RFLP and microsatellite markers (c. 100 markers per animal).

RESULTS

The gestation lengths for the parental species and various hybrids are presented in Table 2. The mean gestation length for the 20 F₁ singleton progeny of PD stags and R hinds was 265.4 days, 31 days longer than the R5R mean and 6 days longer than the expected mid parent mean of 259 days, although there was a significant difference between males (268.8 ± 6.4 , n=10) and females (262.0 ± 4.5 , n=10, standard error of the difference ± 2.4 , P<0.01).

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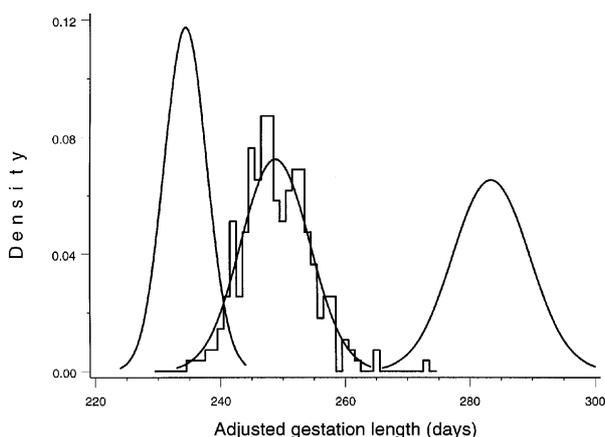
TABLE 2: Gestation lengths for Père David's deer, red deer and their hybrids.

Species	n	Mean \pm SD	Expected ¹
Red (R)	86	234.4 \pm 3.4	-
Père David's (PD)	21	283.4 \pm 6.1	-
(PD x R) female	10	262.0 \pm 4.5	258
(PD x R) male	10	268.8 \pm 6.4	259
(R x (PD x R))	19	242.5 \pm 3.3	247
(PD x R) x R)	275	248.8 \pm 5.5	247

¹ This assumes normal additive genetic variation and thus the expected gestation length is the mid parent mean, or in the case of the $\frac{1}{4}$ PD is based on the grand-parental values and adjusted for sex differences.

The 275 AI observations from the (PDxR) sire backcross were initially analysed using a simple general linear model (SAS, 1988) which revealed significant sire and year effects however the sex effect was not significant. For example, one sire (Mihaka GW903) was significantly different from another (Turnip GW999) by -3.4 days ($P < 0.01$) while in terms of years, 1993 was significantly different from 1995 by -3.1 days ($P < 0.01$). Males had a longer gestation length than females but the difference (0.7 days) was not significant. Figure 1 illustrates the distributions for the three populations corrected for sire, year and sex effects. We conducted a segregation analysis of this data using the procedure of (Wuliji *et al.*, 1993). This procedure is particularly sensitive to the standard deviations used for the parental species and since the robustness of the Père David's data were in question, a range of standard deviations were used. In all cases the analysis suggested 2 normally distributed populations with a difference in means of approximately 7 days (means of 245 and 252 days) as opposed to the null hypothesis of one normally distributed population.

Based on the above results we investigated genetic linkage between DNA markers and gestation length. A

FIGURE 1: Probability density distributions for gestation length. Distributions from left are: red deer (Fennessy *et al.*, 1991), (PDxR)xR) both as a histogram and a normal approximation after adjustment for sire, year and sex effects, and Père David's deer (Wemmer *et al.*, 1989).

simple linear regression approach was used to assess the relationship of individual markers to the variation in gestation length. Due to the large number of tests conducted appropriate 5% thresholds need to be calculated in order to report results which are truly significant. Instead of the empirical permutation method developed by Churchill and Doerge (1994) for determining these threshold values we simulated a normal distribution to determine the true 5% threshold for this data set. This was determined as a single test with a probability of $P < 6.7 \times 10^{-4}$. Using these methods two markers have significant relationships with gestation length namely, GL75 ($P = 0.021$) at -2.4 days and GL236 ($P = 0.033$) at -2.7 days.

DISCUSSION

PD have a gestation length significantly longer than any other deer species except roe deer (around 300 days) which exhibit embryonic diapause. Brinklow *et al.* (1993) showed that there is no evidence for embryonic diapause in Père David's deer so it seems most unlikely that this contributes to the observed gestation lengths.

The 6.8 day difference in gestation length between F_1 males and females is very large compared with sex differences in other ruminant species. For example the differences in sheep (1-2 days, Kassem *et al.*, 1989; Mali *et al.*, 1985), cattle (1.4-2.2 days, Azzam and Nielson, 1987) and red deer (<1 day, Fennessy *et al.*, 1991) are all much smaller; the variance and SD are also large compared with red deer (SD of 3.4 days, Fennessy *et al.*, 1991).

In contrast, in the backcross $\frac{1}{4}$ Père David's the variance for the (R x (PD x R)) backcross hybrid is only about one-third of that in the ((PD x R) x R)) hybrids. However the most interesting difference was the significantly shorter gestation length (6.3 days) in the backcross hybrid progeny of F_1 hinds compared with F_1 stags even though both were out of R dams, albeit following embryo transfer in the former case. The gestation lengths observed are intriguing and raise the issue of imprinting, where maternal and paternal chromosomes are functionally non-equivalent (Latham, 1996). Unfortunately there are insufficient data on F_1 hybrid hinds carrying their own backcross calves to term. While MOET programs have been shown to have some unexpected effects on birthweight (Walker *et al.*, 1996) there is no evidence of this in our data set although that does not preclude other potential side effects.

The control of gestation length in the PD 5 R hybrids is clearly very complex. The genetic linkage analysis indicated that two markers (on the same linkage group) individually accounted for 2.4 and 2.7 days of the variation in gestation length. While there is intense international research effort to dissect the genetic basis of productive traits in farm animals as exemplified by the work of Andersson *et al.* (1994) and Georges *et al.* (1994) we are not aware of any other evidence for QTL for gestation length. However a major gene for gestation length in cattle has been documented (Mead *et al.*, 1949). Thus we have found an intriguing pattern of sex effects and segregation

within populations in terms of gestation length. While direct effects of a major gene or genes for gestation length may account for the differences or a portion of them, other non-genetic (e.g. birth mother or MOET) or non-Mendelian genetic effects (imprinting) or sex effects (including X or Y chromosome) may also be involved. Investigation of the reverse hybrid (red deer male over PD female) and their backcrosses would be of value to elucidate the genetic control of gestation length. In general terms, interspecies hybrids such as these deer may well become an extremely useful tool in the quest to understand the mechanisms or control of complex genetic traits such as gestation length.

ACKNOWLEDGEMENTS

We appreciate the generous help and hours put in by the AgResearch Invermay Deer Crew, John Patene, Colin Mackintosh, Ken Waldrup, Geoff Asher, Ian Scott, Grant Shackell, Mark Fisher, Rayna Anderson, Helen Mathias and many others.

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