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Appendix 1.

Genetic bottleneck in the Père David's deer population.

Based on available records (Flower 1883; Phillips 1925; Sowerby 1949; Bedford 1950; 1951; Dobson 1951; Glover 1980; Jones *et al.* 1983; Chapman 1990) the extent of the genetic bottleneck in the Père David population can best be described as follows. The first record of deer leaving China was in 1869 and there are no records of this species shipped out of China after 1894. Animals were collected at Woburn Abbey, England between 1893 and the first world war and the records of their origins are somewhat scarce and possibly only recorded at Woburn Abbey itself. While there is some literature about the history of the animals at Woburn (Bedford 1950; 1951), specific details about individuals including sex, age and origin have not been published. In addition, deficiencies in other records which prevent a precise determination of the genetic bottleneck include the following: i) lack of records with regard to age, sex, parentage or pedigree of animals held in zoos, deficient shipping records including similar details as above and lack of dates and destinations of animals ii) the lack of information on the source of the Père David's deer at Jardin d' Acclimatation introduces more uncertainty.

If in fact the Jardin d' Acclimatation (Paris) animals are derived from a different stock to those from Berlin zoo and, using the knowledge of the pedigree of animals at Woburn Abbey (Sowerby 1949; Bedford 1950; 1951; Dobson 1951; Jones *et al.* 1983), then the maximum number of individuals that this species can be traced back to is 13 animals. The more likely scenario is that the Jardin d' Acclimatation received animals from Berlin and this would imply the minimum number of individuals the current world population is derived from is 3. Alternatively, if Jardin d' Acclimatation had imported one animal of each sex between 1883 and 1889, which is likely considering Père Armand David was a Frenchman, then the present world population would have derived from 5 individuals. There is also evidence of an even narrower genetic bottleneck with Sowerby (1949) suggesting all animals are the descendants of

one stag from the original consignment of six from Paris. Glover (1980) noted that at the Bronx zoo a placard suggested the genetic bottleneck was estimated at 7 individuals though his attempts to verify this were unsuccessful. Therefore, it appears that the world Père David's deer population is derived from a minimum of 3, a maximum of 13 and most likely between 3 and 7 individuals. The presence of a backcross ¾ Père David's / ¼ red deer hybrid at Jardin d' Acclimatation which was subsequently shipped to Berlin Zoo in 1911 is most likely the offspring of the F_1 born at Jardin des Plantes (Paris) on 31 August 1900.

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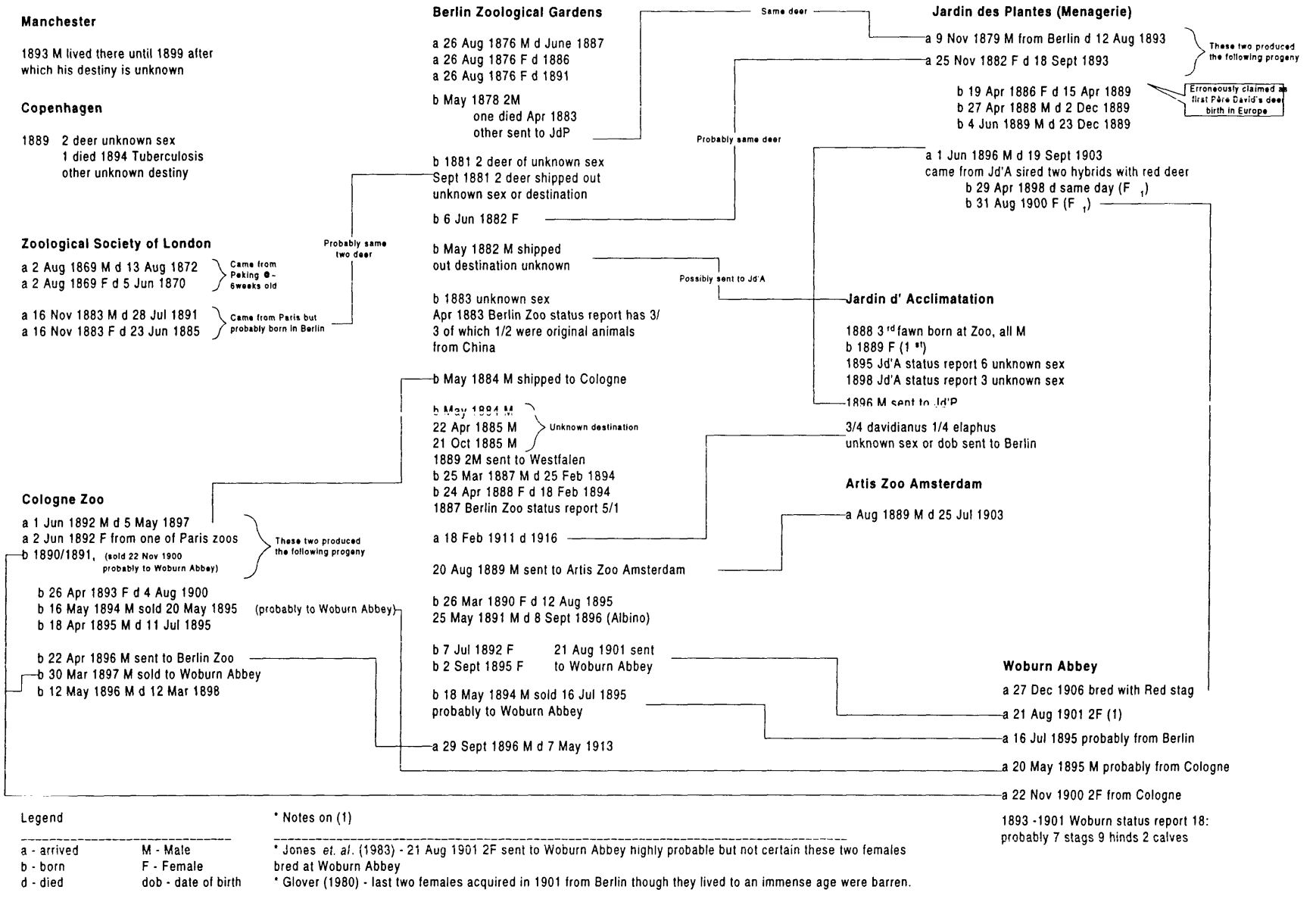
Appendix 1. Flow chart of recorded births, deaths and movements of Père David's deer outside their native China between 1869 and the first World War



Legend

a - arrived	M - Male
b - born	F - Female
d - died	dob - date of birth

* Notes on (1)

* Jones *et. al.* (1983) - 21 Aug 1901 2F sent to Woburn Abbey highly probable but not certain these two females bred at Woburn Abbey

* Glover (1980) - last two females acquired in 1901 from Berlin though they lived to an immense age were barren.

Appendix 2.

Estimates of food intake parameters, maintenance efficiency, growth efficiency and mature live weight in male ¼ Père David / ¾ red deer hybrids and red deer using Equations (1) and (1a) derived from Parks (1982).

Appendix 2. Males - estimates of mature food intake (C), appetance (t*), amplitude (d), phase shift (ϕ), maintenance efficiency (T_o) growth efficiency (AB) and mature live weight (A) in ¼ Père David / ¾ red deer hybrids and red deer males using Equations (1) and (1a) derived from Parks (1982).

		C (MJ ME /week)	t* (weeks)	d (MJ ME /week)	ϕ (weeks)	T_o (kg LW /MJ ME /week)	AB (kg LW/ MJ ME)	A (kg)
Equation (1)								
Hybrid	RW204	178	24.9	-	-	0.836	0.041	149
	WR207	195	28.7	-	-	0.712	0.029	139
	WR216	224	57.2	-	-	0.729	0.035	163
	RW217	188	32.9	-	-	0.897	0.029	169
	RW218	199	32.0	-	-	0.778	0.034	155
	RW221	183	31.4	-	-	0.817	0.045	150
	Mean ± (SD)	**195 ± 16.4**	**34.5 ±11.5**	**-**	**-**	**0.795 ± 0.069**	**0.036 ± 0.006**	**154 ± 10.7**
Red	Y240	168	17.1	-	-	0.916	0.028	154
	Y244	187	24.5	-	-	0.776	0.028	145
	Y257	174	24.5	-	-	0.816	0.032	142
	Y281	212	17.2	-	-	0.608	0.031	129
	Y298	188	25.4	-	-	0.888	0.031	167
	Mean ± (SD)	**186 ± 16.9**	**21.7 ± 4.2**	**-**	**-**	**0.800 ± 0.122**	**0.030 ± 0.002**	**147 ± 14.2**
Equation (1a)								
Hybrid	RW204	160	2.8	52.0	3.2	As above	As above	134
	WR207	168	1.6	46.1	0.6	As above	As above	120
	WR216	158	24.5	35.4	-0.1	As above	As above	115
	RW217	153	2.9	57.4	2.8	As above	As above	137
	RW218	175	18.5	44.5	4.4	As above	As above	136
	RW221	152	3.3	57.9	3.2	As above	As above	124
	Mean ± (SD)	**161 ± 8.9**	**8.9 ± 9.9**	**48.9 ± 8.6**	**2.4 ± 1.7**	As above	As above	**128 ± 9.27**
Red	Y240	163	1.1	81.0	9.0	As above	As above	149
	Y244	181	20.6	38.4	8.8	As above	As above	140
	Y257	161	15.6	38.8	7.9	As above	As above	131
	Y281	209	2.1	71.9	6.2	As above	As above	124
	Y298	166	1.8	68.0	6.6	As above	As above	147
	Mean ± (SD)	**176 ± 20.0**	**8.2 ± 9.2**	**59.6 ± 19.8**	**7.7 ± 1.3**	As above	As above	**138 ± 10.62**

Appendix 3.

Estimates of food intake parameters, maintenance efficiency, growth efficiency and mature live weight in female ¼ Père David / ¾ red deer hybrids and red deer using Equations (1) and (1a) derived from Parks (1982).

Appendix 3. Females - estimates of mature food intake (C), appetance (t*), amplitude (d), phase shift (ϕ), maintenance efficiency (T_o) growth efficiency (AB) and mature live weight (A) in ¼ Père David / ¾ red deer hybrids and red deer females using Equations (1) and (1a) derived from Parks (1982).

		C (MJ ME /week)	t* (weeks)	d (MJ ME /week)	ϕ (weeks)	T_o (kg LW /MJ ME /week)	AB (kg LW/ MJ ME)	A (kg)
Equation (1)								
Hybrid	RW202	222	36.9	-	-	0.784	0.028	174
	RW205	178	30.3	-	-	0.901	0.024	160
	WR206	195	44.3	-	-	0.713	0.035	139
	RW209	140	25.1	-	-	0.811	0.032	112
	WR215	158	42.4	-	-	0.713	0.045	114
	Mean ± (SD)	**179 ± 31.9**	**35.8± 8.1**	**-**	**-**	**0.784 ± 0.078**	**0.033 ± 0.008**	**140 ± 27.5**
Red	Y250	180	25.9	-	-	0.762	0.029	137
	Y255	173	41.9	-	-	0.728	0.043	126
	Y263	211	38.4	-	-	0.713	0.029	150
	Y271	194	34.2	-	-	0.804	0.031	156
	Y293	152	24.8	-	-	0.740	0.036	113
	Mean ± (SD)	**182 ± 22.2**	**33.0 ± 7.5**	**-**	**-**	**0.749 ± 0.035**	**0.034 ± 0.006**	**136 ± 17.5**
Equation (1a)								
Hybrid	RW202	198	24.6	61.4	2.6	As above	As above	155
	RW205	161	19.2	39.3	3.1	As above	As above	145
	WR206	170	31.2	31.0	2.8	As above	As above	121
	RW209	126	10.4	35.7	4.6	As above	As above	102
	WR215	120	15.2	35.2	0.4	As above	As above	86
	Mean ± (SD)	**155 ± 32.3**	**20.1 ± 8.1**	**40.5 ± 12.0**	**2.7 ± 1.5**	As above	As above	**122 ± 28.8**
Red	Y250	177	23.8	36.5	9.9	As above	As above	135
	Y255	135	19.0	27.8	1.1	As above	As above	98
	Y263	170	17.9	41.6	3.1	As above	As above	121
	Y271	191	31.9	31.5	8.3	As above	As above	154
	Y293	149	22.5	21.0	8.9	As above	As above	110
	Mean ± (SD)	**164 ± 22.4**	**23.0 ± 5.5**	**31.7 ± 7.9**	**6.3 ± 3.9**	As above	As above	**124 ± 21.8**

Appendix 4.

Mixture distribution analysis

Likelihood ratio tests can be used in segregation analysis (Elston and Stewart 1971) and complex segregation analysis (Morton and McLean 1974) to discriminate between different modes of genetic inheritance. The main interest in using these techniques are:

i) to test whether the data suggest segregation at major quantitative loci
ii) to make inference about the mode of inheritance (additive, dominant) at the major locus

Segregation analysis has subsequently been widely used for the detection and estimation of the size of major genes in populations (Boichard *et al.* 1990; Liu *et al.* 1994). This analysis involves comparison of the maximum likelihoods of the data under different genetic models. To identify a major gene the likelihood of the data under a polygenic model is maximised with respect to the parameter and effect values and compared with the maximum likelihood of the data under a mixed model which contains both a polygenic component and a major gene component. The test statistic requires a simple calculation involving the two maximum likelihoods under the polygenic and mixed models (Knott *et al.* 1990) and displays properties of a chi squared distribution with degrees of freedom fixed under the polygenic model but maximised under the mixed model. Parameter estimates for the effect and frequency of the major gene in the population are then estimated by maximising the likelihoods through integration procedures.

This type of analysis requires knowledge of the population pedigree structure. The model statement and likelihoods are unique for different pedigree structures and subsequently infer a mode of inheritance of the major gene. Improvements to this method have also been documented and include Hermite integration and modal estimations (Knott *et al.* 1990) which

were designed to overcome problems associated with estimating the likelihoods under the mixed model where the integration of large complex functions becomes mathematically difficult. Enhancements have been included for analysis in large pedigrees (Kerr and Kinghorn 1996) and it has been illustrated that use of marker information provides greater power than segregation analysis without marker information (Knott and Haley 1992).

A graphical technique using quantile-quantile (QQ) plots has also been proposed as a means of detecting the segregation of major genes without the aid of markers (Hoeschele 1988). Using this technique a major locus which accounted for 20% of the phenotypic variance in the trait was clearly detectable whereas there was no evidence for a major locus where the locus accounted for 13% of the phenotypic variance.

In this thesis, mixture distribution analysis refers to the use of a maximum likelihood routine (SAS 1989) which tests the null hypothesis of one normally distributed population against the alternative hypothesis of two normally distributed populations with different means (Wuliji *et al.* 1993). It can be viewed as a simplified form of the above analyses and where a population of a single known pedigree is analysed for evidence of a segregating QTL. The analysis is specific in that it tests for the presence of a single major gene which would manifest itself in this backcross population by the presence of two sub-populations inheriting the two different alleles, red and PD, from the F_1 sire. It does not specifically test for the presence of multiple QTL and assumes the random effects of sire, dam, mendelian sampling and environment that is polygenic and environmental components are normally distributed and there are no other factors aside form the major gene which might tend to distort the population distribution.

This analysis does not use marker information thus providing an alternative test for evidence of segregating populations which are indicative of the presence of QTL. Hence it does not rely on the completeness of genome coverage by markers. This test assumes a known within genotype standard deviation (reasonable from other data) for both environmental and polygenic effects rather than estimating it from the data and assumes that the adjusted data does not contain any other obvious factors which might dichotomise the data or otherwise render them platykurtic.

The nature of this test is such that if the absolute size of the effect is fixed then the greater the number of individual QTL influencing the trait the less chance of detection. Also, if the test has

the ability to detect a QTL of any given size then inclusion of additional QTL of the same size would tend to increase the power of detecting QTL. In light of this, larger effects estimated by this analysis compared with the other methods may indicate the presence of multiple QTL.

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Appendix 5.

Numbers of genotypes scored at each of the 250 genetic markers used for QTL detetction in the hybrid deer population.

Deer map #	Genotypes scored	Deer map #	Genotypes scored	Deer map #	Genotypes scored
1	122	26	119	51	348
2	122	27	331	52	122
3	31	28	348	53	31
4	345	29	104	54	31
5	123	30	339	55	98
6	344	31	120	56	31
7	351	32	344	57	31
8	70	33	308	58	21
9	31	34	116	59	141
10	122	35	82	60	27
11	47	36	351	61	30
12	271	37	117	62	25
13	123	38	123	63	24
14	33	39	229	64	122
15	40	40	122	65	327
16	272	41	116	66	98
17	45	42	118	67	122
18	300	43	318	68	99
19	249	44	343	69	319
20	122	45	123	70	350
21	316	46	347	71	118
22	75	47	288	72	327
23	350	48	94	73	202
24	345	49	122	74	318
25	121	50	351	75	340

Deer map #	Genotypes scored
76	347
77	122
78	123
79	349
80	328
81	117
82	279
83	338
84	30
85	123
86	37
87	123
88	43
89	346
90	99
91	310
92	341
93	350
94	119
95	338
96	306
97	118
98	350
99	293
100	308
101	341
102	344
103	345
104	329
105	115
106	307
107	302
108	351
109	95
110	109

Deer map #	Genotypes scored
111	344
112	350
113	334
114	351
115	332
116	349
117	118
118	123
119	349
120	122
121	348
122	350
123	350
124	114
125	318
126	294
127	317
128	348
129	350
130	299
131	326
132	323
133	336
134	306
135	349
136	351
137	351
138	346
139	350
140	110
141	348
142	319
143	346
144	343
145	351

Deer map #	Genotypes scored
146	120
147	343
148	339
149	341
150	104
151	349
152	349
153	104
154	100
155	344
156	298
157	85
158	66
159	125
160	87
161	87
162	82
163	87
164	132
165	87
166	79
167	136
168	84
169	252
170	87
171	81
172	19
173	149
174	147
175	115
176	87
177	239
178	85
179	68
180	97

Deer map #	Genotypes scored
181	68
182	304
183	40
184	74
185	292
186	86
187	206
188	56
189	89
190	67
191	93
192	41
193	339
194	299
195	87
196	285
197	345
198	317
199	347
200	120
201	337
202	82
203	114
204	121
205	120
206	342
207	145
208	147
209	87
210	256
211	45
212	66
213	52
214	63
215	37

Deer map #	Genotypes scored
216	20
217	47
218	228
219	46
220	23
221	89
222	83
223	17
224	31
225	46
226	76
227	83
228	84
229	84
230	57
231	49
232	49
233	83
234	85
235	83
236	262
237	268
238	55
239	88
240	73
241	84
242	87
243	80
244	46
245	75
246	81
247	62
248	60
249	80
250	32

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 F_1 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 F_1 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 (F_1 dams), the gestation length of 242.5 ± 3.3 days (n=19) was significantly shorter than the backcross hybrid progeny of F_1 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 *et al* (1991)
Père David's	283.4 ± 6.1	Dec/Jan	Oct/Nov	Wemmer *et al* (1989)

MATERIALS & METHODS

All F_1 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 F_1 hybrid (PDxR) semen or multiple ovulation and embryo transfer (MOET) using F_1 hinds (PDxR) as donors (R sire) and R hinds as recipients. Semen from 5 F_1 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 F_1 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 F_1 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 F_1 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 Pére David's deer, red deer and their hybrids.

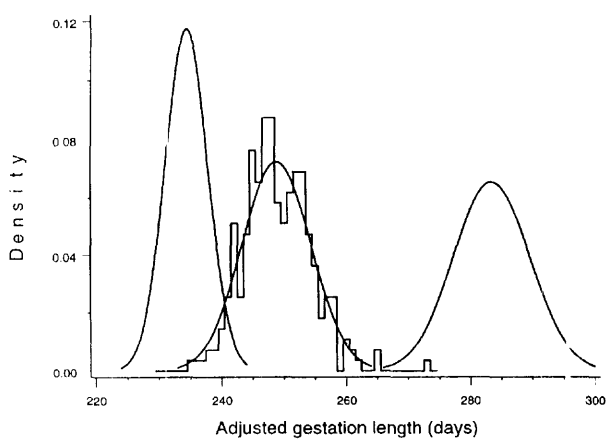
Species	n	Mean ± SD	Expected[1]
Red (R)	86	234.4 ± 3.4	-
Père David's (PD)	21	283.4 ± 6.1	-
(PD x R) female	10	262.0 ± 4.5	258
(PD x R) male	10	268.8 ± 6.4	259
(R x (PD x R))	19	242.5 ± 3.3	247
(PD x R) x R)	275	248.8 ± 5.5	247

[1] This assumes normal additive genetic variation and thus the expected gestation length is the mid parent mean, or in the case of the 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 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 $P<6.7\times10^{-4}$. 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.

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).



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 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.

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GENETIC ANALYSIS OF BIRTH AND WEANING WEIGHT IN AN INTERSPECIES HYBRID IN DEER

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SUMMARY

We provide good evidence (LOD=3.04) for the existence of a birth weight quantitative trait locus (QTL) in an interspecies hybrid between Père David's deer (*Elaphurus davidianus*) and red deer (*Cervus elaphus*). In backcross hybrids the size of this effect was 0.64 kg and the mean birth weight was 9.31 ± 1.29 (SD). The QTL explained 6.0% of the phenotypic variance in birth weight and mapped near marker GL41 on deer linkage group 4 which is analogous to human chromosome 19p.
Keywords: Père David's deer, red deer, birth weight, pre-weaning gain, QTL

INTRODUCTION

Considerable efforts are being conducted worldwide in the quest to find quantitative trait loci (QTL) in a wide variety of species, for example, dairy cattle (Georges *et al.* 1995), sheep (Crawford *et al.* 1997) and pigs (Andersson *et al.* 1994). We have generated interspecies hybrids between Père David's (*Elaphurus davidianus*, PD) and red deer (*Cervus elaphus*, R) as a tool in the search for QTL in deer. A significant feature of this hybrid is that the genetic divergence between the parental species is so large that almost all DNA polymorphisms identified are species specific thus providing a very powerful gene mapping resource (Tate *et al.* 1995). In addition the species also show large differences in morphology, production traits and we have previously presented evidence for gestation length QTL (Goosen *et al.* 1997). In this paper we conducted a genetic analysis of birth weight, weaning weight and pre-weaning gain in this unique deer hybrid.

MATERIALS AND METHODS

F_1 hybrids were generated by artificial insemination (AI) of R hinds with PD semen and backcross hybrid progeny (¼ PD x ¾ R) were generated over a period of six years using AI of R hinds with F_1 hybrid (PDxR) semen (Asher *et al.* 1993) and synchronised natural mating techniques (Fennessy *et al.* 1991). Semen from the six F_1 stags was used in a total of 841 laparoscopic intrauterine inseminations. A more detailed description of the methods is given by Tate *et al.* (1997). A total of 305 backcross progeny were generated of which 275 were by artificial insemination with the remainder being produced by synchronised natural mating. During the calving season hinds were monitored daily, newborn calves tagged and birth weight, sex and dam recorded. The hybrid status of all backcross hybrids was confirmed by DNA typing and that of F_1 hybrids by DNA and/or protein testing (Tate *et al.* 1995). The segregation of up to 250 genetic markers were analysed in the backcross herd: including restriction fragment length variants (RFLV), protein variants and

microsatellites. The linkage relationships of the markers were analysed using MAPMAKER/EXP as described by Tate *et al.* (1995) using the Kosambi mapping function.

The relationship between gestation length and birth weight was investigated and found to be non significant. The fixed effects for birth weight included sire, year, sex and breeding method with dam live weight at conception fitted as a covariate. Similarly fixed effects for weaning weight and pre-weaning gain were sire, birth day, year, sex and a sex by year interaction with dam live weight at conception fitted as a covariate. Backcross progeny birth weight, weaning weight and pre-weaning gain were analysed using three techniques (linear regression, segregation analysis and interval mapping) to test for associations between chromosome sections and/or genetic markers and trait expression. Linkage analyses were carried out testing across sires and investigated differences in backcrosses which inherited either PD or R alleles The linear regression approach used was similar to that of Soller *et al.* (1976) where individual markers were regressed on corrected phenotypes to test for point associations between genetic markers and traits. Segregation analysis used a maximum likelihood technique to test the null hypothesis of one normally distributed population against the alternative hypothesis of two equal sized normally distributed populations with different means in the backcross hybrid population (Wuliji *et al.* 1993). To ensure both robustness and a conservative test we used the same coefficient of variation as for red deer. In addition the more accurate interval mapping maximum likelihood technique developed by Lander and Botstein (1989) i.e. in MAPMAKER/QTL was used to test for QTL.

RESULTS

Means (±SD) for birth weight, weaning weight and pre-weaning gain were 9.31 ± 1.29 kg, 51.0 ± 4.64 kg and 439 ± 44.5 g/d respectively. Given the large number of single point tests conducted across the genome for the linear regression analysis of trait against marker it was important to determine the true 5% significance threshold. We used a technique which simulated a normally distributed population for the 275 individuals and using 1000 iterations determined that the true 5% genome wide threshold was $P=6.7 \times 10^{-4}$. Using this threshold, backcrosses with the PD allele at marker GL112 had significantly higher birth weights (9.63 vs 9.02 kg, $P<0.05$) compared to those without the PD allele and this accounted for 5.6% of the phenotypic variance in birth weight. Neither weaning weight nor pre-weaning gain produced significant results using regression analysis (Table 1).

The segregation analysis does not utilise marker information and as such was an independent test of the data. The results for all three traits rejected null hypothesis of one normally distributed population in favour of the alternative hypothesis of two normally distributed populations with means $\bar{x}_1$ and $\bar{x}_2$ as is evident from the chi-squared probabilities in Table 1.

For the interval mapping analyses we used the more stringent significance threshold from the linear regression simulation to determine the appropriate significance threshold (Knott *et al.* 1996). The genome wide simulated threshold given above is equivalent to a LOD score of 2.78 (Champoux *et al.* 1995). Interval mapping analysis resulted in significant linkage for a birth weight QTL on linkage

group 4 close to marker GL112. The position of the highest LOD score was at marker GL41, 1.2 cM from marker GL112. The effect size was 0.64 kg and explained 6.0% of the variance in birth weight. Both the regression technique and the segregation technique also indicated significant effects of the PD alleles, although in the case of segregation analysis, the predicted effect of the gene was higher at 1.51 kg.

Table 1. Results of single marker linear regression, segregation and interval mapping maximum likelihood analysis of three traits for QTL in the backcross Père David hybrids

Trait	Regression	Segregation			Interval mapping		
	P	P	$\bar{x}_1$	$\bar{x}_2$	LOD	Effect	$\sigma^2\%$[1]
Birth weight (kg)	2.6×10^{-4}*	1.01×10^{-7}***	8.57	10.08	3.04	0.64	6.0
Weaning weight (kg)	1.1×10^{-2} NS	1.72×10^{-3}**	49.0	52.9	1.46	-	-
Pre-weaning gain (g/d)	2.5×10^{-3} NS	5.17×10^{-3}**	456	422	2.00	-16	3.6

[1] Percentage of variance explained by QTL $\sigma^2\% = ((\text{effect}/2)^2/\sigma^2)$

The LOD for pre-weaning gain was 2.00 and in excess of the "suggestive linkage" threshold of 1.90 proposed by Lander and Kruglyak (1995). This mapped to an interval of 24.5cM on linkage group 19 between markers GL209 and GL7. The effect was -16 g/d and it explained 3.6% of the phenotypic variance in pre-weaning gain. The linear regression did not detect significant linkage for either pre-weaning weight gain or weaning weight but segregation analysis suggested significant differences in the order of 34 g/d and 3.9 kg respectively between the two populations. Weaning weight did not achieve the "suggestive linkage" LOD threshold.

DISCUSSION

For birth weight the most significant markers from the linear regression (GL112) and interval mapping techniques (GL41) are both on linkage group 4 and only 1.2 cM (Kosambi) apart. The one LOD interval for this QTL is 26.4 cM and includes a total of 6 markers. The estimated size of the effect was 0.64 kg and the LOD of 3.04 provides good evidence for a birth weight QTL. Markers GL112 and GL41 were restriction fragment length variants detected by expressed sequences which map to human chromosome 19p. Evaluation of genes in this region of the human genome may provide candidate genes for this effect.

Pre-weaning gain attained a reasonably sized LOD of 2.00 indicating that this region is certainly an area worthy of further investigation. Backcrosses with a PD allele at marker GL112 on linkage group 4 had greater birth and weaning weights but animals with a PD allele at marker GL7 on linkage group 19 had lower live weight gain between birth and weaning compared to backcrosses without a PD allele. The segregation analyses suggest there may be two segregating populations in the backcross hybrid population for weaning weight and pre-weaning gain. Lower numbers of animals

recorded for these traits made linkage more difficult to detect. The trend for red type animals to have higher live weight gains pre-weaning was interesting and indicative of a negative heterosis effect which may well be a reflection of the extreme genetic divergence of the parental species. Pure PD are a larger mature size (Loudon *et al.* 1989) than red deer and hybrids between the two would be expected to express hybrid vigour and weights greater than the mid parent means and in proportion to their genotype.

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