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Hybridisation of farmed wapiti (*Cervus elaphus manitobensis*) and red deer (*Cervus elaphus*)

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Abstract Wapiti (*Cervus elaphus manitobensis*) bulls were run with 106 adult farmed red deer hinds (*Cervus elaphus*) selected for size over three mating seasons. Only some bulls readily mated red hinds and some bulls became sexually exhausted after mating about 20 hinds. Seventy six hinds (72%) produced F1 calves. Mean gestation length of the F1 male calves was 239.6 days, with males born 1.8 (SE = 0.8) days earlier than females and a significant negative relationship between male gestation length and birth weight existed. At birth, males, on average, weighed 14.1 kg and females 13.3 kg. Male calves were significantly heavier at birth (6%) and at weaning (5%) than females. Growth rates of the calves to weaning (11 weeks) averaged 558 (males) and 536 g/day (females). Birth weight was related to dam mating weight, with a 0.8 kg increase in birth weight corresponding to a 10 kg increase in dam live weight. Both birth weight and metatarsus length squared of the new born calf were significantly related to growth to 50 days of age but not to later growth from 50–76 days of age. The F1 progeny were fertile when crossed. The use of wapiti sires over large red hinds can maximise the birth weight and weaning weight of calf rearable by a red hind.

Keywords Wapiti; red deer; hybrids; liveweight; growth rates; gestation length

INTRODUCTION

Hybridisation between Eurasian red deer and North America wapiti in United Kingdom deer parks has been reported by Winans (1913) and Whitehead (1950). North American wapiti were introduced into Fiordland, New Zealand in 1905 (Donne 1924; Wodzicki 1950) and subsequently became sympatric and hybridised with red deer (Murie 1951; Caughley 1971; Smith 1974; Batchelor & McLennan 1977; Dratch & Bell 1987). It is now doubtful that many pure wapiti exist there. The majority of Fiordland deer with wapiti characteristics are more accurately described as wapiti-type rather than New Zealand wapiti.

With the development of the New Zealand deer farming industry, the use of Fiordland wapiti-type bulls as heavy weight sires for mating to the predominantly farmed red deer, has considerable potential to increase venison and antler in velvet production (Moore 1984). The coupling of a heavy-weight sire and a small breeding hind (with relatively modest annual feed costs) has an obvious advantage in the production of faster growing heavy weight calves.

To obtain purebred wapiti a band of 14 male and 9 female wapiti (*Cervus elaphus manitobensis*) were imported from Elk Island National Park, Alberta, Canada to Invermay in 1981. Their adaptation to changed seasons has been reported elsewhere (Moore 1987a). This paper reports on the crossbreeding of the pure wapiti bulls from this band with farmed red deer (*Cervus elaphus*) and the growth and reproductive performance of their F1 calves.

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MATERIALS AND METHODS

Animals

The 14 imported wapiti bulls were aged 4 to 5 years in June 1984. Bulls were selected for breeding on superior liveweight and velvet antler size. Early February liveweights of the principle sires (P18, P7, P16) ranged from 328 to 355 kg as rising 6-year olds (although two were used as sires as rising 5-year olds). Wapiti bulls were run with adult red hinds (aged > 3 years) selected for average and above liveweight (111 ± 5 kg) over three mating seasons (1984–86). The number of individual hinds used was 65: 34 for one season, 21 for two seasons, and

10 for three seasons, giving a total of 106 hind breeding-years. The source of the red deer farmed at Invermay is described elsewhere (Moore et al. 1985).

Mating

In 1984 and 1985, two groups of 15 hinds were joined with 2 or 3 bulls each for mating. In 1986, three mating groups of hinds numbering 17, 15, and 14 were joined with one bull each. Replacement stags (F1's) were used only in 1986. Some bulls were replaced or removed and their hinds joined with another group where a bull was apparently working well. In 1984 and 1985 two primary sires were replaced by other bulls after observations suggested that they were sexually exhausted, because they mounted but were unable to penetrate red hinds in oestrus.

The subsequent calving performance of most of the hinds producing F1 calves was recorded. Sixteen F1 females were single sire mated to two F1 males from 16 months of age to test their fertility. Seven of the females were born in 1982–83 and nine in 1984. The two F1 stags mated to F1 hinds were born on Invermay and aged 3 or 4 years. Their sires were unknown but their dams were not those of F1 females they mated.

Treatments

Between 6 to 10 hinds in each mating group had oestrus synchronised before joining, to facilitate observations on whether bulls were working well. Oestrus was synchronised in the hinds using Controlled Internal Drug Release (CIDR) Devices (Alex Harvey Industries, Hamilton) containing progesterone, inserted into their vaginas. At CIDR withdrawal the hinds were injected i.m. with pregnant mares serum gonadotrophin (PMSG, Folligon, Intervet). Treatments were the same within year but varied with year. In 1984 the treatments were 12% w/w CIDRs for 12 days and 500 i.u. PMSG; in 1985 12% CIDRs for 12 days and 400 i.u. PMSG; in 1986 9% CIDRs for 7 days and 400 i.u. PMSG. Dates of CIDR withdrawal were 7 April 1984, 24 March 1985 and 11 March 1986. To record mounting or mating marks on the synchronised hinds the bulls used for mating had coloured grease applied to the inside of their forelegs and inguinal region while under general anaesthetic [Rompun, Bayer; reversal drug Recervyl (Yohimbine), Aspiring Animal Services], once before joining. This enabled the calculation of gestation length for 24 hinds.

Management

Liveweights of the bulls were recorded in early February and of the hinds, before mating in March. Over winter and spring-summer the pasture and supplementary feed intake of the hinds were controlled until several days after calving. For calving, hinds were set stocked on short pasture and supplemented with feed concentrates. This was to minimise the possibilities of calving problems caused by overfatness in the hinds, particularly in their birth canal, and rumen overfill impeding normal presentation of the oversized calves for birth. Once calves were several days old they were shed out with their dams into an adjacent paddock with good quality ryegrass-clover pasture ad lib.

Calf birth weight, sex, and metatarsus length were recorded within 36 hours of birth. Metatarsus length as an indicator of skeletal size was recorded as the distance from the hock to the distal end of the metatarsus bone. Calves were ear-tagged after birth

Table 1 Means and pooled standard deviations (SD) of dam weight and birth date, mid-lactation, and weaning age for male and female F1 calves born in 1984–86.

Calf sex and year of birth	*n*	Dam mating weight (kg)	Birth date age (days)	Mid-lactation age (days)	Weaning age (days)
Males					
1984	14	111	11 Dec	56	73
1985	10	111	25 Nov	52	88
1986	8	112	1 Dec	43	71
Females					
1984	8	114	8 Dec	59	76
1985	9	109	27 Nov	50	86
1986	14	108	4 Dec	40	68
SD		5	8 days	8	8

to identify individuals and sucking was used to identify their dams. Calves were weighed at about 7 weeks (intermediate weight or mid-lactation) and at around 11 weeks of age (weaning). In this paper growth rate from birth to the mid-lactation weighing will be referred to as early growth rate and growth rate from mid-lactation to weaning as later growth rate. Liveweights were recorded to the nearest 0.1 kg at birth and to the nearest 0.5 kg thereafter. Table 1 summarises dam mating liveweights, calf birth dates, and age at weighings over sex and year.

Statistical analysis

Least squares analyses were carried out on dam mating weight (DW), birth date (BD), gestation length (GL), birth weight (BW), and later liveweights and growth rates. Small adjustments were made to intermediate (mid-lactation) and weaning weights to standardise them to 50 and 76 days, respectively, assuming linear growth between weighing dates. Weight analyses were restricted to single-born calves surviving to weaning, and twin birth weights are also given. After adjustment for year effects, sex, and (where appropriate) progesterone-PMSG treatment and BD, were added to the model.

The relationships between BW and DW and between GL and BW were investigated by regression, with differences between year (which were in no instance significant) corrected for and averaged. Differences in intercept and slope between sexes and between progesterone-PMSG treatments (for the BW on DW regression) were assessed. The allometric relationship between BW and metatarsus length (ML) was analysed by a similar regression between the logs of these variables. Early, late, and overall growth rates to weaning were regressed on ML squared, BW and DW, fitted individually after year and sex. This was for 1984 and 1985 born calves only, since no ML measurements were recorded in 1986. (The use of ML squared followed from the allometric relationship between BW and ML.)

Statistical significance was assessed by the t-test at the 5% level for each model term.

RESULTS

Mating

Not all bulls showed an interest in forming a harem or mating the hinds. Bulls P18 in 1984 and P7 in 1985 were the only ones which commenced rutting and were observed mating synchronised hinds, so all the hinds were boxed together and the other bulls removed. Both these bulls appeared to be sexually exhausted a cycle after the induced oestrus and were replaced by other bulls. P7 worked well again in 1986. In the other two 1986 groups the bulls appeared to be working by herding the hinds, but no calves were born to the first cycle. These two groups of 15 and 14 hinds were boxed and a new bull (P16) used, which sired 14 F1 calves from the 29 hinds during the second cycle.

Calving performance

The calving performance of hinds is shown in Table 2. Over 3 years, 76 of 106 hinds (72%) run with bulls over mating, produced F1 calves and 68 (89%) of these hinds reared a calf to weaning. In 1984, bull P18 sired 21 calves including the set of twins, two bulls sired one calf each and two calves were by bulls of unknown identity. The 21 calves born in 1985 were sired by bull P7, who also successfully mated

Table 2 Calving performance of adult red deer hinds mated to Canadian wapiti bulls.

Year	No. of hinds	Hinds calving (%)	No. sets of twins	Calf losses (% of calves born)	Weaning (% of hinds)
1984	30	24 (80)	1	0/25 (0)	25/30 (83)
1985	30	21 (70)	0	2/21 (10)	19/30 (63)
1986	46	31 (67)	2	8/33 (24)	25/46 (54)

Table 3 Means and standard errors of the differences of birth weight and adjusted liveweight at 50 and 76 days for male and female F1 calves born in 1984-86.

	Birth weight (kg)	Mid-lactation weight (kg) at 50 days	Weaning weight (kg) at 76 days
Male	14.1	42.4	56.7
Female	13.3	40.7	53.9
SED	0.3 *	1.0 (NS)	1.4 *

Table 4 Means and standard errors of the differences of early, later and overall F1 calf gain to weaning for male and female F1 calves born in 1984–86.

	Gain rates (g/day)		
	Early	Later	Overall
Male	566	548	558
Female	555	503	536
SED	18 (NS)	28 (NS)	1 (NS)

17 hinds in 1986 when bull P16 sired the other 14 F1 calves. The number of treated hinds calving to mating at the induced oestrus, by year, were 10 out of 12 (1984), 9 out of 11 (1985), and only 3 out of 26 in 1986 (when two-thirds of the hinds were with bulls not observed mating). Overall, 42 out of 57 (74%) of the treated hinds produced F1 calves, compared to 34 out of 49 (69%) of the non-treated hinds. Of the further eight calves born to an F1 replacement stag in 1986, seven were to treated hinds. The three sets of twins were from hinds treated with progesterone-PMSG to synchronise oestrus. The set of female twins born in 1984 survived to weaning, but a set of male twins was stillborn in 1986, in the other set, the male twin survived but the female did not.

In 1984 two hinds required calving assistance and all calves survived. In 1985 three of the hinds required assistance at calving and one had a dead calf. One other hind slipped her calf after being yarded with a hind requiring assistance with calving. Calf losses in 1986 included the three twins previously mentioned which were assisted dead, three other calves assisted dead, a stillborn dystocia and a calf which became mismothered after going through a fence. Records of the subsequent calving performance of hinds showed 64 out of 70 (91%) of red deer hinds which produced F1 calves produced another calf the following season.

Gestation length

The mean gestation length of male F1 calves ($n = 14$) was 239.6 days, significantly earlier than for females ($n = 10$) at 241.4 days (SED = 0.8).

Calf weights

Table 3 shows mean calf birth weight and adjusted intermediate weight and weaning weight by calf sex. Male calves were significantly heavier by 0.8 kg (6%) at birth and by 2.8 kg (5%) at weaning, although the 4% difference at mid-lactation was not significant. However, there was a significant sex by progesterone-PMSG treatment interaction for birth weight, with untreated males averaging 14.2 kg compared to 12.4 kg for untreated females, and 14.1 and 13.9 kg for treated males and females, respectively. There was no evidence that this interaction was associated with date of birth or that later liveweights varied with progesterone-PMSG treatment.

Birth weights of the sets of twins were: males 9.9, 9.6 kg; females 10.4, 9.6 kg; and the unlike sex set 8.0 (male), 8.2 kg (female).

Calf growth rates

Table 4 gives early, later, and overall growth rate to weaning over sex. In all instances growth rates for male calves were not significantly greater than for females. Early male growth rate on average was only 18 (SE =19) g/day (3%) greater than later growth rate, whereas for females early gain was 52 (SE = 19) g/day (10%) greater than later gain. There was no evidence that growth rates varied with progesterone-PMSG treatment.

Birth weight regressions

There was a significant regression of BW on DW, given by

$$BW = 0.081\ (0.026)\ DW + 4.83 \qquad R^2(adj)\% = 33.9,$$

where the significant interaction of sex and progesterone-PMSG treatment, affecting intercept only, has been adjusted for. There was no evidence that date of birth influenced birth weight. The allometric relationship between ML and BW expressed by their log-log regression, was given by

$$\log BW = 1.77\ (0.30) \log ML + 2.62 \qquad R^2(adj)\% = 49.1,$$

with no significant sex difference in parameters. The estimated slope was not significantly different from 2, indicating that ML squared was a suitable measure of skeletal size for comparison with BW.

The regression of gestation length on birth weight for male F1 calves gave the significant negative relationship,

$$GL = -1.26\ (0.564)\ BW + 257.4 \qquad R^2(adj)\% = 38.0.$$

There was no evidence that dam weight influenced male calf gestation length except through birth weight and no evidence of any relationship for female calf gestation length and birth weight.

Growth rate regressions

Table 5 gives the regression coefficients for early, late, and overall growth rates to weaning on metatarsus length squared, birth weight, and dam weight fitted individually after year and sex. Both birth weight and metatarsus length squared were significantly related to early growth but not to later growth, whereas only metatarsus length squared was related to growth to weaning significantly. In all instances the contribution of dam weight to growth was not significant when fitted after metatarsus length squared or birth weight and barely significant only when fitted first to overall growth to weaning.

F1 Reproductive performance

Table 6 summarises the reproductive performance of F1 hinds in the 1985 and 1986 breeding seasons showing that all hinds calved in at least one of the 2 years. One hind which calved as a 2-year old died the following winter. All three F1 hinds which did not calve as 2-year olds in 1985 calved as 3-year olds in 1986. The loss of one F2 calf in 1985 was caused by dystocia and in 1986 one F2 calf was assisted dead at birth and another died from misadventure.

DISCUSSION

The birth of F1 calves to 72% of the red hinds run with wapiti bulls (Table 2) shows they can be interbred on farms. However, all bulls did not display rutting behaviour towards hinds and the synchronisation of oestrus in some hinds facilitated the identification of bulls which would work. The use of CIDR-PMSG treatments, to synchronise oestrus in hinds, did not adversely affect their calving performance when compared to non-treated hinds (74% v. 69%). The calving percentage is less than the 91% achieved using either red stags or wapiti-type or wapiti hybrid bulls of feral (Fiordland) extraction (Moore 1984). A higher calving percentage from the hinds could likely have been achieved as in 1986 (85% including calves from replacement stags), if replacement stags had been used in the other years. F1 twins are likely to overtax a hind's rearing ability and therefore their incidence should be minimised by using only low dose rates of PMSG and not treating the hinds before the normal breeding season (Moore 1987b). The 1986 result of two out of the three treated hinds calving early producing F1 twins is similar to a result in 1985 when four out of six treated hinds calving early produced twin red deer calves (Moore & Cowie 1986). Poor sire fertility before the normal breeding season was considered responsible for the low number (6 of 45) of pregnant treated hinds calving to mating at the induced oestrus in this other experiment.

Some of the wapiti bulls observed lacked interest in herding or rutting with red hinds and those that rutted sired fewer calves (14–21) than could be expected from a red stag (over 70, Moore et al. 1985). The two primary sires used in 1984 and 1985 each mated only about 20 out of the 30 hinds available to them before showing signs of sexual exhaustion by failing to mate hinds in oestrus. Another cause of bulls not working is apparent intimidation resulting from running them too close to other bulls in adjacent mating groups (Moore unpubl. data).

The feeding management in our study was designed to minimise rumen fill and fatness in the hind's birth canal that could impede the normal presentation and delivery of the F1 calf, rather than aim to reduce calf birth size and possibly viability by severe underfeeding. Although our reasoning has yet to be tested empirically, the results achieved have been more than satisfactory. The production of F1 calves by hinds did not lower their subsequent fertility, with 91% of the hinds calving again the next season, the same as with pure red deer noted above.

Gestation lengths recorded for red deer (Kelly & Moore 1977; Moore unpubl. data) and wapiti (Moore unpubl. data) at Invermay were analysed to enable comparisons with the gestation length of F1 calves. Gestation lengths of red deer calves were 232.7 (males, $n = 49$), 233.6 days (females, $n = 47$) SED = 0.7, and are similar to those reported by others (Guinness et al. 1971; Clutton-Brock et al. 1982).

Table 5 Regression coefficients for early (GR1), late (GR2), and overall (GR) F1 calf growth rates to weaning and metatarsus length squared (ML^2), birth weight (BW), and dam weight (DW) with the sex effect on intercept (1984, 1985 born calves).

y variate	Intercept Male	Intercept Female	Slope	SE (slope)		x variate	R^2 (adj) %
GR1	295	255	0.369	(0.178)	*	ML^2	15.8
GR1	314	280	20.1	(8.5)	*	BW	18.4
GR1	215	167	3.45	(1.85)	NS	DW	14.0
GR2	78	33	0.566	(0.358)	NS	ML^2	14.8
GR2	504	452	2.6	(17.9)	NS	BW	9.1
GR2	–91	–148	5.71	(3.7)	NS	DW	14.5
GR	257	216	0.389	(0.178)	*	ML^2	24.9
GR	368	331	14.6	(8.8)	NS	BW	21.1
GR	154	105	3.80	(1.85)	*	DW	23.9

In the sample of red deer gestation lengths (n = 46) for which calf birth weight and dam mating weight were recorded, there was no significant sex or dam mating weight effect on birth weight or gestation length. The equation for gestation length (GL) on birth weight (BW) was

$$GL = 246.9\ (4.4) - 1.57\ (0.50)\ BW \qquad R^2(adj)\% = 20.1.$$

The gestation lengths recorded for wapiti calves averaged 253.3 (male, n = 3) and 252.3 days (females, n = 4) SED = 1.5, significantly longer than for red calves. There was no significant sex effect as found with the F1 calves. Data in the literature on wapiti gestation length are questionable and confusing (Sadlier 1987). Hence with the small amount of data available on wapiti gestation length it is not realistic to attempt analysis of whether F1 gestation length is intermediate between the parent forms or skewed towards red deer.

However, the significant sex difference in gestation length for F1 calves of the same birth weight, with males on average having a 1.8 day shorter gestation, suggests gestation length can be shortened by calf size interacting with the uterine capabilities of the dam. Further evidence of this is the significant negative relationship of gestation length of F1 males with their birth weight. However, birth must be initiated by the foetus or conceptus because the F1 gestation length is longer than for a red calf. This is in agreement with Liggins (1979), who concluded the conceptus probably dominates the mechanisms stimulating the onset of parturition in most mammalian species.

The results from this F1 study can be compared with those from our Invermay study of factors affecting liveweight gain in red deer calves from birth to weaning (Moore et al. 1988) using calves born in the 1984–85 seasons. The mean dam weight of F1 calves was 111 kg (Table 4), 10 kg heavier than the mean dam weight of the red deer calves.

F1 stag calves weighed 6% more at birth than F1 hind calves, less than the 10% difference in red calves. A 10 kg increase in dam mating weight corresponded to a 0.81 kg increase in F1 birth weight. With the red deer calves a 10 kg increase in dam mating weight corresponded to a 0.33 kg increase in calf birth weight. Thus the dams of the F1's, which were 10 kg heavier on average at mating than the dams of the red calves, had F1 calves 0.48 kg heavier than expected for a corresponding 10 kg increase in dam weight. Dam mating weight therefore appears to have a far larger influence on calf birth weight for the F1's more fully utilising the hinds bearing capacity.

The finding that hinds not treated with progesterone-PMSG produced significantly lighter female calves at birth was unexpected. No explanation can be offered.

The growth rates of F1 stag calves to weaning were not significantly greater than the F1 female calves, unlike the red calves where males were significantly heavier than females by 4.8 kg (13%) at 12 weeks of age (Moore et al. 1988). F1 males were only 2.8 kg (5%) heavier than F1 females at 11 weeks of age. Either there is not the same degree of sexual dimorphism in the growth of young F1's compared to reds and/or more likely the red hind cannot fully meet the greater lactational demands of the F1 stag calf compared to the F1 hind calf.

The rearing of F1 calves to 57 kg (males) and 54 kg (females) at 11 weeks of age achieved weights which were 36% (male) and 46% (female) higher than those of red calves weaned at 12 weeks of age.

The suckling and sucking behaviours of some of the F1 calves in our study were investigated in a comparison with red deer calves by Milne (1987). He observed that F1 calves were suckled for no longer than red calves of similar age. As the mean early gain (to 50 days) of F1 males is 36% greater than male reds (566 g/day v. 415 g/day) it can be concluded that F1 calves suck more milk from a hind over a given sucking period than do red calves and that a red hind fed well over lactation can produce more milk than a red calf can utilise. This is supported by Milne's observation that the dams of F1 calves spent more time grazing during early to mid-lactation than the hinds which produced red calves.

With F1 calves, body size at birth, but not sex of the calf, was the major factor accounting for variability in early growth but not later growth before weaning. The main effect of dam mating weight on calf gain is through calf body size at birth and not directly on calf gain. With the red deer calves, sex was an important factor in accounting for variability in growth.

Table 6 Reproductive performance of F1 deer.

Breeding season	Age in months	No. of hinds	No. of hinds calving	Calf mortality	Sire
1985	28	1	1	0	BY258
	16	5	3	1	BY258
1986	40	1	1	0	BY384
	28	4	4	0	BY384
	16	9	9	2	BY258

There was a highly significant relationship between F1 calf birth weight and the square of metatarsus length at birth (Table 5) as reported for red deer calves (Moore et al. 1988). For the red deer calves it was suggested this relationship could be used to estimate the birth weight of unfresh dead calves as an aid in assessing whether dead newborn calves were over or undersized at birth in studies on causes of perinatal mortality. Likewise this relationship could be of use in monitoring causes of neonatal F1 calf mortality, although most dystocias of F1 calves relate to foetal over size and generally either have a swollen head or require assistance.

The breeding performance of the F1 progeny (Table 6) is proof that they are fertile, confirming the finding of Winans (1913). The crossbreeding of the parent forms and the fertility of their hybrids supports the hypotheses that the wapiti and red deer have not become reproductively isolated and, furthermore, that the original hybridisation of the subspecies in Fiordland could have occurred from the union of a wapiti bull and red hind as proposed by Batchelor & McLennan (1977).

From the view of deer farm production, our study has shown that the use of wapiti sires over large red hinds can maximise the birth weight of calf produceable and rearable by a red hind. As it is through a natural process not involving artificial growth promotants, this has marketing advantages for the venison. The breeding problems and management requirements with pure wapiti sires over hinds suggests their F1 or synthesised F2 type stags as better heavy-weight sires for widespread use over average sized red hinds.

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