



# Final Client Report

Prepared for DEEResearch Ltd Contract No: 2.01

September 2004

## **Reproductive performance of pubertal red deer (*Cervus elaphus*) hinds : Effects of genetic introgression of wapiti subspecies on pregnancy rates at 18 months of age.**

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## Lay Summary

- Within the last decade, the variable but generally poor reproductive performance of young hinds (rising two-year-olds) has been highlighted as a significant productivity issue. Pregnancy rates have varied from 40 to 95%, probably reflecting failure of many hinds to reach puberty at 16 months of age.
- While threshold liveweights for puberty of red deer of Scottish origin (e.g. *Cervus elaphus scoticus*) have been estimated at 65-70 kg at 16 months of age, most yearling hinds in New Zealand are well in excess of this. One consideration is that maybe the genetic constitution of NZ farmed deer has changed in favour of a larger mature hind genotype with higher weight thresholds for puberty.
- Wapiti subspecies (*C.e. nelsoni*, *manitobensis*, *roosevelti*) have been used widely for crossbreeding purposes to capture the benefits of the rapid growth characteristics of crossbred calves. This has resulted in the gradual introgression (merging) of Wapiti genes into the national deer herd.
- Given the extreme two-fold difference in mature body weight between red deer hinds and Wapiti cows, it is likely that threshold weights for puberty will be considerably higher for “crossbred” hinds than for “pure” red deer hinds.
- DEEResearch Ltd commissioned a study to investigate the possible effect of Wapiti introgression on puberty of red deer hinds. The aims were to assist with improved reproductive performance by:
  - (1) assessing levels of variation of physical features within groups of yearling hinds and determining how this variation related to the proportion of Wapiti genes individual hinds carried; and
  - (2) determining the effects of different levels of Wapiti genes on the pregnancy rate of yearling hinds at 18 months of age, particularly in relation to liveweight effects on performance.
- All rising two-year-old hinds on four large Otago/Southland farms over a two-year period were studied, totalling 4,329 individuals.
- The farms had differing policies of excluding or including known or suspected crossbreds within their breeding herds.
- The 18 month old hinds were weighed, measured (e.g. body length, shoulder height, head length and head width), body condition scored (BCS) and scored for “obviousness of Wapiti features” (a 5-point ranking where 1 = no evidence of Wapiti features and 5 = highly obvious Wapiti features) ... called “Wapiti Score”. Hinds

were then ultrasound scanned (via rectum) to assess pregnancy status. A hair sample was collected from every animal for later DNA analysis of a pre-determined sample of 1,258 individuals. The *Elkmeter*<sup>™</sup> analysis of 14 DNA markers estimated the actual level of Wapiti parentage of these individuals.

- Using all of the available information, three measures of “Wapiti parentage” were calculated for each individual ...
  - (1) **Wapiti Score (WS)**; subjectively assess in the field;
  - (2) **Corrected Wapiti Score (CWS)**; corrected for between farm variation in the regression of WS on *Elkmeter*<sup>™</sup>;
  - (3) **Estimated Wapiti Parentage (EWP)**; used the strong association between some of the morphological measurements (i.e. body length, shoulder height and liveweight) and *Elkmeter*<sup>™</sup> to calculate a totally objective measure for every hind of Wapiti parentage.
- Of the 4,329 hinds in the study, 506 (11.7%) were not pregnant, with non-pregnancy rates varying between 4.1 and 37.3% between farms and years. Average hind liveweights ranged from 88-100 kg.
- Generally, there was a positive correlation between WS and *Elkmeter*<sup>™</sup> values, indicating that WS was a useful “ready-reckoner” for indicating the presence and degree of Wapiti introgression within herds.
- All farms showed evidence of some degree of Wapiti introgression, irrespective of genetic management. However, levels were lower for those farms that did actively exclude suspected crossbreds from the breeding herd.
- Irrespective of the measure of Wapiti introgression use (i.e. WS, CWS, ESP), there was a significant negative association between hind Wapiti parentage and confirmed pregnancy, which was strongly influenced by liveweight.
- EWP tells the most compelling story. Within the range of liveweights observed on the four farms, there was little differentiation of performance of animals between 0 and 20% actual Wapiti parentage. However, as Wapiti parentage exceeded 20% the probability of pregnancy relationships changed. Pregnancy rate decreased at a given liveweight. Furthermore, critical liveweights required to achieve a given pregnancy level increased with increasing Wapiti parentage. For example, predicted threshold liveweights required to achieve a 90% pregnancy rate for 0, 10, 20, 30, 40 and 50% Wapiti parentage were 81, 81, 85, 106, 127 and 136 kg, respectively. It was concluded that

- (1) Within “red deer” systems on the four farms, mean liveweight targets and achievement for yearling hinds did not penalise animals with <20% Wapiti but severely penalised animals with >20% Wapiti. Animals with higher levels of Wapiti parentage were simply unable to achieve threshold weights for high pregnancy rates.
- (2) Animals with >20% Wapiti parentage probably need to be managed as “crossbreds” rather than as “red deer” in order to optimise growth performance. Target liveweights for such genotypes need to be considerably higher than presently achieved for “red deer”.

## **Implications of the research results**

If the four farms in the present study are in anyway representative of the national situation, then the effects of Wapiti introgression on pubertal performance of “red deer” hinds cannot be ignored. We would argue strongly that introgression, brought about by the indiscriminate and widespread use of Wapiti x red crossbreeding over the last two decades, has been reasonably pervasive throughout the country. Therefore, the implications may be also pervasive across the country.

By our reckoning of yearling hind numbers presently in the New Zealand herd (90,000-100,000), every 1% increase in weaning rate for yearling hinds represents around 900-1000 extra weaned calves on the ground. This translates to between \$100,000 and \$150,000 potential farm revenues per annum. If the national average weaning rate for yearlings jumps from a present average of ~75% to, say 85% through better genotype management, then this would represent \$1 million to \$1.5 million per annum at current market prices.

The implications of Wapiti introgression of puberty is an entirely manageable situation given our current awareness of the issues. Once farmers have tools to identify animals with significant levels of Wapiti parentage (the present study suggests that >20% Wapiti parentage is biologically significant within present “red deer” systems), the management options available include:

- (1) Do nothing and accept reduced reproductive performance of yearling hinds that carry a high proportion of Wapiti genes.
- (2) Implement early identification of hinds with more than 20% Wapiti parentage (i.e. by using a scoring system or DNA analysis) and
  - a. Remove these animals from the herd of hinds to be recruited into the breeding herd;

- b. Separate these animals as weaners and apply management systems better suited to their genotype. This will improve their chances of growing to their genetic potential in order to attain puberty at 16 months.
- (3) Scan yearling hinds at 18-20 months of age and remove the non-pregnant animals (for slaughter?). Over time this will likely penalise animals with >20% Wapiti parentage and reduce levels of introgression within the base breeding herd.
- (4) Set herd target liveweights higher to accommodate the larger bodymass genotypes present within the herd. This may require a paradigm shift in feed and health management strategy.

### **Further recommendations**

- (1) DEEResearch Ltd to promote industry awareness of the issues of Wapiti introgression in relation to reproductive performance of young red deer hinds in a manner that clearly outlines the range of management options to improve reproductive productivity.
- (2) DEEResearch Ltd to support initiatives to further refine and develop the “Wapiti Score” system into a farmer-usable tool to assess levels of Wapiti introgression in younger (weaner) red deer. It is particularly important that this system clearly identifies animals with >20% Wapiti parentage. This will provide opportunities for the earlier instigation of genetic and/or nutritional management policies to improve overall farm productivity.

## Main Report

Submitted to Animal Reproduction Science, August 2004.

**Reproductive performance of pubertal red deer (*Cervus elaphus*) hinds:  
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### Abstract

Low reproductive productivity of young red deer (*Cervus elaphus*) hinds on New Zealand deer farms appears to reflect high incidences of puberty failure at 16 months of age. This is despite the general attainment of average live weights 15-25 kg in excess of the accepted minimum threshold for puberty in red deer subspecies of western European origin (*scoticus*, *elaphus*, *hippelaphus*) that form the basis of the national farmed herd. The present study tests the hypotheses that introgression of the larger North American wapiti subspecies (*nelsoni*, *manitobensis*, *roosevelti*) into breeding herds (1) can be assessed from morphological features of individuals, (2) that there is a relationship between the level of wapiti parentage and non-pregnancy rate at 18 months of age (a proxy for puberty failure) and (3) that minimum liveweight thresholds for puberty increase with increasing levels of wapiti parentage.

A total of 4329 18-month-old hinds across four "red" deer farms in southern New Zealand were scanned by ultrasonography for pregnancy status. Each hind was assigned a Wapiti Score (WS) as a subjective assessment of the obviousness of wapiti features. They were additionally measured for body length, shoulder height, head length, head width, live weight and body condition score (BCS). A hair follicle sample was collected for DNA analysis (14 markers) to objectively assign subspecies pedigree

(i.e. “Elkmeter”) on a subset of 1258 individuals. A total of 506 (11.7%) hinds were not pregnant at 18 months of age, with rates varying between 4.1% and 37.3% between farms and years. Mean WS differed significantly between farms and reflected the genetic management policy of each farm. WS was positively correlated to Elkmeter for each farm/year ( $<0.05$ ) but regression slopes varied significantly, with strong biases reflecting under-estimation of wapiti influence on farms with highest levels of introgression, and over-estimation on farms with lowest levels of introgression. WS was able to be adjusted for these differences to assign a corrected WS (CWS) for all 4329 individuals that estimated the proportion wapiti parentage. Discriminant analysis of morphological variables relative to Elkmeter showed that shoulder height and body length were good indicators of the degree of wapiti parentage within individuals and enabled the development of an objective estimate of wapiti parentage (EWP). The actual level of such parentage within herds ranged from  $<5\%$  to  $>55\%$ . There was a significant negative association between hind wapiti parentage and confirmed pregnancy, which was strongly influenced by live weight. This was manifest as marked displacement of pregnancy probability curves in relation to live weight between genotype groups, particularly for those groups with  $>20\%$  wapiti parentage. For example, predicted threshold liveweights required to achieve a 90% pregnancy rate for EWP values that represent 0, 10, 20, 30, 40 and 50 percent wapiti parentage were 81, 81, 85, 106, 127 and  $\sim 136$  kg, respectively. Within the study herds, the majority of hinds of 0-20% wapiti parentage exceeded the predicted 90% threshold live weights for their genotype cohort. However, hinds with higher levels of wapiti parentage generally fell below the predicted threshold for their genotype group. The data strongly suggests that under live weight performance levels measured for red deer, hinds with  $>20\%$  wapiti parentage are at increased risk of puberty failure.

**Keywords:** Red deer, wapiti, *Cervus elaphus*, crossbreeding, introgression, puberty, reproduction



## 1. Introduction

Pastoral farming of red deer (*Cervus elaphus*) has been established in New Zealand for about 30 years, with >1.2 million breeding hinds presently held across 4500 farms (NZ Ministry of Agriculture and Forestry, Farm Statistics 2003). Over 65% of the national population are hinds of breeding age ( $\geq 2$  years) and reproductive performance of hinds is a key indicator of on-farm productivity and profitability on most farms (Asher and Pearse, 2002).

Within the last decade, the variable but generally poor reproductive performance of young hinds (i.e. rising two-year-olds) has become a significant productivity issue in New Zealand (Audigé *et al.*, 1998; Beatson *et al.*, 2000). While red deer hinds normally attain puberty (first ovulation) and conceive during their second autumn at 16 months of age (i.e. calve at 24 months of age), about 15% of young hinds in NZ fail to become pregnant as rising-two-year-olds (Asher and Pearse, 2002). Widespread application of real-time ultrasonography to hinds at 18-20 months of age, when foetal ages range from 30-120 days, has revealed pregnancy rates ranging from 40% to 95% across farms. Given that low levels of embryonic/foetal wastage seem to occur in red deer, it is generally believed that the high barrenness rate on many farms represents either failure of many hinds to enter puberty (i.e. ovulate) at 16 months of age or failure of these hinds to be mated at first ovulation (Asher and Pearse, 2002).

A number of factors have been postulated as potentially influencing puberty/conception in young red deer hinds, including social inhibitions, environmental stressors and poor growth of young stock. The latter factor is often related to putative liveweight thresholds for the attainment of puberty once hinds are within the appropriate photoperiodic regimen at 16 months of age (Kelly & Moore, 1997). Early studies on Scottish red deer (*C.e. scoticus*) in Britain indicated a 65 kg threshold for attainment of hind puberty at 16 months of age (Hamilton & Blaxter 1980).

The 65 kg liveweight threshold criterion has been used extensively as a management guide in New Zealand (Kelly & Moore 1977; Fisher & Fennessy 1985), an industry that was originally based on the Scottish subspecies (Fennessy, 1992). However, it has recently become apparent that despite industry average live weights 20-30 kg above the putative threshold, high barrenness rates are common in some farming operations (Beatson *et al.*, 2000). This indicates that the 65 kg threshold may no longer be relevant to the general population of farmed deer in New Zealand. Little consideration has been given to the effects of genetic introgression of other, larger subspecies into the farmed red deer population over the last 15-20 years on puberty liveweight thresholds.

The Scottish red deer, with mature hind body mass of ~100 kg, is the smallest subspecies in a west-east, Eurasian-North American subspecies cline characterised by increasing mature body mass (Harrington 1985). Recent importations into New Zealand of new genotypes have included Eastern European red deer (*C.e. hippelaphus*), with a mature hind body mass of 130-150 kg, and North American wapiti (*C.e. nelsoni*, *roosevelti*, *manitobensis*), with a mature cow body mass of 220-260 kg (Whitehead 1972; Haigh and Hudson, 1993). Both of these genotypes have been widely introgressed into the New Zealand farmed red deer population.

The North American wapiti or elk, in particular, has been widely used for crossbreeding purposes to capitalize on the rapid growth characteristics of crossbred calves while maintaining minimal energy inputs into smaller red deer dams (Moore, 1985; Fennessy & Thompson, 1988; Nicol *et al.*, 2003). Such energetic efficiency presupposes a wapiti terminal-sire option in which all crossbred progeny are slaughtered for venison production (Fennessy & Thompson, 1988, 1989). However, female crossbred progeny were seldom slaughtered and were generally retained for breeding purposes, often as large “red deer” (Pearse and Goosen, 1999). Possibly partly as a result of inadvertent or purposeful introgression, the average mature weight of red deer hinds in New Zealand appears to have increased from ~100 kg to ~120 kg over two decades (Pearse and Goosen, 1999; Asher and Pearse, 2002).

The consequences of wapiti introgression on female puberty have never been assessed previously. The various North American wapiti subspecies are reputedly slower maturing than red deer, with most cows attaining puberty at 27 months of age (Taber *et al.*, 1982) although earlier puberty is common under conditions of good nutrition and growth (Haigh & Hudson, 1993). Given the extreme two-fold difference in mature body mass between red deer hinds and wapiti cows, it is likely that threshold liveweights for attainment of puberty will be considerably higher in wapiti and crossbred cows. Thus, while most young “red deer” hinds in New Zealand exceed the putative threshold for the Scottish subspecies, this may not reflect the weight required for their true genotype in some cases.

The present study aimed to establish levels of wapiti introgression within some large commercial “red deer” herds and to determine the influence of such introgression on hind pregnancy rate at 18 months of age (as indicative of puberty at 16 months of age). The following hypotheses were tested:

1. Wapiti introgression within “red deer” herds is reflected in levels of morphological phenotype variation within a given cohort, and a subjective score based on phenotype for each individual reflects its level of wapiti parentage.

2. Within a given herd, (a) the proportion of wapiti genes, (b) the assigned subjective score of wapiti influence on phenotype, and (c) estimated wapiti influence based on morphological phenotypic measurements, within individuals, is negatively related to the attainment of female puberty at 16 months (i.e. pregnancy at 18 months).
3. As the proportion of wapiti genes within individual females increases, the liveweight threshold for the attainment of puberty increases.
4. For individuals attaining puberty at 16 months (i.e. pregnant at 18 months), conception date is progressively advanced with (a) increasing proportion of wapiti genes and/or phenotype, and (b) with increasing liveweight.

## **2. Materials and Methods**

### *2.1 Animals and management*

All rising-two-year old hinds raised on four Otago/Southland farms over a two-year period were studied (Table 1), with a complete data set collected for a total of 4329 individuals. The four farms chosen represented a range of breeding operations in which the base breeding herd was principally “red deer”, although an unknown degree of wapiti influence was suspected or known to occur on two of the farms (Farms A and B). The remaining two farms (C and D) had a policy of maintaining a “pure” red deer nucleus breeding herd and actively avoided recruitment of known or suspected hybrids. All measurements on hinds were recorded in June/July, at approximately 18 months of age and at least 30 days after removal of stags in the previous mating period. Similar mating practices had been employed across all four farms, in which the young hinds were grouped separately from other hind age groups and joined with similar aged stags at ratios of between 1:8 to 1:12 stags:hinds. The joining period extended from late February/early March to late May, at which time all stags were removed. All management procedures were at the discretion of the individual farm managers and there was no attempt to influence these for the purposes of this study.

### *2.2 Measurements*

Hinds were yarded off-pasture no more than 2-3 hours prior to measurement. Measurements recorded for each animal included liveweight (0.2 – 0.5 kg resolution as measured on electronic scales), shoulder height (measured from a rigid calibrated pole while free-standing), body length (measured from the base of the tail to the nape of the neck using a flexible tape while free-standing), and head length and head width (axis

junction to nose tip, and widest point over skull from the eye orbits, respectively, measured by flexible tape while the hinds were restrained in a crush). Additionally, each hind was assigned scores for body condition and obviousness of wapiti features. Body Condition Score (BCS) was based on the 5-point ranking devised by Audigé *et al.*, 1998) in which a score of 1.0 represents very poor condition (cachexia) and a score of 5.0 represents very good condition (fat). In reality, scoring was performed in 0.5 BCS increments by a single observer throughout the study. Wapiti Score (WS) was a 5-point ranking, with a score of 1 representing individuals with no observable physical features indicative of wapiti parentage and 5 representing individuals that exhibited obvious features of wapiti parentage similar to those of an F<sub>1</sub> cross between red deer and wapiti parents. The scoring was performed by a single observer throughout the study. Assessment of wapiti-like features was based on general body height/length relative to herdmates (taller and longer stature for wapiti), size and colour of the rump patch (larger and paler for wapiti), general body pelage colour (paler for wapiti), colour of the neck and face (darker for wapiti) and the appearance of the neck mane (more pronounced for wapiti). The score was not devised to assess the degree (%) of wapiti parentage, only the obviousness of physical features.

### 2.3 *Pregnancy determination*

While restrained in a pneumatic or hydraulic crush, each hind was subjected to real-time rectal ultrasonography using a 5 MHz linear array transducer (Aloka SSD 210; MedTel Teletronics Ltd, Auckland) to assess pregnancy status. Scanning was timed to ensure foetal ages ranged between 30 and 80 days in order to accurately visualise and measure foetal size. When pregnancy was visualised, foetal age was assessed using foetal dimension criteria described by White *et al.* (1989) to retrospectively calculate conception dates to within  $\pm 5$  days. Determination of non-pregnancy status was based on visualisation of the non-gravid uterus. Such individuals were rescanned 30 days later, or inspected at slaughter within one month of scanning, to confirm the non-pregnancy diagnoses.

### 2.4 *DNA analyses*

Hair follicle samples were pulled from each hind while restrained in the crush, and stored in labelled manilla envelopes at ambient temperatures. All non-pregnant hinds and an equal number of pregnant hinds chosen randomly from within farm and Wapiti Score cohorts (i.e. 1258 individuals) were analysed for DNA markers of hybridisation. For each selected animal, 10 or so follicles were cut from their hair shafts and incubated

in a 200mM NaOH solution, at ~97°C for 20 minutes. The solution was then neutralised with the addition of 200mM HCl and buffer (100mM Tris HCl). This produced polymerase chain reaction (PCR) ready DNA of which 1.5µl was used for each 10µl reaction. The template genomic DNA was PCR amplified for a specially selected cervine suite of 14 DNA microsatellite (short tandem repeat) markers.

The samples in this trial were run on three different types of DNA sequencers over the three years of analysis; ABI 377 agarose gel, ABI3100 capillary and ABI3730 capillary sequencers. The gel images or marker data generated by the sequencers was 'scored' (observed peaks assigned as alleles) using automated macros in Genotyper™ or Genemapper™ software from Applied Biosystems. This automated scoring was manually checked by two people. This procedure is an update of that described by Tate *et al.* (1998a).

The raw data was loaded on to a genotype database where alleles were allocated to 'bins'. These 'bins' accept alleles, for each marker, within specific fragment size range tolerances and reject the rest. The 'bins' are assigned alphabetic characters (e.g. A, D) and stored and analysed using these characters. The data in the genotype database was downloaded using MS Access and analysed for the 'Genometer Elk test' in SAS.

The 14 DNA markers are used to undertake pedigree and crossbred testing for New Zealand farmed red deer, wapiti (or "elk" which is common usage for 'pure' wapiti in New Zealand and North America) and their crossbreds (Genomnz Ltd, Invermay Agricultural Centre, Mosgiel). Markers were selected for the suite for their polymorphism between individuals and their polymorphism between wapiti and red deer. The markers range from being a fairly uninformative pedigree marker but very informative hybrid marker to the converse and cover the whole range between these two extremes of testing types. The 14 marker suite is an update (one marker removed and two new ones added) of the 13 marker suite described by Tate *et al.* (1998a). This marker suite was screened across 500 'standards'; 380 'typical' wapiti samples from North America and 120 red deer samples. The red deer samples were intended to be representative of the pure red deer genotypes present on New Zealand farms obtained prior to widespread use of wapiti sires. Relative allele frequencies for red and wapiti were calculated from the data generated by the screening of the 14 microsatellite markers. The allele frequencies were treated as described by Tate *et al.* (1998b), that no one allele is assumed to be absolutely species or breed specific, even if that allele was not observed in 'standards population' for one species or breed and was observed in the other. The individual's DNA marker data was analysed using the composite breed estimation method described by Dodds *et al.* (1997). This method estimates the genetic proportions of two contributing parental populations in an individual. This test is specifically provided for

wapiti x red crossbreds as the “Genomnz Elkmeter test v 3.0”, hereafter referred to as “Elkmeter”.

In the present analysis the estimated value of crossbreeding was called the “estimated wapiti %”. This is the estimated percentage of wapiti genes in an individual, bounded by confidence intervals. In practice the “estimated wapiti %” can range from approximately 4% wapiti genes (red deer) to 96% wapiti genes (wapiti) (Dodds *et al*, 1997).

## 2.5 Statistical Analyses

Wapiti score was analysed as a continuous variable by least squares, fitting farm, year and their interaction. As only 18 animals across three farms had WS=5, these individuals were included with WS=4 for subsequent analysis (see Table 3). A “corrected wapiti score” (CWS) was defined by allocating to individuals the mean Elkmeter score for their WS on their farm and year (Table 3), and rounding to the nearest value in {0.1, 0.2, 0.3, 0.4}. For example, animals with WS=3 on farm D in both years had CWS=0.3, while animals with WS=1 on farm A in both years had CWS=0.2.

The regression relationship of Elkmeter value on WS was evaluated using the 1258 animals selected for DNA analysis (see Table 1), allowing separate slopes and intercepts for each farm in each year. The relationship between WS and the morphological variables was investigated using discriminant analysis. The relationship between Elkmeter and the morphological variables was analysed using multiple regression, with and without adjustments for farm, year and their interaction.

An explanatory variable was derived to express degree of wapiti introgression as accurately and objectively as possible for all animals. It equalled Elkmeter value for those animals for which it was known, and predicted Elkmeter score for the other animals, based on the multiple regression of elkmeter on all morphological variables, allowing separate slopes and intercepts for each farm. This parameter was termed “estimated wapiti parentage” (EWP). WS was not used in this calculation. Pregnancy status was then analysed using a binomial generalized linear model (McCullagh and Nelder, 1989), adjusting for farm, year and their interaction, and then fitting a spline in EWP, live weight and body condition score in sequence. WS and CWS were also used as alternatives to EWP in this analysis. Conception date was analysed by linear regression, fitting the same explanatory terms.

### 3. Results

#### 3.1 General Farm Productivity

Of the 4329 hinds measured in the study, 506 (11.7%) were not pregnant at ~18 months of age (Table 1). Actual pregnancy rates varied between farms and years from 95.9% (Farm C 2002) to 62.7% (Farm B 2003) (Table 2). While mean conception dates were generally grouped around Day 102-106 (12-16 April) on most farms, two notable exceptions were the earlier conceptions for Farm C 2003 (5 April) and the later conceptions for Farm D 2002 (27 April) (Table 2). These did not appear to relate to stag joining dates, as the farms were fairly uniform in this respect. Mean live weights of hinds at ~18 months of age ranged from 88.5 kg (Farm C 2002) to 100.8 kg (Farm D 2002), with most farms averaging in the 90-94 kg range (Table 2). Mean body condition scores (BCS) ranged between 3.45 and 3.90 (Table 2).

#### 3.2 Measures of wapiti introgression

Mean wapiti scores (WS) differed significantly between farms and years ( $P < 0.05$ ; Table 2), being consistently higher across years for Farms A and B, where there was a known wapiti influence within the breeding herd (i.e. mean scores 1.66-1.96), than for Farms C and D, which had policies of selecting for “pure” red deer breeding herds (i.e. mean scores 1.15-1.33). The frequency of individual WS by farm and year are presented in Table 1.

There was a significant positive regression of Elkmeter value on WS for each farm in each year ( $P < 0.05$ - $0.001$ ), although regression slopes varied significantly between farms and years (Table 3). Thus at  $WS=1$ , Elkmeter values ranged from 0.08 to 0.22, while at  $WS=4+$  values ranged from 0.22-0.49. The main biases appeared to be a general underestimation of wapiti influence at low WS for farms A and B (i.e. known wapiti influence), and a general overestimation of wapiti influence at low-mid WS for farms C and D (i.e. avoidance of wapiti influence).

Using the within-farm and year regression coefficients, all WS were adjusted for differences between farm and year cohorts to calculate “corrected wapiti score” (CWS) for all 4329 individuals. This essentially gave 32 discrete values (scores) for assessed level of wapiti parentage. For subsequent analysis, these values were grouped into four categories (i.e.  $<0.15$ ,  $0.15$ - $0.25$ ,  $0.26$ - $0.35$  and  $>0.36$ ) that each defined a range of assigned wapiti parentages (i.e. percent wapiti).

The result of the discriminant analysis of the morphological variables and WS is given in Table 4. The first canonical vector is the only one to make a substantial contribution,

and shows that the combination of shoulder height and body length is a good indicator of the degree of wapiti introgression as measured by WS, with some positive influence from liveweight, but little from the head measurements. The group means of the first vector increment evenly with wapiti score. The stepwise multiple regression of Elkmeter on morphological data, without and with adjustment for farm and year, is given in Table 5. In both cases the strongest contributions come from shoulder height and body length, although after adjustment for farm and year, body length is fitted subsequent to head length. In both cases body condition score had a significant negative slope. On the basis of this analysis, EWP parameter was calculated for each individual.

### 3.3 *Relationship between wapiti introgression and pregnancy rate*

The summary statistics for the binomial-logit regression of pregnancy rate on EWP, without and with the addition of the other explanatory variables, are given in Table 6, and the pregnancy rate versus elkmeter relationship is graphed in Figure 1. The linear component of the curve is strongly negative, while for the simple regression on EWP there is an upward curvature to the fitted spline for scores greater than 0.4 – 0.45. This, therefore, does not exclude the hypothesis that the observed decline in pregnancy rate may be due to effects of “negative heterosis” or even epistatic gene interactions, rather than a negative effect of wapiti parentage. In the former case the pregnancy rate versus Elkmeter score would trend upwards again for Elkmeter scores over the range 0.5 – 1.0 (for which there are few observations), while in the latter case it would continue to trend downwards. However, when live weight was then added to the model there was a strong positive slope in liveweight (Table 6), while the curvature in the spline curve for high Elkmeter scores (0.4 – 0.6) was reduced (Figure 1). This curve has been adjusted to an overall mean live weight of 91 kg. Thus, 60% wapiti hybrids weighing 91 kg have an 18% chance of pregnancy, while pure red deer weighing 91 kg have a 95% chance. Curves adjusted to other live weights are parallel to the given curves on the logit scale.

Figure 2 represents the regression with liveweight on the x-axis, with separate curves for WS values of 1, 2, 3 and 4+ (Figure 2a) and for CWS values of <0.15, 0.16-0.25, 0.26-0.35 and >0.35 proportion wapiti parentage (Figure 2b). These profiles show a clear differentiation in the probability of pregnancy throughout the various levels of estimation of wapiti introgression. This is most obvious for WS, which was earlier shown to be subject to subtle biases across different farms. For CWS, which accounts for some of these biases, differentiation between profiles for the lower categories of introgression (i.e. <0.15 and 0.15-0.25) were not as marked as for WS 1 and 2. Thus, the predicted liveweights required to achieve a 90% pregnancy rate for WS of 1, 2, 3 and 4+ are 83, 95, 115 and 129 kg, respectively, and for CWS groupings of <0.15, 0.15-0.25, 0.26-0.35



and >0.35 wapiti parentage are 79, 92, 118 and 132 kg, respectively. As shown by the thicker portion of each profile line (representing the 10<sup>th</sup> and 90<sup>th</sup> percentiles of actual hind liveweights for each WS and CWS value), most hinds of WS=1 and CWS <0.15 were between 80 and 100 kg in liveweight, and were above the predicted threshold for a 90% herd pregnancy rate. In marked contrast, most hinds at higher WS and CWS fell below their predicted threshold, particularly for WS = 3 and 4+ and CWS >0.25.

Figure 3 then represents the same regression with liveweight, with separate curves for fixed EWP values of 0, 0.1, 0.2, 0.3, 0.4 and 0.5. The obvious feature of this graph, which is based on an entirely objective measure of wapiti introgression, is the absence of any clear differentiation in curves for EWP values of 0, 0.1 and 0.2 (0-20% wapiti parentage) but marked displacement of probability curves for the higher levels of wapiti introgression (i.e. 30-50% wapiti parentage). Thus, the predicted liveweight required to achieve a 90% pregnancy rate for EWP values of 0, 0.1, 0.2, 0.3, 0.4 and 0.5 are 81, 81, 85, 106, 127 and 136 kg, respectively (note that no hinds of >50% wapiti parentage attained this weight). For EWP values of 0 – 0.2 (0 – 20% wapiti parentage), the majority of hinds were above the predicted threshold liveweight, whereas for higher values the majority of hinds were below this threshold.

There was no evidence ( $p>0.05$ ) that variation in conception date was related to percentage of wapiti genes or live weight.

#### **4. Discussion**

There is no doubt that the “red deer” population presently farmed in New Zealand has become a complex mix of introgressed subspecies, and concepts on reproductive productivity developed originally from studies of the small Scottish subspecies (*Cervus elaphus scoticus*) are of reduced relevance to this population. While overall seasonal reproductive physiology has probably altered little, selection emphasis on increased growth performance has been clearly associated with increased mature animal size (Fennessy, 1992; Pearse and Goosen, 1999). This means that the dynamics of the interactions between growth, body mass and reproduction (e.g. female puberty) have undoubtedly changed. The North American wapiti (at least three subspecies introduced into New Zealand) arguably represents the most notably introgressed genotype because of the extreme difference in body mass (a factor of at least two) to that of the European subspecies. Indiscriminant use of wapiti-type sires and dams, and the retention of most female crossbred progeny within the national breeding herd has resulted in rapid introgression over the last two decades. Clearly, however, introgression is not uniform, and populations may contain a mix of individuals with variable wapiti parentage.

The main outcomes of the present study on young red deer hinds across four New Zealand deer farms are (1) the demonstration of various levels of wapiti introgression within each population and (2) the finding that pregnancy rate of rising-two-year-old hinds was negatively associated with increasing level of wapiti parentage. These outcomes have major implications for management of young hinds to improve overall reproductive productivity of farmed herds. While the findings relate to only pubertal hinds, these animals may represent between 10% and 20% of the national breeding herd in any one year (Asher and Pearse 2002).

It is clearly not possible from the present study to draw inferences on the total levels of wapiti introgression with the national herd. The four farms in the study may not necessarily represent the range of types of breeding herds. However, two contrasting genetic management principles were represented; (1) implementation of practices to recruit only “red deer”-type hinds into the breeding herd and avoidance of the use of crossbred sires within the nucleus herds that supply replacement hinds, and (2) recruitment of larger replacement hinds irrespective of genotype, and active use of crossbred sires over all hinds in the herd. In this respect, it is important to note that few operations in New Zealand utilize purebred wapiti or high-level crossbred (i.e. >70% wapiti) sires over red deer hinds to generate F1 or similar progeny, due to animal management and health issues. However, many New Zealand deer farms utilise low-level crossbred sires (i.e.  $\leq 50\%$  wapiti) over red deer hinds to generate progeny (20-25% wapiti) of high growth potential (Yerex, 1991). It is the female progeny from this grouping that are commonly incorporated into breeding herds, often as large “red deer”. This first-cross in itself may not have marked impacts on yearling reproductive rate, as indicated by results of this study, but repeated indiscriminant use of this mating system will lead to individual hinds which contain significant (>25%) proportions of wapiti and have decreased chance of becoming pregnant in their second year.

The differing genetic policies of the study farms was clearly reflected in the actual levels of introgression observed. However, introgression was evident on all four farms and at higher levels than the herd managers had anticipated. In particular, the demonstration that some animals on farms A & B had Elkmeter and EWP values of >0.55 (i.e. >55% wapiti genes) was not in accord with the farmers’ perceptions of the level of wapiti parentage of the sires used, and perhaps indicates an overall paucity of knowledge of actual levels of introgression occurring within the base hind herd and the period of time over which introgression has been occurring.

As expected with the introgression of morphologically distinct strains, there was a detectable and measurable level of morphological variation observed on each farm. Wapiti characteristics that clearly emerge within introgressed populations include

increased body mass, body height and body length, as well as pelage colour characteristics, including size and colour of the rump patch and neck-mane colour. The “Wapiti Score” (WS) devised for the present study combined a visual assessment of these features to provide a relative ranking of the obviousness of wapiti genes within individual animals. Correlation with the DNA marker assessment of wapiti parentage (i.e. Elkmeter) demonstrated that the score did indeed identify wapiti introgression within the study herds, and that, in general, increasing WS indicated increasing level of wapiti parentage for individuals. However, there were some within-farm biases in application of WS. In particular, herds with lower levels of actual wapiti introgression (Farms C and D) tended to have an overestimation of wapiti introgression based on WS (i.e. a higher proportion of red deer ranked as exhibiting wapiti features), indicating an observer’s natural bias towards subconsciously recalibrating the scoring system to include all scores within a population. Herds with higher actual levels of introgression (Farms A and B) clearly showed better separation of scores relative to actual wapiti parentage, as the higher level crossbreds had strikingly obvious wapiti features. The development of the “corrected Wapiti Score” (CWS) based on within-farm regression coefficients (i.e. Elkmeter over WS) provided a more accurate reflection of between-farm differences in observable introgression. In this respect, it is an objective calibration of a subjective assessment system. The morphometric information provided additional quantification of wapiti introgression. The major explanatory variables of body height and body length correlated well with the Elkmeter assessment of wapiti parentage, allowing for an objective assessment of the wapiti parentage (i.e. EWP) for each individual in the study. Thus, the subsequent analyses on reproductive performance relative to level of wapiti introgression were able to draw upon subjective (WS), semi-objective (CWS) and objective (EWP) measures of wapiti parentage.

The measure of reproductive productivity used in the present study was pregnancy rate of hinds at 18 months of age. Given the difficulty in assessing ovulation status in red deer, pregnancy status was used as a proxy for the incidence of puberty (first ovulation) at 16 months of age. While recognition is given to other forms of reproductive wastage that can occur between 16 and 18 months (e.g. mating failure, fertilization failure, embryonic wastage and early foetal death), these are likely to be of minor consequence in this study given the management systems used (i.e. high-ratio multi-sire mating) and our understanding of red deer reproductive performance (Asher and Adam, 1985; Asher and Pearse, 2002). Furthermore, it is noted that while the present study used 18-month-old liveweight as a proxy for puberty weight, this is normally defined at 16 months of age when hinds initiate ovulatory activity. It is probable that this 2-month age difference is associated with some change in liveweight, although most published studies indicate that this is in the order of only 2-3 kg increase (Beatson *et al* 2000). Therefore, we have

not accommodated any adjustment for this, but acknowledge that young hinds are still growing after puberty. It is clear from the present study that the proportion of wapiti genes within individuals (by whatever means of assessment was used) was negatively related to the attainment of female puberty. Thus, groups of females with increasing wapiti parentage exhibited increasing rates of barrenness (non-pregnancy). More important, however, was the demonstration of a significant interaction between wapiti parentage and liveweight on pregnancy rate (hence puberty). Within each genotype cohort (e.g. % wapiti class) increasing liveweight was associated with an increasing probability of pregnancy. The displacement of the probability curves for each genotype cohort is entirely consistent with the paradigm of an upward shift in the liveweight threshold for attainment of puberty with increasing potential mature liveweight, as would be expected from wapiti introgression. It is unfortunate that the study was not able to extend to securing information on mature liveweight of the study animals to model the theoretical puberty threshold (critical liveweight at which 50% of individuals enter puberty) for each genotype cohort. However, interpolation of the profitability functions gives some insight into threshold liveweights. The median intercept for Scottish red deer (mainly *Cervus elaphus scoticus*), the genetically smallest of the red deer subspecies, has been assessed as 65 kg at 16-months of age (Hamilton and Blaxter 1980). However, as the liveweight range of the 18-month-old hinds in the present study did not extend below 73 kg, the probability models could not reliably project this threshold point for hinds showing little or no evidence of wapiti parentage (i.e. true "red deer"). Overall, this group of hinds (i.e. WS=1, CWS=0.1, EWP=0-0.1) exhibited pregnancy rates in excess of 95%. Similarly, animals with a relatively low level of introgression (i.e. WS=1, CWS<0.25, EWP<0.2) were clearly consistently above the liveweight threshold, and the 50% threshold point could not be reliably assessed. However, the puberty threshold for hinds with higher levels of wapiti parentage (e.g. CWS>0.25 EWP  $\geq$  0.3) ranged from 77-85 kg at 25-35% wapiti to 98-103 kg for >35% wapiti.

From a practical perspective, however, the liveweight pregnancy probability analysis can best be used to calculate the liveweights required for each genotype cohort to attain specified performance targets. For example, using the probability curves based on WS, a 90% pregnancy rate target would require the attainment of cohort liveweights of 83, 95, 115 and 129 kg for WS 1, 2, 3 and 4+, respectively. Clearly the majority of study animals in WS 2, 3 and 4 fell well below the mean liveweights required.

While the predicted probabilities of pregnancy (e.g. Figures 2 and 3) apply to an individual hind, and can be used to determine a target live weight in order to achieve an expected pregnancy result (for a given genotype), in practice these targets will be applied to groups of animals. Group variation in liveweight may cause the target mean

liveweight required to achieve a certain group pregnancy rate to differ from the target liveweight for an individual hind. The target mean weight for a group of animals to achieve a given pregnancy rate can be obtained by calculating the integral of the function describing probability of an individual becoming pregnant (given liveweight and genotype) multiplied by an assumed distribution of liveweight for the group. This calculation was performed using the functions describing probability of pregnancy based on EWP and assuming a normal distribution with coefficient of variation of 5%. In this case it was found that target mean liveweight to achieve 90% group pregnancy rate were not markedly different from the target liveweight on an individual basis. However, this result may not apply for all situations, particularly where group liveweight distributions are skewed or group variance in live weight is greater than 5%.

It is noteworthy that there are some secondary discrepancies between the various methods of assessment of wapiti introgression in the relative positioning of the live weight/pregnancy probability curves. The analysis based entirely on the subject WS exhibits a fairly uniform displacement of probability curves across the range of scores 1-4. WS is not aligned to any objective assessment of the actual level of wapiti parentage and, therefore, cannot be reliably related to the proportion of wapiti genes within each score cohort. In contrast, more objective measures based on or alongside DNA markers (CWS and EWP), better reflect true levels of wapiti introgression. In these cases the probability curves for cohorts of  $\leq 20\%$  wapiti 0.1 parentage (e.g. EWP = 0, 0.1 and 0.2) are more closely aligned than for WS, whereas those for cohorts of greater wapiti parentage (e.g. EWP = 0.3 – 0.5) are markedly displaced from the former and from each other. Use of the probability constructs based on CWS and Elkmorph to calculate mean liveweight thresholds for a 90% pregnancy rate target provides a slightly different picture than for constructs using WS. For example, the liveweight targets based on the EWP probability curves are 81, 81, 85, 106, 127 and 136 kg for cohorts 0, 10, 20, 30, 44 and 50% wapiti, respectively; the main difference being a lack of differentiation between cohorts of  $\leq 20\%$  wapiti percentage. Again, this seems to reflect the actual levels of liveweight performance attained by the study animals, which are well above critical liveweight thresholds calculated previously for red deer. It could be argued that with a herd mean liveweight in excess of 90 kg, the majority of hinds in the 0, 0.1 and 0.2 EWP categories are placed within a biologically “safe” range. Had the range of actual liveweights extended considerably lower than was observed, the probability functions for these cohorts may have exhibited a greater degree of displacement. These data do suggest, however, that low levels of wapiti introgression (i.e.  $<25\%$  wapiti genes) may have little biological consequence on puberty performance within the range of hind liveweights commonly attained on New Zealand deer farms (85-96 kg; Beatson, *et al.*, 2000). In contrast, higher levels of introgression have pushed the mean liveweight

thresholds well above the performance levels presently achieved on most New Zealand “red deer” farms.

This raises an important question: why have the hinds with >25% wapiti genes generally failed to express their genetic potential for growth, failing to surpass the puberty liveweight threshold for their genotype? Given that in the present study these animals were incorporated into herds containing a higher proportion of smaller-bodied genotypes and managed under nutritional regimens designed for red deer, overall management may have been the limiting factor. For example, feed budgeting for the herd may simply not have accommodated the increased energy requirements of the wapiti-type animals. However, further considerations include the possibility that other aspects of herd management which suit red deer may place crossbred animals at a competitive disadvantage in a mixed-genotype situation. It is well established that “higher-order” wapiti crossbreds (i.e. >70% wapiti) and purebred wapiti have specific management needs over and above those required for red deer. These relate to increased susceptibility to copper deficiency, gastro-intestinal parasitism and certain pasture-based mycotoxins that can seriously impede growth performance (Orr *et al.*, 1990; Yerex, 1991; Parsons *et al.*, 1994). It is probable that increasing wapiti parentage in the “lower-order” crossbred is associated with increased impacts of these “wapiti” characteristics. This would indicate the desirability of managing such animals separately from red deer in order to accommodate their different management needs (which is essentially the case in farming higher-order crossbreds and purebred elk).

Consideration also needs to be given to the possibility that wapiti are, genetically, a later maturing genotype. Genetic factors may limit the rate at which females attain a critical liveweight threshold. Thus, while the smaller-bodied red deer may readily attain >70% of potential mature body mass by 16 months of age, such proportional targets may be more difficult to attain in wapiti. Certainly, puberty at 16 months has been demonstrated for pure wapiti cows on North American farms (Haigh and Hudson, 1993) but this may represent the result of accelerated growth under optimum nutritional environments. Most North American literature points to a more common phenomenon of female puberty in wapiti at about 27 months of age (Taber *et al.*, 1982). This raises the intriguing possibility that specific genes or gene complexes acquired from the wapiti lineage may operate to delay puberty processes. These genes may not necessarily operate via control of growth. If this were the case it may be possible through breeding and selection to segregate the favourable wapiti growth genes from the unfavourable wapiti puberty genes to produce a genotype exhibiting positive characteristics for growth without the negative impact on puberty identified in this study.

Although no association was found relating conception date to other variables, this does not exclude the possibility that such a relationship exists. We note that calculating conception date is subject to high sampling error, both because of the back-estimation measurement process and the inherent discreteness of ovulatory cycles. Recent studies in New Zealand have indicated that adult F<sub>1</sub> crossbred hinds exhibit seasonal onset of oestrous activity about 9 days earlier than red deer herdmates (Asher *et al* 2000). Thus, we predicted that, for those hinds attaining puberty, the animals with higher levels of wapiti parentage would exhibit clear evidence of earlier conception dates. The fact that this was not apparent from the data may reflect countering effects poorer relative growth characteristics of crossbred animal retarding the onset of puberty.

## Acknowledgements

This study was funded by DEEResearch Ltd with venison levy contribution by New Zealand deer farmers. We are grateful for assistance given by Des Ford, David Peek, Ollie Dickinson and Steve Mitchell. We also thank A.J. Pearse for valuable and heroic assistance during the course of the field work.

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**Table 1:** Sample sizes by farm and year, including total numbers of yearling hinds measured, non-pregnancy rate, numbers of hinds selected for DNA analysis and distribution of wapiti scores.

Farm	Year	Total number of hinds	Number of non-pregnant hinds	% non-pregnant	Number of hinds selected for DNA analysis (non-pregnant: pregnant)		Frequency of Wapiti Scores*				
							1	2	3	4	5
A	2001	612	58	9.5	150	(58:92)	277	279	37	19	0
A	2002	625	125	20.0	242	(124:118)	208	278	102	27	10
B	2002	357	51	14.3	154	(51:103)	217	69	48	21	2
B	2003	343	128	37.3	206	(127:79)	208	37	54	38	6
C	2002	1283	53	4.1	205	(51:154)	1115	148	18	1	0
C	2003	435	29	6.7	100	(28:72)	337	54	26	12	0
D	2002	489	48	9.8	148	(45:103)	328	85	59	16	0
D	2003	185	14	7.6	53	(14:39)	163	14	5	3	0
<b>Total</b>		<b>4329</b>	<b>506</b>	<b>11.7</b>	<b>1258</b>	<b>(498:760)</b>	<b>2853</b>	<b>964</b>	<b>349</b>	<b>137</b>	<b>18</b>

\* Eight missing values for Wapiti Score (Farms B2002, B2003 and C2002)

**Table 2:** Pregnancy rate and mean ( $\pm$  sem) conception date, wapiti score, body condition score and morphological measurements of yearling hinds by farm and year.

Farm	Year	% Pregnant	Conception Date (Days from 1 January)	Liveweight Kg	Wapiti Score	Body Condition Score	Shoulder Height (cm)	Body Length (cm)	Head Length (cm)	Head Width (cm)
A	2001	90.5	105.4 (0.11)	90.2 (0.23)	1.67 (0.03)	3.53 (0.016)	102.7 (0.21)	96.4 (0.21)	40.1 (0.005)	14.1 (0.003)
A	2002	80.0	106.0 (0.65)	91.9 (0.30)	1.96 (0.04)	3.45 (0.015)	103.3 (0.15)	98.3 (0.13)	39.4 (0.006)	17.2 (0.005)
B	2002	85.7	104.1 (0.65)	92.6 (0.55)	1.66 (0.05)	3.46 (0.018)	100.3 (0.27)	94.3 (0.29)	39.1 (0.008)	17.5 (0.005)
B	2003	62.7	102.3 (0.71)	91.1 (0.59)	1.83 (0.06)	3.56 (0.020)	99.5 (0.22)	89.2 (0.21)	37.1 (0.009)	18.2 (0.006)
C	2002	95.9	102.2 (0.29)	88.5 (0.22)	1.15 (0.01)	3.70 (0.009)	100.3 (0.10)	87.3 (0.12)	39.7 (0.004)	19.0 (0.002)
C	2003	93.3	95.0 (0.32)	90.0 (0.35)	1.33 (0.04)	3.70 (0.017)	98.9 (0.13)	89.7 (0.13)	39.4 (0.006)	18.1 (0.003)
D	2002	90.2	116.7 (0.36)	100.8 (0.34)	1.51 (0.04)	3.90 (0.013)	101.7 (0.16)	88.9 (0.18)	39.8 (0.006)	18.9 (0.003)
D	2003	92.4	105.2 (0.81)	93.3 (0.48)	1.18 (0.04)	3.72 (0.025)	100.1 (0.24)	88.6 (0.19)	39.4 (0.008)	17.8 (0.004)

**Table 3:** Mean observed<sup>1</sup> and predicted<sup>2</sup> “Elkmeter” values, and “Elkmeter” values for each Wapiti Score based on regression analysis

Farm	Year	Mean (sem) observed “Elkmeter”		Mean (sem) predicted “Elkmeter”		Wapiti Score				Regression intercept	Regression slope	S.E. (Slope)	Sig.	
						1	2	3	4/5					
A	2001	0.23	(0.009)	0.23	(0.003)	0.18	0.23	0.29	0.22	0.180	0.022	0.0095	*	
A	2002	0.28	(0.010)	0.26	(0.004)	0.18	0.24	0.29	0.49	0.067	0.089	0.0066	***	
B	2002	0.26	(0.012)	0.21	(0.006)	0.17	0.22	0.33	0.40	0.078	0.080	0.0081	***	
B	2003	0.30	(0.010)	0.24	(0.007)	0.22	0.29	0.34	0.40	0.169	0.056	0.0062	***	
C	2002	0.13	(0.005)	0.15	(0.002)	0.10	0.15	0.19	0.41	0.051	0.051	0.0112	***	
C	2003	0.16	(0.013)	0.15	(0.004)	0.08	0.13	0.21	0.40	-0.036	0.094	0.0103	***	
D	2002	0.21	(0.011)	0.20	(0.004)	0.13	0.19	0.29	0.37	0.047	0.080	0.0087	***	
D	2003	0.15	(0.019)	0.15	(0.006)	0.11	0.13	0.25	0.48	-0.001	0.092	0.0170	***	
										Pooled	0.079	0.070	0.0031	***

<sup>1</sup> n = 1258

<sup>2</sup> n = 4329

**Table 4:** Canonical vectors, group means by wapiti score, and roots from the discriminant analysis of morphological data in relation to wapiti score (n=4296).

Variable	Canonical vector		
	first	second	third
BCS	-0.061	0.0288	-0.0667
Shoulder height	0.722	-0.4034	0.2514
Body length	0.630	0.7823	-0.2777
Head length	-0.078	0.4228	-0.7447
Head width	0.021	-0.3945	-0.6528
Live weight	0.260	-0.6804	0.4638

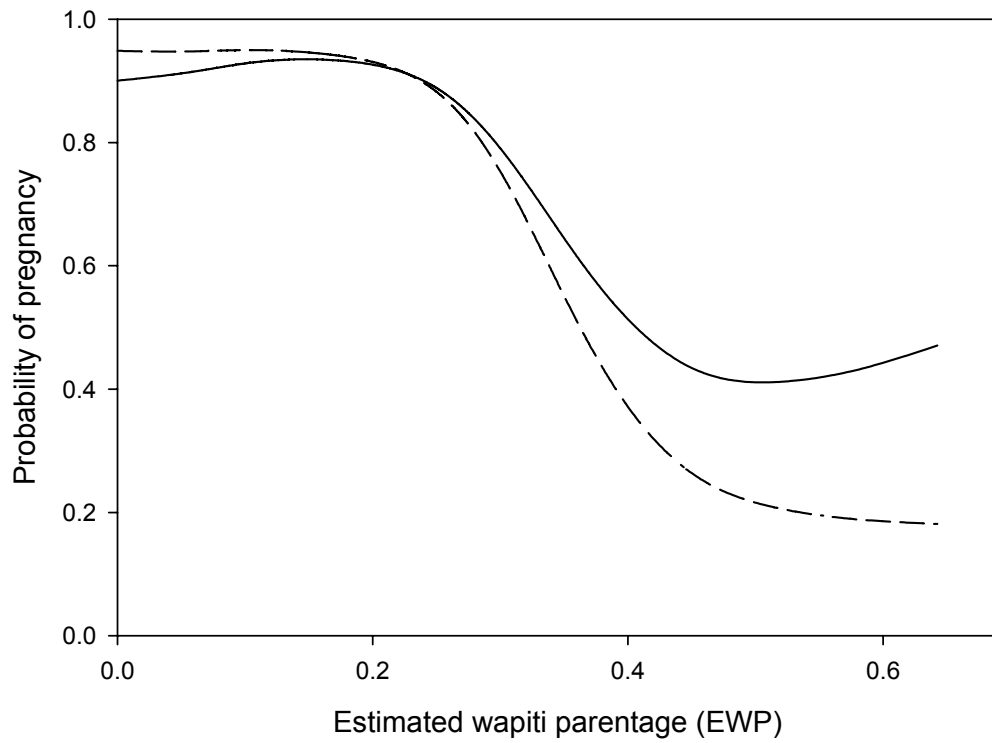
Wapiti score	Group mean		
1	-0.56	-0.0669	-0.0001
2	0.73	0.3444	-0.0491
3	1.45	-0.0698	0.2208
4	2.69	-0.757	-0.1853
Root	0.7558	0.0502	0.0057

**Table 5:** Slope parameters (with standard errors) from the multiple regression of elkmeter value on all morphological variables, (a) without and (b) with adjustment for farm, year, and their interaction.

	<b>Slope parameter</b>	<b>standard error</b>	<b>t-value</b>
(a) Without adjustment for farm, year, and their interaction			
Shoulder height	0.0087	0.00116	7.45
Body length	0.0059	0.00081	7.32
Live weight	0.0026	0.00044	5.96
BCS	-0.053	0.0090	-5.94
Head length	-0.0010	0.00023	-4.23
Head width	0.0010	0.00037	2.63
(b) Adjusted for farm, year, and their interaction			
Shoulder height	0.0076	0.00110	6.89
Head length	0.0011	0.00026	4.30
Body length	0.0045	0.00101	4.50
BCS	-0.028	0.0086	-3.31
Live weight	0.0010	0.00048	2.15
Head width	0.0008	0.00041	1.99

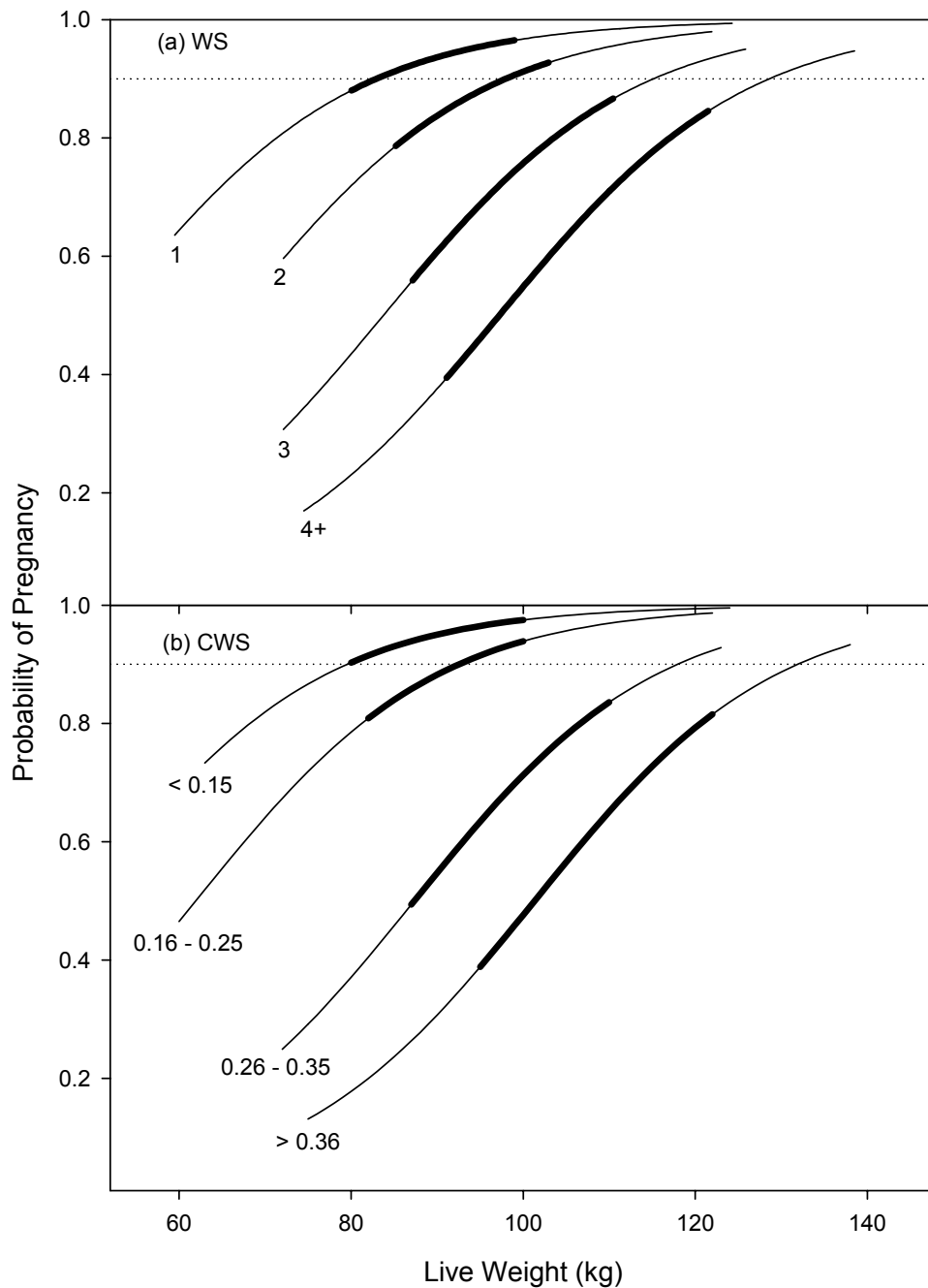
**Table 6** Slopes with standard errors (se) and significance of slope (sig), residual mean deviance (rmd) and residual degrees of freedom (df) for the binomial-logit regression of pregnancy rate on estimated wapiti parentage (EWP; calculated by Elkmeter score with missing values predicted from morphological and farm data) with liveweight and body condition score (BCS) added to the model.

<b>model</b>	<b>slope</b>	<b>se</b>	<b>sig</b>	<b>df</b>	<b>rmd</b>
Lin (EWP)	-6.88	0.39	***	4303	0.629
Lin (EWP)	-9.53	0.53	***	4294	0.591
+ Live weight	0.074	0.0072	***		
+ BCS	0.427	0.143	**		

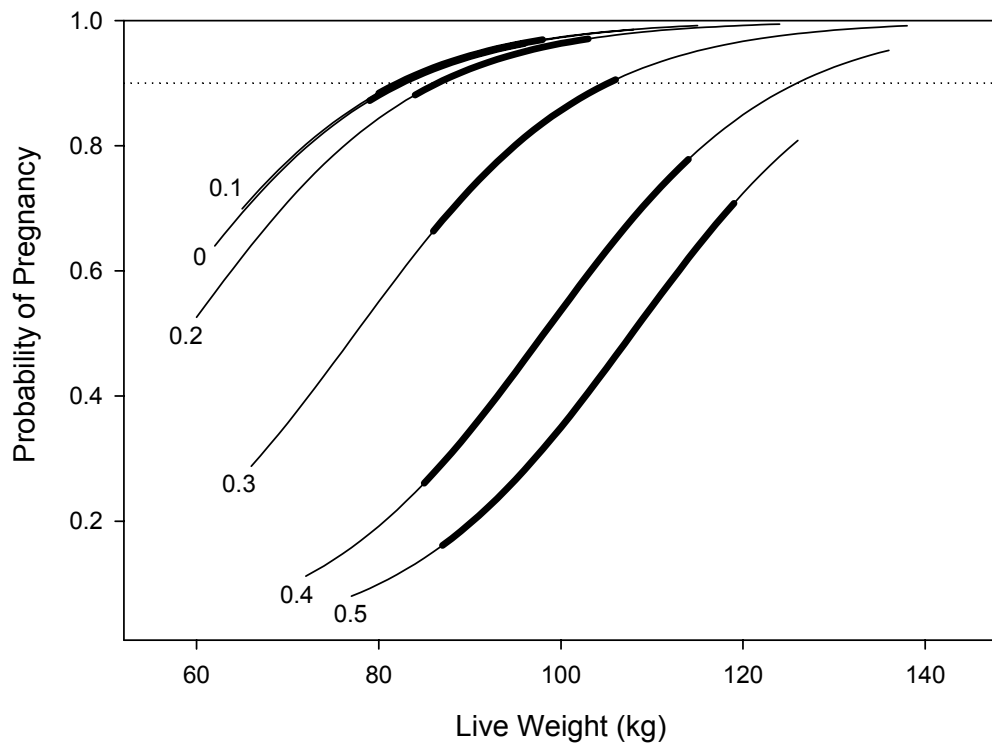


**Figure 1** Predicted probability of pregnancy, modelled (a) as a spline function of estimated wapiti parentage (EWP; calculated by Elkmeter score with missing values predicted from morphological and farm data) (solid line), and (b) as for (a) with live weight added and adjusted to an overall mean live weight of 91 kg (dashed line).





**Figure 2** Predicted probability of pregnancy of hinds at 18 months of age as a function of liveweight for **(a)** wapiti score (WS; based on actual scores recorded in the field) and **(b)** corrected wapiti score (CWS; based on given fixed values that represent nominated ranges for level of wapiti parentage). The actual observed range of liveweights is delineated by each line, with the thick portion of each line representing the 10<sup>th</sup> – 90<sup>th</sup> quantiles in liveweight. The dotted lines define the intercepts for 90% probability of pregnancy.



**Figure 3** Predicted probability of pregnancy of hinds at 18 months of age as a function of assessed level of wapiti parentage (plotted as discrete values) based on the correlation between DNA markers (“Elkmeter”) and descriptive morphological measurements (i.e. EWP values). The actual observed range of liveweights is delineated by each line, with the thick portion of each line representing the 10<sup>th</sup> – 90<sup>th</sup> quantiles in liveweight. The dotted lines define the intercepts for 90% probability of pregnancy.