Chapter 3.

3. Patterns of food intake, efficiency and growth in red deer (*Cervus elaphus*) and their hybrids with Père David's deer (*Elaphurus davidianus*).

3.1 Abstract

The pattern of food intake and growth in red deer (reds) and hybrids with Père David's deer (¼ Père David's / ¾ red deer, hybrids) of both sexes were described using the approach of Parks (1982). This uses an exponential function of food intake against time which plateaus to an asymptote; to allow for the seasonal pattern of food intake in deer an annual sine oscillation was imposed on the relationship. The model then derived energy requirements for both growth and maintenance. Red males reached their peak metabolisable energy (ME) intake significantly earlier than hybrids (1 January 1994 vs 24 January 1994, $P<0.05$) while for females there was no difference with both genotypes reaching peak ME intake on 18 January 1994. There were no significant differences between genotypes within sex groups in other key parameters tested including mature food intake (MJ ME/week, C), mature live weight (kg, A), food efficiency (kg LW/MJ ME, AB) or maintenance efficiency (kg LW/MJ ME/week, T_o). Mean food efficiency was 0.034 kg live weight/MJ ME/week which was slightly higher than other estimates for domestic ruminants as well as other estimates for red deer. Mean maintenance efficiency was 0.782 kg live weight/MJ ME/week which is slightly lower than other estimates for red deer. There were large oscillations in food intake for all genotype/sex groups but no evidence for seasonal oscillations in either maintenance or growth efficiencies.

Keywords: deer, seasonal patterns, food intake, growth modelling, Père David's deer.

3.2 Introduction

Deer, as well as some other temperate and arctic species of herbivores, exhibit considerable seasonality in their patterns of food intake and live weight change (French *et al.* 1956; Wood *et al.* 1962; Mitchell *et al.* 1976; Hamilton and Blaxter 1980; Blaxter and Boyne 1982; Worden and Pekins 1995; Weber and Thompson 1997). These persist even under *ad libitum* feeding

using high energy diets (Bandy et al. 197C; McEwan and Whitehead 1970; Fennessy 1982; Loudon et al. 1989; Weber and Thompson 1997). In both red deer and Père David's deer, similar patterns are apparent, namely a seasonal cycle where food intake is higher in summer and lower in winter (Blaxter et al. 1974; Suttie et al. 1987; Loudon et al. 1989), together with a severe reduction in food intake associated with the breeding season or rut in males (Fennessy 1982; 1991c). The features of the rut (e.g. aggression, feeding behaviour, weight loss) have been documented in both red deer (Clutton-Brock et al. 1982) and Père David's deer (Schaller and Hamer 1978).

There is also evidence in sheep (Blaxter and Boyne 1982) and white-tailed deer (Silver et al. 1969; Moen 1985) of a cyclical or seasonal relationship between food intake and basal metabolic rate, although the latter is somewhat controversial (Perkins et al. 1992; Worden and Pekins 1995). The seasonal cycles in food intake in deer are daylength related but the regulatory mechanism/s are not known. However, there is evidence of seasonal patterns in a number of hormones such as prolactin in both red deer and Père David's deer hinds (Loudon et al. 1989), growth hormone and insulin-like growth factors in red deer stags (Suttie et al. 1989), and thyroid hormones in white-tailed deer (Bubenik and Leatherland 1984). The rut-associated reduction in food intake is apparently related to the high levels of circulating testosterone (Fennessy et al. 1988) and in this respect, a cause-effect relationship between testosterone administration and feed intake has been shown (Newman et al. 1992). The reduction in food intake associated with the rut commonly results in losses of 10 to 20% in body weight from pre-rut weight and sometimes as high as 30% (Kelly et al. 1987; Fennessy et al. 1991c).

Consequently understanding or dissecting the mechanisms which control food intake patterns could potentially be useful if it were possible to manipulate these. In this light, detailed studies of food intake patterns and live weight change are an important component in developing an understanding of basal rhythms. The conventional approach to describing growth is a two dimensional weight by age approach. A potentially more powerful and descriptive approach is the one proposed by Parks (1982) in which growth is described using a three dimensional model including live weight, age and food intake. Thus, using red and ¼ Père David / ¾ red deer hybrids of both sexes differences in growth patterns and underlying rhythms in food intake, live weight change, maintenance efficiency and food efficiency in a controlled

environment were investigated. This method estimates individual animal mature food intake, mature live weight, the age at which the animal reaches two thirds of its mature food intake and both maintenance and growth efficiencies.

3.3 Materials and Methods

To quantify genotype and sex differences in patterns of intake and live weight a total of 24 deer, comprising seven ¼ Père David's / ¾ red deer hybrids (hybrid, average age 31.4 weeks) and five red deer (red, average age 28.9 weeks) of each sex were individually housed and fed a concentrate ration *ad libitum* for a period of 64 weeks. Pens allowed the deer visual contact with their neighbours. The pen dimensions were $2.8 \times 1.7 m^2$ and $2.2 \times 1.1 m^2$ (3m in height) for males and females respectively. The animals were fed a pelleted, high concentrate ration *ad libitum*, plus 0.5 kg of chaffed lucerne hay per 10 kg of concentrate and had unrestricted access to water. The composition of the diet is presented in Table 3.1. Individual animal live weight and food intake were recorded on a weekly basis. During the experiment three animals died from malignant catarrhal fever (MCF) (Orr and Mackintosh 1988), including two female hybrids (one at 5 weeks and the other at 20 weeks) and a red male (at 54 weeks). In addition to this one hybrid male was excluded from the analyses, as its food intake fluctuated and it failed to thrive. There were no signs of subclinical MCF in any other animals. Live weights (kg) at the end of winter (23 August) for the four groups suggested no evidence for MCF; hybrid males (78, 72, 59, 75, 74 and 74), red males (69, 66, 65, 70 and 70), hybrid females (77, 76, 66, 64 and 52) and red females (65, 58, 59, 62 and 57). All animals were allowed to exercise twice weekly for 4 - 6 hours in a $14 \times 14 m^2$ outdoor exercise pen with water but no food available. During the rut the males (M) and females (F) were exercised separately to avoid unwanted pregnancies. All antler was removed at the hard stage (i.e. cleaned of velvet)

Table 3.1 Composition of the pelleted diet fed to ¼ Père David's / ¾ red deer hybrids and red deer.

Component	%	Component	%
Barley	48.5	Sodium bentonite	2.0
Broll	20.5	Crystallised lime	1.5
Rapeseed meal	7.5	Zeolite	1.0
Peas	7.5	Salt (NaCl)	1.0
Extracted cottonseed meal	4.0	Molasses	1.0
Oat husks	2.5	Urea	1.0
Fishmeal	2.0	Vitamins and minerals	0.25

The vitamin and mineral mix contained 25 g/kg dicalcium phosphate, 2500 iu/kg Vitamin A, 1000 iu/kg Vitamin D3, 10 iu/kg Vitamin E and 0.15 mg/kg of selenium as sodium selenate. Broll is a 50/50 mix of bran and pollard.

unless it had to be removed due to injury (4 stags) in which case a standard local anaesthetic procedure was used. The deer had a 6 week period of adjustment to the diet and environment before full data recording commenced. The artificial breeding techniques used in generating the hybrids meant that mean birth dates were 6 (± 8.1) November 1992 for hybrids and 23 (± 2.5) November 1992 for reds.

All animals were fed three times per week at 1.1. to 1.2 times their expected intake and subsequently combined into weekly food intake, food wastage was minimal. Feed bins were checked daily to ensure food supply was *ad libitum* and residues were removed weekly. Individual animal residues, the concentrate ration and lucerne hay were sampled on a weekly basis for dry matter determination. The metabolisable energy (ME) content of the diet was estimated using an *in vitro* digestibility procedure and using standard formulae (Alderman 1985; CSIRO 1990). Using this technique the pelleted concentrate ration was estimated at 11.7 ± 0.20 MJ ME/kg and the lucerne hay at 9.1 ± 0.58 MJ ME/kg.

3.3.1 Growth modelling

Parks (1982) proposed that growth can be described as an input/output system in which food intake is partitioned between growth and maintenance parameters which are characteristic of the species, diet and environment. He used a number of exponential functions, including parameters for mature food intake, appetance (the age in weeks at which an animal reaches 0.63 of its mature food intake), growth and maintenance efficiency and mature weight of the animal to describe food intake and growth functions. He proposed that the parameters for growth and maintenance efficiency are independent of the mode of feeding (i.e. whether animals are fed *ad libitum* or on a controlled feeding regime), although a controlled feeding regime obviously impacts on the food intake (both appetance and mature food intake) and mature weight parameters. However, if an animal on a controlled feeding regime is later rehabilitated to *ad libitum* feeding, the *ad libitum* feeding and growth parameters will again be operative.

It is well documented that deer exhibit a highly seasonal physiology both in their breeding and feeding habits (Mitchell *et al.* 1976; Drew 1985). The animals in this study underwent the expected seasonal fluctuations in food and energy intake. In addition to this, stags underwent severe voluntary food restriction during the rut. It was therefore appropriate that the

relationship between live weight and food intake be described using the controlled growth function proposed by Parks (1982), even though they had access to *ad libitum* food throughout the experiment. The same approach has been used to identify patterns of growth to maturity in red stags (Fennessy *et al.* in preparation).

The pattern of weekly food intake and corresponding live weights were analysed using an exponential term which plateaued at a mature food intake (Parks 1982) as in Equation (1).

$$dF/dt = C (1 - EXP (-t/t^*)) \tag{1}$$

Where

dF/dt = weekly food intake (MJ of ME/week)

C   = mature food intake (MJ of ME/week)

t   = age (weeks)

t^* = appetance (the exponential decay constant for food intake, weeks)

Live weight was described using the controlled growth function proposed by Parks (1982):

$$W_{(t)} = (T_o f_{(t)} - W_{(t-1)}) (1 - EXP (-AB/T_o)) + W_{(t-1)} \tag{2}$$

Where

$W_{(t)}$ = live weight at age t (kg)

T_o = maintenance efficiency (kg live weight /MJ of ME /week)

$f_{(t)}$ = weekly food intake (MJ of ME /week)

$W_{(t-1)}$ = live weight at age t-1 (kg)

(AB) = food efficiency factor or exponential decay constant for live weight per unit of food intake (kg live weight /MJ of ME)

Maintenance efficiency (T_o) estimates the period of time that a unit of live weight can be maintained by a unit of food intake. This has been found to be a constant value at all live weights to and including maturity (Taylor *et al.* 1981). Parks (1982) therefore defined T_o as a constant which was calculated as the ratio of mature live weight and mature food intake (i.e. A/C). Thus if T_o and C are known, it is possible to estimate mature live weight, A as follows

$$T_o = A / C \tag{3}$$

Where

T_o = maintenance efficiency (kg live weight /MJ of ME /week)

A = mature live weight (kg)

C = mature food intake (MJ of ME /week)

Equation (1) was fitted to the weekly food intake data using non linear procedures (SAS 1989a) for individual animals including the period of feed intake associated with the rut. Unfortunately the rut could not be excluded as by Fennessy *et al.* (in preparation) because the end of the rut could not be defined; while the onset of the rut could be defined as that time when food intake began to decline by some arbitrary factor, the end of the rut could not be defined in a similar manner because the experiment was terminated prior to a new plateau in food intake. The fitting of mature food intake (C) and appetance (t*) using Equation (1) led to distinct sinusoidal oscillations in the residuals for all animals. Therefore Equation (1) was altered to include a sine oscillation, where the frequency of the sine curve was fixed at an annual oscillation (i.e. $2\pi / 52.14 = 0.1205$ in units of radians per week), as in Equation (1a).

$$dF/dt = C\,(1 - EXP\,(-t/t^*)) + (d \sin (0.1205^*(t + \phi))) \tag{1a}$$

Where

dF/dt = weekly food intake (MJ of ME/week)

C = mature food intake (MJ of ME/week)

t = age (weeks)

t* = appetance (the exponential decay constant for food intake, weeks)

d = amplitude (MJ ME/week)

ϕ = phase shift of the sine oscillation (weeks)

The live weight data were fitted to Equation (2) as a function of weekly food intake for individual animals using non-linear procedures. Mature food intake and live weight were estimated using Equation (3). The non-linear procedures included application of both

derivative and derivative-free methods to estimate the parameters to ensure the model converged to stable values.

The non-linear procedures used derivative and derivative free methods to estimate parameters as well as different starting points to ensure global solutions instead of local maxima or minima in the residual patterns.

Using the derivative of Equation (1a) with respect to age (in weeks) the ages and dates at minimum and maximum ME intakes were determined as those points where the gradient changed from negative to positive and *vice versa*.

3.4 Results

At the conclusion of the feeding period there were no significant differences in live weight between genotypes, although males were markedly heavier than females (125 vs 108kg, $P<0.01$). There were no significant differences between sex genotype groups in their date of minimum ME intake while for one animal (Y293) it was not possible to determine the date at minimum intake because the change in gradients of ME intake around that time were not sufficiently large to generate a true minimum. The dates at minimum ME intake were 17 July 1993, 20 July 1993, 29 June 1993 and 14 June 1993 for the hybrid males, red males, hybrid females and red females respectively. The dates at maximum ME intake were 24 January 1994 and 1 January 1994 for hybrid and red males while both female genotypes reached peak ME intake on 18 January 1994.

The two alternative models were fitted to the data. For all individual animals Model (1a) provided a significantly better fit than Model (1). We expected this since Model (1a) incorporates a second feature which allows for a seasonal oscillation in food intake in addition to an asymptotically increasing food intake with age. The raw data, Model (1) fit, and the significantly better fit with Model (1a) are illustrated in Figure 3.1 for one animal of each genotype/sex group. The differences between parameters derived from the two models are important. For example, there was a significant difference between male genotypes in appetance from Model (1) which disappeared when the sine oscillation was included in Model (1a). However in this latter model, the sex difference in appetance was significant (M, 8.6 vs F, 21.6, $P<0.01$). There was also a significant ($P<0.05$) genotype by sex interaction for amplitude

with hybrid females exhibiting a greater amplitude than reds while the reverse was the case for males. The hybrids also exhibited less phase shift than reds (M, 2.4 vs 7.7 weeks, P<0.01, F, 6.3 vs 2.7 weeks, P<0.05) with their maximum food intake 5.3 weeks (M) and 3.6 weeks (F) later than their red counterparts. The full individual animal data are presented in Appendices 2 and 3. After adjusting for the 2 and 3 week earlier birth dates for hybrid males and females the differences in phase shift between genotypes reduced to -2.6 (4.6 - 7.2) and -0.6 (5.7 - 6.3) weeks respectively.

The mean ME intake patterns for each genotype / sex group are presented in Figure 3.2 and illustrate the differences between the genotypes within sex. Clearly the reds appear to reach their peak intakes at an earlier age.
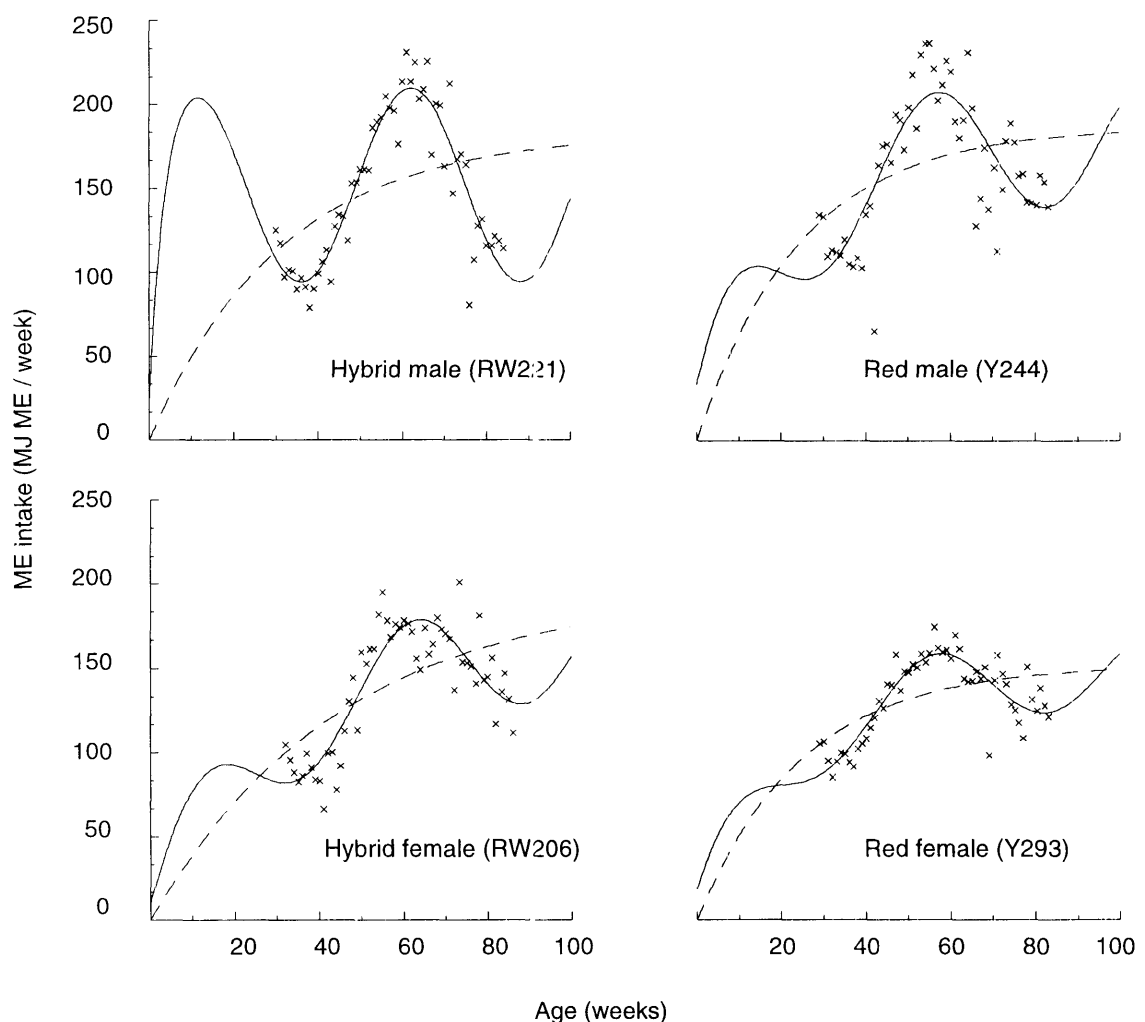

Figure 3.1 Plots of raw data and fits using Models (1---) and (1a —) of an animal from each of the four genotype/sex groups.

Table 3.2 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 of both sexes using Equations (1) and (1a) derived from Parks (1982).

	C (MJ ME /week)	t* (weeks)	d (MJ ME /week)	ϕ (weeks)	To (kg LW /MJ ME /week)	AB (kg LW / MJ ME)	A[2] (kg)
Equation (1)							
Males							
Hybrid (6)	195	34.5	-	-	0.795	0.036	154
Red (5)	186 NS[1]	21.7 *	-	-	0.801 NS	0.030 NS	147 NS
Females							
Hybrid (5)	179	35.8	-	-	0.784	0.033	140
Red (5)	182 NS	33.0 NS	-	-	0.749 NS	0.034 NS	136 NS
SED (approximate)							
within sex between genotypes	14.2	5.36	-	-	0.052	0.004	11.5
between sexes	9.8 NS[3]	3.71 [4]	-	-	0.363 NS	0.003 NS	8.0 NS
Equation (1a)							
Males							
Hybrid	161	8.9	49	2.4	As above	As above	128
Red	176 NS	8.2 NS	60 NS	7.7 **	As above	As above	139 NS
Females							
Hybrid	155	20.1	41	2.7	As above	As above	122
Red	164 NS	23.0 NS	32 NS	6.3 *	As above	As above	124 NS
SED (approximate)							
within sex between genotypes	13.6	5.42	8.5	1.47	As above	As above	12.0
between sexes	9.6 NS	3.70 **	5.6[4]	1.02 NS	As above	As above	8.5 NS

[1] Comparisons between hybrid and red deer are made within sex and noted beside red. * P<0.05; ** P<0.01

[2] A= To x C, where C is dervied from Equation (1) and To is derived from Equation (2).

[3] Comaprisons between male and female deer are noted beside the between sexes SED. * P<0.05; ** P<0.01

[4] Genotype by sex interaction
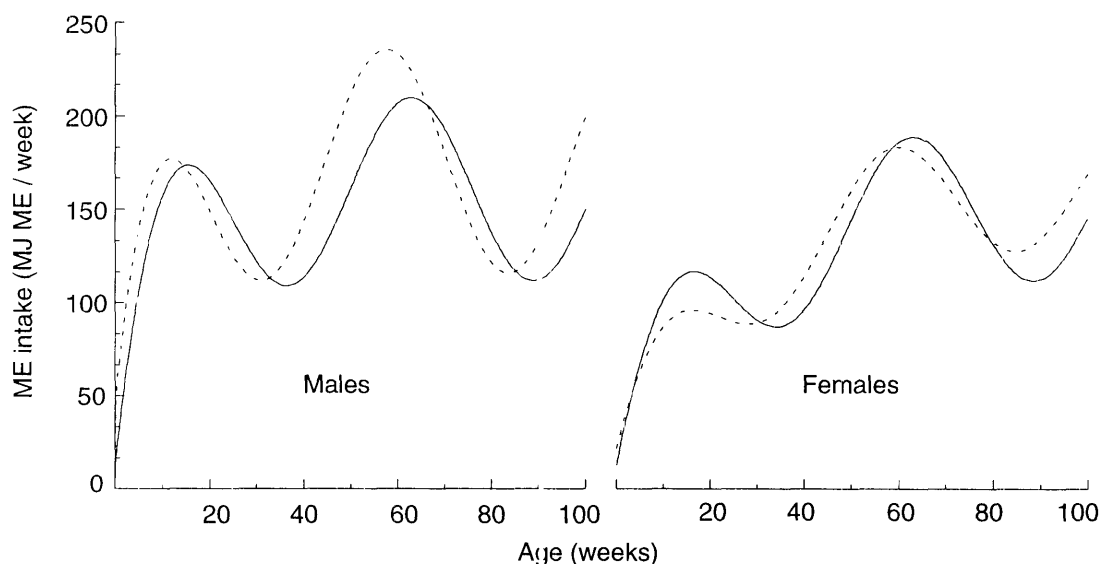
Figure 3.2 Patterns of food intake (ME) using Model (1a) for hybrids (—) and reds (---) of each sex.

Ages at maximum ME intakes were determined using the derivative of Equation (1a) and subsequently corrected for date of birth to allow comparisons at the same date. These suggested red males peaked 23 days earlier than hybrids (Table 3.3) compared with the 18 day earlier difference (2.6 weeks) using phase shift adjusted for date of birth.

Subsets of the data were analysed to ascertain the effect of including the initial stages of the experiment in the models (i.e. to allow time for animals to acclimatise to conditions and diet). However there were no significant effects on the model parameters (results not presented).

Table 3.3 Genotype differences in the occurrence of peak ME intake using phase shift (ϕ, weeks) estimates and the maximum turning point from the first derivative of Equation (1a).

	Date		
	Hybrid (SE, days)	Red (SE, days)	Diff (days)
Males			
using phase shift (ϕ)	-	-	-18
using max turning point	24 Jan 94 (9.9)	1 Jan 94 (10.9)	-23
Females			
using phase shift (ϕ)	-	-	-4
using max turning point	18 Jan 94 (10.9)	18 Jan 94 (12.2)	0

3.5 Discussion

The seasonal trend in food intake with maximum intake in summer and minimum intake in winter was large and consistent with other reports in seasonal deer (Suttie *et al.* 1987; Worden and Pekins 1995). Model (1), which excluded the sine oscillation, yielded C and t* parameters notably higher than those from Model (1a), which included the sine oscillation. Model (1a) was a more stable model giving consistent results using different starting values and both derivative and derivative-free convergence methods. Compared to another study which used the same techniques (Fennessy *et al.* in preparation) these results for C, t*, d, ϕ and A estimates are similar despite the differences in the length of the two studies (55 weeks in the present study compared to a minimum of 129 in the other). Mature food intakes (C) were between 152 and 209 MJ ME/week compared with 161 to 249 MJ ME/week in Fennessy *et al.* (in preparation). Appetance (t*, weeks) estimates of -0.1 to 9.0 weeks from Model (1a) are much lower than those of 35 to 47 weeks in Fennessy *et al.* (in preparation). The difference in length of data recording undoubtedly contributed to the unstable parameter estimates for all animals using Model (1a) despite the significantly better fit with the sine function. Using Model (1), t* is an estimate of the age at which food intake attains 63% of mature food intake. This parameter is likely to be influenced by the starting date of the experiment and may generate different estimates for animals born out of season. Fennessy *et al.* (in preparation) started their experiments at older ages and hence were effectively estimating a value of t* prior to the actual start of their experiment. The estimates of mature live weight (A) may also reflect the length of the experiment, particularly for stags as the live weights are well below actual live weights of mature males. However values for red females (124kg) are reasonable (Kelly *et al.* 1987). Amplitude estimates were very similar being between 27 and 61 MJ ME/week in our study compared to 31 and 52 MJ ME/week in Fennessy *et al.* (in preparation).

The phase shift (ϕ) values for both genotypes in Table 3.2 indicate consistent differences between the genotypes in the order of 3.6 to 5.3 weeks (M, hybrids 2.4 vs reds 7.7, P<0.01; F, hybrids 2.7 vs reds 6.3, P<0.05) with reds reaching peak food intakes earlier than hybrids. After adjusting for birth dates, the differences in phase shift (-18 and -4 days) between genotypes were more consistent and in the same direction (-23 and 0 days) as those estimated using the maximum turning point from the first derivative of Equation (1a). The phase shift in sinusoidal feed intake provided an indication of the time required for the genotypes to respond

to changes in daylength. The estimates for the lag in food intake oscillation after adjusting for differences in birth dates were 2.6 and 0.6 weeks earlier in red males and females respectively. This suggests red genotypes are more responsive to changes in daylength than hybrids although the differences are not large. This lag is clearly not a sudden event but the result of a progressive or cumulative response to a change in daylength detected by the genotypes. The reported seven week lag between manipulated photoperiod and antler cleaning and casting dates in red stags (Suttie *et al.* 1984a) corresponds well with this study where the lags are estimated at 7.2 weeks for red stags and 6.3 weeks for red hinds.

Considering the live weights of pure PD and red deer (Loudon *et al.* 1989) and the potential for heterosis in an interspecies hybrid we would expect these hybrids to have higher mature live weights than red deer. The significantly lower appetance factor (t*) in males compared to females and the similarity of mature food intake (C) in males and females using Model (1a) are perplexing and two factors are likely to contribute. Firstly, the models were unable to effectively fit the rut (expressed in males) which meant that this depression in food intake effectively reduced the apparent maximum food intake in early summer. Secondly, the experiment only lasted for 64 weeks so that animals did not express their food intake pattern for a second spring-summer.

The food efficiency factor (AB) is the exponential decay constant for live weight per unit of ME intake, or the marginal efficiency of conversion of ME to live weight gain, free of any maintenance component (Parks 1982). The mean values for stags and hinds respectively were 0.033 and 0.034 kg live weight/MJ ME, which were slightly higher than other values reported for domestic ruminants. Other derived estimates include 0.027 to 0.037 for red stags (Fennessy *et al.* in preparation), 0.023 and 0.026 for sheep (Thompson and Parks 1983; Thompson *et al.* 1985) and 0.023 calculated for cattle (Taylor *et al.* 1985) (note: where appropriate values have been converted to units of MJ of ME from those which were published in terms of kg feed dry matter intake). These suggest a 1.3 to 1.5 fold feed efficiency advantage of red deer over cattle and sheep but there was no significant difference between the hybrids and red deer.

The basic pattern of feed intake was best described by a simple exponential function with a sine oscillation because of the narrow window of data collected. For some animals, including RW221 (Figure 3.1), the fitted food intake model prior to actual data recording is clearly an

inappropriate model because it suggests a very high level (200 MJ ME/week) of feeding at a young age (approximately 10 weeks). Attempts to further improve this sine model by including an exponentially increasing (sine) amplitude with age were successful for some animals however tended to create an overspecified model for others as was indicated by poor fits (results not presented).

Maintenance efficiency (T_o) is an estimate of the amount of body weight that a MJ of ME will maintain for a week, which is equal to the time period (in weeks) that a MJ of ME will maintain one kg of live weight. The values for stags and hinds were 0.798 and 0.767 kg live weight/MJ ME/week respectively, values which are very similar to those of Fennessy *et al.* (in preparation) estimated to be between 0.802 and 0.958 in red deer stags.

Inclusion of sine oscillations in either or both the maintenance efficiency (T_o) or food efficiency (AB) parameters did not reveal any robust annual oscillations in these parameters (results not presented). This may not preclude any seasonal pattern in these parameters but rather it indicates that a robust relationship could not be established by simplistically adding sine oscillations to the parameters in this model More intensive studies monitoring inputs (food intake) and much more accurate outputs in terms of body tissue accretion for at least two annual cycles using techniques such as computer-aided tomography to assess body composition (Jopson *et al.* 1997) would be necessary to answer this question.

In order to compare key growth and maintenance parameters with other studies the data was analysed using the regression relationship between live weight gain and ME intake (Fennessy *et al.* 1981). In this study, ME requirements for red stags indoors were estimated at 37 MJ ME/ kg live weight gain and 0.57 MJ ME/$kg^{0.75}$ /day for maintenance (Fennessy *et al.* 1981). Using the same approach the ME requirements for hybrid males, red males, hybrid females and red females were 32, 33, 37 and 30 MJ ME/kg live weight gain and 0.48, 0.46, 0.48 and 0.52 MJ ME/$kg^{0.75}$ /day for maintenance. These are also similar to the range of 0.45 to 0.55 derived in other red deer studies (Simpson *et al.* 1978a; 1978b) using a calorimetric approach. Alternatively using simple maths the maintenance value of 0.8 kg LW /MJ ME /week from the Parks (1982) analysis is equivalent to 0.54 MJ ME /$kg^{0.75}$ /d for an 80 kg animal and 0.57 MJ ME /$kg^{0.75}$ /d for a 100 kg animal.

In New Zealand deer are managed outdoors where they are exposed to environmental extremes including low temperature, wind and rain particularly through the winter. These conditions necessitate increased energy and hence food intake to compensate for increased body heat loss. This is particularly critical for adult stags which have been shown to have low fat reserves at the end of the rut or breeding season (Drew 1985). Younger animals are generally still on a growth plane although this tends to be somewhat retarded through the winter. Estimates of the increased energy requirement for stags over wintered outdoors are 50% greater than for stags housed indoors (Fennessy et al. 1981). In this light, shelter would assist with reducing the energy requirements of deer managed on pasture. Overall, the appreciation and understanding of the seasonal nature of growth in deer and the impact of the environment on the energy requirements will assist in the development of practical and cost effective management systems for deer.

The model Parks (1982) developed appears to estimate key growth parameters well in species where live weight approaches a maximum asymptotically over time. This model did fit our data, but not as well as in another experiment with a larger sampling window (Fennessy et al. in preparation). Including a sine function to account for seasonal oscillations in feed intake associated with deer significantly decreased the residual sums of squares and hence increased the fit of the model. Unfortunately, inclusion of this sine function was somewhat simplistic, and led to some unstable parameter estimates. Parameters estimated were indicative of growth patterns but showed small differences between genotype/sex groups. This model may have been more stable if data had been collected for a longer period as is indicated by other research (Fennessy et al. in preparation). An alternative approach to the (Parks 1982) model, may be to use a model which can more appropriately adjust for fixed (genotype/sex) and random (animal) effects and fit a regression without imposing any function per se. In the following chapter a B-spline regression analysis was used as an alternative form of analysis which might illustrate differences in growth patterns of the genotype/sex groups.

Acknowledgements

Chapter 4.

4. Patterns of food intake and growth in red deer (*Cervus elaphus*) and their hybrids with Père David's deer (*Elaphurus davidianus*).

4.1 Abstract

Marked differences in patterns of voluntary food intake were evident between ¼ Père David / ¾ red hybrids (hybrid) and red deer (red) Red males (M) consumed more metabolisable energy (ME) during the spring/summer period between early October 1993 and early to mid February 1994. The two female genotypes had similar patterns of feed intake. There were significant differences between male genotypes in age at maximum ME intake (red 56.4 weeks vs hybrid 61.0 weeks, P<0.01) and age at minimum ME intake in both sexes (M: red 36.2 vs hybrid 38.7, P<0.01; and F: red 34.2 weeks vs hybrid 37.0 weeks, P<0.01). There were sex differences in maximum and minimum ME consumption with males consuming significantly (P<0.01) more than females. In addition, red males consumed significantly more ME at maximum ME intake compared to hybrid males (254 vs 211 MJ ME/week, P<0.05).

Keywords: deer, seasonal patterns, food intake, growth modelling, Père David's deer.

4.2 Introduction

Deer, as well as some other temperate and arctic species of herbivores, exhibit considerable seasonality in their patterns of food intake and live weight change (French *et al.* 1956; Wood *et al.* 1962; Mitchell *et al.* 1976; Hamilton and Blaxter 1980; Blaxter and Boyne 1982; Worden and Pekins 1995). These persist under *ad libitum* feeding using either high or low energy diets (Bandy *et al.* 1970; McEwan and Whitehead 1970; Fennessy 1982; Loudon *et al.* 1989; Weber and Thompson 1997). In both red deer and Père David's deer, similar patterns are apparent, namely a seasonal cycle where food intake is higher in summer and lower in winter (Blaxter *et al.* 1974; Suttie *et al.* 1987; Loudon *et al.* 1989), together with a severe reduction in food intake associated with the breeding season or rut in males (Fennessy 1982; Fennessy *et al.* 1991c). The features of the rut (e.g. aggression, feeding behaviour, weight loss) have been

documented in both red deer (Clutton-Brock *et al.* 1982) and Père David's deer (Schaller and Hamer 1978). There is also evidence in sheep (Blaxter and Boyne 1982) and white-tailed deer (Silver *et al.* 1969; Moen 1985) of a cyclica! or seasonal relationship between food intake and basal metabolic rate, although the latter is somewhat controversial (Perkins *et al.* 1992; Worden and Pekins 1995). The seasonal cycles in food intake in deer are daylength related although the regulatory mechanism/s are not known. However there is evidence of seasonal patterns in a number of hormones such as prolactin in both red deer and Père David's deer hinds (Loudon *et al.* 1989) growth hormone and insulin-like growth factors in red deer stags (Suttie *et al.* 1989) and thyroid hormones in white-tailed deer (Bubenik and Leatherland 1984). The rut-associated reduction in food intake is apparently related to the high levels of circulating testosterone (Fennessy *et al.* 1988) and in this respect, a cause-effect relationship between testosterone administration and feed intake has been shown (Newman *et al.* 1992). The reduction in food intake associated with the rut commonly results in losses of 10 to 20% in body weight from pre-rut weight and sometimes as high as 30% (Kelly *et al.* 1987; Fennessy *et al.* 1991c).

Consequently understanding or dissecting the mechanisms which control food intake patterns could potentially be useful if it were possible to manipulate these. In this light, detailed studies of food intake patterns and live weight change are an important component in developing an understanding of basal rhythms. Large differences between pure Père David's and red deer hinds have been reported (Loudon *et al.* 1989) for both breeding season and food intake patterns. Thus, using red deer and ¼ Père David / ¾ red deer hybrids of both sexes differences in growth patterns and underlying rhythms in food intake and live weight change in a controlled environment were investigated.

4.3 Materials and Methods

To quantify genotype and sex differences in patterns of intake and live weight a total of 24 deer, comprising seven ¼ Père David's / ¾ red deer hybrids (hybrid, aged 31.4 weeks) and five red deer (red, aged 28.9 weeks) of each sex were individually housed and fed a concentrate ration *ad libitum* for a period of 64 weeks.

Hybrid generation began with the production of F_1 hybrids using Père David semen in red females (Asher *et al.* 1988; Fennessy and Mackintosh 1992) and specialised techniques

Table 4.1 Composition of the pelleted diet fed to ¼ Père David's / ¾ red deer hybrids and red deer.

Component	%	Component	%
Barley	48.5	Sodium bentonite	2.0
Broll	20.5	Crystallised lime	1.5
Rapeseed meal	7.5	Zeolite	1.0
Peas	7.5	Salt (NaCl)	1.0
Extracted cottonseed meal	4.0	Molasses	1.0
Oat husks	2.5	Urea	1.0
Fishmeal	2.0	Vitamins and minerals	0.25

The vitamin and mineral mix contained 25 g/kg dicalcium phosphate, 2500 iu/kg Vitamin A, 1000 iu/kg Vitamin D3, 10 iu/kg Vitamin E and 0.15 mg/kg of selenium as sodium selenate. Broll is a 50/50 mix of bran and pollard.

developed for deer (Fennessy *et al.* 1990, 1991a; Asher *et al.* 1993; Fennessy *et al.* 1994). Subsequently, backcross progeny were generated using these F_1 hybrids in both artificial insemination ((PDxR)xR)) and multiple ovulation and embryo transfer programs (MOET) (Rx(PDxR)) (Tate *et al.* 1997).

The animals were introduced to their new environment in April 1993 and allowed 9 weeks to adapt before 55 weeks of full data recording commenced between June 1993 and June 1994. Pens allowed the deer visual contact with their neighbours. The pen dimensions were $2.8 \times 1.7 m^2$ and $2.2 \times 1.1 m^2$ (3m in height) for males and females respectively. The animals were fed a pelleted, high concentrate ration *ad libitum* (Table 4.1), plus 0.5 kg of chaffed lucerne hay per 10 kg of concentrate and had unrestricted access to water.

Individual animal live weight and food intake were recorded on a weekly basis. During the experiment three animals died from malignant catarrhal fever (MCF) (Orr and Mackintosh 1988), including two female hybrids (one at 5 weeks and the other at 20 weeks) and a red male (at 54 weeks). There were no signs of subclinical MCF in any other animals. Live weights at the end of winter (23 August) for the four groups suggested no evidence for MCF; hybrid males (78, 72, 59, 75, 74 and 74), red males (69, 66, 65, 70 and 70), hybrid females (77, 76, 66, 64 and 52) and red females (65, 58, 59, 62 and 57). In addition to this, one hybrid male was excluded from the analyses (as its food intake fluctuated and it failed to thrive). All animals were allowed to exercise twice weekly for 4 - 6 hours in a $14 \times 14 m^2$ outdoor exercise pen with water but no food available. During the rut the males (M) and females (F) were exercised separately to avoid unwanted pregnancies. All antler was removed at the hard stage (i.e. cleaned of velvet) unless it had to be removed due to injury (4 stags) in which case a

standard local anaesthetic procedure was used. The deer had a 6 week period of adjustment to the diet and environment before full data recording commenced. The artificial breeding techniques used in generating the hybrids resulted in mean birth dates of 6 (± 8.1) November 1992 for hybrids and 23 (± 2.5) November 1992 for reds.

All animals were fed three times per week at 1.1 to 1.2 times their expected intake and subsequently combined into weekly food intake, food wastage was minimal. Feed bins were checked daily to ensure food supply was *ad libitum* and residues were removed weekly. Individual animal residues, the concentrate ration and lucerne hay were sampled on a weekly basis for dry matter determination. The metabolisable energy (ME) content of the diet was estimated using an *in vitro* digestibility procedure and the formulae of Alderman (1985) and CSIRO (1990). Using this technique the pelleted concentrate ration was estimated at 11.7 ± 0.20 MJ ME/kg and the lucerne hay at 9.1 ± 0.58 MJ ME/kg.

Testes diameters measured between July (c. 8 months of age (8m)) and February (c. fifteen months of age (15m)) were used as indicators of seasonality and testes growth patterns over this period for the two male genotypes.

4.3.1 Growth modelling.

The relationship between weekly food intake and age (weeks) was modelled using B-spline regression (Chambers and Hastie 1992). This type of regression represents the mean response over time as a "wavy" curve by using certain parametric functions of the sample times, termed spline bases, as independent variables. Diagnostic plots of the raw food intake data suggested six bases would be adequate to reliably represent intake as a smooth function over time both globally and locally at the minimum and maximum intakes. The actual sampling times (weekly between weeks 28 and 87) were transformed into six other variables which model different parts of the curve; the summation of the individual parts led to the mean response over the range of samplings. The correlations amongst residuals due to repeated measures on each animal were accounted for by including random effects for each animal and its interactions with the six spline bases (Diggle *et al.* 1994).

The statistical model for the metabolisable energy intake (ME) of animal k in group j at time t (days) is

$$ME_{jkt} = \beta_{j0} + \sum_{i=1}^{6} \beta_{ji} x_{it} + u_k + \sum_{i=1}^{6} \theta_{ki} x_{it} + \varepsilon_{jkt}$$

Where

x_{it} denotes the value of the ith basis function at time t (days),

β_{j0} is the overall mean for group j

β_{ji} are the coefficients of the B-spline curve for group j,

u_k is the random effect of animal k,

θ_{ki} are the coefficients of the interactions of animal k with the spline bases, and

ε_{jkt} is experiment error.

The assumptions of the model were that each random effect and the residuals were distributed independently with normal distributions. The model was fitted using the REML algorithm in S-PLUS (Statistical Sciences 1995). Maximum and minimum ME values and their associated times for each animal were extracted from the fitted curves. A 95% confidence interval was constructed for each curve from the predicted values and their standard errors as ME ± 2 * SE(ME). The confidence limits for the times at which the minimum (or maximum) occurs are the times at which the confidence envelope of the curve equals minimum (or maximum) ME. An illustration of this is shown in Figure 4.1.

Testes analysis. Genotypes were compared for testes diameter at 8 and 15m of age. The model fitted included genotype as a class variable and both date of birth and live weight as covariates. In addition genotype growth in testes diameter between these two ages were compared using a model which fitted genotype as a class variable and date of birth as a covariate.

4.4 Results

The B-Spline regressions of metabolisable energy intake (MEI) as a function of age for each genotype/sex group were determined and their fits are presented in Figures 4.1 and 4.2. In all cases the model fits were significant (P<0.01).

Table 4.2 Key definitive growth pattern parameters (mean±SD) for the four genotype/sex groups derived from the coefficients in Tabel 4.2.

Genotype/ sex group	Minimum intake			Maximum intake			Ratio (max MEI: min MEI)	
	Date	Age (weeks)	MJ ME	Date	Age (weeks)	MJ ME		
Males								
Hybrids	5 (± 7.2) Aug 1993 NS	38.7 ± 1.37 *[1]	100 ± 13.2 NS	8 (± 11.4) Jan 1994 NS	61.0± 1.41 *	211 ± 16.3 *	2.12	± 0.221 NS
Reds	5 (± 8.0) Aug 1993	36.2 ± 1.10	112 ± 19.8	25 (± 3.8) Dec 1993	56.4± 0.55	253 ± 33.4	2.28	± 0.301
Females								
Hybrids	18 (± 5.9) Jul 1993 NS	37.0 ± 0.71 **	84 ± 11.3 NS	6 (± 14.5) Jan 1994 NS	61.6± 1.82 NS	187 ± 36.9 NS	2.21	± 0.211 NS
Reds	22 (± 3.8) Jul 1993	34.2 ± 0.84	90 ± 7.3	8 (± 30.4) Jan 1994	58.4± 4.51	184 ± 23.0	2.03	± 0.180

[1] Comparison of hybrids with reds within sex; * P<0.05; ** P<0.01.

Date at minimum intakes did not differ significantly between hybrid and red males (5 Aug 93 vs 5 Aug 93, SED 4.1) and females (18 Jul 93 vs 22 Jul 93, SED 4.1) (Table 4.2). Similarly there were no significant differences in dates at maximum voluntary food intake between genotypes for both males (8 Jan 94 vs 25 Dec 93, SED 10.6) and females (6 Jan 94 vs 8 Jan 94, SED 10.6). The significant differences in age at minimum and maximum intakes are a function of the 2 and 3 week earlier mean birth dates in hybrid males and females compared to reds.

Whilst the patterns of food intake were in phase for all genotype/sex groups, males consumed significantly more ME at minimum (106 vs 87 MJ ME /week, $P<0.01$) and maximum (232 vs 185, $P<0.01$) intakes than females and red males consumed significantly ($P<0.05$) more at maximum MEI (Table 4.2). Females did not differ between genotypes in maximum or minimum MEI.

The average minimum weekly MEI were 100, 112, 84 and 90 MJ ME/week for the hybrid males, red males, hybrid females and red females respectively. Similarly the average maximum MEI for the four groups were 211, 253, 187 and 184 MJ ME/week respectively (Table 4.2).
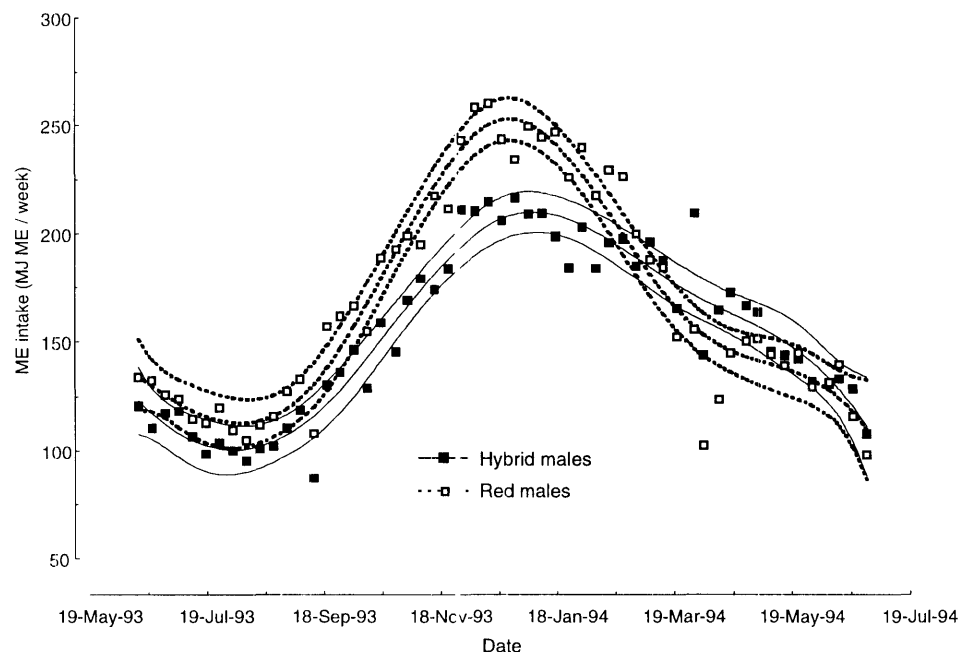

Figure 4.1 Patterns of metabolisable energy (ME) intake in male Père David x red hybrids and red deer between June 1993 and June 1994. Regression curves are mean ± 2 SE.

As is also shown in Table 4.2 there were no significant differences in the ratio of maximum to minimum MEI (i.e. amplitude) between genotypes or sexes, with mean ratios varying from 2.03 to 2.28.

The patterns of MEI (overall means ± 2 SE) for the male genotypes are presented in Figure 4.1 with the excellent fit of the model clearly evident for both groups. Where the 95% confidence intervals for the two genotypes do not overlap indicates significant differences between genotypes. Thus male genotypes showed clear differences in intake patterns with red deer consuming more ME between early October 1993 and early to mid February 1994. Red males also consumed less between late March 1994 and mid May 1994 than hybrids. At other times MEI for the two male genotypes were almost indistinguishable. Energy intakes for the two female genotypes were more similar than for the males (Figure 4.2) with the confidence intervals overlapping for the entire experiment. Female red deer ME consumption was higher than hybrid females between mid May 1994 and the end of the experiment in late June 1994. At all other times MEI for the two female genotypes were almost indistinguishable. The patterns of live weight are presented in Figure 4.3. Reds were significantly lighter (M, 51.9 vs 64.8kg, P<0.001; F, 49.9 vs 64.9kg, P<0.001) than hybrids at the start of the experiment but
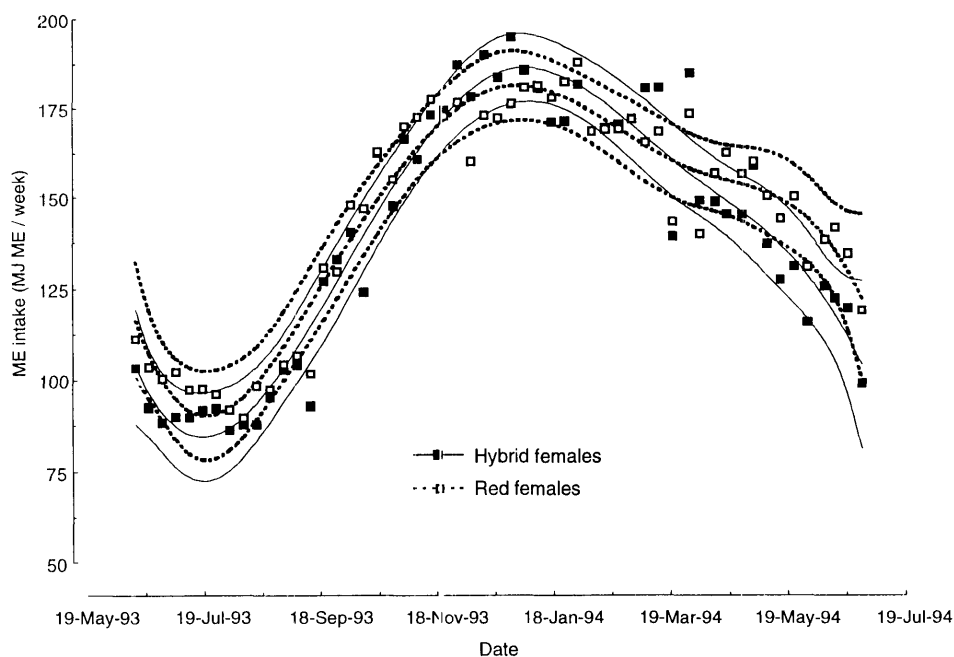

Figure 4.2 Patterns of metabolisable energy (ME) intake in female Père David x red hybrids and red deer between June 1993 and June 1994. Regression curves are mean ± 2 SE.
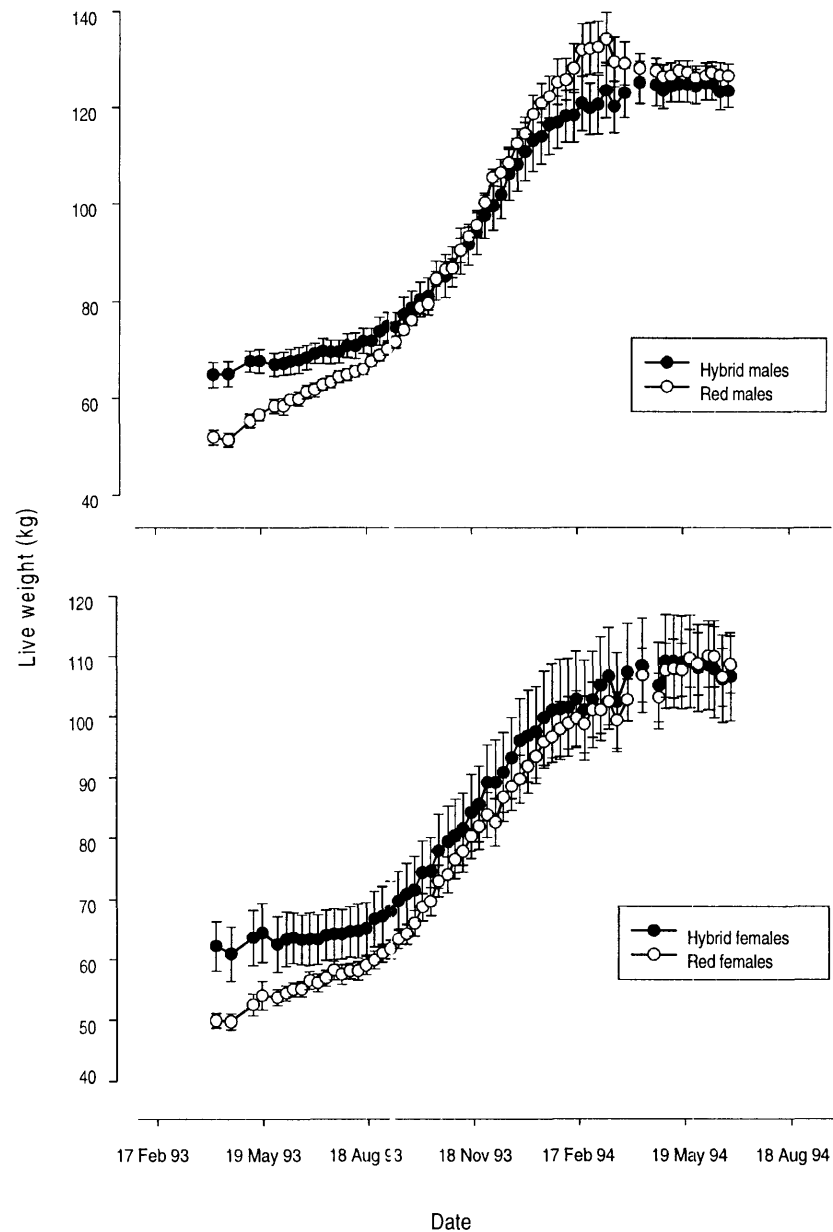
Figure 4.3 Patterns of live weights in hybrids and red deer from April 1993 to June 1994 (64 weeks).

were heavier 16 months later (M, 126.7 vs 123.7, F, 108.7 vs 106.7, NS SED = 6.8) reflecting significant differences in the average rate of live weight gain (M, 169 vs 132g/d, P<0.01, F, 132 vs 94g/d, P<0.01). Red males reached a clear peak in live weight in autumn (14 March) just prior to the commencement of the rut while the peak for hybrid males (12 April) was later and not as pronounced.

Point comparisons between hybrid and red males (at 8 and 16m) for testes diameter, after adjusting for live weight as a covariate, approached significance early in the experiment (26
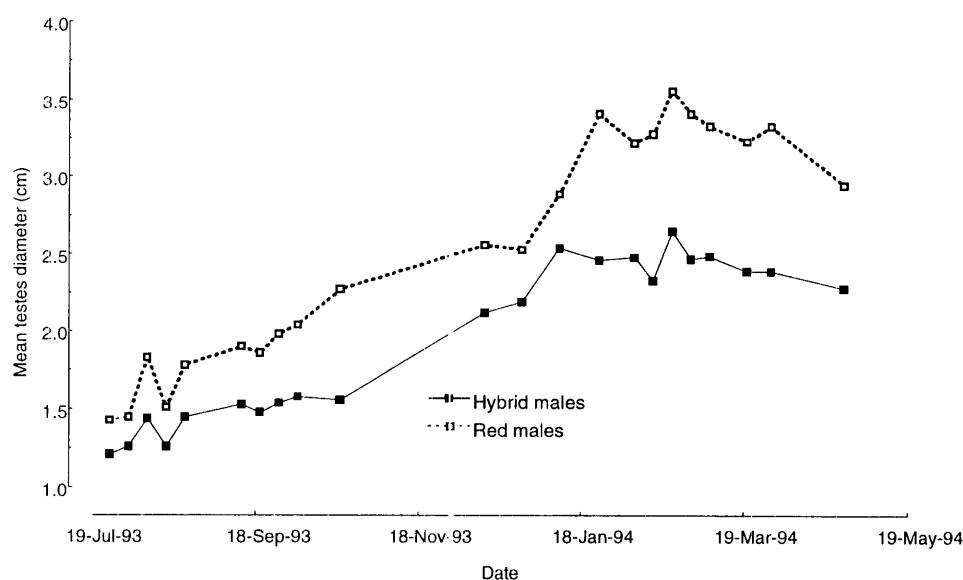
Figure 4.4 Pattern of testes growth in hybrids and red deer from July 1993 (8.5 months) to April 1994 (17.5 months).

July 1993, 1.1 vs 1.6cm, P=0.066) and were significantly different at their peaks on 21 February 1994 (2.5 vs 3.8cm, P<0.05) reflecting the significant differences in the increase in testes size (hybrids 0.7×10^{-2} vs 1.0×10^{-2}cm, P<0.01). For the comparisons at 8 and 16m, the model adjusted animals to common live weights of 67.2 kg and 126.1 kg respectively. The pattern of testes growth (averaged over the two testes) is presented in Figure 4.4.

4.5 Discussion

The seasonal food intake patterns observed in this experiment are similar to those described in sheep (Blaxter and Boyne 1982), others species of deer (French *et al.* 1956; Wood *et al.* 1962; Mitchell *et al.* 1976; Worden and Pekins 1995) and in red deer (Hamilton and Blaxter 1980; Fennessy *et al.* in preparation) with winter consumption lower than that observed in summer. The increases in food intake from winter to summer in growing sheep and deer have been estimated at between 32 to 42% and 54 to 70% respectively depending on the quality of the diet. Deer appear more analogous to cattle in their ability to digest poor quality foods (Milne *et al.* 1978). The foods offered consisted of different preparations of grass species (dried vs pellets vs cold stored) and the deer used were essentially unselected wild deer. These diets compare poorly with the much higher quality food offered in the current study and where progressive selection has increased deer live weights since deer farming became legal in New

---

Zealand in 1972. These two factors partly explain the large increase in MEI of between 2.03 to 2.28 times the winter levels in the current study and in this respect were more similar to other Invermay data e.g. Suttie et al. (1987) and to penned deer in Scotland fed a high quality barley based diet (Suttie and Simpson 1985). These differences are slightly larger than the 1.8 fold difference for red hinds and less than the 3 fold difference for pure Père David's (Loudon et al. 1989).

In contrast to a study where adult non pregnant female black-tailed deer (Bandy et al. 1970) showed less marked seasonal cycles of growth and intake in comparison with bucks, this was not the case in the present study although there was a clear difference in the ages of animals between these two studies. Differences in voluntary food intake (VFI) between sheep breeds have been documented, with Dorset Horns showing considerably less seasonal variation in VFI than Scottish Blackface and Shetland sheep (Iason et al. 1994). The most seasonal of the sheep breeds appears to be the primitive Soay sheep which experiences a greater amplitude in food intake than Suffolk x Finn-Dorset sheep, but less than that experienced by deer when exposed to 6 month photoperiodic cycles (Kay 1979). Changes in metabolic rate and voluntary food intake have been reported in deer (Silver et al. 1969; Simpson et al. 1978a; Renecker and Hudson 1986) and sheep (Blaxter and Boyne 1982; Argo and Smith 1983). In Soay rams a sinusoidal seasonal change of approximately 26% in estimated metabolisable energy requirements for maintenance and changes in metabolic rate which precede those of appetite suggest a causal relationship (Argo and Smith 1983).

The differences in patterns are similar to other studies of food intake in males and females with males reaching higher peak energy intakes and experiencing a self-induced anorexia during the rut (Suttie and Simpson 1985; Suttie et al. 1987) while females appear to go through a less erratic yet still oscillating pattern of food intake (Weber and Thompson 1997). It is interesting that the ratio of maximum/minimum energy intake was not significantly different between sexes, indicating the proportional shift in intakes were similar for both sexes. The observed marked reduction in energy intake associated with the rut was consistent with previous studies and of the magnitude expected for first rut animals (Suttie and Simpson 1985; Suttie et al. 1987). Other studies show that the severity of the rut tends to increase in magnitude with age (Kelly et al. 1987; Fennessy et al. 1991c). It has previously been shown that high testosterone

Table 4.3 Comparison of ME intake (kg$^{0.75}$ basis) in red and Père David's deer and their hybrids.

	Minimum intake (MJ ME/kg$^{0.75}$/d)	Maximum intake (MJ ME/kg$^{0.75}$/d)	Study
Females			
Hybrids	0.531	0.861	This study
Reds	0.615	0.879	This study
Père David's	0.570	0.912	Loudon *et al.* (1989)
Reds	0.523	0.941	Loudon *et al.* (1989)
Males			
Hybrids	0.590 *	0.877 **	This study
Reds	0.695	1.054	This study

levels at the time of the rut significantly reduce feed intake in male deer (Newman *et al.* 1992). The rut-induced lower intake was more pronounced in red stags than in the hybrids.

On average red females reached their maximum energy intake on 8 Jan 1994 at while hybrids reached theirs on 6 Jan 1994. Red males reached their peak energy intake on 25 December 1993 at 56.4 weeks of age, 4.6 weeks younger than hybrids but because of the differences in birth dates, the timing of maximum and minimum MEI levels did not differ significantly between genotypes. This was surprising in view of the differences in the timing of the antler cycle between F_1 (PDxR) and red males (the other major seasonal cycle) at around 57 days (Fennessy and Mackintosh 1992) and the timing of the breeding season in females at around three months (Loudon *et al.* 1989). Similarly there were no differences between males and females in the pattern of food intake. Using a different technique (Parks 1982), the seasonal oscillations in food intakes of these genotypes were estimated (see Chapter 3). Using this technique there were consistent differences between hybrids and reds of both sexes in their phase shifts (ϕ) with the reds appearing to attain peak food intakes prior to hybrids by 2.6 weeks in males and 0.6 weeks in females after adjusting for the 2 and 3 week earlier birth dates for hybrid males and females respectively. This compares favourably with the 2 week and 2 day differences using the current analysis.

Minimum and maximum energy intakes on a metabolic live weight basis in female hybrids and reds compare well with values for pure PD and red deer (assuming lucerne ME of 9.5 MJ/kg) (Loudon *et al.* 1989). At peak energy intakes, PD and their hybrids appear to consume less ME per unit metabolic weight than reds but the same is not true at their point of lowest ME

intake where the results of this study and those of Loudon *et al.* (1989) are dissimilar. Male hybrids and reds differed significantly in their metabolic energy intakes at both minimum and maximum intakes (Table 4.3). This suggests that relative to reds, hybrids consumed lower quantities of energy thus hinting at potential differences in efficiency of energy utilisation as was also suggested by Loudon *et al.* (1989).

Loudon *et al.* (1989) showed that Père David hinds have different patterns of growth compared to red deer but these differences did not manifest themselves until the animals were 11 months old. Adult Père David hinds reached their peak voluntary feed intake 60 days prior to reds whereas pre-pubertal PD hinds reached their peak only 21 days earlier than their red counterparts. Prolactin levels in the adult and pre-pubertal PD hinds reached their peaks 56 and 66 days prior to their red contemporaries respectively. The differences between the pure species in onset of the breeding season in adults and onset of first oestrous cycle in yearling hinds were a consistent 3 months. In addition the difference between adult species in the onset of anoestrous was also a three month period but there were no differences in the length of breeding season, indicating the seasonal breeding rhythms in these deer species are more rigid and their large differences allow easier detection than differences in feeding patterns. These seasonal inconsistencies suggest that the maturity patterns and synchronisation with environmental queues (or the genetic control of these) are different for PD and red deer hinds. Consequently it seems possible that the differences in date of maximum and/or minimum food intake might have stabilised to values more consistent with genotype classification at maturity if the animals had been recorded during their second annual cycle. There is also evidence to suggest the differences in key seasonal parameters between F_1 hybrid (PDxR) and red males (Fennessy and Mackintosh 1992) are of a magnitude consistent with the differences observed in females above (Loudon *et al.* 1989). It was interesting that the hybrid males appeared to have smaller testes than red males at their peak even after adjusting for live weight.

An interesting observation by Loudon *et al.* (1989) was that both post and pre-pubertal Père David's hinds ate less than their red counterparts all year except during a ten week period in the spring/early summer after scaling for metabolic weight. This alludes to the possibility of differences in maintenance and/or growth efficiencies between these species. In addition, when changes in live weight were adjusted for VFI by covariance analysis in the adult animals there was a highly significant ($P<0.01$) difference between species, indicating possible greater

Table 4.4 Comparisons of energy requirements for maintenance and live weight gain in deer, sheep and cattle.

Species /genotype	Energy requirement for maintenance (MJ ME/kg$^{0.75}$/d)	Energy requirement for LW gain (MJ ME/kg LWG)	Reference
Male			
Hybrids	0.482	32	This study
Reds	0.462	33	This study
Female			
Hybrids	0.480	37	This study
Reds	0.516	30	This study
Male reds	0.570	37	(Fennessy *et al.* 1981)
Male reds	0.415 - 0.535	-	(Simpson *et al.* 1978a)
Female reds	0.529	-	(Brockway and Maloiy 1968)
Sheep	0.413	-	(ARC 1980)
Cattle	0.525	-	(ARC 1980)

efficiency of utilisation of intake for growth and maintenance in Père David's deer. (note: maintenance efficiency is defined as the food or energy required to maintain a kilogram of (metabolic) live weight for a given time period and growth efficiency is the food or energy required to gain a kilogram of live weight.) ME requirements for red stags indoors have previously been estimated at 37 MJ ME/ kg live weight gain and 0.57 MJ ME/kg$^{0.75}$ /day for maintenance (Fennessy *et al.* 1981). Using the same approach, the ME requirements for maintenance and live weight gain for the four genotype/sex groups were calculated (Table 4.4). These estimates are similar to previous values (Fennessy *et al.* 1981) and those derived using a calorimetric approach (Simpson *et al.* 1978a, 1978b). Estimates for maintenance energy requirements in sheep and cattle in Table 4.4 imply deer require about 1.2 times as much energy for maintenance compared to sheep and very similar energy for maintenance compared to cattle.

Using a different technique, the growth efficiency or the marginal efficiency of conversion of ME to live weight gain, free of any maintenance component has been estimated for several species (Parks 1982). Using this technique mean values for stags and hinds respectively were 0.033 and 0.034 kg live weight gain/MJ ME, which were slightly higher than other values reported for domestic ruminants (see Chapter 3). Other derived estimates include 0.027 to 0.032 for red stags (Fennessy *et al.* in preparation) 0.023 and 0.026 for sheep (Thompson and Parks 1983; Thompson *et al.* 1985) and 0.023 calculated for cattle (Taylor *et al.* 1985) (note: where appropriate these values have been converted to units of MJ of ME from those which

were published in terms of kg feed dry matter intake). These suggest a 1.3 to 1.5 fold feed efficiency advantage of red deer over cattle and sheep but there was no significant difference between the hybrids and red deer.

Considering the 50% increase in energy requirements of animals managed on pasture (Fennessy *et al.* 1981), the cold winter conditions experienced in New Zealand and the fact that deer up to 15 months of age are still generally in a growth phase emphasises the importance of feed management systems which will allow animals to reach optimum weights at 15 months. Also an appreciation of the seasonal nature of growth in deer and their energy requirements will assist in the development of practical management systems for deer.

The patterns of food intake and live weight gain in the Père David's deer hybrids investigated in this study appear to be similar to farmed New Zealand red deer and as such may not convey advantages in terms of their seasonality. This was somewhat surprising in view of the large differences in live weight gains and food intakes reported previously between the pure species (Loudon *et al.* 1989). The New Zealand venison schedule is a highly seasonal one, which is a reflection of the seasonal demand for this high quality product in traditional European and North American markets and there is financial incentive for producing carcasses to specification earlier in the season which these hybrids may have offered.

Acknowledgements