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Tissue mobilization rates in male fallow deer (*Dama dama*) as determined by computed tomography: the effects of natural and enforced food restriction

N. B. Jopson[1]†, J. M. Thompson[1] and P. F. Fennessy[2]

[1]*Department of Animal Science, University of New England, Armidale NSW 2351, Australia*
[2]*AgResearch, Invermay Agricultural Centre, Private Bag 50034, Mosgiel, New Zealand*

Abstract

The breeding season in temperate species of deer is characterized by the rut, a period of intense sexual activity when the male eats very little and competes for access to females. Males have been reported as losing proportionately up to 0·30 of live weight over a 6- to 8- week period. The majority of the live-weight loss is accounted for in loss of depot fat, with smaller losses in muscle reserves. The effects of body composition, hormone status and season on these changes in fat and muscle reserves were examined in mature fallow bucks (Dama dama).

The experiment was conducted in two stages, the 'rut' (February to May), and 'spring' (June to November). For the 'rut' period, bucks were randomly allocated to either ad libitum *feeding, entire (HiEnt), matched group feeding, castrated (CAST), or entire bucks restricted to 7·6 kg dry matter per week (LoEnt) treatment groups (no. = 4, 4 and 6, respectively). Three bucks from each of the HiEnt and LoEnt groups were selected for the 'spring' period. Bucks were given food* ad libitum *until mid October, whereupon they were restricted to 2·5 kg dry matter per week for 4 weeks (SPRING). Group food intake and individual live weights were measured weekly throughout both periods. Body composition was measured by computed tomography on five and three occasions during the 'rut' and 'spring' stages, respectively.*

Comparisons of the relative losses of total fat and muscle relative to empty body weight (EBW) using the allometric model ($y = aX^b$) *revealed significant treatment differences. HiEnt bucks had a high relative rate of fat and a low rate of muscle mobilization* (b = *5·23 and 0·38, respectively). Only the CAST group had lower* ($P < 0·1$) b *coefficient for fat than the HiEnt group at 2·79. The LoEnt group was the only group in which the* b *coefficient for muscle (at 1·07) was not significantly lower than 1·0. Visceral organ weight was lost at the same rate as EBW across all treatments. There was no net loss or gain of bone for any treatment group as the* b *coefficients were not significantly different from zero. Fat depots were analysed relative to the total fat depot using the allometric model. The HiEnt group displayed a pattern of fat mobilization whereby the external depots were mobilized at the greatest relative rate and the internal fat depots at the lowest rate* (b *coefficients were 1·86, 1·23 and 0·68 for the subcutaneous, intermuscular and internal fat depots, respectively). CAST and SPRING groups were not significantly different from HiEnt bucks in the relative mobilization of fat depots. All fat depots in the LoEnt group were mobilized at the same relative rate as total fat, as the* b *coefficients were not significantly different from 1·0.*

Keywords: *body composition, computed tomography, fallow deer, food restriction, tissue mobilization.*

Introduction

The annual growth cycle in male deer is characterized by a seasonal pattern of food intake and live-weight gain, even when given *ad libitum* access to food (Kay, 1979; Fennessy *et al.*, 1991). Live weight is gained in spring and summer, lost in the autumn during the breeding season, and generally maintained throughout the winter (Bandy *et al.*, 1970; Asher *et al.*, 1987; Fennessy and Milligan, 1987). The annual reproductive cycle interacts with the growth cycle, producing a marked decline in food intake, and consequently live-weight loss during the autumn rut (Fennessy *et al.*, 1991).

† Present address: AgResearch, Invermay Agricultural Centre, Private Bag 50034, Mosgiel, New Zealand.

The rut-associated fast is an example of a seasonal anorexia, a widespread adaptation in many species to situations where time spent eating may compromise other important activities (Mrosovsky and Sherry, 1980). In male deer, natural selection has favoured breeding activity at the expense of feeding activity. The rut is a special time in the seasonal physiology of male deer as it appears they are able to regulate the relative losses of their lean and fat reserves throughout the rut-associated fast. The majority of the live-weight loss over the rut may be accounted for by the preferential mobilization of fat stores (Drew, 1985; Wallace and Davies, 1985). There is also evidence to suggest that fat depots are mobilized in a preferential manner, with the relative mobilization of the subcutaneous depot being greater than the intermuscular depot (Wallace and Davies, 1985). The mechanisms that control these processes are poorly understood and studies to date have generally been limited by the necessity to slaughter animals to obtain data and by the use of small numbers of animals.

In the experiments reported in this paper, the hypothesis proposed was that testosterone modified the pattern of tissue mobilization in response to a fast. To this end the experiments investigated the effects of manipulating pre-fast fat reserves, and the presence or absence of testosterone, on the relative mobilization rates of fat and lean body reserves during food restriction in mature fallow bucks. The food restriction periods were either natural (the rut-associated seasonal anorexia) or enforced. The computed tomography (CT) scanner was considered the best available means of collecting information on changes in body composition over time. It enabled the repeated measurement of body composition on individuals to be made and could be used to give accurate results over a wide range of ages and body compositions (Thompson and Kinghorn, 1992).

Material and methods

General experimental details

The experiment was conducted in two stages. In stage I (rut: February to May 1991), a total of 14 mature fallow bucks were randomly allocated (stratified by weight) to one of three treatment groups in November 1990. The treatment groups comprised: a high nutrition treatment (HiEnt, no. = 4), a castration treatment (CAST, no. = 4) and a low nutrition treatment (LoEnt, no. = 6). In the pre-experimental period the HiEnt bucks were grazed on high-quality pasture from November to February. They were then group-fed a pelleted diet *ad libitum* for the experimental period. The CAST group comprised bucks that after randomization were also maintained on high-quality pasture from November to January. They were then castrated and kept on pasture for another 6 weeks. During the experimental period, the CAST treatment was group-fed at the same level as, but a week behind, the HiEnt bucks in order to induce an equivalent live-weight loss. This failed to occur and so the CAST group were restricted for a further 4 weeks (at 1·89 kg dry matter (DM) per week) to achieve an equivalent live-weight loss to the HiEnt group. During the pre-experimental period the LoEnt group were restricted on pasture from November to February in order to achieve a 10 kg lower live weight than the HiEnt bucks at the commencement of the experiment in February. Thereafter this group was given a maintenance food allowance of 7·6 kg DM per head per week from February to May. The expectation was that rising testosterone levels associated with the onset of the rut would further restrict food intake inducing live-weight loss.

In stage II (SPRING: June to November 1991) six entire bucks (three from each of the HiEnt and LoEnt groups) were given food *ad libitum* from May to mid October and then restricted to 2·83 kg DM per head per week for 4 weeks (equivalent to the minimum food intake of the HiEnt group over the rut, adjusted for differences in activity). This treatment was applied to test the body composition response to food restriction outside of the rut. In spring, entire bucks are functional castrates with low or undetectable concentrations of testosterone (Suttie *et al.*, 1992).

Bucks were group-fed a pelleted diet (Table 1) in outdoor pens measuring 20 × 40 m in which vegetative growth was eliminated by regular spraying with glyphosate ('Round-up', Monsanto). Live weight and food intake were measured weekly. The bucks were CT-scanned to estimate body

Table 1 *Components and dry matter composition of the pelleted diet*†

Components (g/kg)		Dry matter composition	
Lucerne	600	Organic matter (g/kg)	932
Wheat grain	300	Crude protein (g/kg)	192
Soya-bean meal	100	Metabolisable energy (MJ/kg)	10·23

† To 100 kg of this diet was added: 1 kg finely ground limestone, 0·25 kg NaCl and 0·8 kg of a vitamin-mineral pre-mix (0·8 kg pre-mix contained 29 g retinol, 0·1 g cholecalciferol, 80 g α-tocopherol, 8 g cobalt, 8 g iodine, 8 g molybdenum, 0·8 g selenium, 120 g iron, 160 g manganese and 400 g zinc). A new batch of food was used from August 1991 in which the vitamin-mineral pre-mix contained an additional 8·4 g sodium molybdate, 50 g sulphate of ammonia and 59·2 g sodium sulphate per 100 kg diet.

composition at regular intervals. For the 'rut' period, bucks were CT-scanned on five occasions, namely: 18 February; 18 March; 15 April; 6 May; and 31 May. For the 'spring' period, bucks were CT-scanned on three occasions, namely: 15 October, 29 October and 12 November. Plasma samples were collected over ice prior to each CT scanning to measure testosterone concentration.

Procedures for X-ray computed tomography of deer

Bucks were scanned using a CT-scanner (Hitachi CTW-430, X-ray computed tomography system) following the procedure described by Thompson and Kinghorn (1992). Prior to scanning, bucks were fasted for 24 h and then anaesthetized with an intramuscular injection of 4 mg/kg live weight of xylazine hydrochloride ('Xylazine 100', Pitman-Moore, Coopers Animal Health Australia Limited) and 8 mg/kg ketamine hydrochloride ('Ketavet 100', Delta Veterinary Laboratories Pty Limited). If necessary a further intravenous injection of 4 mg/kg ketamine hydrochloride was given. Following scanning (*ca.* 45 min), the sedation was reversed by an intravenous injection of 0·5 mg/kg yohimbine hydrochloride ('Reverzine Injection', Parnell Laboratories Australia Pty Limited). A 5-ml intramuscular injection of 150 mg/ml procaine penicillin G, 112·5 mg/ml benathine penicillin, ('Norocillin LA', Norbrook Laboratories, United Kingdom) was given as a preventative measure against inhalation pneumonia.

Animals were scanned with forelimbs flexed and hindlimbs extended. Scans comprised a series of cross-sectional images recorded at 50-mm intervals along the length of the body, from a point behind the rump (i.e. distal to the proximal hind limb muscles) to the first cervical vertebrae. Scans were 420 mm in diameter and 5 mm in width. On average 21 scans were recorded for each buck.

Image analysis procedure

Images were analysed using the program 'CATMAN' (Thompson and Kinghorn, 1992). This required images to be transferred to a PC and the CT number rescaled to a 256 grey scale which maximized the differences between lean and fat tissue. The program separated the image into areas associated with up to six tissue depots, comprising subcutaneous, intermuscular and internal fat (all visible fats in the thoracic and abdominal cavities), muscle, viscera (which contained all abdominal and thoracic organs, excluding the lungs, and rumen and caecal contents) and bone. Tissue areas from each scan were numerically integrated to estimate tissue volume for that depot (Gundersen *et al.*, 1988). This was then corrected for density to provide an estimate of tissue weight based on the relationship between Hounsfield units and density (Fullerton, 1980). Empty body weight (EBW) was defined as the sum of the total fat, muscle, bone and viscera weights.

Testosterone radioimmunoassay

Plasma testosterone concentrations were determined in duplicate by an extraction radioimmunoassay. The antisera used in the assay ('6050'; CSIRO Prospect, Blacktown, Australia) was raised in sheep against testosterone-3-0-carboxymethyloxine-BSA conjugate. The inter- and intra-assay coefficients of variation were 0·155 and 0·121 respectively. The sensitivity of the assay was 0·1 μg/l and the mean non-specific binding was 2·8%. Cross-reactivities were; dihydrotestosterone 31%, androstan-17β-ol-3-one 30%, androstenedione 1·3%, all oestrogens tested <1%.

As testosterone is released into the blood in a pulsatile manner there are difficulties interpreting results from single samples. To resolve this problem, the results are presented as the proportion of animals displaying evidence of a testosterone pulse (plasma concentration >0·5 μg/l).

Statistical analysis

The allometric model has conventionally been used as a tool to describe relative growth and development of tissues in growing animals (Huxley, 1931). The model is generally computed in the linear form after log transformation ($\log_{10}y = \log_{10}A + b \log_{10}x$, where y = component weight, A is the scaling factor, b the allometric coefficient and x the sum of the component weights). In this study the allometric model was used to describe relative rates of tissue loss, using the following nomenclature based on the b coefficient. High mobilization described those tissues that had a b coefficient greater than one, indicating that they were mobilized at a greater rate than the total. Average mobilization described those tissues with a b coefficient which was not significantly different from one, indicating that they were mobilized at the same rate as the total. Finally low mobilization described those tissues with a b coefficient significantly less than one, indicating that they were mobilized at a lower rate than the total. Repeated compositional measurements on individual animals allowed changes to be examined on a within-animal basis, rather than measurements from each scan being considered as an independent observation as in a serial slaughter design. Log component weights of the body (total fat, muscle, viscera and bone) were analysed in a model which contained terms for treatment, log EBW, animals nested within treatment and the interaction between treatment and log EBW. Effects were tested against the appropriate error term using the Proc MIXED option in Statistical Analysis Systems Institute (1992).

For changes in fat partitioning, the dependent variable comprised log weights of subcutaneous, intermuscular and internal fat using total fat weight as the covariate.

Results

Live weight

The general patterns of live weight for the four treatment groups are shown in Figure 1. As the rut progressed the HiEnt bucks lost live weight at 0·28 kg/day, from a mean pre-rut live weight of 70 kg. The LoEnt bucks lost live weight whilst restricted at pasture, although when placed on the restricted pelleted diet they gained considerable weight (7 kg) in the first 2 weeks, and then 3 kg over the next 5 weeks before losing 5 kg over the last 7 weeks. The rut-associated period of weight loss was delayed and greatly reduced in the LoEnt animals, with bucks losing weight at an average rate of 0·12 kg/day from week 10 to the end of the experiment.

When the CAST bucks were given food at the same level as the HiEnt bucks, they also lost weight at 0·28 kg/day. As the HiEnt bucks increased their intakes out of the rut, the food intake of the CAST bucks was increased accordingly and consequently their live weight also increased. However as the CAST group had lost less total live weight than the HiEnt bucks (Figure 1), a second period of food restriction was enforced so that they again lost live weight at a rate of 0·28 kg/day until the end of the study.

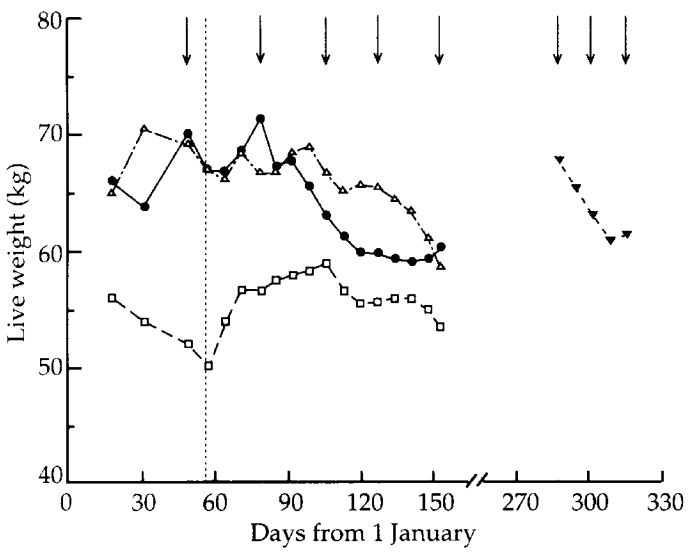

Figure 1 Patterns of live weight in adult fallow entire and castrated bucks on various nutritional regimes. The dashed line and arrows indicate the start of food intake measurements and scanning dates respectively. ● = HiEnt; ❑ = LoEnt; Δ = CAST; ▼ = SPRING.

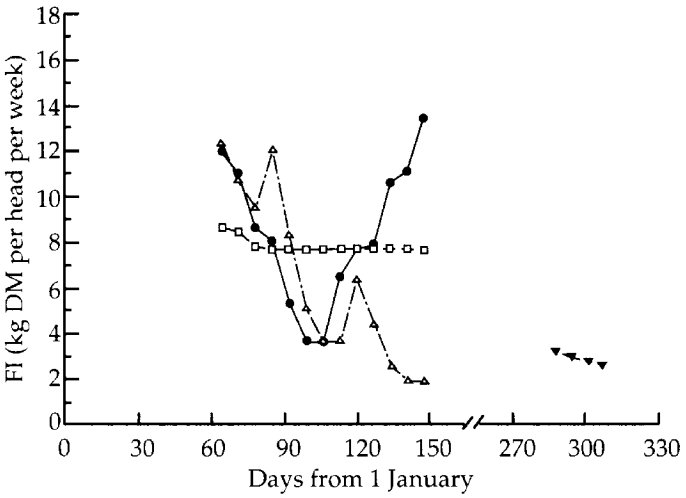

Figure 2 Weekly food intake (FI) (kg dry matter per head) of a pelleted diet in entire adult fallow bucks given food *ad libitum* (HiEnt, ●) or restricted prior to rut (LoEnt, ❑), castrated (CAST, Δ), pair fed with the HiEnt group, and entire males restricted in the spring (SPRING, ▼).

The SPRING group underwent a 4-week period of restriction, which resulted in a live-weight loss of 0·23 kg/day.

Food intake

Food intake data for the HiEnt and LoEnt, CAST and SPRING restriction groups are shown in Figure 2.

Food intake in the HiEnt bucks decreased from 12·0 kg DM per head per week at the beginning of March, to 3·6 kg DM per head per week at the beginning of April. Having reached a nadir, food intakes increased steadily to reach 13·5 kg DM per head per week by the end of study in June. When the LoEnt group was moved from pasture into the outdoor pens, they were offered the pelleted diet at a rate of 8·6 kg DM per head per week (Figure 2), which was reduced to 7·6 kg DM per head per week over the first 2 weeks to stabilize live weight. Food intake for the LoEnt group was maintained at this level for the remainder of the study.

The CAST group were 'matched group' fed at the same level of food that the HiEnt group consumed the previous week. At the same level of food intake the CAST group lost less live weight than the HiEnt bucks during the rut and so were restricted for a further 4 weeks (at 1·89 kg DM per head per week) to achieve an equivalent live-weight loss. Food intake in the SPRING group was reduced to 2·83 kg DM per head per week over a 4-week period to ensure a rapid live-weight loss.

For the HiEnt and LoEnt bucks, data in Figures 1 and 2 revealed a delay of around 3 weeks between the

Table 2 *Plasma testosterone† at each scanning day for the four treatment groups‡*

	Evidence of pulse (proportion of bucks)			
Date	HiEnt	LoEnt	CAST	SPRING
19 Feb.	1·00	0·80	0·00	
19 Mar.	0·75	0·66	0·00	
16 Apr.	1·00	1·00	0·00	
7 May	0·25	0·66	0·00	
31 May	0·25	0·66	0·00	
15 Oct.				0·00
29 Oct.				0·00
12 Nov.				0·00

† Single blood samples were taken at *ca.* 08.00 h: any concentration > 0·5 μg/l was taken as evidence of a pulse.
‡ Treatments were *ad libitum* (HiEnt) and restricted (LoEnt) feeding of entire males over the rut, castrated (CAST) males pair-feeding with the HiEnt group and entire males on *ad libitum* feeding into spring then given the same amount as the HiEnt group during the rut (SPRING).

change in food intake and the live-weight response to that natural restriction. This lag was not evident in the CAST or SPRING groups.

Testosterone

The proportion of bucks displaying evidence of a testosterone pulse are presented in Table 2. Testosterone pulses were present in a high proportion of both HiEnt and LoEnt bucks throughout the entire experimental period. This indicates that the nutritional regime applied to the LoEnt bucks did not interfere with the increase in testosterone pulsatility around the rut. Testosterone concentrations were never greater than 0·5 μg/l in either the CAST or SPRING treatments groups. The SPRING group were indeed functional castrates, with very low or undetectable concentrations of testosterone throughout the weight loss period.

Body composition

Mean tissue weights, as estimated by CT-scan, for the four treatment groups at their estimated peaks are presented in Table 3. The LoEnt group had the least fat with only 1·57 kg, whilst the HiEnt, CAST and SPRING groups had similar weights of peak fat, ranging between 6·78 and 10·5 kg. There was around a four- to seven-fold difference in peak fat weight between the HiEnt, CAST and SPRING groups compared with the LoEnt group. In comparison, there was a 0·18 proportional difference between treatments in muscle weights, with less than 5 kg separating the four groups. All treatment groups had similar bone weights.

Gross composition and fat partitioning

Table 4 presents the allometric analyses for body tissue weights relative to EBW. Two bucks (from a total of six) from the LoEnt group with very low levels of fat (approx. 1·3 kg) were excluded from the analyses, as the change in EBW was less than 2 kg and little confidence could be placed in the body tissue/EBW relationships.

The *b* coefficients for the various fat and lean depots in CAST, SPRING and LoEnt bucks need to be compared with the HiEnt bucks in order to test the hypothesis that testosterone modified the pattern of tissue mobilization in response to a fast. First, testosterone influenced the pattern of tissue mobilization during the rut. CAST bucks mobilized fat at a lower rate than HiEnt bucks ($P < 0·01$), with *b* coefficients of 2·79 and 5·23, respectively (Table 4). While there was a trend for CAST bucks to mobilize both muscle and viscera at higher rates than HiEnt bucks, the differences were not significant ($P > 0·05$). There was a significant difference between CAST and HiEnt bucks in the pattern of bone mobilization/deposition ($P < 0·05$). In the CAST bucks bone mass decreased slightly as the animals lost EBW ($b = 0·19$), while in the HiEnt bucks there was a slight gain relative to EBW ($b = -0·21$).

Secondly, tissue mobilization in spring (when testosterone was undetectable) was different from that of the autumn rut. SPRING bucks mobilized fat at a slightly lower rate than HiEnt bucks (4·02 and

Table 3 *Mean body composition and date of peak live weight for body components from animals at the commencement of the weight loss due to natural or enforced food restriction for the four treatment groups†*

		Live weight (kg)		Fat (kg)		Muscle (kg)		Bone (kg)	
Treatment	Date	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.
HiEnt	19 Mar.	70	11	7·42	3·34	30·4	3·12	4·65	0·54
LoEnt	15 Apr.	59	6	1·57	0·27	25·6	2·08	4·53	0·39
CAST	19 Mar.	69	9	10·5	2·26	27·5	2·80	4·71	0·28
SPRING	15 Oct.	68	4	6·78	1·59	29·6	1·35	4·71	0·39

† For treatments see Table 2 footnote.

Table 4 *The intercept (log a) and slope (b) of the log transformed allometric for the mobilization of body components relative to empty body weight (EBW) for the four treatment groups*†

	log *a*						*b* coefficient					
	HiEnt	LoEnt	CAST	SPRING	Average s.e.	Significance	HiEnt	LoEnt	CAST	SPRING	Average s.e.	Significance
Total fat	−18·64	−12·40	−8·62	−13·75	3·91		5·23	3·49	2·79	4·02	0·71	*
Muscle	1·90	−0·68	1·28	0·62	0·40	***	0·38	1·07	0·52	0·71	0·08	***
Viscera	−0·81	−1·47	−1·24	−1·56	1·12		0·73	0·92	0·82	0·91	0·20	
Bone	2·34	1·29	0·74	1·67	0·88		−0·21	0·06	0·19	−0·02	0·16	
Change in EBW (kg)							6·90	3·61	7·97	7·39		

† For treatments see Table 2 footnote.

5·23, respectively), although the difference was not significant ($P > 0·05$). Muscle was mobilized at a higher rate ($P < 0·01$) in SPRING bucks than in HiEnt bucks (*b* coefficients of 0·71 and 0·38, respectively). There was no difference in the *b* coefficients for bone between the SPRING and HiEnt bucks.

Thirdly, a comparison of changes in body composition (relative to EBW) with food restriction revealed significant differences between the SPRING and CAST groups. The rate of muscle mobilization relative to EBW change was significantly ($P < 0·05$) higher in SPRING bucks than in CAST bucks as was evidenced by the differences in *b* coefficients (0·71 and 0·52, respectively). The relative rate of fat mobilization was also higher in SPRING bucks than in CAST bucks but the difference was not significant ($P > 0·05$). The *b* coefficients for bone mobilization were not different between the SPRING and CAST bucks ($P > 0·05$).

Finally, there were different relative rates of tissue mobilization between LoEnt and HiEnt bucks, which appeared to be associated with fat reserves prior to the rut. LoEnt bucks tended to have a lower *b* coefficient for total fat relative to EBW than HiEnt bucks, although the difference was not significant ($P > 0·05$). The difference between *b* coefficients for muscle in LoEnt and HiEnt bucks was significant (1·07 and 0·38, respectively; $P < 0·05$) indicating a higher rate of mobilization in bucks with lower energy stores at the commencement of the rut. The results from the allometric analysis of fat depots relative to total fat weight are presented in Table 5. The mobilization of subcutaneous fat relative to total fat was significantly greater in HiEnt than in CAST bucks ($P < 0·05$), with *b* coefficients of 1·86 and 1·41, respectively, and both were significantly greater than 1·0. Likewise, the relative mobilization of intermuscular fat was greater in HiEnt than in CAST bucks at 1·23 and 0·75, respectively ($P < 0·05$). However, neither of these *b* coefficients was significantly different from 1·0. The *b* coefficients for internal fat were not significantly different ($P > 0·05$) for the two treatment groups (Table 5).

Comparing the relative rates of fat mobilization in the HiEnt and SPRING groups, the HiEnt bucks tended to have higher *b* coefficients in all three depots, with the greatest differences occurring in the

Table 5 *The intercept (log a) and slope (b) of the log transformed allometric function for the mobilization of fat depots relative to total fat for the four treatment groups*†

	log *a*						*b* coefficient					
	HiEnt	LoEnt	CAST	SPRING	Average s.e.	Significance	HiEnt	LoEnt	CAST	SPRING	Average s.e.	Significance
Subcutaneous fat	−3·15	−2·92	−1·78	−2·32	0·39	*	1·86	1·23	1·41	1·72	0·16	**
Intermuscular fat	−2·04	−2·24	−1·38	−1·88	0·36		1·23	1·23	0·75	1·03	0·15	
Internal fat	−0·04	−0·24	−0·36	−0·17	0·10	**	0·68	0·97	0·76	0·65	0·04	***
Change in total fat (kg)							4·52	0·66	4·98	3·19		

† For treatments see Table 2 footnote.

intermuscular depot (1·23 *v.* 1·03 for the HiEnt and SPRING bucks, respectively). However, the differences did not reach statistical significance in any depot. There were clear differences in *b* coefficients for the fat depots relative to total fat between the HiEnt and LoEnt groups (Table 5). In the subcutaneous depot, the HiEnt bucks had a greater *b* coefficient ($P < 0·05$) than LoEnt bucks at 1·86 and 1·23, respectively. The opposite trend was observed in the internal fat depot with the HiEnt bucks having a lower *b* coefficient ($P < 0·05$) than the LoEnt bucks at 0·68 and 0·97, respectively. The *b* coefficient was significantly lower than 1·0 in HiEnt ($P < 0·05$) but not in LoEnt bucks. There was no difference between groups in the *b* coefficient for intermuscular fat and in neither case were the *b* coefficients significantly different from 1·0.

The relative rates of fat mobilization in SPRING as compared with CAST bucks failed to reach significance in any of the fat depots examined (Table 5).

Discussion

The initial amount of fat reserve and presence or absence of testosterone produced clear differences in the pattern of body tissue mobilization in fallow bucks. Muscle was conserved at the expense of body fat in rutting bucks when accumulation of adequate body fat stores had occurred prior to the rut. The same degree of muscle conservation did not occur in the absence of testosterone, or when there were low pre-rut fat reserves. The ability to conserve muscle mass over the rut represents an adaptation to cope with the rut-associated seasonal anorexia and presumably serves to improve the buck's ability to compete for access to females during the rut in the wild.

Live weight and food intake

The pattern of live weight change for the HiEnt bucks was similar to that reported for a number of deer species (Bandy *et al.*, 1970; Fennessy, 1981; Asher *et al.*, 1989), as was food intake (Fennessy and Milligan, 1987). The HiEnt group exhibited the normal pattern of changes in body weight and food intake over the rut. The mechanism for the week delay between the decline in food intake and the associated fall in live weight is unknown. The failure to observe a similar delay in the CAST or SPRING groups indicates that the effect is probably related to the presence of testosterone. This delay between the timing of the decline in food intake and live-weight loss is not unique in that it has been reported in red deer stags (P. F. Fennessy, personal communication), harbour seals (*Phoca vitulina;* Renouf and Noseworthy, 1991) and in some of the hibernating species (Mrosovsky, 1976; Young, 1976). There is an accumulation of data relating to deer which indicate that some of the difference may be accounted for in an increase in body water immediately prior to the rut. The greatest carcass water content in red deer is immediately prior to the rut-associated fall in live weight (Drew, 1985). Also, the water : protein ratio of the neck musculature is greater in entire red stags during the rut than in castrated stags at the same time (Tan and Fennessy, 1981). The importance of maintaining size by retaining water cannot be overlooked in a species where reproductive success in males is highly related to body size (Clutton-Brock *et al.*, 1982).

Pre-rut fat proportion has been shown to be positively related to the duration of the rut and negatively related to the time of the onset of the rut in red deer (Gibson and Guinness, 1980). In the present experiment, the start of the rut in the LoEnt bucks could not be determined from food intake data but food restriction prior to the breeding season appeared to delay the rut by around 2 weeks based upon the onset of live-weight loss. The expression of the rut was also altered in the same animals as food intake never dropped below the 7·6 kg DM per head per week allowance. Bucks in poor condition prior to the rut appear to compensate for their initial fat-depleted state by consuming more food throughout the period of the rut. Some true hibernators display a programmed decrease or falling set point for body weight (Mrosovsky and Powley, 1977), or body fat (Mrosovsky and Sherry, 1980) over the winter phase of the hibernation cycle. When forced below the programmed level of fat weight, food intake is increased to compensate. Parallels between hibernators and deer are indicated here but further experimentation is required to examine whether deer adjust food intake to keep fat reserve losses within defined limits. In the wild, an increase in time spent eating by an individual buck would compromise the ability of that buck to compete for access to females, such that the buck would be unlikely to mate in that year.

The fact that CAST bucks lost less live weight than HiEnt bucks when given the equivalent amount of food suggests that the CAST group were more efficient during their fast. It should be noted that energy expenditure is elevated in red deer stags during the rut (Bobek *et al.*, 1990). Although this was not measured in the present experiment, it appeared to be the case as the HiEnt bucks were more aggressive during handling when compared with the CAST bucks, both to the handlers and to other bucks in their group. Further, the pair feeding of CAST bucks was based on the group intake of the HiEnt group. If individual bucks were not synchronized in

their food intake nadir, then the individual CAST bucks did not experience as severe a fast as individuals from the HiEnt group. An experiment in which castrated males and bucks are individually fed over the rut is required to resolve the contribution of these factors to the apparent difference in 'efficiency' between entire and castrated deer.

Tissue mobilization

Bucks from all treatment groups were well able to use their stores of body fat to meet the energetic requirements of a fast. During the rut in both wild and farmed red deer stags the proportional drop in live weight is in the order of 0·15 to 0·30 (Mitchell *et al.*, 1976; Drew, 1985; Kelly *et al.*, 1987), with mobilization of the majority of fat reserves. The relative rate of fat mobilization in the present experiment was considerably greater than the gain of lipid in the carcass of growing fallow deer bucks, with Gregson and Purchas (1985) reporting an allometric growth coefficient for fat relative to carcass weight of 2·1. On this basis, it should be noted that a period of weight loss is not simply the reversal of a period of weight gain. The *b* coefficients were also higher than those reported during live weight loss in Merino sheep by Aziz *et al.* (1992). While directly comparable results for individual depots were not presented, they could be calculated by substituting terms from the various regression equations. The *b* coefficients for the mobilization of subcutaneous fat relative to EBW during live-weight loss were 2·22 and 9·73 for Merinos (Aziz *et al.*, 1992) and the HiEnt bucks, respectively. For the intermuscular depot, *b* coefficients of 1·41 and 6·43 were recorded, respectively. A comparison of the kidney and channel fat depot in Aziz *et al.* (1992) with the internal fat depot in the present experiment produced *b* coefficients of 1·54 and 3·55, respectively.

Removal of the animal-within-treatment term from the model in the statistical analysis of the present experiment always resulted in reduced *b* coefficients. For example, the *b* coefficients for total fat relative to EBW were 5·23 and 4·35 for models including animal within treatment and models excluding animal within treatment, respectively. Models that did not include animal within treatment may be thought of as equivalent to a slaughter experiment. The *b* coefficients calculated by Gregson and Purchas (1985) and Aziz *et al.* (1992) may be underestimated because they were measured from slaughter data and could not account for the random effect of animal. The extremely high weight loss coefficients of body and depot fat reported here are considerably greater than estimates for other species in the literature. Taken in conjunction with the low coefficients for muscle loss, this indicates that, during the rut, mature fallow bucks protected muscle mass by biasing their metabolism towards utilization of fat.

Use of a CT scanner allowed a detailed examination of the patterns of tissue or depot mobilization. The presence or absence of testosterone clearly modified the pattern of tissue mobilization over the rut. The group experiencing a natural rut-induced fast in the presence of testosterone (the HiEnt bucks) protected, or spared, their muscle reserves to a greater degree than those bucks fasted without testosterone. It would appear that entire bucks have evolved mechanisms which spare muscle mass during a predictable period of general body-weight loss but these mechanisms do not appear to operate as efficiently at other times of year (i.e. in the SPRING bucks), or in CAST bucks at the same time of year. The anabolic effects of testosterone in ruminants are well documented (Schanbacher *et al.*, 1980; Unruh, 1986). Also, the rut-associated depression in food intake in fallow deer is at least in part induced by the action of testosterone as it can be produced outside of the rut by administering exogenous testosterone (Newman *et al.*, 1992). Testosterone obviously has major effects on the partitioning of fat and lean tissues during growth and the present experiment demonstrates that it also influences the partitioning of fat and lean depot loss during food restriction. Whether this effect was due to actual protection of protein mass or simply due to increased stores of body water over the rut could not be resolved in this study due to the fact that it was not possible to divide muscle mass, as determined by CT, into protein and water.

However, the muscle sparing action of testosterone over the annual rut failed when insufficient stores of body fat had been accumulated prior to the rut. The relatively high mobilization of muscle mass in the LoEnt group, in conjunction with the failure of bucks in this group to further restrict their food intake in the rut, indicates that when loss of condition is severe this overrides some of the effects of the rut. The LoEnt bucks were still in a state of negative energy balance, as was evidenced by the loss of live weight, lean and fat reserves. However, the question raised is whether live-weight loss, and therefore muscle and fat mobilization, would have been completely avoided had the bucks had *ad libitum* access to food during the rut. It should be noted that the LoEnt bucks did experience a rut based on behavioural and live-weight data, and so theoretically attempted to compete reproductively, albeit at a reduced level due to the increased need to eat. The implications are that in a situation where the logical endpoint of gambling resources on attempting to reproduce in that year is a lack of reproductive success and likely death, then a buck

may minimize this effect by employing a strategy of limiting rutting activities, so conserving energy while also maintaining a reasonable level of energy intake.

The deposition of fat in spring and summer certainly appears to be a reproductive strategy in deer as suggested by Tyler (1987). Failure to deposit large stores of fat prior to the rut resulted in higher food intake during the rut, which would compromise efforts to gain access to females for breeding. Fat is not used for winter survival in fallow bucks as they exited the rut with almost all of their pre-rut stores exhausted. If male deer cannot consume enough food to maintain weight over the winter, carcass and visceral protein stores are mobilized (Wolkers *et al.*, 1994) and death may result in extreme cases. The extreme mobilization of fat during the rut appears to preserve as much muscle mass as possible. This process is regulated in some manner by testosterone (or one of its metabolites) as the same preservation of muscle mass was not seen in bucks that had undetectable levels of testosterone.

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References

Asher, G. W., Day, A. M. and Barrell, G. K. 1987. Annual cycle of liveweight and reproductive changes of farmed male fallow deer (*Dama dama*) and the effect of daily oral administration of melatonin in summer on the attainment of seasonal fertility. *Journal of Reproduction and Fertility* **79:** 353-362.

Asher, G. W., Peterson, A. J. and Bass, J. J. 1989. Seasonal pattern of LH and testosterone secretion in adult male fallow deer, *Dama dama*. *Journal of Reproduction and Fertility* **85:** 657-665.

Aziz, N. N., Murray, D. M. and Ball, R. O. 1992. The effects of live weight gain and live weight loss on body composition of Merino wethers: dissected muscle, fat, and bone. *Journal of Animal Science* **70:** 1819-1828.

Bandy, P. J., Cowan, I. M. and Wood, A. J. 1970. Comparative growth in four races of black-tailed deer (*Odocoileus hemionus*). 1. Growth in body weight. *Canadian Journal of Zoology* **48:** 1401-1410.

Bobek, B., Perzanowski, K. and Weiner, J. 1990. Energy expenditure for reproduction in male red deer. *Journal of Mammalogy* **71:** 230-232.

Clutton-Brock, T. H., Guinness, F. E. and Albon, S. D. 1982. *Red deer: behaviour and ecology of two sexes.* University of Chicago Press, Chicago.

Drew, K. R. 1985. Meat production from farmed deer. In *Biology of deer production* (ed. P. F. Fennessy and K. R. Drew), *The Royal Society of New Zealand, bulletin 22,* pp. 285-290.

Fennessy, P. F. 1981. Nutrition of red deer. In *Proceedings of a deer seminar for veterinarians, Deer Advisory Panel, NZVA,* pp. 8-15.

Fennessy, P. F. and Milligan, K. E. 1987. Grazing management of red deer. In *Feeding livestock on pasture* (ed. A. M. Nicol), *occasional publication no. 10, New Zealand Society of Animal Production,* pp. 111-118.

Fennessy, P. F., Thompson, J. M. and Suttie, J. M. 1991. Season and growth strategy in red deer: evolutionary implications and nutritional management. In *Wildlife production: conservation and sustainable development* (ed. L. A. Renecker and R. J. Hudson), pp. 495-501. University of Alaska, Fairbanks.

Fullerton, G. D. 1980. Fundamentals of CT tissue characterisation. In *Medical physics of CT and ultrasound: tissue imaging and characterisation* (ed. G. D. Fullerton and J. A. Zagzebski), *medical physics monograph, no. 6, American Institute of Physics,* pp. 125-162.

Gibson, R. M. and Guinness, F. E. 1980. Behavioural factors affecting male reproductive success in red deer (*Cervus elaphus*). *Animal Behaviour* **28:** 1163-1174.

Gregson, J. E. and Purchas, R. W. 1985. The carcass composition of male fallow deer. In *Biology of deer production* (ed. P. F. Fennessy and K. R. Drew), *The Royal Society of New Zealand, bulletin 22,* pp. 295-298.

Gundersen, H. J. G., Bendtsen, T. F., Korbo, L., Marcussen, N., Møller, A., Nielsen, K., Nyengaard, J. R., Pakkenberg, B., Sørensen, F. B., Vesterby, A. and West, M. J. 1988. Some new, simple and efficient stereological methods and their use in pathological research and diagnosis. *Acta Pathologica, Microbiologica et Immulogica Scandinavica* **96:** 379-394.

Huxley, J. 1931. *Problems of relative growth, first edition.* Methuen, London.

Kay, R. N. B. 1979. Seasonal changes of appetite in deer and sheep. *ARC Research Review* **5:** 13-15.

Kelly, R. W., Fennessy, P. F., Moore, G. H., Drew, K. R. and Bray, A. R. 1987. Management, nutrition, and reproductive performance of farmed deer in New Zealand. In *Biology and management of the Cervidae* (ed. C. M. Wemmer), pp. 450-460. Smithsonian Institute Press, Washington, DC.

Mitchell, B., McCowan, D. and Nicholson, I. A. 1976. Annual cycles of body weight and condition in Scottish red deer (*Cervus elaphus*). *Journal of Zoology, London* **180:** 107-127.

Mrosovsky, N. 1976. Lipid programmes and life strategies in hibernators. *American Zoology* **16:** 685-697.

Mrosovsky, N. and Powley, T. L. 1977. Set points for body weight and fat. *Behavioural Biology* **20:** 205-223.

Mrosovsky, N. and Sherry, D. F. 1980. Animal anorexias. *Science* **207:** 837-842.

Newman, R., Weston, R., Foldes, A., Jarratt, P. and Wynn, P. 1992. Administration of exogenous testosterone reduces feed intake in male fallow deer. *Proceedings of the Australian Society of Animal Production* **19:** 420.

Renouf, D. and Noseworthy, E. 1991. Changes in food intake, mass, and fat accumulation in association with variations in thyroid hormone levels of harbour seals (*Phoca vitulina*). *Canadian Journal of Zoology* **69:** 2470-2479.

Schanbacher, B. D., Crouse, J. D. and Ferrell, C. L. 1980. Testosterone influences on growth, performance, carcass characteristics and composition of young market lambs. *Journal of Animal Science* **51:** 685-691.

Statistical Analysis Systems Institute. 1992. *SAS technical report P-229, SAS/STAT software: changes and enhancements, release 6.07.* SAS Institute Inc, Cary, NC.

Suttie, J. M., Fennessy, P. F., Corson, I. D., Veenvliet, B. A., Littlejohn, R. P. and Lapwood, K. R. 1992. Seasonal pattern of luteinizing hormone and testosterone pulsatile secretion in young adult red deer stags (*Cervus elaphus*) and its association with the antler cycle. *Journal of Reproduction and Fertility* **95:** 925-933.

Tan, G. Y. and Fennessy, P. F. 1981. The effect of castration on some muscles of red deer (*Cervus elaphus* L.) *New Zealand Journal of Agricultural Research* **24:** 1-3.

Thompson, J. M. and Kinghorn, B. P. 1992. CATMAN — A program to measure CAT-scans for prediction of body components in live animals. *Proceedings of the Australian Association of Animal Breeding and Genetics* **10:** 560-564.

Tyler, N. J. C. 1987. Body composition and energy balance of pregnant and non-pregnant Svalbard reindeer during winter. *Symposium of the Zoological Society of London*, pp. 203-229.

Unruh, J. A. 1986. Effects of endogenous and exogenous growth-promoting compounds on carcass composition, meat quality and meat nutritional value. *Journal of Animal Science* **62:** 1441-1448.

Wallace, V. and Davies, A. S. 1985. Pre- and post-rut body composition of red deer stags. In *Biology of deer production* (ed. P. F. Fennessy and K. R. Drew), *The Royal Society of New Zealand, bulletin 22*, pp. 291-293.

Wolkers, H., Wensing, T., Schonewille, J. T. and Klooster, A. T. van 't. 1994. Undernutrition in relation to changed tissue composition in red deer (*Cervus elaphus*). *Canadian Journal of Zoology* **72:** 1837-1840.

Young, R. A. 1976. Fat, energy and mammalian survival. *American Zoology* **16:** 699-710.

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