Body compositional changes during fasting periods in fallow deer bucks
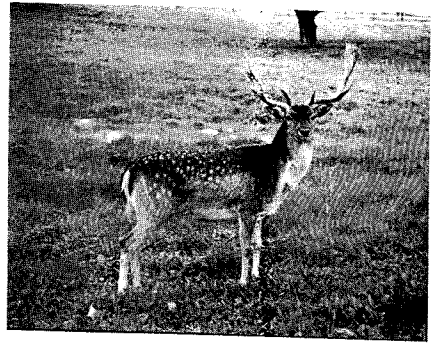
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Summary

Fallow deer bucks are adapted to use their body fat stores to meet their energetic requirements during the rut-associated period of food restriction. If fat stores are adequate there is capacity to conserve stores of carcass lean over this period.

Body fat stores after the rut are closely related to fat stores prior to the rut. The greater the fat stores prior to the rut, the greater the weight of fat remaining after the rut, albeit after mobilising a greater proportion of initial stores.

Compared with entires during the rut, entires during the spring and castrates during the rut mobilised more lean body mass at the same level of initial fat reserves.

Introduction

The behaviour, morphology and physiology of fallow deer, like that of other temperate deer species (including red, white-tailed, black-tailed and mule deer), reflect the adaptations developed to meet the seasonal constraints of the environments in which they evolved. Male deer of the temperate species clearly display two types of seasonal patterns, namely those of a cyclical nature with an annual frequency and those which are associated specifically with the mating period.

The annual cycle of food intake is evident in both male and female temperate deer, with intake levels high in summer and low in winter (Blaxter et al., 1974; Suttie,1987; Fennessy et al., 1991). This pattern appears to be related to photoperiod, with a lag phase of approximately two months in red deer

(Fennessy et al., 1991). The mechanisms controlling this cycle are poorly understood, although it is obviously under endogenous control as it continues when excess quantities of high quality food are available (McEwan & Whitehead, 1970; Bandy et al.,1970; Loudon et al.,1989; Fennessy et al.,1991).

The males have superimposed on the annual cycle an additional depression in food intake that is associated with the mating period (Fennessy et al., 1991). Temperate species of deer are seasonal breeders with a well-defined period of sexual activity, called the rut, occurring in the autumn months. Autumn timing of the rut ensures that births occur at the time of the year in which the probability of survival of the offspring is greatest when raised in the moist temperate environments in which they evolved (Lincoln & Short,1980).

During the rut, the male dramatically reduces food intake, loses a substantial amount of liveweight (Wood et al., 1962; Kay,1979; Asher et al., 1987) and displays marked aggression towards other males (Geist,1974; Clutton-Brock et al.,1979). These traits have evolved in the wild because they increase the probability of reproductive success of the individual males that display them. Natural selection will maximise the lifetime reproductive output of successful individuals (Maynard Smith, 1976). In the wild, the rut represents a considerable risk on the part of the buck as it must channel substantial resources into meeting the energetic requirements of the rut and also risk injury in fights with other bucks.

The rut is characterised by extremely high levels of plasma testosterone in contrast to the low or undetectable concentrations at other times of the year (Fennessy et al., 1988). There appears to be

an inverse relationship between the concentration of testosterone and the level of food intake, as food intake is reduced while the concentration of testosterone is elevated. Also, treatment of fallow bucks with testosterone prior to the start of the rut results in a rut-like reduction in food intake (Newman et al., 1992). The decline in food intake during the rut is reflected in substantial body weight loss (Fennessy,1981). Individual fallow bucks may lose up to 30 per cent of their pre-rut body weight at a rate of 450 g/day in a three to four week period (Asher, 1986). The depression in food intake and therefore the magnitude of the body weight loss, increases with age (Fennessy, 1981; Fennessy et al., 1991).

Studies by Drew (1985) and Wallace & Davies (1985) have reported that the loss in body weight over the rut in mature red deer stags results in differential rates of tissue loss, with rapid mobilisation of fat and only a small loss of muscle. For the domesticated species there are limited data on the loss of body components during weight loss in mature animals, although a study in mature Merino ewes showed the greatest loss in fat weight, a substantial loss of muscle and a small loss in bone weight (Thompson, J. M., Hinch, G. N. and Saka, K.; unpublished data). This prompts the question as to whether the low loss of muscle mass over the rut in mature male deer from the temperate species is associated with the high testosterone concentrations encountered during the rut.

While previous work has provided much useful data on the changes in body composition in deer during the rut, there are limitations due to the way in which body composition was measured. Traditional assessment of body composition has relied on a serial slaughter design in which groups of animals are slaughtered at set times, or weights. The greatest drawback with this design is that individual animals can only be assessed once. Also to ensure that treatment differences are simply not a reflection of differences between individual animals, it is necessary to sample a large number of animals. A much more efficient design is to use techniques which allows the same individual to be assessed a number of times throughout the experimental period. There are now a number of techniques available which measure the body composition in the live animal (for review see Wells, 1991). This means that the body composition of the animal may be measured on a number of occasions and that a smaller number of experimental animals are needed to achieve the same degree of accuracy. The CAT-scanner is an ideal tool for measuring body composition because it is accurate, relatively easy to use, can be applied to a wide range of ages and compositions and most importantly, can be applied to the live animal with little disturbance to subsequent performance of that animal.

The rut is a unique period in the yearly cycle of the deer. It reflects the result of generations of natural selection to give the individual male the maximum opportunity of passing on his genetic information to the next generation. The occurrence of the rut is exhibited in changes in food intake, live weight, body composition and behaviour, which in the wild are all means used to improve an individuals chances of reproductive success. In this paper the CAT-Scanner is used to examine the effect of both rut-induced and artificial fasts on tissue mobilisation in fallow deer. The implications of these evolutionary strategies on management of fallow bucks are also discussed.

Materials and methods

Animals and management: In January 1991, 17 mature fallow bucks (three years of age and older) were randomly allocated to three treatments, comprising high nutrition entire (6), low nutrition entire (6) and castration (5) groups. Bucks allocated to the latter group were castrated under anaesthetic on 1 February 1991. For the first month the high nutrition entire and castration groups had ad libitum access to both pasture and pellets (see Table 1 for composition), while the low nutrition entire group grazed a restricted pasture area. On 26 February, the animals were split into the three groups and moved into bare pens. Animals were given a week to acclimatise to the pens and then group intakes were recorded weekly. The high nutrition entire animals were group fed the pelleted ration ad libitum from 5 March until 3 June 1991, whilst the castration group were fed the amount the high nutrition entire group consumed the previous week. At this level of food intake the castrates did not lose as much weight as the high nutrition entire group by the end of the rut, and so on 9 May 1991 the castrate group was restricted further (minimum 1.9 kg dry matter per head per week) to give a comparable weight loss to the high nutrition group. The low nutrition entire bucks were fed at a level to maintain their live weight approximately 15 per cent below the peak live weight of the high nutrition entire group using the formula given by Fennessy et al. (1981).

This first phase of the experiment continued until 3 June 1991, whereupon three bucks from both the high and low nutrition entire groups were selected and placed in two pens to form the spring restriction

group. All the castrates and the excess bucks from the high and low nutrition groups were removed from the experiment. This group was fed *ad libitum* from 6 June 1991, for 18 weeks (until 13 October 1991), whereupon they were placed on a restricted ration and fed 1.9 kg dry matter per animal per week for four weeks to simulate a rut-like fast.

All groups were kept in pens measuring 20 x 40 m that were regularly sprayed with glyphosate ('Round-up', Monsanto) to eliminate pasture growth. Animals were weighed weekly from 1 February until 3 June, except the spring restriction group which was weighed from 11 June until 12 November. Residual food was removed and weighed weekly and group food intakes calculated.

Over the period of the experiment three animals died. The first was in the castration group with the cause of death diagnosed as stress associated with the castration operation. Two bucks from the high nutrition group died from inhalation pneumonia from the first scan. After these deaths the scanning procedure was modified to include a 12 hour fast off food and a 5 ml intramuscular injection of antibiotic ('Norocillin L.A.', 150 mg/ml procaine penicillin G, 112.5 mg/ml benathine penicillin, Norbrook Laboratories, United Kingdom).

Scanning procedure: Animals were scanned on 10 occasions. The high nutrition entire, low nutrition entire and castration groups, were scanned on five occasions, namely; 18 February, 18 March, 15 April, 6 May and 31 May. Similarly the spring restriction group was also scanned on five occasions, namely; 23 July, 10 September, 15 October, 29 October and 12 November. Animals were scanned at a rate of six per day.

Deer were anaesthetised in individual transport boxes with an intramuscular injection of a mixture of 4 mg/kg 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.). A further injection of 4 mg/kg ketamine hydrochloride was administered if required to ensure adequate sedation throughout the scanning period. The scanning procedure generally took 0.5 hours. Immediately after scanning, sedation was reversed with an intravenous injection of 0.5 mg/kg yohimbine hydrochloride ('Reverzine Injection', Parnell Laboratories Australia Pty. Limited).

Once anaesthetised, deer were securely strapped to a plywood bed to ensure that the animal would fit through the CAT scanner aperture and to minimise any movement by the animal. A firm foam rubber block was placed underneath the base of the deer's neck to provide drainage for saliva and rumen contents and reduce the risk of inhalation pneumonia.

A 300 mm longitudinal scanograph was taken to position the crossectional scans. The first scan was placed randomly at a small distance behind the rump and then slices taken every 50 mm thereafter. The size of the aperture was set at 420 mm diameter and the scan width at 5 mm. The end point for scanning was set at the first image taken past the first cervical vertebra. An average of 22 scans were required to scan the deer from the rump to the first cervical vertebra.

The image files were transferred to a personal computer and the pixel range rescaled to a 256 grey scale. The image analysis program 'CATMAN' (Thompson & Kinghorn, 1992) was used for all image analysis measurements. The program allowed the user to shade and fill regions in an image to calculate area and density of individual tissues or organs. The area and mean pixel number were calculated in every image for that particular animal. As the images were taken at regular intervals, the weight of a tissue depot was calculated as the sum of the areas, multiplied by the distance between slices and the average density of the tissue. Empty body weight was defined as the weight of all tissue components in the body, calculated from the sum of the total areas for each slice, excluding the content of the reticulo-rumen and large intestine.

For individual animals the weight of total body fat and carcass lean (Y) were regressed against empty body weight (X) using the allometric equation (Y=AXb), where A was a scaling factor and b the

allometric coefficient. The rate of tissue mobilisation relative to empty body weight was calculated as the first derivative of the allometric function. For the purposes of this paper only tissue mobilisation rates for total body fat and carcass lean tissue weights are reported.

Results and Discussion

The pattern of food intake from late February until November for the four treatment groups is shown in Figure 1. It appeared that the bucks in the high nutrition entire group had already commenced the decline in food intake associated with the rut when food intake recording began. Food intake was reduced to 30 per cent of the level at the start of the experiment. Newman et al. (1992) reported a similar drop in food intake for fallow deer treated with exogenous testosterone prior to the normal rut. Ad libitum food intake in that study fell from 10.3 to 4.5 kg/week prior to and during testosterone treatment, respectively.
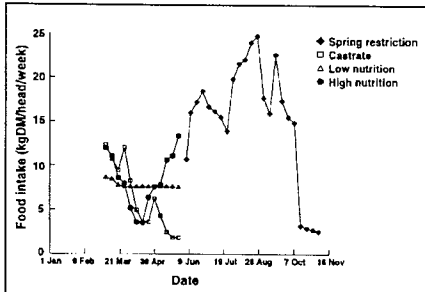

Figure 1: Mean weekly dry matter food intake in groups of entire and castrated adult fallow bucks fed various diets of a pelleted ration

The bucks stayed at the low level of food intake for 2 weeks before food intakes began to increase, so that within 2 months food intakes had returned to the levels recorded at the start of the study. Even though the level of food intake had begun to increase at the end of the rut, this was not reflected in liveweight that had troughed at approximately 59 kg until the final week of the experiment.

As expected, the rapid decline in food intake associated with the onset of the rut resulted in a substantial loss in liveweight. The bucks lost an average 8.2 kg of liveweight over the rut, a 12 per cent loss of pre-rut liveweight at an average rate of 280 g/day. Asher et al. (1988) reported a 32 per cent loss of live weight for a group of actively rutting 5 year old fallow bucks, considerably higher than the bucks in the present study. However, individual

bucks in the present study approached this level of liveweight loss with the largest buck losing 25 per cent of his pre-rut liveweight. A similar range of liveweight losses have been reported for red deer stags, varying between 15 per cent (Wallace & Davies, 1985) and 26 per cent (Drew, 1985).

It is noteworthy that the decline in food intake was not immediately matched by a decline in liveweight (Figures 1 and 2). Rather, there was a lag phase of at least three weeks after food intake began to decline before a decrease in liveweight was evident. This lag phase was not evident in either the castrate or spring restriction groups, which had both begun to decrease liveweight within one week of food restriction. Although not reported here, mobilisation of fat stores in the high nutrition group of bucks had begun while empty body weight was still increasing (N. Jopson; unpublished data). A similar delay of liveweight loss in mature red deer stags after food intake had begun to decline was also evident in data collected by P. F. Fennessy, (unpublished data). While the exact mechanisms are unknown, results from several studies suggest that this delay in liveweight response may be due in part to an increase in body water content at the start of the rut. Drew (1985) reported that the greatest carcass water content was immediately prior to the rut, whilst Tan & Fennessy (1981) reported that the water to protein ratio of the neck musculature was greater in entire red stags during the rut than in castrates. This results suggest that an increase in water content may be sufficient to offset the loss of liveweight due to loss of fat reserves and gut contents in the early stages of the rut.
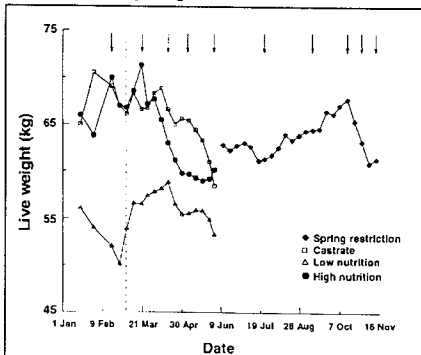

Figure 2: Change in mean liveweight in adult fallow entire and castrated bucks on various nutritional regimes. The dashed line and arrows indicate the start of food intake measurements and scanning dates respectively.

The castrates were restricted to the same level of intake as the high nutrition entires until the end of the rut, whereupon intakes were restricted further to 2 kg DM/week. Whilst being pair fed, the castrates lost about half the weight loss shown by the high nutrition entire group (4 kg to 8.2 kg, respectively). After their intake was further restricted, the castrates lost an additional 6.4 kg so that their total weight loss over the 3 month period was 10.4 kg (15 per cent of their pre-food restriction liveweight), which was similar to that of the high nutrition group. Again, one animal dominated the weight loss figures, with a 22 per cent decrease in liveweight.

The low nutrition entire group was initially restricted at pasture, prior to being placed in the pens and fed the pelleted ration. During this pasture restriction period they lost weight at a rate of 151 g/day. The level of maintenance feeding was estimated at 7.6 kg DM/head/week using the formula for metabolisable energy requirements of adult red stags from Fennessy *et al.* (1981). This proved to be an overestimate of the energy requirements of fallow bucks and consequently, mean liveweight of the low nutrition group increased prior to the rut. Examination of the data for individual animals in this group showed that three bucks either maintained, or lost weight, throughout the entire pellet feeding period. The rise and fall in liveweight displayed in Figure 2 was produced by the individual responses of the other 3 animals. Mean liveweight increased for a period of 7 weeks and peaked at approximately 59 kg when weight loss began. It is suggested that this decline was the result of animals undergoing a less intense rut. Although not reported in this paper, the suggestion that the animals did enter the rut was confirmed by elevated testosterone levels and the observation that aggression between animals increased during this period. In total, 9% of the peak liveweight in the low nutrition group was lost, even though the bucks were on a constant level of intake which was twice that of the trough for the high nutrition group.

Food intake for the spring restriction group increased over the 19 weeks of *ad libitum* feeding from 10.7 to a peak of 24.6 kg DM/head/week, whereupon it was restricted to a mean of 2.8 kg DM/head/week for the remaining four weeks. Liveweight increased at a rate of 39 g/day under *ad libitum* feeding. During the first three weeks of the food restriction period, 6.9 kg liveweight was lost at an average rate of 329 g/day. In the fourth week of the food restriction, there was a slight gain in weight which was possibly due to the bucks eating quantities of nylon shade cloth during this week.

Birds were observed consuming feed in all *ad libitum* periods. This loss appeared greater in the second part of the experiment than in the first part. *Ad libitum* feed intakes for the spring restriction group must therefore be considered an overestimate of actual food intake.

The repeated measurements on body composition made using the CAT-Scanner allowed the rates of tissue mobilisation to be calculated for individual animals during both the rut and the enforced fasting periods. Within treatments there was considerable variation in both initial composition and also the intensity of the rut and therefore rate of tissue mobilisation was considered as a function of initial composition, rather than a conventional between treatment analysis. The treatments therefore were considered to have generated animals of differing body compositions prior to a period of fasting.

Body weight loss was partitioned into total body fat and carcass lean. Figure 3 shows a strong positive relationship between the rate at which body fat was mobilised relative to empty body weight and the weight of total body fat prior to the period of food restriction ($R^2=0.70$). This figure demonstrates that treatment differences in the rate of body fat mobilisation were largely a function of variation in the weight of total body fat prior to a period of body weight loss. That is, animals that had the greater weight of fat prior to a period of food restriction exhibited the greatest rate of fat mobilisation during that restriction. Animals in the castrate and spring restriction groups, which were artificially forced to lose weight, appeared to simply follow the same function which described body fat mobilisation in the high and low nutrition entire bucks during the rut
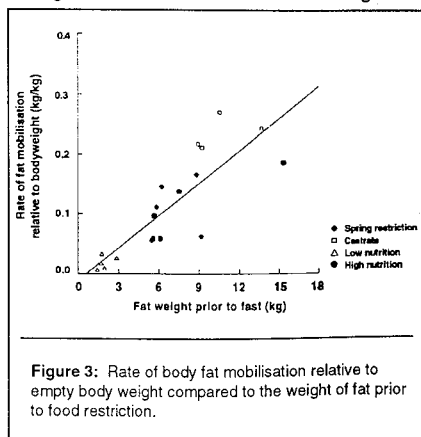

Figure 3: Rate of body fat mobilisation relative to empty body weight compared to the weight of fat prior to food restriction.

Figure 4 shows a strong negative curvilinear relationship between the rate at which carcass lean was mobilised relative to empty body weight and the weight of total body fat prior to the food restriction period for both groups of entire bucks over the rut period. Entire bucks are represented by the small solid circles in Figure 4 to demonstrate the fit of the data to the prediction curve. Entire bucks that were unable to accumulate large stores of fat prior to the rut compensated by increasingly drawing on lean tissue stores to meet the energy requirements of the rut. Our results suggest that he low rates of carcass lean tissue mobilisation reported by Drew (1985) and Wallace & Davies (1985) were most likely a reflection of substantial reserves of body fat prior to the rut.
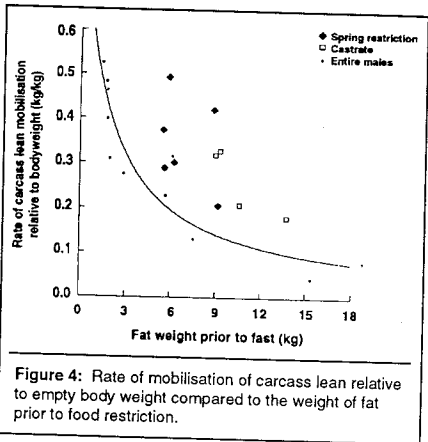

Figure 4: Rate of mobilisation of carcass lean relative to empty body weight compared to the weight of fat prior to food restriction.

It is intriguing that both the castrate and spring restriction groups lay above the fitted line for the entire bucks in Figure 4. This suggests that at the same initial level of fat, more lean body mass was lost during the period of food restriction compared with entires during the rut (Table 2). As the spring restriction group were functional castrates during their period of food restriction, it would appear that testosterone, or some factor associated with the rut, was to a degree protecting the reserves of lean tissues in entire males. 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.

Figure 5 illustrates a positive relationship between fat weight at the commencement and end of the rut, which suggests that initial fat reserves play a major role in determining the intensity of the rut. The mean initial fat weight of the high nutrition group was approximately 8.6 kg, of which 6.5 kg was lost

Table 2: Predicted• and actual rates of carcass lean mobilisation compared to empty body weight in castrated and entire fallow bucks fasted in autumn and spring respectively.

Treatment	Predicted (kg/kg)	Actual (kg/kg)(s.e.)	
Castrate	0.12	0.26	0.038
Spring restriction	0.18	0.35	0.042

•Predicted values derived from the relationship between lean tissue mobilisation and initial fat for entire stags over the rut {y=0.904/(1+0.604x); F2,8=19.6, P<0.001}

during the rut. In this group the bucks relied principally on body fat reserves to meet energy demands during the rut. This contrasts with the low nutrition group which had only 2 kg body fat prior to the rut and lost 1 to 1.5 kg of fat over the rut. The greater reliance on body fat reserves for the high nutrition group meant that food intake could drop to very low levels. Lack of fat reserves in the low nutrition group meant that food intake never dropped below the restriction level, which was twice the ad libitum intakes of the high nutrition bucks at their trough. This implies that in the wild the low nutrition bucks would have to spend a greater proportion of their time grazing and, therefore, less time in rutting behaviour, making them potentially less competitive and, therefore, less reproductively successful
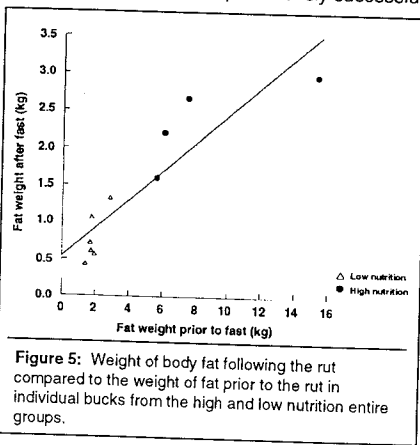

Figure 5: Weight of body fat following the rut compared to the weight of fat prior to the rut in individual bucks from the high and low nutrition entire groups.

The practical implications of these results are that the body fat reserves at the end of a rut are largely a function of the pre-rut reserves. However, even though the post-rut fat reserves were greater in those bucks that had substantial initial fat re-

serves, all bucks had less than 5 per cent of their liveweight as fat. The subtle differences in fat reserves at the end of the rut suggest that all bucks were in relatively poor condition going into winter. High initial fat reserves serve to conserve carcass lean and presumably allow bucks to increase their probability of reproductive success by spending more time in rutting activities. These results support the hypothesis that fat is used as a means of increasing reproductive success rather than winter survival in deer (Tyler, 1987; Fennessy et al., 1991). It is therefore vital to supply high quality feed to all bucks after the cessation of the rut and through the winter until body fat reserves are replenished.

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