

Winter food restriction and summer compensation in red deer stags (*Cervus elaphus*)

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1. Twelve red deer stags (*Cervus elaphus*) penned individually from weaning were fed on a concentrate diet. Six stags received the diet to appetite throughout the study, and the other six were restricted to 70% of the intake of the first group during winter and then fed to appetite during summer.

2. The winter-restricted stags showed remarkable compensatory growth during summer. Compared with the unrestricted stags they showed greater food intake, greater daily live-weight gain and increased food conversion efficiency. Nonetheless, they failed to compensate fully for the previous undernutrition.

3. The hind-foot of the restricted stags failed to grow as long as that of the unrestricted stags.

4. Poor winter nutrition, particularly during the first year of life, and subsequent failure to compensate during the short periods of summer plenty, provides an explanation for the small mature size of wild stags in Scotland.

5. Although the winter-restricted stags were less fat both grossly and relative to body-weight than the unrestricted stags, both groups showed the same relationship of level of fatness to empty-body-weight. In both the groups of stags, extensive fat deposition began once they had reached about half their expected mature weight, a much later stage of development and age than in sheep and cattle.

6. The annual cycle of growth and appetite is considered to form part of a complex adaptive system to enhance survival in a harsh seasonal environment followed by a mild seasonal environment. On Scottish hills deer reach a size appropriate to their environment rather than their genetic potential size.

The red deer (*Cervus elaphus*) has a wide distribution throughout the temperate regions of the world. Stags from different locations show an enormous variation in body-weight (Mitchell *et al.* 1977). Whitehead (1950) gave live weights of 145–227 kg for representative English park stags and also quoted record weights of over 300 kg for English park stags as compared with 127–145 kg for Scottish Highland stags (Whitehead, 1964). Within Scotland there is much variation in stag body size; the largest (160 kg) are from Glen Fiddich, the smallest (100 kg) are from Glen Prosen (Staines, 1970, 1978; Michell *et al.* 1976).

The small size of these Highland deer seems to be an acquired rather than an inherited characteristic. Red deer stags in New Zealand, derived in the past from Scottish stock, may attain weights of 160 kg at 3 years of age (Moore & Brown, 1977). Indigenous red deer in the Grizedale Forest in Cumbria, a favourable habitat, are genetically similar to Scottish red deer (Lowe & Gardiner, 1974) yet the mature body size of stags is about twice that of stags on the Scottish hill (Mitchell *et al.* 1981). Scottish stag calves raised by hand and given a concentrate diet weighed over 160 kg at 2 years of age (Blaxter *et al.* 1974).

Studies of many wild herbivores have shown that these animals have a characteristically lean carcass containing less than 100 g fat/kg body-weight (Ledger, 1968; Blaxter *et al.* 1974; Drozd *et al.* 1975; Weiner, 1977), much less than is found in well-grown domestic animals (Callow, 1947, 1948, 1958; Callow & Searle, 1956). Moreover, in the dressed carcasses of wild animals, fat is usually deposited only intermuscularly rather than both inter- and intramuscularly as in domestic animals. Fat deposits in wild herbivores have been shown to vary seasonally (Krog *et al.* 1976; Mitchell *et al.* 1976) and with age (Blaxter *et al.* 1974; Robbins *et al.* 1974).

The main aim of the present study was to test the hypothesis that poor winter nutrition,

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particularly during the first winter of life, and subsequent failure to compensate fully during the periods of summer plenty, are responsible for the small size of Scottish deer. A subsidiary aim was to investigate the body composition of red deer stags given unrestricted or seasonally-restricted dietary regimens during winter, for 2 or 3 years.

MATERIALS AND METHODS

Between 7 and 16 June 1977, twelve wild stag calves were captured in Kincardineshire and brought to the Rowett Research Institute. Their date of birth was unknown but assumed to be 7 June. The animals were penned individually in two adjacent rooms, each with a single window. Light intensity, measured 1 m above the floor at 12.00 hours, varied between 700 lx on bright days and 160 lx on dull days. Out-of-doors light intensity always exceeded 2000 lx. Temperature reflected that of the external environment. The calves were bottle-fed a standard ewe-milk substitute (Nutrilamb; Scottish Agricultural Industries Ltd) and then weaned at 9 weeks of age to a pelleted barley diet. This diet contained 869 g dry matter (DM)/kg and provided 15.28 MJ gross energy and 160 g crude protein (nitrogen \times 6.25)/kg DM.

When 10 weeks old, on 16 August 1977, the calves were ranked according to live weight and allocated alternately from lightest to heaviest to form two groups. The mean (with SE) live weight of animals in group A was 26.2 (0.9) kg and in group B 26.9 (1.6) kg. Group A stags were offered food in excess of their estimated requirements at 08.00 hours. Uneaten food was collected and weighed, and daily food intake thus determined. Group B stags were offered a daily ration that was 0.7 times the mean voluntary intake of group A during the previous week, all food intakes being calculated as g DM/kg body-weight^{0.75}. The food restriction continued until May 1978 (Fig. 1) then, over a period of 3 weeks, the feeding levels were adjusted to 80, 90 and 100% of the intake of the unrestricted stags and then increased until the previously-restricted stags were also feeding to appetite. In November 1978 the food restriction was reimposed in group B and continued until May 1979 when the stags were progressively realimented and then fed to appetite as before. The same pattern of feeding was imposed for a third cycle from November 1979 until the study ended in September 1980. Water was freely available at all times.

The stags were weighed at weekly intervals from June 1977 until October 1978 and thereafter at 3-weekly intervals until May 1980 and again in September 1980. At 3-weekly intervals the hind-foot length was measured from the tip of the calcaneum to the junction between the fused metatarsi and the phalanges, using a flexible metal tape.

From February 1978, deer no. 2, a rather intractable animal, had to be sedated by intramuscular injection of Rompun (Bayer; 20 mg/l, 1.5 ml/100 kg body-weight) to permit weighing and measuring. Deer nos. 6 and 9 required the same treatment from May and the remaining stags from August 1978. From September 1979 the Rompun was injected by means of a dart rifle (Paxarm Ltd, New Zealand).

Unless otherwise stated, analysis of variance was used to test level of significance ($P < 0.05$).

As far as possible, unrestricted and restricted stags were slaughtered in pairs on the same date. However, this goal was to some extent thwarted by the deaths of four of the twelve experimental animals due to malignant catarrhal fever (W. Corrigan, personal communication).

Subcutaneous, rump (covering the pelvis), abdominal (from the proximal tip of the kidney to the pelvic canal), channel (pelvic canal) and omental (associated with the gut) fat depots were dissected and weighed separately.

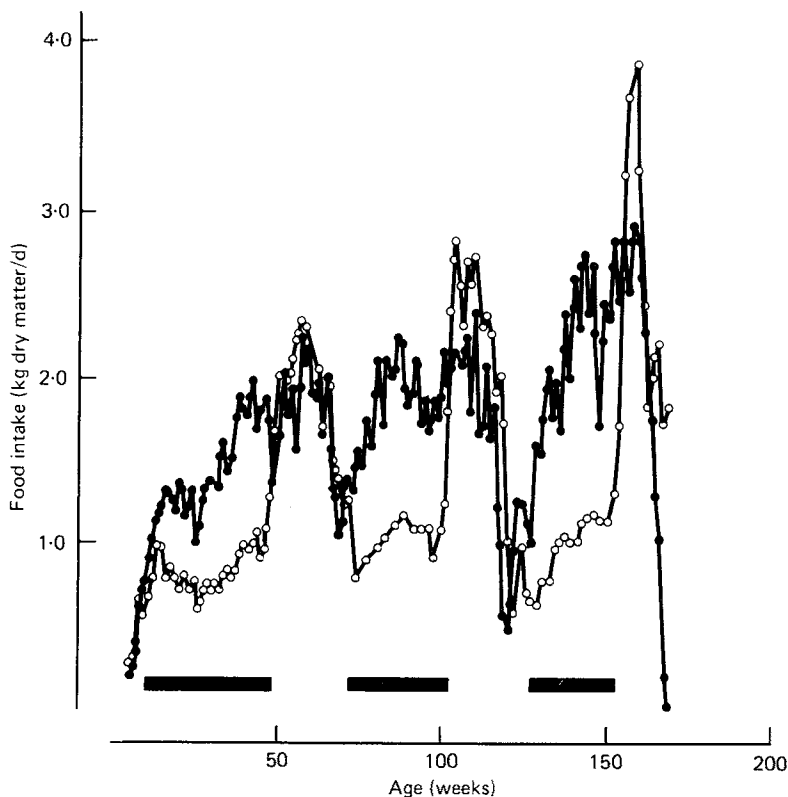


Fig. 1. The food intakes (kg dry matter/d) of stags given a concentrated diet at levels of unrestricted (group A) (●) and restricted (group B) (○) intake. (■), Periods of nutritional restriction. Standard errors were smaller than the size of the points.

Chemical analysis

The empty-body-weight (live weight less gut contents) was divided into four parts for analysis: (1) the left side of the carcass with the channel, rump and all subcutaneous fat removed; (2) all internal organs, channel, abdominal and omental fat, the reproductive tract, the spinal processes and tail; (3) the subcutaneous and rump fat; (4) the head, feet and skin.

Each part was minced through an 8 mm screen and mixed thoroughly. Three samples, weighing approximately 160 g each, were taken from the resultant mince and frozen pending freeze-drying. The freeze-dried samples were ground through a 4 mm screen then stored at room temperature before analysis for dry matter, ash, protein and fat. Dry matter was determined by placing weighed subsamples in an oven at 38° for 48 h and then reweighing. The subsamples were then placed in a muffle furnace at 500° for 24 h and the ash remaining was weighed. Protein was determined by the method of Davidson *et al.* (1970) and fat by the method of Atkinson *et al.* (1972).

RESULTS

The changes in DM intake are shown in Fig. 1. The daily DM intake of group A, the unrestricted group, increased from weaning until it reached a plateau during the first winter. It rose in spring before falling slightly in May and June. In July and August it was again

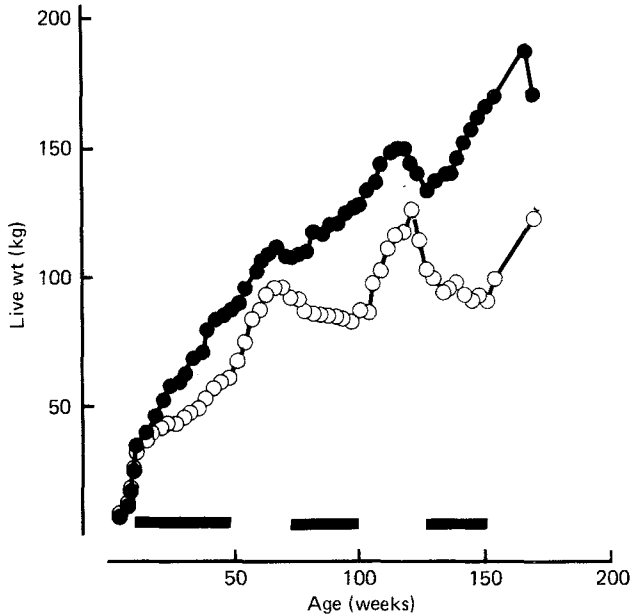


Fig. 2. The live weights (kg) of stags given a concentrated diet at unrestricted (group A) (●) and restricted (group B) (○) levels of intake. (■), Periods of food restriction. Standard errors were smaller than the size of the points.

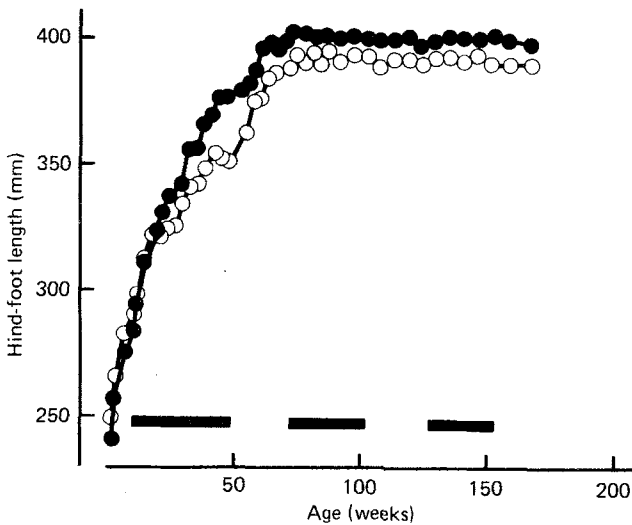


Fig. 3. The hind-foot length (mm) of stags given a concentrated diet at unrestricted (group A) (●) and restricted (group B) (○) levels of intake. (■), Periods of food restriction. Standard errors were smaller than the size of the points.

high before it dropped during the rut in October. This pattern was repeated during the second and third years of the study although food intake peaks were higher and troughs lower. The stags in group B raised their DM intake to above that of group A each summer but invariably reduced their intake, voluntarily, in late summer before the rut. Thus they voluntarily curtailed the period of rehabilitation.

Table 1. Food intake and live weight changes of stags during the summer periods of unrestricted food intake and the winter periods of restricted food intake

(Mean values with pooled estimates of standard errors)

	Group A Mean	Group B Mean	Pooled SE	Group A Mean	Group B Mean	Pooled SE
	Period 1			Period 3		
DM intake (kg/d)	1.52	0.83***	0.055	1.85	1.01***	0.062
Live wt (kg)	69.2	50.5***	2.56	119.2	88.9***	3.77
DM intake (kg/100 kg metabolic live wt)	6.30	4.37***	0.138	5.12	3.49***	0.134
Live-wt gain (kg/d)	0.21	0.11***	0.014	0.05	0.01***	0.029
Food conversion efficiency	7.31	8.11	0.641	— All values negative —		
	Period 2			Period 4		
DM intake (kg/d)	1.89	2.04	0.101	2.02	2.60*	0.219
Live-wt (kg)	102.5	84.4***	3.48	144.6	107.3***	5.45
DM intake (kg/100 kg metabolic live wt)	5.88	7.39***	0.285	4.86	7.73***	0.592
Live-wt gain (kg/d)	0.22	0.30*	0.029	0.17	0.28*	0.038
Food conversion efficiency	8.882	6.84*	0.848	12.20	9.27*	1.059

DM (dry matter) intake is the mean of weekly values; live weight and DM intake/metabolic live weight are mean values estimated for the mid-point of each week; live-weight gain was estimated as a regression coefficient from all weighings during each summer period; food conversion efficiency is the ratio of DM intake (kg): live-weight gain (kg).

Periods 1 and 3 are the periods of restriction from November 1977 until 15 May 1978 (n 12) and 6 November 1978 until 14 May 1979 (n 11) respectively. Periods 2 and 4 are the periods of unrestricted food intake from 5 June 1978 until 22 September 1978 (n 12) and 4 June 1979 until 10 September 1979 (n 9) respectively. Where $n = 11$, SE should be multiplied by 1.044 and where $n = 9$ by 1.155 to allow for the fact that there are less than twelve values.

Significance of difference: * $P < 0.05$, *** $P < 0.001$.

Fig. 2 shows the changes in live weight for each group. Group A grew well after weaning and showed only a slight weight loss during the rut (weeks 66–69) and a reduced rate of weight gain for 8 weeks following the rut. During the second year of the study they continued to grow but less rapidly than previously and lost about 20 kg during the second rut and again showed a slight reduction in weight gain after it. During the third year the two remaining stags grew quickly and the last animal attained a maximum individual weight of 189.6 kg before rut in September 1980. Group B grew at the same rate as group A until checked by dietary restriction in August 1977. They continued to gain weight, albeit at a slow rate, until realimented in May 1978. Although they grew quickly during the period of realimentation, they did not fully compensate for the previous period of undernutrition, that is, they did not catch up on the weights of group A stags before they voluntarily reduced their food intake in September 1978. During the second period of restriction they lost weight but showed a rapid recovery after food allowance was increased, although as before they failed to exhibit full compensation for previous undernutrition. During the third period of restriction the remaining two stags in group B lost weight and after realimentation, despite a large compensatory increase in food intake, only managed to recover the weight they had lost.

Table 2. *The distribution of dissectable fat in the carcasses of red deer stags given a concentrate diet at unrestricted and restricted levels of intake*

Deer no.	Date of slaughter	Plane of nutrition	Percentage distribution of total dissectable fat				
			Abdominal	Channel	Omental	Rump	Subcutaneous
2	15 May 1979	Unrestricted	15.37	3.86	23.71	11.51	45.55
01	9 May 1979	Restricted	100.00	0	0	0	0
5	11 Sept. 1979	Unrestricted	12.22	5.84	37.28	10.34	34.32
9	9 Sept. 1979	Restricted	15.96	8.73	33.03	8.27	34.01
02	13 Nov. 1979	Restricted	15.69	3.30	29.27	5.26	46.48
3	6 May 1980	Unrestricted	17.50	2.46	38.03	8.76	33.18
4	9 Sept. 1980	Unrestricted	10.28	3.61	46.61	7.30	32.20
00	9 Sept. 1980	Restricted	11.26	7.14	36.85	6.54	38.25

Table 3. *Gradients and intercepts of regression equations relating carcass composition to age (x) where $y = ax + b$ for carcass constituents for two groups of stags (three animals per group) given a concentrated diet at unrestricted (group A) and restricted (group B) levels of intake*

Carcass constituent (y)	Component	Group	a	b	y at x = 30 months
Carcass less subcutaneous fat	Water	A	-1.214	656.427	620
		B	-4.792	792.038	648
	Protein	A	-0.431	237.346	224
		B	-0.663	237.782	218
	Fat	A	3.470	-11.349	93
		B	5.220	-88.800	68
	Ash	A	-1.820	117.000	62
		B	0.241	58.707	66
Internal organs	Water	A	-9.991	821.143	521
		B	-9.272	932.94	655
	Protein	A	-3.194	225.229	129
		B	-2.362	229.292	158
	Fat	A	13.817	-80.513	334
		B	11.795	-175.224	178
	Ash	A	-0.264	16.778	9
		B	-0.354	22.031	11
Subcutaneous and rump fat	Water	A	-1.419	169.304	127
		B	2.442	66.375	139
	Protein	A	-1.578	101.011	54
		B	0.475	33.175	47
	Fat	A	3.236	721.278	818
		B	-2.900	897.500	810
	Ash	A	0.062	4.092	2
		B	0.017	2.950	2
Head, feet and skin	Water	A	0.556	537.479	576
		B	-4.099	679.504	556
	Protein	A	0.156	28.932	34
		B	0.088	30.572	53
	Fat	A	0.020	5.351	6
		B	0.237	3.074	4
	Ash	A	-0.192	11.951	6
		B	0.084	4.551	7

The stags were slaughtered at 23, 27 and 39 months of age. Data were analysed within groups across time intervals. Predictions of composition of g/kg of component weight are given for a standardized slaughter time of 30 months.

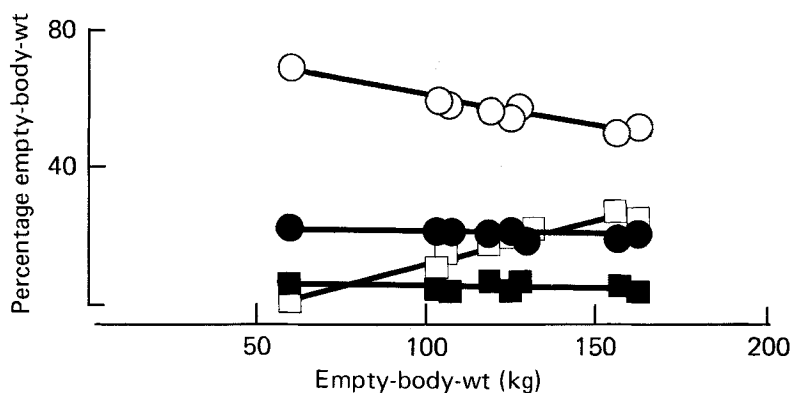


Fig. 4. The relationship between empty-body-weight (live weight less gut contents) and contents of water (○), protein (●), fat (□) and ash (■) in empty-body-weight in red deer stags given a concentrate diet. The linear regression equations for protein, water, fat and ash with correlation coefficients and levels of significance are:

$$\begin{aligned} \text{Fat: } & y = 0.224x - 10.61, r \ 0.961, P < 0.001 \\ \text{Protein: } & y = -0.03x - 25.09, r \ 0.784, P < 0.05 \\ \text{Water: } & y = -0.166x + 77.728, r \ 0.955, P < 0.001 \\ \text{Ash: } & y = 0.022x + 7.788, r \ 0.713, P < 0.05 \end{aligned}$$

where y is the carcass constituent and x is the age of the stag (months).

The changes in hind-foot length are shown in Fig. 3. In group A the feet grew quickly from birth onwards until an asymptote was reached at 70–75 weeks. In group B there was a period of slow or arrested growth between weeks 40–48, towards the end of the first period of food restriction. After realimentation foot length increased quickly to reach an asymptote at the same time as in group A (70–75 weeks). Group B did not fully catch up with group A, however, and the means of each group were significantly different ($P < 0.05$, $t \ 2.57$, $n \ 5$, unpaired two-tailed t test) at this time. After the asymptote was reached no further growth was seen in individual stags even during the second and third periods of realimentation, although the mean values were affected by successive removal of animals from the groups.

Table 1 compares food intake, body-weight change and food conversion efficiency during the first two periods of winter restriction and the first two summers of unrestricted food intake. Although the previously restricted stags of group B ate more than the stags of group A in absolute terms, this only achieved statistical significance during the second period. However, since group B stags were significantly lighter than group A stags, their food intake on a metabolic body-weight basis was substantially and significantly greater in both periods. Group B converted food to weight gain significantly more efficiently than group A in both summer periods but in both groups conversion efficiency was poorer during the second period.

During both periods of food restriction the group A stags were larger and consumed more food than group B stags and during the first winter period gained significantly more weight. There were no significant differences in food conversion efficiency during the first winter and no effect was measurable during the second year as weight gains were low or absent.

The relative distribution and importance of the different fat depots is shown in Table 2. The major fat depots were subcutaneous and omental. Within slaughter pairs, and generally as the stags became older and heavier, the omental depot became larger relative to the subcutaneous depot.

Table 3 shows regression equations for the composition of parts of the empty body with

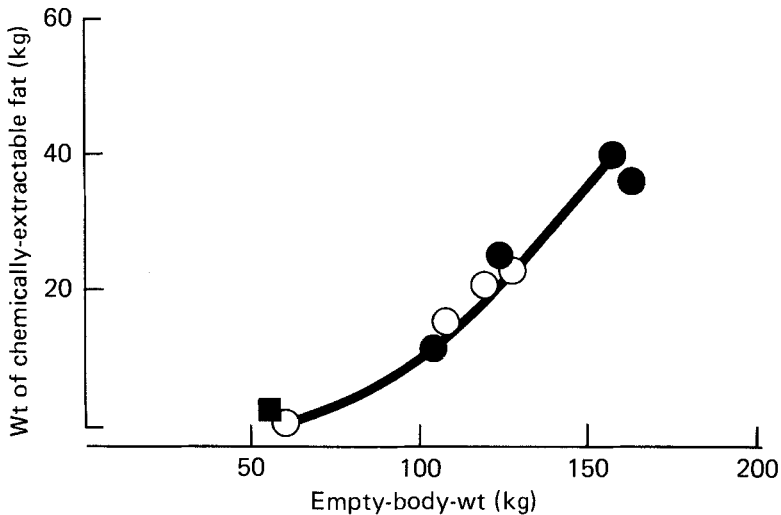


Fig. 5. The relationship between empty-body-weight (live weight less gut contents) and the total fat content of the body, determined chemically, in red deer stags given a concentrated diet at unrestricted (●) or restricted (○) levels of intake. (■), Young farm stags (Kay *et al.* 1981).

age. The composition of the lean carcass showed a trend towards an increase in fat and a decrease in water as the stags become older and heavier. Protein and ash contents remained relatively constant throughout the study. The previously described pattern was consistent for the composition of internal organs and of the subcutaneous fat, but the composition of the head, feet and skin varied little within pairs or with age.

The percentage composition of the total body (excluding gut contents) of water, protein, fat and ash is illustrated in Fig. 4. As empty-body-weight increased the fat content increased, water decreased and the protein and ash remained about the same. The relationship between the weight of chemically-extractable fat and the empty-body-weight is given in Fig. 5. This shows that the fat content of the body was closely related to body-weight, above a certain threshold, and so with the differing planes of nutrition fat content was largely independent of time of slaughter and age. The lean stags analysed by Kay *et al.* (1981) fit the curve drawn for the stags in the present study.

DISCUSSION

The stags on the unrestricted plane of nutrition, group A, showed a pronounced annual cycle of voluntary food intake. This is in agreement with other studies on male deer, caribou (*Rangifer tarandus*) (McEwan, 1968; McEwan & Whitehead, 1970), roe-deer (*Capreolus capreolus*) (Drozd & Osiecki, 1973; Drozd, 1979) and red deer (Simpson, 1976; Kay, 1979). Bandy *et al.* (1970), in addition to showing a seasonal pattern of food intake in male black-tailed deer (*Odocoileus hemionus columbianus*), found that there were two phases of inappetence. The first deep trough was associated with the rut but this was followed by a short recovery phase and then a shallow trough in the winter before intake levels rose to the summer peak. The second shallow trough coincided with the female inappetent phase and it was concluded that this was the basic cycle and the male superimposed an additional inappetent phase due to the rut, not shown by the female. In the present study the intake of unrestricted stags increased sharply after the rut and continued to rise until spring when an inappetent phase occurred. Thus in one annual cycle two peaks of food intake occurred, one in early spring, the other in summer. The early spring peak was associated with a

resurgence of sexual activity, as indicated by increased testis size, a rise in testosterone and a fall in prolactin, that like inappetence was conspicuous in some, mainly group A stags, and absent in others. This subject is considered more fully by Suttie (1980, 1981).

The growth of the stags in group A was good in comparison with published accounts. At 27 months old they were approximately twice the weight of stags of similar age at Glenshagh (Blaxter *et al.* 1974) and they were also heavier than 27-month-old wild stags from Glenfeshie (Mitchell *et al.* 1977). They were equivalent in weight to stags fed to appetite at the Rowett Research Institute (Blaxter *et al.* 1974) and in New Zealand (Moore & Brown, 1977). Group B stags grew better in the first year of life than wild Scottish calves (Mitchell *et al.* 1977) or farmed calves (Blaxter *et al.* 1974), but clearly showed exaggerated cycles of weight loss and gain caused by the nutritional regimen. Compensatory growth from May to November, although remarkable, did not allow group B to catch up completely with group A during any phase of realimentation. It is concluded that although the winter-restricted stags of group B were larger than their wild counterparts, the nutritional regimen imposed indeed prevented the stags reaching their genetic potential weight.

The hind-foot continued to grow from birth until an asymptote was reached at the same age, about 17 months, in both groups despite the significant body-weight difference. The restricted group B stags continued to increase the length of the hind-foot through most of the first period of undernutrition; this is in agreement with Blaxter *et al.* (1974) and Mitchell *et al.* (1976) who showed that farmed and wild stags respectively continued to grow skeletally throughout their first winter. However, skeletal growth rate of group B stags was less during the restricted period than that of the unrestricted group A stags and, despite increased skeletal growth rate during realimentation, the difference was never made up and by the time growth ceased their legs were significantly shorter.

Previous studies on compensatory growth of white-tailed deer (*O. virginianus*) (French *et al.* 1956; McEwen *et al.* 1957; Long *et al.* 1959; Cowan & Long, 1962) did not involve repeated periods of nutritional restriction. The present study showed that repeated severe nutritional deprivation has profound deleterious effects on body and skeletal growth.

Over the range of body-weights obtained, the percentage of fat and water varied reciprocally while protein and ash remained more or less constant in the carcass, internal organs and subcutaneous fat. Within the slaughter pairs the restricted stags always had a higher proportion of water to fat, an effect previously noted by Drew & Reid (1975). The values for the percentage of fat in the carcass were similar to those quoted by Blaxter *et al.* (1974) of 9.5–15% of the carcass for stags fed on dried-grass or concentrates indoor. This contrasts sharply with the values obtained for wild hinds (2.7–8.7%) and domestic red deer calves (1.3–7.8%) in the same report.

The trend for water content to decrease and fat to increase as empty-body-weight increases is shown graphically in Fig. 4. Robbins *et al.* (1974) showed that while the amount of protein remained at around 200 g/kg and ash at 60 g/kg, water fell from 750 to 550 g/kg and fat rose from 0 to 20 g/kg in the empty bodies of male and female white-tailed deer as weight increased from 4 to 68 kg. Almost exactly the same relationship was found in the present study for red deer. The composition of red deer is also within the normal ranges for domestic sheep, cattle and pigs (Berg & Butterfield, 1976).

It is an apparent paradox that the relationship between percentage body fat and empty-body-weight is linear but the relationship between the weight of chemically-extractable fat and empty-body-weight is curvilinear. This may be resolved because although stags become relatively fatter as they get older, hence the curvilinearity, at any given body-weight laying down of fat displaces water linearly, hence the percentage fat content is linearly related to empty-body-weight.

The relationship between the weight of chemically-extractable fat and empty-body-weight

(Fig. 2) closely resembles those reviewed by Searle (1977) for sheep, cattle and rats. The main difference between deer and other ruminants is the intercept on the x -axis; deer only begin to deposit substantial amounts of body fat above 85–90 kg body-weight, about half their mature size, whereas sheep and cattle begin to fatten at lower body-weights and at an earlier stage of development. However, above this intercept, body-weight is the major indicator of fatness in deer as in sheep or cattle. Deer may only be attractively lean animals at low body-weight; at high body-weight they may become as fat as cattle.

The present study emphasizes an important phenomenon; that deer are adaptable in reaching the maximum size their environment can maintain, thus approaching as closely as possible the genetic potential size within the constraints of the environment. The animal appears to be physiologically programmed to deal with periods of inadequate nutrition and to follow them with periods of compensatory growth.

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REFERENCES

- Atkinson, T., Fowler, V. R., Garton, G. A. & Lough, A. K. (1972). *Analyst, London* **97**, 562–568.
- Bandy, P. J., Cowan, I. M. & Wood, A. J. (1970). *Canadian Journal of Zoology* **48**, 1401–1410.
- Berg, R. T. & Butterfield, R. M. (1976). *New Concepts of Cattle Growth*. Sydney: Sydney University Press.
- Blaxter, K. L., Kay, R. N. B., Sharman, G. A. M., Cunningham, J. M. M. & Hamilton, W. J. (1974). *Farming the Red Deer*. Edinburgh: H.M. Stationery Office.
- Callow, E. H. (1947). *Journal of Agricultural Science, Cambridge* **37**, 113–131.
- Callow, E. H. (1948). *Journal of Agricultural Science, Cambridge* **38**, 174–199.
- Callow, E. H. (1958). *Journal of Agricultural Science, Cambridge* **51**, 361–369.
- Callow, E. H. & Searle, S. R. (1956). *Journal of Agricultural Science, Cambridge* **48**, 61–73.
- Cowan, R. L. & Long, T. A. (1962). *Pennsylvanian Cooperative Wildlife Research Unit Progress Report* no. 107.
- Davidson, J., Mathieson, J. & Boyne, A. W. (1970). *Analyst, London* **95**, 181–193.
- Drew, K. R. & Reid, J. T. (1975). *Journal of Agricultural Science, Cambridge* **85**, 193–204.
- Drozd, A. (1979). *Acta Theriologica* **24**, 137–170.
- Drozd, A. & Osiecki, A. (1973). *Acta Theriologica* **18**, 81–91.
- Drozd, A. & Weiner, J., Gebczynska, Z. & Krasinska, M. (1975). *Polish Ecological Studies* **1**, 85–101.
- French, C. E., McEwen, L. C., Magruder, N. D., Ingram, R. N. & Swift, R. W. (1956). *Journal of Wildlife Management* **20**, 221–232.
- Kay, R. N. B. (1979). *ARC Research Review* **5**, 13–15.
- Kay, R. N. B., Sharman, G. A. M., Hamilton, W. J., Goodall, E. D., Pennie, K. & Couts, A. G. P. (1981). *Journal of Agricultural Science, Cambridge* **96**, 79–87.
- Krog, J., Wika, M., Lund-Larsen, T., Nordfjell, J. & Myrnes, I. (1976). *Norwegian Journal of Zoology* **24**, 407–417.
- Ledger, H. P. (1968). *Symposium of the Zoological Society of London* **21**, 289–310.
- Long, T. A., Cowan, R. L., Wolfe, C. W., Rader, T. & Swift, R. W. (1959). *Pennsylvanian Agricultural Experimental Station Progress Report*, no. 209.
- Lowe, V. P. W. & Gardiner, A. S. (1974). *Journal of Zoology (London)* **174**, 185–201.
- McEwen, E. H. (1968). *Canadian Journal of Zoology* **46**, 1023–1029.
- McEwen, E. H. & Whitehead, P. E. (1970). *Canadian Journal of Zoology* **48**, 905–913.
- McEwen, L. C., French, C. E., Magruder, N. D., Swift, R. W. & Ingram, R. H. (1957). *Transactions of the 22nd North American Wildlife Conference*, pp. 119–132.
- Mitchell, B., Grant, W. & Cubby, J. (1981). *Journal of Zoology (London)* **194**, 279–284.
- Mitchell, B., McCowan, D. & Nicholson, I. A. (1976). *Journal of Zoology (London)* **171**, 141–152.
- Mitchell, B., Staines, B. W. & Welch, R. (1977). *Ecology of Red Deer*. Cambridge: I.T.E.
- Moore, G. M. & Brown, C. G. (1977). *New Zealand Journal of Agricultural Science* **11**, 175–178.
- Robbins, C. T., Moen, A. N. & Reid, J. T. (1974). *Journal of Animal Science* **38**, 871–876.
- Searle, T. W. (1977). *Proceedings of the Nutrition Society of Australia* **2**, 53–60.
- Simpson, A. M. (1976). A study of the energy metabolism and seasonal cycles of captive red deer. PhD Thesis, University of Aberdeen.
- Staines, B. W. (1970). The management and dispersion of a red deer population in Glen Dye, Kincardineshire. PhD Thesis, University of Aberdeen.
- Staines, B. W. (1978). *Journal of Zoology (London)* **184**, 403–419.

- Suttie, J. M. (1980). *Proceedings of the 2nd International Reindeer/Caribou Symposium*, pp. 341–349.
- Suttie, J. M. (1981). The influence of nutrition and photoperiod on the growth, development and endocrine status of captive red deer and Soay Rams. PhD Thesis, University of Aberdeen.
- Weiner, J. (1977). *Acta Theriologica* **22**, 3–24.
- Whitehead, G. K. (1950). *Deer and Their Management in the Deer Parks of Great Britain and Ireland*. London: Country Life Ltd.
- Whitehead, G. K. (1964). *The Deer of Great Britain and Ireland*. London: Routledge and Kegan Paul.