THE INFLUENCE OF NUTRITION AND PHOTOPERIOD ON THE GROWTH OF ANTLERS OF YOUNG RED DEER

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ABSTRACT

The present study tested the interaction between nutrition and photoperiod on antler development. Twelve male red deer calves were allocated to either of 2 equal groups; 1 group was fed to appetite for 3 years while the other was fed 70% as much from each November-May and to appetite from each May-November. All stags were kept indoors and no manipulation of photoperiod was made. The stags were observed daily for antler development and weighed at weekly intervals. The unrestricted stags commenced pedicle development at 19.0 ± 2.22 S.E. weeks of age and at a decreasing photoperiod of 10.98 ± 1.00 hrs. of light, while the restricted stags began pedicle development at 31.0 ± 1.96 weeks of age at an increasing photoperiod of 8.31 ± 0.49 hrs. The difference between the means for each group ws statistically significant ($p < 0.01$). However, the body weights at which this event occurred, 41.2 ± 1.07 kg for the unrestricted group and 44.1 ± 1.54 kg for the restricted group, did not differ significantly ($p > 0.05$). Throughout the growth of the first antler the unrestricted group began each stage (onset of pedicle growth, onset of antler growth and cleaning of velvet) significantly earlier than the restricted group, but each stage occurred when the stags had attained the same body weight. Further, the unrestricted group grew antlers when the photoperiod was decreasing whereas the opposite would have been expected. During subsequent cycles antlers were grown, cleaned and cast in response to fluctuations in photoperiod irrespective of body weights. The major stages of the development of the first antler appear to me more closely related to the nutritional status of the deer as reflected by body weight than to the prevailing photoperiod. This may have adaptive value as young stags are spared the burden of antler growth until they are physiologically capable. KEY WORDS: Antlers, Deer, Growth, Nutrition, Photoperiod.

Goss (1969*a*, *b*) and Jaczewski (1954) have shown that deer cast and regrow their antlers each year in response to changes in the day-length. Goss (1969*a*) suggested that the onset of antler growth is entrained by increasing day-lengths. Antlers are cast and regrown in response to an endogenous rhythm whose duration can be adapted to the prevailing photoperiod but which reverts to circannual on constant, long or short days and disappears on simulated equatorial lighting conditions (Goss 1969*b*, 1980). Fawns exposed to a day-light regime of 12 hours light/12 hours dark, which would not stimulate antler growth in adult males, grew pedicles and antlers during their second summer of life but subsequently failed to cast them. He concluded that production of a stag's first set of antlers was determined more by its chronological age than the photoperiod (Goss 1969*b*). In a further study he showed that fawns born on a regime in which day-length was decreasing grew antlers at approximately the same age as deer kept outside. However,

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these antlers were shed and replaced ½ year earlier than would have occurred in normal light. He concluded that renewed antler growth is triggered by lengthening days irrespective of the age of the deer (Goss 1980).

Lincoln (1971) considered that the pedicle was a secondary sexual character in red deer (*Cervus elaphus*) that developed in response to an increase in testosterone after the onset of puberty. He suggested that the age of puberty is related to the plane of nutrition, although the exact time of year puberty occurred was influenced by other factors, such as photoperiod.

Long et al. (1959) showed that nutritional deprivation of white-tailed deer (*Odocoileus virginianus*) in the spring for periods of 5-10 weeks hastened antler casting if the feed restriction was during the shedding period. In contrast, Watson (1971) showed that antler casting among red deer was delayed by feed restriction brought about by severe weather conditions, but supplemental feeding could reverse this trend. Poor nutrition typically causes small, weak antlers (French et al. 1956; Cowan and Long 1962; Hyvarinen et al. 1977).

Although the influence of nutrition in relation to the photoperiod has been discussed by several authors, there is no published evidence for such an effect. The present study set out to provide this evidence.

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METHODS

Two investigations were carried out on young red deer on the extent of compensatory growth following periods of winter undernutrition. The full rational for this experimental approach is given in Suttie (1981).

Study 1

Between 7-16 June 1977, 12 stag calves born to wild hinds were captured within 3 days of birth from a Scot's estate and brought to the Rowett Institute. The animals were penned individually, although they could hear, see, and smell each other. There was a single window in each room, and no manipulations of photoperiod were made. Temperature reflected that of the external environment. Light intensity in each pen measured 1 m above the floor at 1200 hr varied between 700 and 160 lux. Outside light intensity was always > 2000 lux. Calves were bottle fed a standard ewe milk substitute (Nutrilamb, Scottish Agricultural Industries, Ltd) and were weaned at 9 weeks of age onto a diet containing 84% ground barley and 13% fish meal, with a mineral and vitamin supplement. The ration provided 15.28 KJ gross energy/g dry matter and 16% crude protein.

Since the exact age of each calf at capture was unknown, it was assumed that all calves were born on 7 June 1977, which is about the modal date of calving in Scotland. When the stags were 10-weeks-old, each was allocated to either of 2 groups such that the mean body weight of each group was sim-

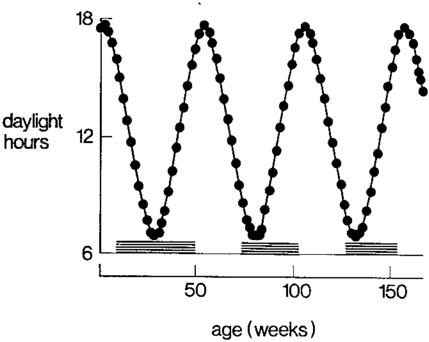

Fig. 1. The fluctuations in day-length throughout the study. The hatched area indicates the period of restriction. The periods of compensatory growth occurred between the hatched areas.

ilar (26.2 ± 0.9 kg and 26.9 ± 1.6 kg). The first group, designated the unrestricted group, was fed in excess of requirements at 800 hr each day; uneaten feed was collected and weighed so that feed intake could be calculated. The mean daily intake of the unrestricted group was measured in terms of $g/kg^{0.75}$ body weight. This value was multiplied by 0.7, and the resulting figure was multiplied by the body weight in $kg^{0.75}$ of each stag in the second or restricted group to determine the feed to be offered each animal for the next week. This food restriction continued for 10 months until May 1978 (Fig. 1) for the restricted animals. Then, over a period of 3 weeks, the feeding levels of the restricted animals were increased to 80%, 90%, and 100% of the intake of the unrestricted stags and then increased progressively until all stags in both groups were feeding to appetite. This was necessary since the previously restricted stags ate more relative to their metabolic body weight than the continuously fed stags. Between May 1978-November 1978, all stags were fed to appetite. In November 1978 the food restriction was reimposed on the group that had previously been restricted 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 time from November 1979 until the study ended in September 1980.

The stags were weighed weekly from June 1977 until October 1978, thereafter every 3 weeks until May 1980 and again in September 1980. At 3 week intervals throughout the study, the length of each antler was measured to the nearest millimeter from the base of the pedicle to its tip with a metal tape placed on the medial surface. The number of points on each antler was recorded, and it was noted whether the antlers of each stag were in velvet, cleaning, or in hard antler. The stags were observed daily to determine the exact date of cleaning and casting.

After the antlers of each stag were clean of velvet, they were sawn off approximately 1 cm above the antler pedicle junction. Each antler was weighed on a top pan balance to the nearest 0.1 g on the day it was removed and then weighed under water. They were then oven-dried at 38°C for 48 hours and reweighed. Specific gravity was calculated from the following:

$$\text{Antler Specific Gravity g DM/ml} = \frac{\text{Oven-dry Weight (g)}}{\text{Weight in Air (g)} - \text{Weight in Water (g)}}$$

Study 2

Twenty-one stag calves born at Glensaugh Experimental Deer Farm during June-July 1977 and reared by their dams were weaned in September and assigned to 2 groups on 1 December 1977 such that mean live weight of each group was nearly equal. The groups were housed indoors in separate pens and bedded on straw. The first group (10 calves) was fed 1.1 kg/head daily of a mixture of 90% loose barley, 10% pelleted protein, and vitamins; the second group (11 calves) was fed 0.23 kg/head daily of the same diet. Medium quality hay and water were available to appetite. No manipulations of photoperiod were made.

At intervals of approximately 3 weeks, each animal was weighed and the antlers were measured to the nearest 0.1 cm. In mid-May 1978 both groups were released onto a 81 ha paddock, and at irregular intervals thereafter they were gathered for weighing and measuring. Antlers were removed when they were clean of velvet and treated as in Study 1.

RESULTS

The unrestricted stags began pedicle ($P < 0.01$) and antler growth ($P < 0.001$) earlier on a decreasing light regime and at a significantly younger age than the winter restricted group (Table 1). However, pedicle initiation began when the stags had reached a similar body weight. The unrestricted stags cleaned their antlers of velvet when day-length was increasing significantly earlier ($P < 0.001$) but not at a significantly different weight than the restricted group. Thereafter, events in the antler cycle were closely linked to changes in the photoperiod and were independent of weight differences. There was a non-significant trend for antlers of the unrestricted group to be cast 1-2 weeks before the restricted group.

The only significant difference in antler parameters was in number of points per antler ($P < 0.05$) during the second cycle of antler development (Table 2). Although antler length, growth rate, body weight, and relative antler weight increased for the first to the second antler, no significant difference was shown between the groups. The specific gravity was similar both between treatments and years.

In Study 2 stags initiated their pedicles and antlers and cleaned their antlers at the same weight irrespective of nutritional plane, but the low plane group was significantly older at each event ($P < 0.001$, $P < 0.001$, $P < 0.01$, respectively) (Table 3). However, this study differed from the previous

Table 1. The effects of age, day-length, and body weight on the antler cycles of red deer fed *ad libitum* and restricted rations.

Antler cycle	Stage of antler growth	Age (Weeks)						Day-length (hours)						Body weight (kg)					
		Unrestricted			Restricted			Unrestricted			Restricted			Unrestricted			Restricted		
		$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE	N
1	Pedicle																		
	Initiation	19.0	2.2	6	31.0	2.0	6	10.98 D[a]	1.0	6	8.31	0.49	6 I[a]	41.2	1.1	6	44.1	1.5	6
	Antler																		
	Initiation	28.0	1.3	6	40.0	2.0	6	7.71 D	0.21	6	11.37	1.03	6 I	62.1	2.2	6	55.1	2.0	6
	Cleaned	39.0	1.8	6	52.2	2.2	6	10.47 I	0.82	6	15.87	0.55	6 D	98.1	5.6	6	88.8	3.6	6
	Cast	81.0	6.4	6	95.0	2.3	6	11.39 I	1.49	6	12.99	1.19	6 I	117.8	5.8	6	88.0	2.2	6
2	Cleaned	112.4	0.8	5	113.5	1.1	4	16.22 D	0.30	5	15.58	0.48	4 D	149.2	4.7	5	118.1	4.4	4
	Cast	135.5		2	139.0		1	7.35 I		2	8.75		1 I	144.3		2	95.6		1
3	Cleaned	167.0		1	169.0		1	14.92 D		1	13.88		1 D	188.9		1	122.5		1

[a]D = prevailing light decreasing; I = prevailing light increasing.

Table 2. Antler characteristics of red deer fed *ad libitum* and restricted rations.

Antler cycle	Antler length (cm)						Antler growth rate (cm/wk)						Antler weight (g DM)					
	Unrestricted			Restricted			Unrestricted			Restricted			Unrestricted			Restricted		
	$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE	N
1	28.83	2.30	6	33.25	1.94	6	2.05	0.16	6	2.09	0.26	6	160.6	31.70	6	146.5	10.5	6
2	49.80	1.70	5	46.00	2.18	4	3.19	0.13	5	2.81	0.34	4	460.3	21.60	5	367.9	47.9	4
3	72.50		1	48.5		1	2.69		1	1.67		1	707.8		1	419.5		1
	Antler specific gravity (g DM/ml)						Relative antler wt. (g/kg body wt)						No. of points/antler					
	Unrestricted			Restricted			Unrestricted			Restricted			Unrestricted			Restricted		
	$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE	N
1	1.31	0.03	6	1.23	0.05	6	3.72	0.46	6	3.30	0.28	6	1.09	0.03	6	1.17	0.09	6
2	1.09	0.07	5	1.27	0.06	4	6.11	0.44	5	6.20	0.67	4	3.60	0.26	5	2.50	0.29	4
3	1.36		1	1.52		1	7.49		1	6.85		1	4.00		1	2.00		1

one in that the high-plane group had heavier ($P < 0.005$), longer ($P < 0.001$), antlers with more points ($P < 0.05$) than the low plane group; the specific gravity was not significantly greater (Table 4).

Further evidence for the influence of nutrition on the onset of pedicle development was kindly provided by Dr. P. F. Fennessy (Table 5). Red deer stags penned indoors in New Zealand grew pedicles when they reached a threshold body weight, which was hastened by a high plane of nutrition ($P < 0.005$). Likewise, antlers were initiated at a similar body weight, but significantly ($P < 0.025$) earlier age in well-fed stags. However, casting of this first antler occurred at the same time irrespective of the slight non-significant difference in weight.

The time taken to grow the pedicle and antler was remarkably consistent within and between the studies (Table 6). The stags at Invermay took only 8.2 ± 0.5 and 8.6 ± 0.4 weeks ($t = 0.6$ n.s.) from pedicle initiation to antler initiation for the pelleted diet fed and the meadow hay fed groups respectively.

DISCUSSION

Young red deer stags began pedicle development when they attained a certain body weight irrespective of age or prevailing photoperiod. This exact weight differs between these studies, and this may represent genetic differences between the stags used. In addition, if pedicle initiation, as a secondary sexual character, is a consequence of the onset of puberty, then the weight at which this occurs may be a portent of the maximum genetic potential size of the stag.

The data explain the finding by Goss (1969*b*) that pedicles were initiated in young sika deer (*Cervus nippon*) despite the simulated equatorial photoperiod and confirm the supposition of Lincoln (1971) that plane of nutrition controls pedicle development. Lincoln, however, thought that photoperiod might actually control the timing of pedicle development, but there is no support for this concept from the present study.

The weight at which antlers were initiated appeared consistent within, but not between studies. This may be due to the different planes of nutrition offered to the groups of stags. The timing between each event is consistent (Table 6). Therefore, if nutrition is poor, this must indicate that the restricted stags will grow less well than the well-fed stags during this period. However, antler growth and cleaning are an inevitable consequence of pedicle initiation. Although these events are not related to the photoperiod, much less their timing, they may not necessarily be related to plane of nutrition either.

In contrast, antler casting is strongly dependent on an increasing photoperiod for stimulation. It was during the period between cleaning and casting of the first antler that the winter restricted group in Study 1 "caught up" on the unrestricted group and remained thereafter in synchrony with the photoperiod. In this study there is a slight non-significant trend for the unre-

Table 3. Effects of supplemental feed during the first winter on antler cycle of red deer.[a]

	Weight (kg)						Age (weeks)					
	High supplement			Low supplement			High supplement			Low supplement		
	X̄	SE	N	X̄	SE	N	X̄	SE	N	X̄	SE	N
Pedicle initiation	47.9	1.49	9	47.4	0.8	10	37.9	0.7	9	52.8	3.2	10
Antler initiation	57.9	1.7	9	56.7	1.3	10	52.0	2.7	9	64.1	1.1	10
Antler cleaned	63.8	0.6	5	62.0	1.5	4	64.3	0.6	5	72.5	1.8	4

[a]Supplement was mixture of 90% barley, 10% protein pellets, and vitamins; hay and water *ad libitum*.

Table 4. Effect of supplemental feed during first winter on antler characteristics of red deer.[a]

	Weight (g)			Specific gravity (g DM/ml)			Length (cm)			Number of points per antler		
	X̄	SE	N	X̄	SE	N	X̄	SE	N	X̄	SE	N
High supplement (1.1 kg/day)	48.4	7.6	8	0.8	0.1	8	22.3	2.0	8	1.22	0.1	8
Low supplement	18.3	2.9	10	0.59	0.08	10	10.1	1.0	10	1.0	0.0	10

[a]Supplement was mixture of 90% barley, 10% protein pellets, and vitamins; hay and water *ad libitum*.

Table 5. The effect of dietary protein in the antler cycle of red deer stags penned indoors.[a]

		Pedicle initiation			Antler initiation			Casting		
	Ration[b]	X̄	SE	N	X̄	SE	N	X̄	SE	N
Live weight (kg)	Pelleted diet (17.2% C.P.)	50.4	1.5	5	59.7	1.4	5	120	8.2	5
	Meadow hay (6.1% C.P.)	47.4	1.5	5	63.8	1.8	5	115	2.8	5
Age (wks)	Pelleted diet	32.6	1.4	5	40.7	1.5	5	97.1	0.5	5
	Meadow hay	38.8	0.4	5	47.4	1.5	5	97.2	0.7	5

[a]Data courtesy of P. F. Fennessy, Invermay Agricultural Research Center
[b]Rations fed *ad libitum* for 10 weeks, June-August.

stricted group to cast a few weeks before the restricted group. This supports Watson (1971) but contrasts with Long et al. (1959).

Although photoperiod may be the principal environmental cue for antler casting, nutrition or stress (Topinski 1975) may also act as modifying controls. Geist and Bromley (1982) suggested that antlers were cast in order that exhausted male deer may mimic females after the rut and thus escape predation. While this may be the selective force influencing the time of casting, it fails to predict why red deer cast later due to poor nutrition and white-tailed deer cast earlier.

Retention of antlers must confer some selection advantage to red deer. Lincoln (1972) showed that the presence of antlers was related to dominance at antler casting time. It may, therefore, be beneficial for a stag in poor con-

Table 6. The effects of feed restriction (study 1) and supplemental feed (study 2) in the weeks between antler cycle events in red deer stags.

	Study 1						Study 2					
	Unrestricted			Restricted			High Supplementation			Low Supplementation		
	$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE	N
Pedicle initation to antler initiation	9.0	1.0	6	9.0		6	14.1	2.5	9	14.3	3.1	7
Antler initiation to velvet cleaning	10.5	1.1	6	12.2	0.8	6	14.0	2.2	6	15.0		1
Velvet cleaning to antler casting	42.5	5.2	6	42.8	2.7	6						
Antler casting to second velvet cleaning	32.8	7.7	5	15.25	1.7	4						
Second velvet cleaning to antler casting	23.0		2	26.0		2						
Antler casting to third velvet cleaning	32.0		1	30.0		1						

dition, and presumably low in the dominance hierarchy, to retain his antlers for as long as possible in order to benefit nutritionally from his short-lived period of antler-dependent-dominance. Red deer stags would gain little from sharing the females' range; if poor white-tailed bucks did and if their acceptance by females was related to the presence or absence of antlers, then it may be adaptive for them to look like females during this period in order to join them.

Plane of nutrition had little effect in Study 1 on parameters of antler size. The restricted deer grew their antlers mainly during phases of feeding to appetite, which may account for this result. Relative antler weight tends to increase with age as shown by Huxley (1931) and Hyvarinen et al. (1977). In Study 2 the stags that had received the highest level of winter supplementation had larger, longer antlers than the other group. This may be reconciled with the result from Study 1 since the plane of summer nutrition for both groups in Study 2 was substantially lower than for those in Study 1. The group recovering from the low level of winter supplementation in Study 2 probably had less energy in excess of maintenance with which to grow antlers than the previously restricted group in Study 1.

Bergerud (1976) presents data for the dates at which a captive male caribou (*Rangifer tarandus*) grew, cast, and cleaned its 2nd-5th set of antlers. In successive years it took 21 and 22 weeks to grow antlers and 27, 28 and 27 weeks between cleaning and casting them. Thus, although the time taken for these events is different for caribou than red deer, nevertheless the timing is constant within the species between years. In addition, an age effect was noted such that each event occurred a few days earlier each year throughout the study.

The present studies have shown that pedicle initiation, a consequence of puberty, leads to antler development irrespective of the direction of the prevailing photoperiod. It is imperative, therefore, that the young stag be in such a condition that it can cope with the nutritional stress of antler development. The threshold weight for pedicle development prevents initiation of this process before any animal is of sufficiently good condition. Lincoln (1971) points out that Scot's red deer living in very severe conditions may not grow pedicles until they are 2 or 3 years of age. Hummels, antlerless stags, may, in part, be caused by severe undernutrition beyond the age at which the presumptive pedicle region is responsive to changes in luteinizing hormone and testosterone associated with puberty.

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