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Growth and mineralisation of antlers in red deer (*Cervus elaphus*)

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Abstract In a study of antler growth and mineralisation, 18 red deer stags aged 4 years and older were individually penned immediately before and during antler growth and offered one of three pelleted rations which varied in protein and calcium (Ca) content. One antler was removed from a stag in each treatment group at 28, 42, 56, 70, 91, and 112 days of growth. The contralateral antler was removed when epidermal tissue began to be shed (velvet shedding). No effect of nutritional treatment on antler growth was detected. Mean time of velvet shedding was 164 days after the start of antler growth. Date of antler casting (range = 56 days) was more variable than date of velvet shedding (range = 24 days). Increase in length and weight followed a typical growth curve with the most rapid phases, 0.67 cm/day and 13.7 g/day respectively, occurring between 28 and 112 days after casting. By 112 days, antlers had achieved about 95 and 127% of final length and weight. Three phases of mineralisation were demonstrated. The first was a zone of initial rapid mineralisation 5.0–7.5 cm behind the poorly mineralised antler tip. The second phase was a gradual general increase with time in density of bone matrix and its degree of mineralisation throughout the antler shaft. The third phase occurred between 91 and 112 days of growth. It coincided with cessation of growth in length and was characterised by rapid deposition of matrix throughout the antler with immediate and high rates of mineralisation. Maximum rate of Ca deposition in an antler ultimately weighing 3 kg was calculated to be 8.4 g/day, and occurred between 91 and 112 days of growth.

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INTRODUCTION

Antlers are secondary sexual structures carried on pedicles formed from the frontal bones of the skull by the males of most species of deer. Growth consists of rapid differentiation of vascular cartilaginous tissue, during which phase the antlers are covered with epidermal tissue known as 'velvet'. Subsequently, mineralisation occurs and epidermal tissue is shed. Casting of mineralised 'hard' antler occurs by separation at the antler-pedicle junction during spring when new antler growth is initiated.

In red deer, antler weight is related to bodyweight and age (Huxley 1926, 1931; Muir 1985) but only anecdotal evidence is available on specific nutrient requirements for antler growth. Vogt (cited by Whitehead 1950) suggested that feeding sesame cake, with a high protein content, increases hard antler weight. Huxley (1926) noted a decrease in hard antler weight following the cessation of liming of pasture which he considered may reflect decreased herbage calcium (Ca) concentration. There is some evidence that dietary restrictions adversely affect antler growth in white-tailed deer (French et al. 1956; Ullrey 1983).

The very rapid development and external nature of antler tissue may provide a useful model for the study of the regulation of hard-tissue growth in farm animals. Such speculation is constrained, however, by the paucity of data on antler growth and composition, and on its response to nutritional or other stimuli. The present study provides some of these data for red deer (*Cervus elaphus*).

EXPERIMENTAL METHODS

Animals and treatment

The trial was conducted between August and February (spring and summer in New Zealand). Eighteen stags aged 4 years and older were held under cover but exposed to natural lighting, in individual concrete-floored pens (1.6 × 2.4 m) with

Table 1 Formulation (%) and analysis of the three rations[a] offered.

	A Control	B High protein	C Low Ca
Ingredient			
Barley	-	10.0	-
Wheat	66.8	40.0	74.0
Wheat pollard	20.0	-	15.0
Peas	10.0	10.0	10.0
'Protected' linseed	-	36.0	-
Limestone	2.2	2.4	-
Salt	1.0	1.0	1.0
Analysis			
Crude protein (g/kg DM)	130	199	132
Ca (g/kg DM)	7.6	6.7	3.0
P (g/kg DM)	5.0	5.5	5.7
ME[b] (MJ/kg DM)	12.5	12.5	12.5

[a] Vitamin and trace element pre-mix was added to all rations.
[b] Determined from digestible energy content (DE) measured in sheep at maintenance levels of feeding and converted to metabolisable energy (ME) using DE × 0.8.

sawdust as lairage. They were adjusted to pelleted concentrate rations for 2-3 weeks and allocated, on the basis of previous antler growth and current liveweight, to three groups. A basal diet (Group A), or the same diet enhanced with formaldehyde-treated linseed meal (high protein, Group B), or deficient in Ca (low Ca, Group C) was offered. The composition of the diets, which were isocaloric, is given in Table 1. Feed was offered once daily at the rate of 0.95 MJME/kg bodyweight ($W^{0.75}$). This was calculated to provide for bodyweight gain of 300 g/day. Animals were weighed weekly and individual dry matter (DM) intake recorded daily.

Individual stags from within each group were allocated, at random, to one of six dates for removal of the left antler, viz. 28, 42, 56, 70, 91, and 112 days after casting of remnants of the previous antler. The right antler was removed, and the trial ceased when epidermal tissue (velvet) commenced shedding (velvet shedding). Regrowth on the stump of the cut left antler was also removed at this time.

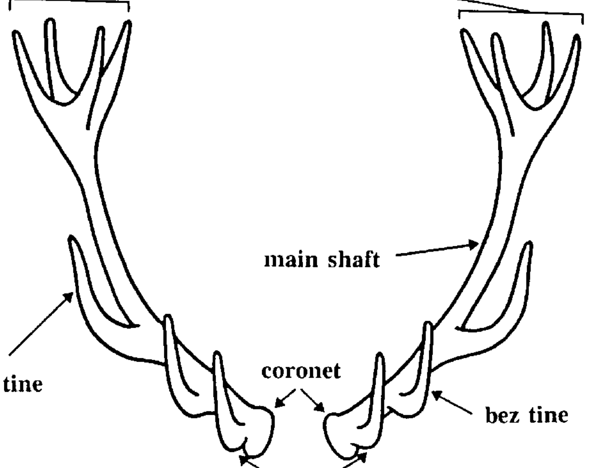

Fig. 1 Antler nomenclature in red deer.

Antlers were removed following sedation of stags with 60 mg xylazine hydrochloride (Rompun®, Bayer) and blockage of nervous conduction in infratrochlear and zygomaticotemporal branches of the trigeminal nerves with 20 mg lignocaine hydrochloride (Xylocaine®, Astra). A tourniquet was applied and the tissue removed 1 cm above the antler-pedicle junction using a bone saw.

Antlers were inverted on removal to prevent blood loss, weighed and length of the main shaft and tines recorded around their greater curvature. Circumference of the antler shaft was measured immediately above its intersection with the bez tine and that of the brow tine immediately above its attachment with the mainshaft. The length of antler remaining on the pedicle was assessed visually. A description of red deer antler nomenclature is given in Fig. 1.

The main shaft and tines of all developing antlers were cut at 5 cm intervals from tip to base. The cylinders thus produced were then bisected medially and one half used for chemical analysis. Tissue from nine antlers which had shed velvet, three from each treatment group, and all regrowth tissue from the left antler, was subjected to similar procedures before chemical analysis.

Subsequently, tissue between 0 and 10 cm from the tip which had been stored at −20°C was

Table 2 Mean (± SED) antler weight, length, and degree of mineralisation at velvet shedding, casting date, velvet shedding date, and duration of antler growth in mature red deer stags subjected to three nutritional treatments.

	Treatment group A	B	C	SED
No. of stags	6	4	6	
Weight (kg)	1.12	1.32	0.99	± 0.214
Length (m)	0.71	0.71	0.72	± 0.326
Mineralisation (A:R)	1.76	1.72	1.72	± 0.068
Mean casting date (days)	8 Sep	19 Sep	15 Sep	± 8.6
Mean velvet shedding date (days)	20 Feb	27 Feb	26 Feb	± 4.1
Duration of antler growth (days)	166	161	164	± 8.4

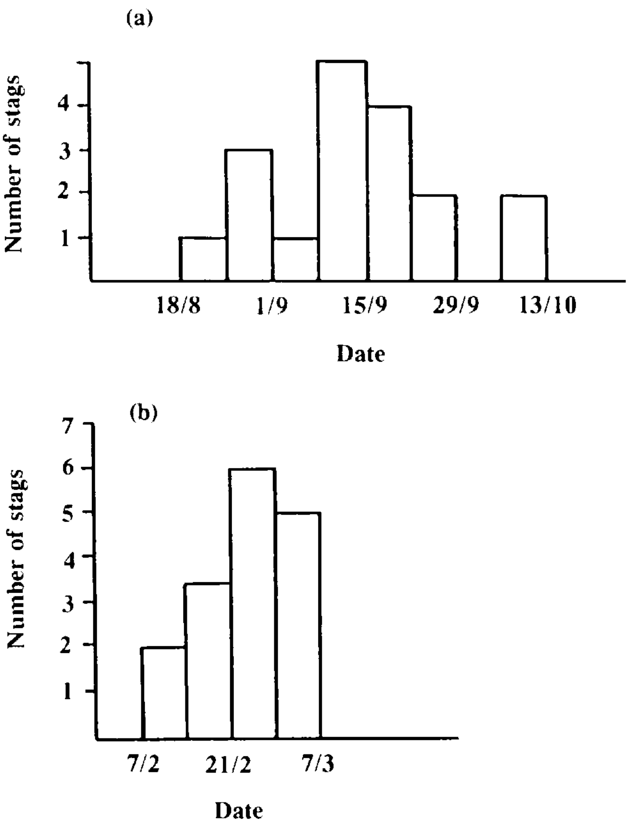

Fig. 2 Distribution pattern of date of (a) hard antler casting ($n = 18$); and (b) velvet shedding ($n = 16$), in red deer stags.

further subdivided at 2.5 cm intervals and subjected to the same analyses.

Chemical analyses

The half cylinders of tissue were weighed, immersed in water for 8 h before measurement of volume (V) by water displacement and then dried at 100°C for DM determination. Fat was extracted by boiling twice in petroleum ether for 6 h and fat-free dry weight (W) determined by re-drying at 100°C. The half cylinder was then ashed at 550°C, ground and digested in 2*N* HCl at 60°C to provide weights of ash (A) and organic matrix (R, R = W − A).

Feed DM was determined after drying at 60°C for 48 h. Samples were then passed through a 1 mm sieve and nitrogen (N) concentration determined by the methods of Sykes et al. (1979). Samples were incinerated at 550°C and the ash digested for 15 min in 2*N* HCl at 60°C.

Inorganic phosphorus (P) in feed and antlers was measured by the method of Hurst (1964), adapted by Kraml (1966), and Ca by atomic absorption spectrophotometry (Willis 1960).

Statistical analyses

Treatment effects were examined by analysis of covariance, using liveweight as the covariate. In some analyses variation between animals in length and weight of the left antler was reduced by expressing this value as a proportion of that of the contralateral antler at velvet shedding.

The possibility of mathematical description of antler growth was examined using polynomial and more specific growth equations. Where the latter provided a better fit they were used and their use indicated. Regression analysis techniques were used to describe variation in composition within an antler.

Means are given in tables and text with one standard error unit.

RESULTS

Animal health, feed intake, and liveweight gain

Two deaths, attributed to malignant catarrhal fever, occurred in Group B, one after sampling at Day 28 and the other after Day 56. Both stags were apparently healthy at antler removal, and data were retained where appropriate. Feed intake and bodyweight change were not affected by treatment

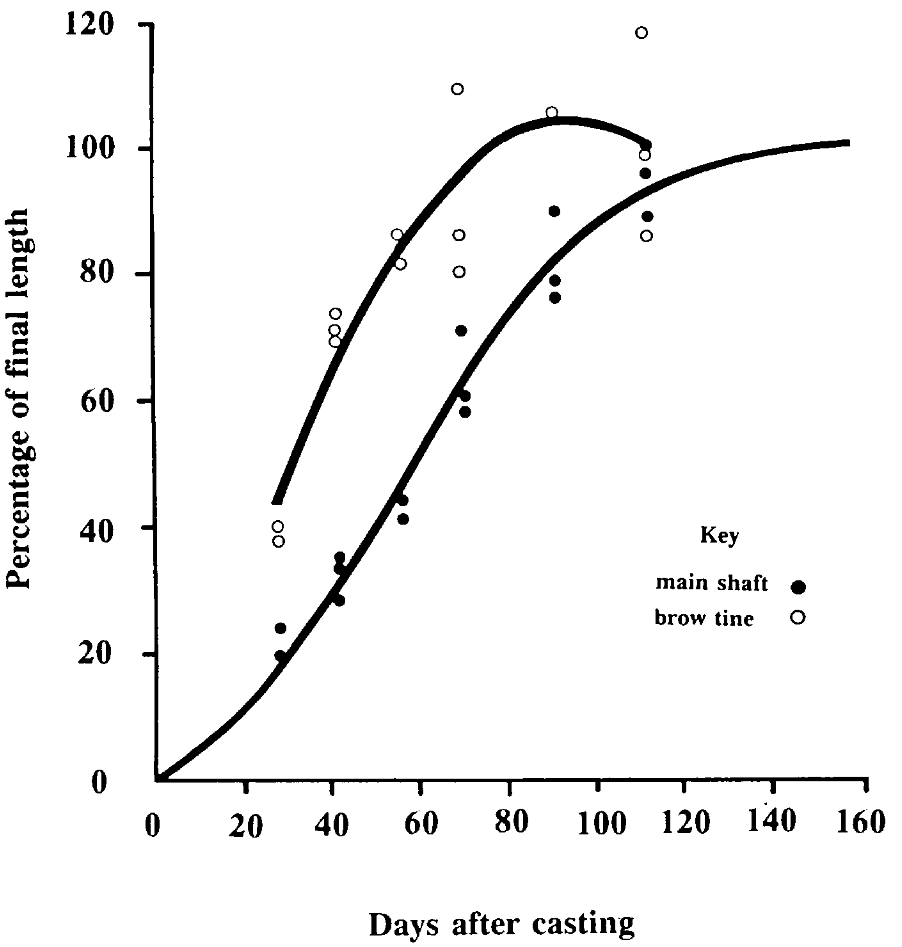

Fig. 3 Elongation of antler shaft and brow tine in relation to stage of antler growth. See text for equations.

Table 3 Mean (± SED) hard antler weight, length, degree of mineralisation, and bodyweight (at velvet shedding) in relation to time of removal of the contralateral antler.

	Time of removal of contralateral antler (days after casting)						
	28	42	56	70	91	112	SED
No. of stags	2	3	2	3	3	3	
Weight (kg)	1.38	1.25	1.32	0.99	1.11	0.85	± 0.317
Length (m)	0.73	0.72	0.76	0.68	0.72	0.69	± 0.046
Mineralisation (A:R)	1.72	1.65	1.85	1.69	1.79	1.72	± 0.091
Bodyweight (kg)	162.3	176.7	201.0	178.7	190.2	167.5	± 19.69

Table 4 Weight of regrowth antler (percentage of the weight at velvet shedding of the contralateral antler) in relation to time of antler removal.

	Date of antler removal (days after casting)					
	28	42	56	70	91	112
No. of stags with regrowth antler/no. of stags sampled	2/2	3/3	2/2	2/3	2/3	0/3
Mean regrowth antler weight (percentage of hard antler)	48.0	42.8	31.0	19.9	19.3	-

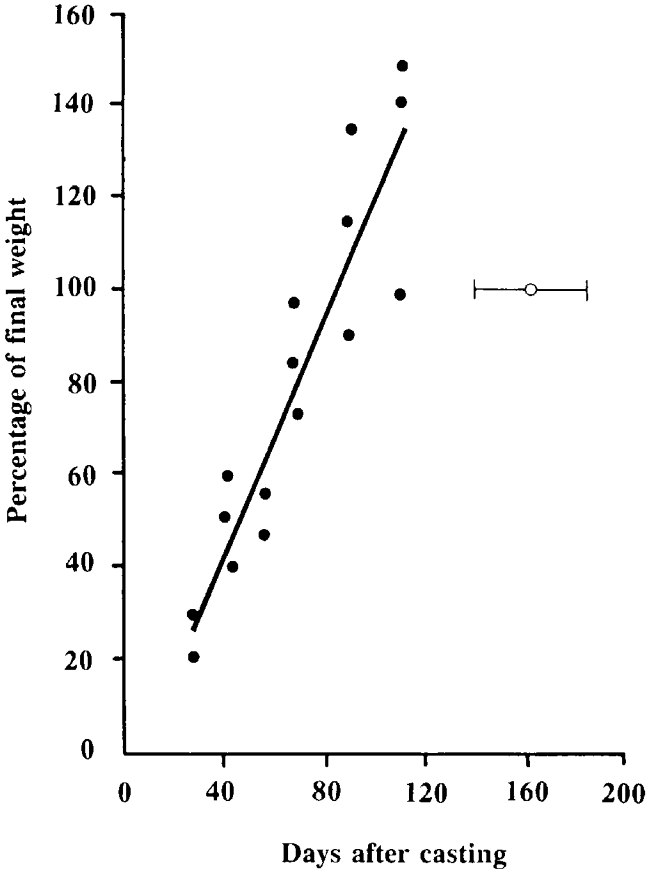

Fig. 4 Increase in weight of antler in relation to stage of growth. Open circle and bar represent mean and range respectively of velvet shedding dates of hard antler. See text for equation.

and data were combined. Intake (kg DM/day) increased from 1.75 ± 0.048 in mid August to 2.75 ± 0.055 in early November and then remained constant until the trial ceased four months later. Mean bodyweight (kg) was 121.0 ± 2.67, 125.0 ± 2.93, and 179.1 ± 5.08 respectively, on entry to the trial, at mean date of antler casting (26 days after the trial started), and at velvet shedding. Mean bodyweight gain during the period of antler growth was 327 ± 16.9 g/day.

Antler growth

There were no significant effects of treatment on hard antler length, duration of antler growth, or in degree of mineralisation. Antlers from stags in Group B tended to be heaviest, but not significantly so. Data were combined to describe the pattern of antler growth and composition (Table 2).

At velvet shedding the right antler tended to be heavier when the contralateral antler was removed early (Table 3), being 1.31 and 0.98 kg when the contralateral antler was removed before 56 days or after 70 days, respectively.

Date of casting of previous antler remnants was normally distributed (Fig. 2); mean date was 13 September, with a range of 56 days (18 August - 13 October). Left and right antler stumps were cast within 1.7 ± 0.5 days. Shedding of velvet from the intact and regrowth antler occurred simultaneously, and both were removed together. Mean date of shedding was 24 February with a range of 24 days (Fig. 2). The period of antler growth (casting to shedding) ranged from 142 to 187 days, mean 164 days, and was negatively correlated ($r = -0.88$**) with the date of casting of antler remnants.

The number of antler tines per antler (Fig. 1) varied between 3 and 6, with a mean of 4.1. Brow tines were present on all antlers and bez tines on 9 the of 18 antlers removed during growth and on 7 of 16 antlers removed at shedding. Trez tines were present on all the latter antlers. Royal tine number ranged from 1 to 3, mean 1.6. Six stags had an unbranched upper main shaft which was counted as a single royal tine.

Growth in length of the main shaft, expressed as a proportion of final length of the contralateral antler (Fig. 3) followed a normal growth curve to which the following Gompertz equation was fitted:

$$Y = 0.000 + 102.332 (-e (-0.033 (X - 46.944)))$$

(SE at midpoint = 2.2)

where Y = proportion of final antler length and X = days after casting. Between Days 28 and 112 length increased by 0.62 cm/day. Final length was, on average, 0.71 ± 0.013 m. There was large variation in brow tine length (mean 0.23 ± 0.014 m) and between contralateral brow tines from the same stag. The relationship which best described growth in length of the brow tine (Fig. 3) was:

$$Y = -17.0 + 2.53 X - 0.0132 X^2 \ (r = 0.91^{**}, \text{RSD} = 10.4)$$

where Y = final brow tine length and X = days after casting, suggesting a more curvilinear pattern of growth than that of the shaft. Growth in length between 28 and 56 days averaged 0.53 cm/day, and was almost complete (92%) after 70 days (Fig. 3).

The mean weight of whole antler at velvet shedding was 1.12 ± 0.092 kg, which was 78% of its maximum weight at 112 days. Increase in weight was most rapid, mean 13.7 g/day, between 28 and 112 days (Fig. 4) and was described by a linear relationship as:

$$Y = -7.70 + 1.26 X \ (r = 0.92^{**}, \text{RSD} = 15.9)$$

where Y = percentage of final hard antler weight and X = days after casting.

Antler tissue re-grew from the stump of the cut antler in 11 of the 16 stags. The extent of regrowth was related to the date at which tissue had been removed, being greater in earlier cut antlers (Table 4). Regrowth did not occur when antler tissue was

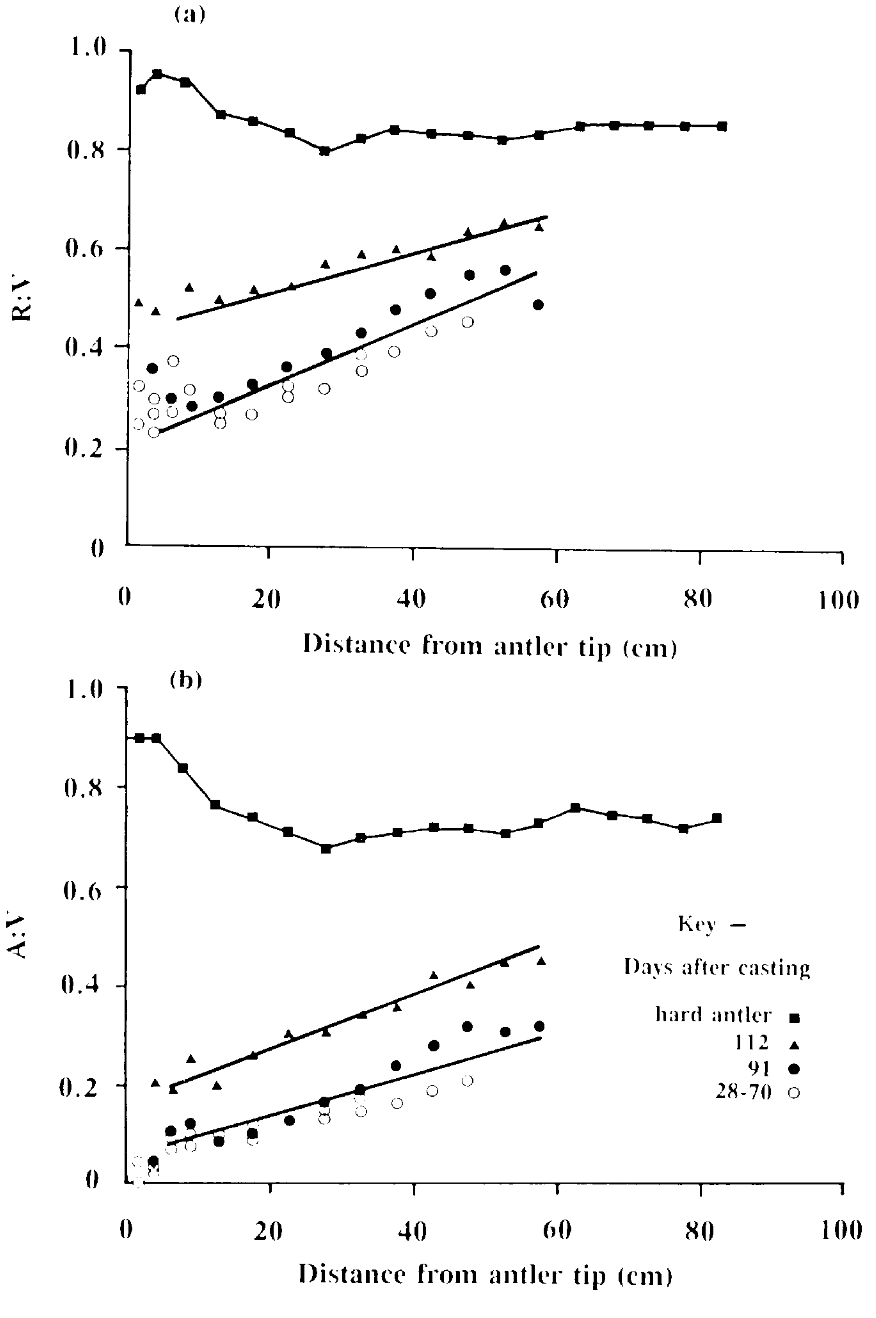

Fig. 5 Ratio of (a) fat-free organic matter to volume (R:V); and (b) ash to volume (A:V), in the shaft of antlers removed at 7 stages of growth. Each point is the mean of sections from three antlers. From 28 to 91 days after casting, $Y = 0.105 + 0.00306\,X$ (r = 0.89**, RSD = 0.02) for R:V; $Y = 0.0564 + 0.00420\,X$ (r = 0.50**, RSD = 0.09) for A:V. At 112 days after casting, $Y = 0.214 + 0.00208\,X$ (r = 0.72**, RSD = 0.04) for R:V; $Y = 0.160 + 0.00564\,X$ (r = 0.87**, RSD = 0.05) for A:V. In all instances Y = ratio, X = distance (cm) from the antler tip.

removed later than 11 December; in this experiment this coincided with a minimum of 89 days growth.

Antler mineralisation

The densities of organic matrix and of ash in unit volume of tissue (R:V, g:ml and A:V, g:ml, respectively) are given in Fig. 5. R:V and A:V ratios both increased from tip to base in antlers removed at all stages. However, whereas a gradual progressive increase in R:V ratio was seen at all stages, except in the shedding antler, a rapid increase in A:V ratio was observed in the distal 5 cm of all antlers removed up to 112 days (Fig. 5). Regression of R:V and A:V on distance from the tip at each sampling time, but excluding data from the poorly mineralised distal 5.0 cm in the latter case, revealed no significant differences in slope or elevation between antlers removed between 28 and 91 days of growth for either parameter and common regression equations were fitted. Both R:V and A:V ratio increased with distance from the antler tip, the gradient of change being greater for the latter. Antlers removed after 112 days had significantly greater R:V and A:V ratios than

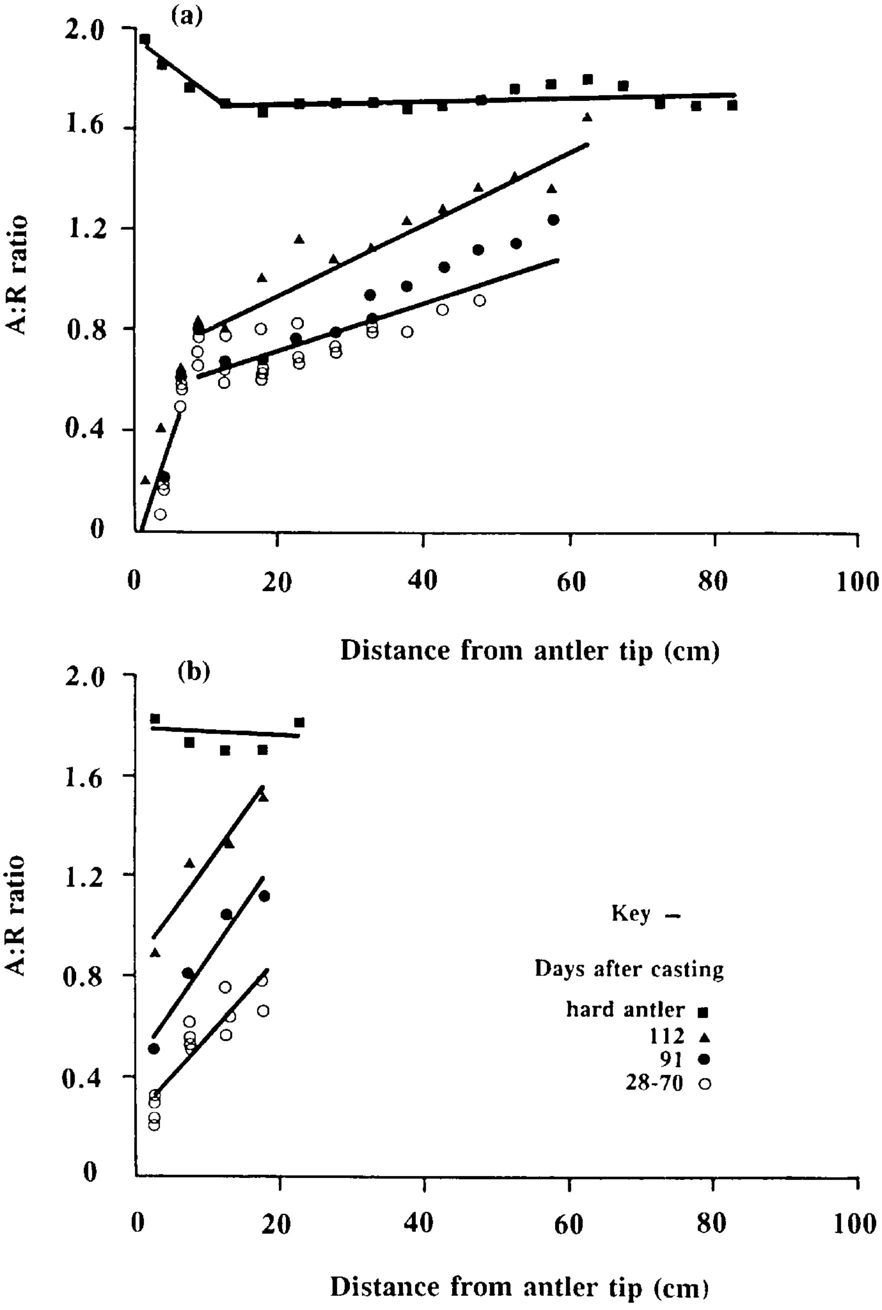

Fig. 6 Degree of mineralisation in (a) antler shaft and (b) brow tine, of antlers removed at 7 stages of growth. Each point is the mean of sections from three antlers. Between 28 and 112 days mineralisation was described as $Y = 0.0805 + 0.875\,X$ ($r = 0.87$**, RSD = 0.14) in tip sections and as $Y = 0.530 + 0.0960\,X$ ($r = 0.79$**, RSD = 0.17) in the rest of the shaft. After 112 days, mineralisation beyond 10 cm of the tip was described as $Y = 0.648 + 0.0144\,X$ ($r = 0.068$**, RSD = 0.11). In the brow tine, mineralisation was described as $Y = 0.231 + 0.0329\,X$ ($r = 0.85$**, RSD = 0.15) between 28 and 70 days after casting, as $Y = 0.445 + 0.0421\,X$ ($r = 0.85$**, RSD = 0.16) 91 days after casting, and as $Y = 0.847 + 0.040\,X$ ($r = 0.73$**, RSD = 0.16) at 112 days after casting. In all instances Y = A:R ratio, X = distance (cm) from antler tip.

antlers removed between 28 and 91 days (** in both cases – Fig. 5). A further major increase in R:V and A:V occurred after 112 days, particularly in sections within 20 - 30 cm of the antler tip.

Differential development of ash and matrix was examined as the ratio of ash to organic matter (A:R, g:g) in the antler shaft and brow tine (Fig. 6). Until 112 days there was a steep gradient of change in A:R ratio in the region 0 - 7.5 cm below the tip of the antler shaft (Fig. 6a), but mineral deposition in the tip subsequently increased rapidly. There was a significant linear increase in A:R from 7.5 cm below the tip to the antler base between 28 and 91 days. A higher (**) A:R ratio was observed at 112 days (Fig. 6a). In the antler shedding velvet A:R ratio had further increased, particularly in the sections nearest to the tip.

A:R ratio in brow tines increased linearly from tip to base until 112 days of growth (Fig. 6b); intercept values in the regression of A:R on distance from the tip were significantly different at 112, 91, and combined 28 - 70 day antlers. The gradient of mineralisation from the tip was much greater in the brow tine than in the antler shaft, as judged by regression coefficients of 0.36 and 0.12, respectively.

Table 5 Degree of mineralisation (A:R ratio, mean ± SEM, $n = 3$) of brow tine and antler shaft in relation to stage of antler growth.

	Stage of antler growth (days after casting)						
	28	42	56	70	91	112	Velvet Shedding
Brow tine	0.39 ±0.038	0.44 ±0.017	0.56 ±0.20	0.64 ±0.093	0.82 ±0.166	1.28 ±0.090	1.75 ±0.022
Antler shaft	0.51 ±0.035	0.65 ±0.019	0.65 ±0.029	0.71 ±0.033	0.86 ±0.35	1.20 ±0.117	1.73 ±0.030

The chronological sequence of mineralisation of the antler shaft compared with that of the brow tine is given in Table 5. Brow tine initiation was not recorded, and consequently A:R ratio has been expressed in relation to initiation of antler growth. Degree of mineralisation (A:R), although tending to be lower in the brow tine in the early stages of growth, had caught up with that of the main shaft by 112 days.

Antler regrowth removed at velvet shedding tended to be less well mineralised (A:R, 1.62 ± 0.046) than the contralateral hard antler removed at the same time (A:R, 1.71 ± 0.045) though the difference was not significant.

The composition of ash was not constant within antlers. Ash from tip sections of antlers removed between 28 and 91 days contained 21.1 ± 1.33 g Ca/100g ash compared to a value of 35.7 ± 0.65 g Ca/100g ash in tip sections removed after 112 days or from hard antlers. The difference was significant (**). Changes in P concentration showed a similar but less marked trend. In tip sections Ca to P ratio increased from 1.5 ± 0.07 between 28 and 91 days of growth to 2.1 ± 0.03 at 112 days and 1.8 ± 0.05 in hard antlers. This had negligible effect on total Ca (35.8 ± 0.33 g/100g ash), or total P concentration (19.7 ± 0.24 g/100g ash), or on Ca to P ratio (1.8) in the ash of antlers varying in stage of development from 28 days to velvet shedding.

To calculate rates of total ash deposition, the ash content of each antler removed was expressed as a proportion of the ash weight in the contralateral antler at velvet shedding (Fig. 7). The proportion of ash deposited increased exponentially with time and could be described by the relationship:

$$Y = 0.000120\ X^{2.81}\ (r = 0.96^{**},\ \text{RSD} = 6.7)$$

where Y = the proportion of final antler ash weight and X = days after casting. Maximum rate of ash deposition occurred between 91 and 112 days when 33% of total ash was deposited.

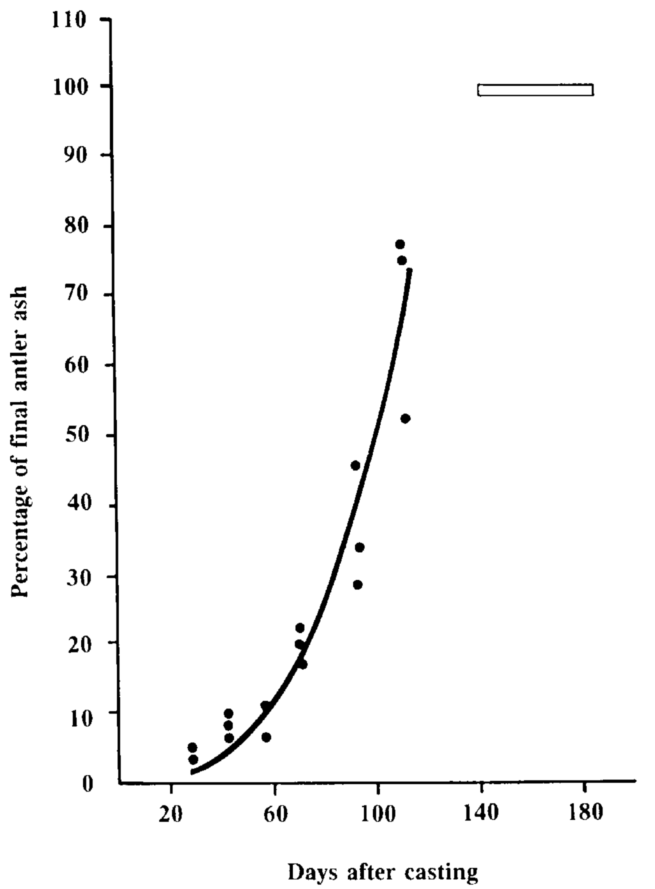

Fig. 7 Ash deposition in relation to stage of antler growth. Horizontal bar indicates range of dates of velvet shedding of hard antler. See text for equation.

DISCUSSION

The overall pattern of growth in length of antlers with time followed a sigmoidal (Gompertz) growth curve similar to that observed in spike antlers of yearling red deer (Fennessy 1982) and in antlers of a single mature moose (*Alces alces*) (van Ballenberghe 1983). Growth in length (and weight) occurred most rapidly between 28 and 112 days after casting, with 94.7 and 127% of final antler length and weight, respectively, being attained by Day 112. In accord with the classical study of Rorig (1906; cited by Goss 1983), elongation of the brow tine followed a different pattern to that of the main shaft. The former was almost fully formed 56 days after casting (84% of final brow tine length), whereas the antler shaft was still growing actively. Elongation in the brow tine appears, therefore, to be controlled either by a different mechanism to that in the antler shaft or to respond differently, locally, to the same mechanism. It may well simply be subject to earlier restriction of nutrient supply, possibly through circulatory differences and our own data (Muir et al. 1987a) suggest that blood content of the brow tine may be only 50% of that in the shaft. Differential regulation of growth within an individual bone is not however, a novel phenomenon. For instance, the proximal and distal epiphyses of the radii of sheep appear to close at markedly different times, respectively (Smith 1956).

The duration of antler growth, ranging from 142 to 187 days between casting and velvet shedding, was comparable to the 165 days estimated for the process in mature white-tailed deer (*Odocoileus virginianus*) by Anderson & Medin (1971). Variation in the duration of antler growth was associated with greater variation in casting date (range 56 days) than in velvet shedding date (range 24 days).

The slightly heavier antlers removed from stags offered the protected protein ration may support the finding of Vogt (cited by Whitehead 1950) for increased antler weight with increase in dietary protein supply. The lack of significant effect may simply reflect the very large variation in hard antler weight observed between animals (0.55 - 1.90 kg). Resolution of the effects, if any, of protein or energy intake on antler growth will require experiments with much larger numbers than used here or the selection of groups of animals with similar potential for antler growth. The fact, however, that within individual animals removal of one antler early in the growth phase resulted in a trend for a heavier contralateral antler at velvet shedding (Table 3) is perhaps a further indication that antler growth is sensitive to supply of a particular nutrient. It is possible, however, that a phenomenon akin to compensatory growth of other paired organs after unilateral resection has operated in the present situation.

It had been anticipated that the low Ca diet would contain only 1.0 g Ca/kg DM rather than the 3.0 g Ca/kg DM actually offered. Removal of one antler would further reduce demand for Ca and sensitivity to Ca intake was perhaps not tested. Subsequent experiments have, however, suggested that despite high Ca intake, extensive skeletal demineralisation may be a normal phenomenon during antler growth (Muir et al. 1987b); this is also suggested by earlier studies (Kay & Staines 1981).

The distal 2.5 cm of the antler (i.e., the tip) remained poorly mineralised during active growth and the Ca to P ratio in ash, at 1.5, was similar to the 1.48 in initial mineral deposits in epiphyseal cartilage of bone (Urist 1976). The increase in Ca and P concentration in the 112-day antler, together with the appearance of mineralised cartilage close to the antler tip (Muir et al. 1987a) and slowing or cessation of growth at this stage, suggests a process equivalent to epiphyseal plate closure in long bones.

Three distinct phases of mineralisation were apparent. The first was that which occurred in a discrete band 5.0 - 7.5 cm below the antler tip, and corresponded with a transition from mineralised cartilage to trabecular bone (Muir et al. 1987a). In contrast Kay et al. (1982) described a zone of mineralisation only 2 - 4 cm below the antler tip of 10 - 15 cm antlers from 2-year-old stags, the age and weight of which were unknown. The difference between these and the present results may be the result of differences in size of the antlers. On the other hand, in the present studies, the zone of mineralisation in the brow tine appeared to be much closer to the tip than in the antler shaft.

A second phase of mineralisation could be described as a gradual increase in density and degree of mineralisation of trabecular bone in the antler shaft with distance from the tip and possibly, therefore, time during which mineralisation could occur.

The third phase, which might be described as terminal mineralisation, occurred very rapidly between 91 and 112 days of growth (Fig. 7). It may reflect the formation of cortical bone (Muir et al. 1987a) which contains more ash per unit of matrix than trabecular bone (Arnold 1960). This phase appeared to coincide with cessation of growth and a decrease in antler blood content (Muir et al. 1987a).

The rate of Ca deposition and Ca requirement can be calculated from the pattern of Ca deposition (Fig. 7) and knowledge of ultimate antler size. Hard antlers weighing 3 kg (DM, 81.1 ± 0.77; ash, 63.0 ± 0.34% in DM and with Ca concentration in antler ash of 35.0%) would contain 537 g of Ca. Maximum rate of Ca deposition (33% of total antler Ca), would occur between 91 and 112 days of antler growth at 8.4 g Ca/day. This may appear large, but on a bodyweight basis it is about 50 mg/kg W per day and quite modest compared with Ca requirements for milk secretion in sheep of 60 - 110 mg/kg W per day (Braithwaite 1978, 1983; Sykes & Geenty 1986). If faecal endogenous loss was 2.7 g/day, based on estimates of endogenous loss for sheep and cattle of 16 mg/kg W per day (Agricultural Research Council 1980) and mean stag liveweight of 170 kg, maximum total daily net requirement for Ca would be 11.1 g Ca/day. If one assumes a value of 0.68 for availability of Ca (Agricultural Research Council 1980), dietary Ca requirement is 16.3 g/day. For stags showing compensatory growth after winter under-nutrition, intake of herbage should readily supply this. It has generally been found, however, that skeletal porosity increases during antler growth (Meister 1956; Banks et al. 1968) suggesting that bone mineral may inevitably be mobilised. Our own Ca kinetic studies (Muir et al. 1987b) with stags consuming forages, have shown that the skeleton may supply 30 - 60% of Ca requirement, even when Ca intake is considerably greater than requirement.

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