Antler growth and extinction of Irish elk

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ABSTRACT

Adult male Irish elk (*Megaloceros giganteus*) grew the largest antlers of any extinct or extant cervid. These antlers have often been implicated in the extinction of the Irish elk, although the effects of antler growth on Irish elk physiology have not been analysed quantitatively. We used a simulation model of energy and mineral metabolism to compare nutritional requirements for antler growth in Irish elk and moose (*Alces alces*), the largest extant cervid. The model simulates intake, metabolism, deposition, and excretion of energy, nitrogen, ash, calcium and phosphorus with mass balance for each of these nutrients on a daily time step. Predicted energy requirements for antler growth by moose are half as large as energy requirements for summer fat and protein deposition. In contrast, the predicted energy requirements for antler growth by Irish elk were about 75% as large as energy requirements for summer fat and protein deposition. Irish elk antlers weighing 40 kg at the end of velvet shedding would have contained 2.1 kg nitrogen, 7.6 kg calcium and 3.8 kg phosphorus. The nitrogen requirements for antler growth were met by forage intake. The model predicts that, to grow 40 kg antlers in a 150 day period, more than 60 g of calcium and more than 30 g of phosphorus were deposited in antlers daily for 60 consecutive days when antler mineralization rate was highest in mid-summer. Simulated Irish elk depleted skeletal mineral reserves to support antler growth more than extant moose, even when hypothesized adaptations to reduce skeletal mineral resorption were implemented. Even though Irish elk fit the allometric relationship between antler size and body size in extant cervids, mineral metabolism does not scale allometrically in the same manner. About 6% of the calcium and 10% of the phosphorus in the antler were resorbed from the skeleton because dietary intake of minerals was insufficient to meet requirements for antler mineralization. The minerals resorbed from the skeleton in summer would have to be replenished by dietary intake over the following winter. Pollen records document a shift in plant species composition from a tall willow–spruce community during the Allerod interstadial to a tundra during the Younger Dryas cold episode with reduced forage density coincident with the extinction of the Irish elk about 10,600 years before present (B.P.). The reduction in forage density would have made replenishing calcium and phosphorus in the skeleton even more difficult, as well as making it more difficult for male Irish elk to replenish fat reserves depleted during the rut. Sexual selection pressures for larger antlers and larger body size were opposed by selection pressures for smaller antlers and smaller body size imposed by environmental change. We suggest that the inability to balance these opposing selection pressures in the face of rapid environmental change contributed to extinction of the Irish elk 10,600 years B.P.

Keywords: antlers, Cervidae, energetics, Irish elk, *Megaloceros giganteus*, metabolism, mineral nutrition, nutrient requirements, simulation model.

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INTRODUCTION

Irish elk (*Megaloceros giganteus*) grew the largest antlers of any extinct or extant cervid (Gould, 1974). Irish elk from the Allerod interstadial (11,000–12,000 years ago) on Ireland were larger than other populations of Irish elk in the fossil record (Lister, 1994). The larger body and antler size corresponds to a period of climatic amelioration with a longer plant growing season and a shorter winter. Then, about 11,000 years ago, the Younger Dryas cold episode was initiated when Milankovitch variations in the Earth's orbital parameters reduced solar radiation (Berger, 1978, 1992). The Younger Dryas lasted for several centuries and the reduction in summer temperatures may have been as much as 12°C in Ireland (Ahlberg *et al.*, 1996). Pollen records indicate the temperature decrease precipitated a rapid change in vegetation in which shrub willows were replaced by a dwarf willow and grasses gave way to species of *Artemesia*, *Sedum*, *Crucifera* and *Polygonum* (Mitchell and Parkes, 1949; Barnosky, 1986). The decreased size of bones and antlers of Irish elk that died during the Younger Dryas suggests that the last surviving animals were nutritionally stressed (Barnosky, 1985).

This record of climate and vegetation change, coinciding with a decrease in both antler and skeletal size just prior to extinction of the Irish elk, suggests that an analysis of physiological requirements for antler growth in Irish elk may shed light on its extinction. The largest Irish elk antlers weighed about 40 kg, 30% heavier than the antlers of moose (*Alces alces*), the largest extant cervid (Geist, 1987). Despite their large antlers, Irish elk conformed to the expected allometric relationship between body size and antler size (Gould, 1974). In contrast, moose have antlers that are smaller than expected from this allometric relationship (Geist, 1987).

Irish elk antlers are physically and chemically similar to antlers of extant cervids (Kitchener, 1987; Kitchener *et al.*, 1994; Tataruch and Wolfsperger, 1995), and the physiology of antler growth is evolutionarily conservative among cervids (Chapman, 1975). Therefore, a model developed to simulate the nutritional requirements for antler growth in extant cervids (Moen and Pastor, 1998a,b) should be suitable for examining antler growth in Irish elk. Simulations of mineral metabolism must account for metabolic responses to changing mineral requirements during antler growth. Skeletal minerals are resorbed when requirements for deposition of calcium and phosphorus in the antlers cannot be met by dietary intake (Banks *et al.*, 1968). Mineral requirements are high because the antler dry matter contains 55% ash. A set of 40 kg antlers with a 10% water content would contain almost 20 kg of mineral elements. Calcium and phosphorus, primarily present as hydroxyapatite ($Ca_5(PO_4)_3OH$), constitute 38% and 18% of the ash, or approximately 21% and 10% of the dry mass of the antlers, respectively (Chapman, 1975). The skeletal mineral reserves are repleted during the subsequent fall and winter through dietary intake.

We predicted nutritional requirements for antler growth and the effects of antler growth on mineral metabolism in Irish elk during the Allerod and during the Younger Dryas cold episode. We also used the model to simulate extant moose under current climatic conditions to provide a baseline against which the Irish elk simulations could be compared. Finally, we used the model to simulate possible changes in Irish elk physiology, behaviour and morphology that might have reduced resorption of skeletal minerals, and to perform a factorial sensitivity analysis on skeletal resorption and energy requirements for antler growth.
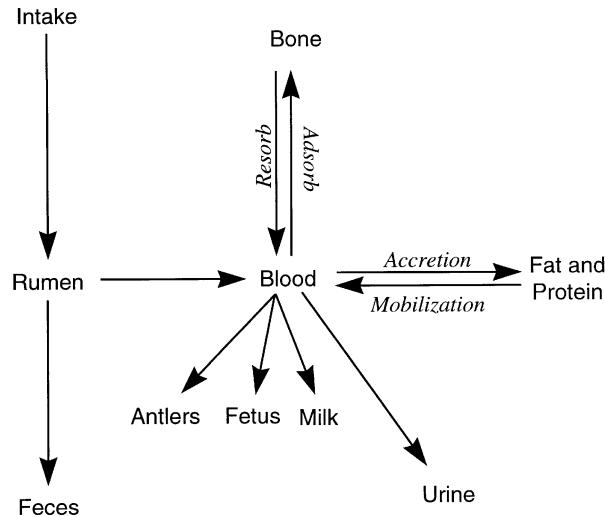
Fig. 1. Schematic representation of the flow of nutrients in the simulation model. Each nutrient (energy, protein, calcium and phosphorus) is treated independently. Energy reserves are stored in fat and protein, whereas mineral reserves are stored in the skeleton. If dietary intake is insufficient to meet the requirements for antler growth, body reserves are used to meet the deficit.

METHODS

Model description

Nitrogen, calcium and phosphorus metabolism (Moen and DelGiudice, 1997; Moen and Pastor, 1998a,b) were integrated into a previously validated model of energy metabolism (Moen *et al.*, 1997). The model maintains mass balance of each of these nutrients. The daily balance of energy, nitrogen, calcium and phosphorus is determined from forage intake, availability of each nutrient and requirements for maintenance and production. Metabolic fecal and endogenous urinary nitrogen, calcium and phosphorus are accounted for. If the simulated animal ingests excess nutrients, body fat and protein reserves are increased, and minerals are deposited in the skeleton if it is not replete (Fig. 1). If requirements for production and maintenance cannot be met from dietary intake, body reserves are used to make up the deficit.

The major storage depot for both calcium and phosphorus is the skeleton, which contains about 99% of the calcium and more than 75% of the phosphorus in the body (Agricultural Research Council, 1980). Skeletal minerals are resorbed when requirements for deposition of calcium and phosphorus in the antlers cannot be met by dietary intake (Banks *et al.*, 1968). Calcium and phosphorus are more efficiently extracted from the diet as skeletal reserves are depleted, with measured extraction efficiencies of 35–65% (Braithwaite, 1983; Muir *et al.*, 1987; Heaney, 1990). The ash content of the ingesta- and fat-free body in a replete skeleton is 5.5%, and the model allows up to 20% of the ash in a replete skeleton to be resorbed if dietary intake is insufficient (Moen and Pastor, 1998b). These resorption rates are in accordance with skeletal resorption in deer, other ruminants and humans (Smith *et al.*, 1975; Parfitt, 1981; Buckwalter *et al.*, 1995).

Nutrient concentrations in the diet

Simulated diet digestibility, protein, calcium and phosphorus followed seasonal patterns with smooth transitions between minimum and maximum values occurring over 20 days in both spring and fall (Moen *et al.*, 1997). Peak diet digestibility was 65% in summer and declined to 40% in winter. Peak crude protein in the diet was 18% in summer and 6% in winter. Concentrations of calcium in the diet ranged from 0.75% in winter to 1.25% in summer, and concentrations of phosphorus in the diet ranged from 0.40% in winter to 0.85% in summer. These concentrations of calcium and phosphorus are similar to concentrations in diets of free-ranging moose and caribou today (Kubota, 1974; Oldemeyer *et al.*, 1977; Staaland *et al.*, 1983; Staaland and Saebo, 1993; Chase *et al.*, 1994) and are higher than concentrations of calcium and phosphorus in tundra plant genera (Chapin, 1980; Chapin *et al.*, 1986; Shaver and Chapin, 1991) present on Ireland when the Irish elk became extinct (Mitchell and Parkes, 1949).

Growing season length

During the period of climatic amelioration of the Allerod, the plant growing season was longer than it was during the Younger Dryas cold episode or it is today. We simulated the Younger Dryas environment and current-day conditions with a 120 day plant growing season which began on 15 May and ended on 12 September, and we simulated the Allerod with a 150 day plant growing season which began on 15 April and ended on 12 September.

   The length of the antler growth period during the Allerod is unknown, but evidence indicates that it was longer than during the Younger Dryas or today (Guthrie, 1984). The simulated length of the antler growth period must be consistent with antler growth in extant cervids. Antler growth is controlled by photoperiod (Goss, 1983) and the rut is timed so that calves are born at the start of the plant growing season. Antlers must have completed growth and be fully mineralized prior to the rut when males engage in physical combat (Clutton-Brock and Albon, 1980; Clutton-Brock, 1982; Kitchener *et al.*, 1994). The length of antler growth in moose today is about 150 days (Van Ballenberghe, 1982). We used a 150 day length of antler growth for Irish elk during the Younger Dryas simulations, and a 165 day length of antler growth in the Allerod simulations.

Irish elk and moose

Simulations of moose allow us to use the physiological effects of antler growth in the extant moose as a baseline reference against which the predicted physiological effects of antler growth in Irish elk can be compared. We standardized simulation conditions for both species so that energy intake during the antler growing period was sufficient to increase body mass by 30% (Franzmann *et al.*, 1978; Schwartz *et al.*, 1987) and complete antler growth (Table 1). Fat content of the ingesta-free body was 5% on the first day of antler growth and about 13% on the last day of antler growth. Initial skeletal repletion was set at 100% for both calcium and phosphorus. Digestible energy intake required to meet the weight gain goal ranged from 1.36 to 1.45 $MJ \cdot kg^{-0.75} \cdot day^{-1}$ (Table 1).

Possible adaptations of Irish elk

We tested the effect of several hypothesized behavioural, physiological and morphological adaptations which might have reduced resorption of minerals from the skeleton. These

Table 1. Initial parameter values for each species and changes in body mass and composition[a]

| | Moose | Irish elk | |
		Allerod	Younger Dryas
Initial body mass (kg)	460	460	460
Pre-rut body mass (kg)	600	600	600
Initial body fat (%)	5	5	5
Pre-rut body fat (%)	13	13	13
Antler mass (kg)	30	40	40
Antler mass/MBW	247	330	330
Maximum food intake			
(dry matter as % of body mass)	2.45	2.38	2.53
Energy intake (MJ/MBW)	1.40	1.36	1.45

[a] Antler and pre-rut body masses are from Geist (1987). Body fat is expressed as a percentage of ingesta-free and antler-free body mass. Interspecific comparisons are made on the basis of body mass in $kg^{0.75}$ (MBW).

adaptations were tested for Irish elk under conditions simulating the Younger Dryas cold episode (Table 1). First, we increased dietary calcium concentrations to 1% in winter and 1.5% in summer, and we increased dietary phosphorus concentrations to 0.5% in winter and 0.95% in summer. These dietary calcium and phosphorus concentrations are higher than would be ingested by free-ranging moose and caribou (Kubota, 1974; Oldemeyer *et al.*, 1977; Staaland and Saebo, 1993; Chase *et al.*, 1994) and thus probably represent maximum dietary concentrations Irish elk would have ingested. Second, we increased the maximum extraction of dietary calcium and phosphorus from 65 to 75%. This is a higher extraction efficiency than has been measured in extant cervids (Stephenson and Brown, 1984; Muir *et al.*, 1987; Grasman and Hellgren, 1993). Third, larger bones in Irish elk may have provided supplemental calcium and phosphorus for resorption during antler growth (Lister, 1994). We increased the ash content of the lean body mass from 5.5 to 6.0% to simulate this, an increase of 9% in skeletal calcium and phosphorus reserves. When calculating skeletal depletion for animals with an increased ash content, we assumed that the additional calcium and phosphorus served no structural purpose and was only used as a calcium and phosphorus reserve. Fourth, mean body mass of male Irish elk is usually estimated at about 600 kg (Coope, 1973; Geist, 1987), but it has been suggested that mean pre-rut body mass could have been as high as 700 kg (Stuart, 1991). Therefore, we increased initial body mass to 540 kg and final body mass to 700 kg.

Sensitivity analysis

We used a factorial sensitivity analysis to determine how skeletal resorption and energy requirements affected the predicted antler mass of Irish elk. The factors varied in the sensitivity analysis were the available mineral reserves in the skeleton, the efficiency with which energy was used for antler growth, and the energy intake per day. A sensitivity analysis on the maximum resorption of skeletal minerals and the efficiency with which energy is used for antler growth in the model is desirable because experimental work is limited (Goss, 1995) and therefore parameter values for these factors had to be estimated.

The model allows up to 20% of skeletal mass to be resorbed. If in error, we believe this

estimate to be too high (Moen and Pastor, 1998a). Therefore, in the sensitivity analysis, we used factor levels of 10–20% in increments of 2.5% as the maximum amount of skeletal mass that could be resorbed. The efficiency of energy use for antler growth is set at 25% in the model, midway between the efficiency of energy use for gestation and the efficiency of energy use for fat and protein accretion (Moen and Pastor, 1998a). In the sensitivity analysis, we varied the efficiency of energy use for antler growth from 20 to 45% in increments of 5%. The last factor in the sensitivity analysis was the digestible energy intake per day. We used six digestible energy intakes evenly spaced between 1.26 and 1.46 $MJ \cdot kg^{-0.75} \cdot day^{-1}$ to cover the estimated daily energy intakes of extant ruminants during the plant growing season (Moen, 1978; Gillingham and Bunnell, 1985).

For each factorial combination, we determined the maximum antler mass that could be grown when all available skeletal minerals were resorbed. Because the antler growth model is deterministic, we only performed one simulation at each combination of factor levels. Maximum predicted antler mass was determined to the nearest 0.01 kg under the standardized simulation conditions of the Younger Dryas cold episode (Table 1). We also determined the effect of each factorial combination on the body mass and the repletion status of the skeleton at the end of antler growth.

RESULTS

Comparing Irish elk to moose

Energy requirements

Energy intake in the simulations was adjusted for moose and Irish elk until each species gained 30% body mass over the summer resulting in pre-rut body fat contents of 13% (Table 1). Energy intake was larger in Irish elk because more energy was required to grow their 40 kg antlers. The basal metabolic rate is commonly used to compare the relative importance of different energy costs (Hudson and White, 1985). Peak energy requirements for antler growth in a single day were approximately equal to the basal metabolic rate in the extant moose, about 120% of basal metabolic rate in the Allerod Irish elk, and about 133% of basal metabolic rate in the Younger Dryas Irish elk (Table 2). The Allerod Irish elk maximum daily energy requirement was smaller because energy costs of antler growth were spread over a 165 day period of antler growth.

Energy above maintenance is allocated either to antler growth or to fat and protein accretion in males. Stored fat is an important energy reserve both during the rut and throughout winter. Over the entire period of antler growth, energy requirements for antler growth were about 50% of basal metabolic rate in moose, and almost 70% of basal metabolic rate in Irish elk (Table 2). A consequence of the smaller antlers in moose was that proportionately more energy could be allocated to fat and protein accretion than to antler growth. Moose invested about twice as much energy into fat and protein accretion as into antler growth, while Irish elk could only invest about 1.3 times as much energy into fat and protein accretion as into antler growth if they were to grow 40 kg antlers (Table 2).

Nitrogen requirements

The model predicts that nitrogen intake would not limit antler growth of either moose or Irish elk. Irish elk would need to incorporate only 2.1 kg of nitrogen into 40 kg antlers out

Table 2. Predicted nutritional requirements to grow antlers and increase body mass by 30% in summer for moose under current growing conditions, and Irish elk under growing conditions during the Allerod and the Younger Dryas[a]

| | Moose | Irish elk | |
		Allerod	Younger Dryas
Peak requirements (% of BMR)			
antlers	101	121	133
fat and protein accretion	171	157	174
Seasonal requirements (% of BMR)			
antlers	52	63	69
fat and protein accretion	96	83	89
Dietary contribution to antler (% of intake)			
energy	16	20	21
nitrogen	4	5	5
calcium	26	31	32
phosphorus	20	24	25
Resorbed mineral as % of mineral in antler			
calcium	5	7	7
phosphorus	9	10	10

[a] Energy requirements for antler growth and fat and protein accretion are contrasted as a percent of the basal metabolic rate (BMR), as are the percentage of dietary energy, protein, calcium and phosphorus incorporated into the antler. Finally, the percent of antler calcium and phosphorus that is predicted to be resorbed from the skeleton is given for each species.

of about 44 kg of nitrogen ingested during the period when antlers are metabolically active (Table 2). More than 90% of the ingested nitrogen is excreted in either feces or urine in summer.

Calcium requirements

Moose deposit 5.7 kg of calcium in their 30 kg antlers and Irish elk deposited 7.6 kg of calcium in their 40 kg antlers. Irish elk incorporated just over 30% of ingested calcium into antlers (Table 2). The model predicts that Irish elk deposited more than 60 g of calcium per day into antlers for about 60 days in the middle of antler growth (Fig. 2a). Peak deposition was 102 g calcium in a single day for Irish elk during the Younger Dryas, and 93 g in a single day for Irish elk in the Allerod. Dietary calcium intake increased greatly after a switch from dormant vegetation to green vegetation at the beginning of the plant growing season (Fig. 2a). However, dietary intake was insufficient to support antler growth in both moose and Irish elk. Therefore, 5–7% of calcium in the antlers is from bone resorption (Table 2). About 39% of available calcium was resorbed from the skeleton in moose under current growing conditions, and about 81% of available calcium was resorbed from Younger Dryas Irish elk at the peak of resorption (Fig. 2a). By the end of antler growth, moose and Allerod Irish elk had completely restored skeletal calcium reserves, and Younger Dryas Irish elk had almost restored their calcium reserves.
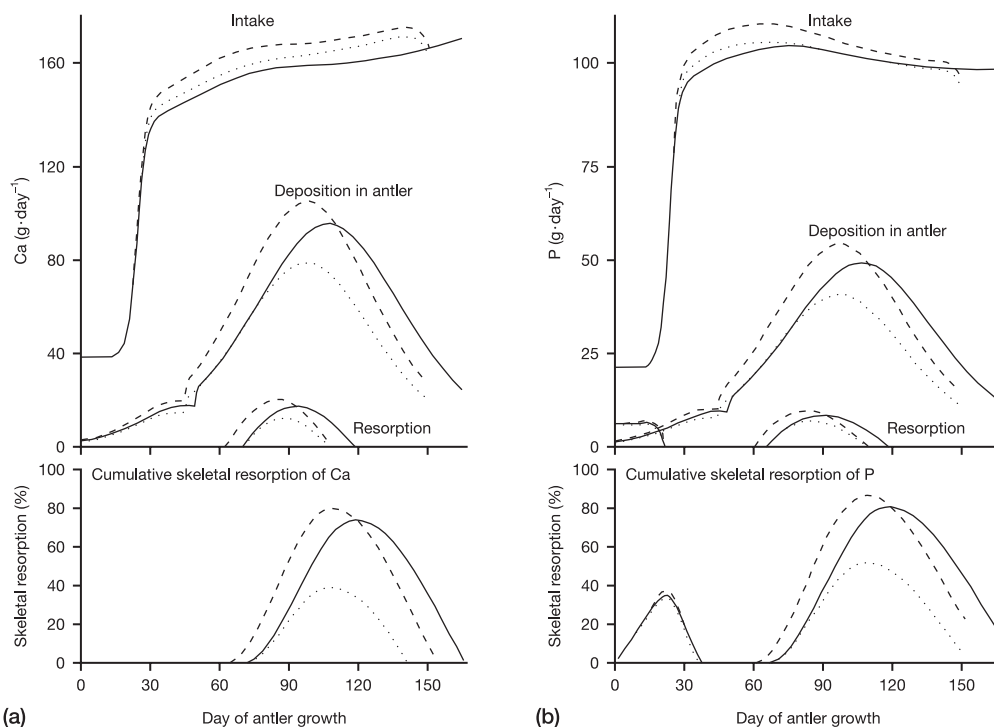
Fig. 2. (a) Simulated calcium (Ca) intake and predicted calcium incorporated into antlers, calcium resorption from skeleton and skeletal calcium resorption during antler growth for current-day moose (dotted lines) and Irish elk during climatic conditions corresponding to the Allerod (solid lines) and the Younger Dryas (dashed lines). (b) Simulated phosphorus (P) intake and predicted phosphorus incorporated into antlers, phosphorus resorption from skeleton and skeletal phosphorus resorption during antler growth for current-day moose (dotted lines) and Irish elk during climatic conditions corresponding to the Allerod (solid lines) and the Younger Dryas (dashed lines). Each species began the summer with bones 100% replete and resorption occurred when dietary intake was insufficient to meet requirements for antler growth. For initial conditions, see text and Table 1.

Phosphorus requirements

Moose deposit 2.8 kg of phosphorus into their 30 kg antlers and Irish elk deposit 3.8 kg of phosphorus into their 40 kg antlers each year. Dietary phosphorus intake increased greatly at the beginning of the plant growing season, and then declined slightly over the summer because the concentration of phosphorus in forage declined (Fig. 2b). Phosphorus requirements for antler deposition peak in mid- to late-summer. Irish elk deposited more than 30 g of phosphorus per day into antlers for about 60 days during the middle of antler growth. Peak deposition was 51 g phosphorus in a single day for Younger Dryas Irish elk, and 46 g in a single day for Allerod Irish elk (Fig. 2b). About 25% of phosphorus ingested during the antler growing season was incorporated into the antler in Irish elk, and about 20% in the extant moose (Table 2). Because peak phosphorus requirements for antler mineralization occurred during the middle of antler growth, and because all ingested phosphorus could not be absorbed across the gut wall, dietary intake of
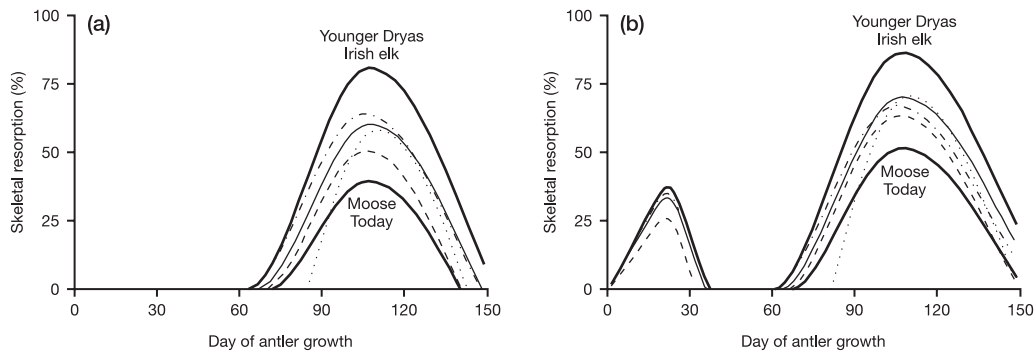
Fig. 3. Effect of hypothesized adaptations on skeletal depletion of (a) calcium and (b) phosphorus during antler growth in Irish elk. The Younger Dryas Irish elk and the current-day moose (bold lines) are shown as a standard for comparison. Dotted and dashed lines, extraction efficiency; thin solid lines, body mass; dashed lines, diet calcium and phosphorus concentration; dotted lines, bone density.

phosphorus was insufficient and skeletal minerals were incorporated into the antler. About 10% of phosphorus in the antlers is from bone resorption (Table 2). At peak resorption of phosphorus from the skeleton, 51% of available phosphorus in extant moose and 85% in the Younger Dryas Irish elk was resorbed from the skeleton (Fig. 2b). By the end of antler growth, the moose had almost completely restored its phosphorus reserves, while Irish elk still had a deficit of 20–25% of the skeletal pool of available phosphorus to be restored.

The model predicts a 21 day period of phosphorus resorption early in the antler growing season before plants begin to grow. The deficit is made up in early summer before peak mineral requirements in the middle of antler growth (Fig. 2b). The existence of this negative phosphorus balance in live animals will depend on whether or not initiation of antler growth is synchronized with spring green-up. If antler growth is delayed until spring green-up, as suggested for moose (Van Ballenberghe, 1982), this period of negative phosphorus balance may be reduced. However, a consequence of delaying antler growth is that peak demand for calcium and phosphorus during antler mineralization would increase.

Adaptations to reduce resorption

The model predicts that skeletons of Irish elk in the Younger Dryas were not fully mineralized at the end of antler growth if they grew 40 kg antlers. Each adaptation we simulated in this section is a possible compensatory mechanism to reduce skeletal resorption of calcium and phosphorus during antler growth. These adaptations may also have been present in Allerod Irish elk. None of the adaptations were as effective in reducing resorption as decreasing antler mass to 30 kg, the antler mass of extant moose (Fig. 3). Increasing dietary concentrations of calcium and phosphorus, a behavioural mechanism, decreased resorption more than any other adaptation tested. Resorption from the skeleton decreased from about 80% to about 50% of the available calcium, and from 85% to 60% of the available phosphorus, when dietary concentrations of calcium and phosphorus were increased (Fig. 3).

Increasing the fraction of ash in the lean body mass provided an additional source of calcium and phosphorus during peak mineralization. Even though we assumed that the new

Table 3. Effects of digestible energy intake, efficiency of energy use for antler growth and maximum skeletal resorption on antler mass, body mass and skeletal depletion at the end of antler growth[a]

Factor	F-value	Low mean	High mean
Antler mass (kg)			
digestible energy intake	$F_{6,209} = 31283$	36	46
efficiency of energy use for antler growth	$F_{5,209} = 1028$	40	42
maximum skeletal resorption	$F_{4,209} = 1858$	40	42
Body mass (kg)			
digestible energy intake	$F_{6,209} = 3417$	567	630
efficiency of energy use for antler growth	$F_{5,209} = 3595$	564	621
maximum skeletal resorption	$F_{4,209} = 56$	595	601
Skeletal phosphorus resorption (%)			
digestible energy intake	$F_{6,209} = 7432$	17	30
efficiency of energy use for antler growth	$F_{5,209} = 663$	22	26
maximum skeletal resorption	$F_{4,209} = 61293$	9	37

[a] The analyses of variance were highly significant ($P < 0.001$) for each factor. The low and high means for each factor level are an indication of how important that factor was in determining antler mass, body mass and skeletal depletion.

calcium and phosphorus had no structural purpose, peak resorption of the two minerals was still greater than in moose (Fig. 3). It is unlikely that a small increase in bone density resulting from this increased ash content would be sufficient to meet peak mineralization requirements, because only 5–10% of calcium and phosphorus in antlers is resorbed from the skeleton (Table 2). However, increasing bone density did provide a biologically significant benefit. Resorption of structural calcium and phosphorus began about 20 days later when bone density was increased (Fig. 3). More importantly, at the end of antler growth, just prior to the rut, structural calcium and phosphorus in the skeleton were completely restored.

Sensitivity analysis

Antler mass, body mass and skeletal depletion at the end of antler growth in the Younger Dryas Irish elk were all affected by the factors varied in the sensitivity analysis with $P < 0.001$ for each factor (Table 3). The factor which most affected antler mass was digestible energy intake. Mean antler mass was 36 kg when digestible energy intake was $1.36 \, MJ \cdot kg^{-0.75} \cdot day^{-1}$ and 46 kg when digestible energy intake was $1.45 \, MJ \cdot kg^{-0.75} \cdot day^{-1}$. In contrast, mean antler mass only differed by 2 kg between low and high factor levels for both the efficiency of energy use for antler growth and the maximum skeletal resorption allowed.

Final body mass was affected by both digestible energy intake and efficiency of energy use for antler growth. At low digestible energy intake and at low efficiency of energy use for antler growth, the mean body mass was about 565 kg; at high digestible energy intake and high efficiency of energy use for antler growth, mean body mass was 625 kg. The efficiency of energy use for antler growth affected body mass because energy was partitioned to either antlers or protein and fat accretion. When the efficiency of energy use for antler growth increased, more energy was available for fat and protein accretion, and pre-rut body mass increased. Digestible energy intake affected body mass because, at higher
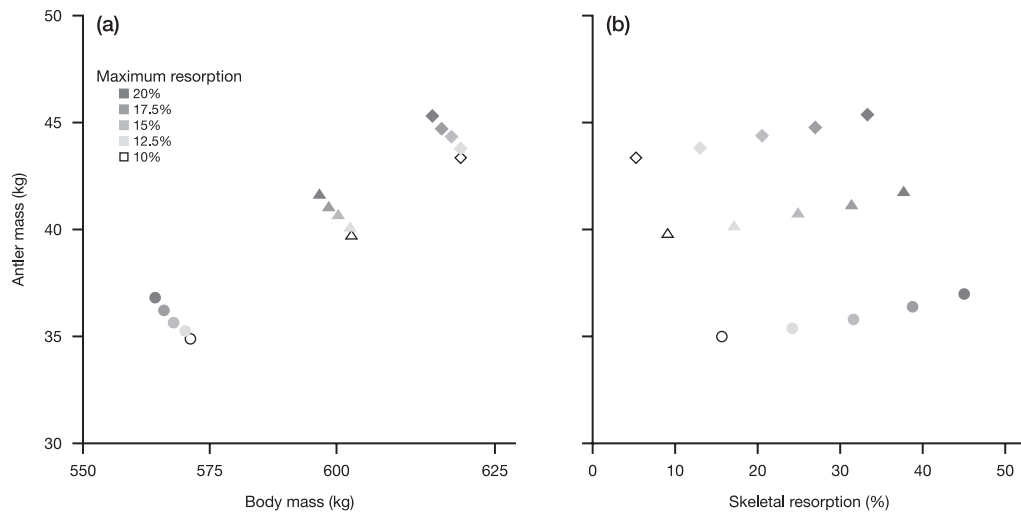
Fig. 4. Maximum antler mass predicted by the simulation model at three levels of digestible energy intake ($\diamond = 1.46$, $\triangle = 1.38$ and $\bigcirc = 1.26\ \mathrm{MJ \cdot kg^{-0.75} \cdot day^{-1}}$) and five levels of maximum skeletal reserves available for resorption (20, 17.5, 15, 12.5 and 10%). Efficiency of energy use for antler growth was fixed at 30%. Antler mass increased as additional skeletal reserves were made available at each digestible energy intake level. A consequence of the increase in antler mass was (a) a decrease in body mass at the end of antler growth and (b) an increase in skeletal mineral depletion at the end of antler growth.

digestible energy intake levels, more energy was available for both antler growth and protein and fat accretion.

Skeletal depletion at the end of antler growth (and the beginning of the rut) was most affected by the maximum allowed resorption. Mean depletion was 9% at the lowest factor level of allowing 10% of skeletal minerals to be resorbed, and mean depletion was 37% of available phosphorus at the highest factor level of allowing 20% of skeletal minerals to be resorbed. The absolute amount of depletion at peak mineralization is the determinant of pre-rut skeletal repletion. When 20% of the skeleton is resorbed, it is not possible for the simulated animal to make up this deficit in the approximately 30 days at the end of antler growth when mineral balance is positive. In contrast, when 10% of skeletal mass is available to be resorbed, the absolute size of the deficit is smaller and the simulated animal could almost make up the deficit with dietary intake before the end of antler growth.

The relationships among antler mass, body mass and skeletal resorption illuminate a dilemma faced by male Irish elk, and probably by other male cervids as well. Digestible energy intake was most important in determining final antler mass, suggesting that male Irish elk should eat as much as possible each day in summer. However, energy must be allocated either to antlers or to body fat and protein accretion. At a fixed digestible energy intake level, increasing antler mass resulted in a lower body mass (Fig. 4a) and a more depleted skeleton (Fig. 4b).

DISCUSSION

Irish elk faced the largest physiological challenge in calcium and phosphorus metabolism of any cervid because they grew antlers as large as expected from the allometric relationship

between body size and antler size (Gould, 1974; Geist, 1987). Although the large size of antlers in Irish elk has traditionally been a focal point for investigations, the results of the model illustrate how body mass and skeletal repletion are physiologically linked to antler mass. A consequence of increasing antler mass was a reduced body mass and a skeleton depleted of minerals because energy was diverted from fat and protein accretion to antler growth. In extant red deer (*Cervus elaphus*), body mass and antler mass are both correlated with success in dominance fights during the rut (Clutton-Brock and Albon, 1980). The orientation of hydroxyapatite crystals in Irish elk antlers indicates that bulls fought to establish dominance during the rut (Kitchener, 1987; Kitchener *et al.*, 1994). Furthermore, a depleted skeleton could lead to brittle bones that would be more easily broken when fighting with other males during the rut. The high incidence of fractured ribs and scapulas in male moose today may in part be explained by a seasonal osteoporotic condition induced by antler growth (Bubenik, 1998). If the depletion of bone calcium and phosphorus was not replenished from the fall and winter diet before antler growth in the following year, the resorption could lead to permanent osteoporosis or reduced antler growth, either of which would be likely to reduce the genetic fitness of affected individuals.

The maximum antler mass predicted by the model under Younger Dryas growing conditions was similar to Irish elk antlers that have been found on the assumption that skull mass is 2 kg (Gould, 1974). Antler masses predicted at higher energy intakes in the sensitivity analysis would correspond to antler masses of Irish elk during the Allerod. Some predicted antler masses were heavier than the largest antlers found to date, but any estimates of maximum antler size from the fossil record are subject to severe sampling problems (Guthrie, 1984).

The sensitivity analysis indicated that antler mass was most strongly affected by energy intake (Table 3). This relationship is supported by antler growth in extant cervids. The largest antlers in caribou (*Rangifer tarandus*) are grown in maritime climates, especially in years with long plant growing seasons (Bergerud, 1976; Geist, 1987). At a fixed daily energy intake, heavier antlers could be grown if forages were selected for mineral content rather than energy content, if alternative sources of calcium or phosphorus were available, or if mineralization rate was increased early in antler growth. Phosphorus is more likely to limit antler growth than calcium because plants move phosphorus from leaves to shoots and roots later in the growing season, whereas calcium concentrations in leaves remain constant or increase (Shaver and Chapin, 1991).

The closest modern analogue to the *Salix auritica–S. phylicifolia*–graminoid habitat of the Irish elk during the Allerod that has been studied is the 1–2 m tall *S. pulchra*–graminoid tundra in riverine environments (Shaver and Chapin, 1991). Annual phosphorus and calcium uptake rates in this modern analogue are 2.7 kg phosphorus per ha and 21.2 kg calcium per ha (Shaver and Chapin, 1991). Large herbivores typically consume ≤10% of net above-ground primary production (NAPP) in northern ecosystems (Jefferies *et al.*, 1994). To deposit 3.8 kg phosphorus and 7.6 kg calcium in 40 kg antlers, a single male Irish elk consuming 5% of NAPP with an extraction efficiency of 50% would consume the NAPP from 56 and 14 ha of modern shrub tundra analogue solely to supply antler requirements for phosphorus and calcium, respectively. When the vegetation changed during the Younger Dryas, the new dwarf willow community would cycle even less phosphorus and calcium than a *S. pulchra* community (Shaver and Chapin, 1991), forcing Irish elk to range over even larger areas or browse local areas more heavily to acquire sufficient energy and minerals for antler growth. Browsing over larger areas would have increased the energy cost of foraging,

reducing energy available for antler growth and protein and fat deposition. Heavy browsing locally could have decreased food supplies in subsequent years through concentration of phosphorus in antlers and export of phosphorus from the summer ranges when antlers were dropped in wintering areas.

As the vegetation changed, the sexual selection pressures for larger antlers and larger body size were opposed by selection pressures for smaller antlers and smaller body size imposed on Irish elk by environmental change. The rate of change in the environment was apparently sufficiently great that Irish elk could not decrease antler size fast enough to meet mass balance constraints of nutrient availability and at the same time meet the sexual selection requirements for large antlers. We suggest that the inability to balance these opposing selection pressures in the face of rapid environmental change contributed to extinction of the Irish elk about 10,000 years B.P. If nutritional limitations contributed to extinction of Irish elk, we would expect that a smaller cervid, such as caribou, would survive longer because of lower requirements for antler growth and maintenance (Moen and Pastor, 1998a,b). Caribou bones have been dated to at least 200 years after the last Irish elk bone date (Woodman *et al.*, 1997). Although this supports our hypothesis, the fossil record is not complete enough to confirm that caribou survived in Ireland throughout the entire Younger Dryas (Woodman *et al.*, 1997).

It may also be possible to test for mineral limitation by searching for histological evidence of osteoporosis and measuring the calcium and phosphorus content of bones and antlers in museum species of Irish elk. Museum bones are from animals that died at the end of winter and not in summer when antlers are growing (Barnosky, 1985). If low levels of calcium and phosphorus and osteoporosis pits persist through late winter during the Younger Dryas but are not present in Irish elk bones from the Allerod, this would support the idea of seasonal physiological osteoporosis (Banks *et al.*, 1968) gradually being supplanted by permanent osteoporosis. If osteoporosis pits are not present in Irish elk bones, but are present in extant moose, this would suggest that some aspect of mineral metabolism in Irish elk was different from mineral metabolism in extant cervids.

Although further model development and analysis of museum specimens is needed, we believe that nutritional physiology of cervids is sufficiently well understood that it is possible to make quantitative predictions of the physiological requirements for antler growth in Irish elk. The ultimate cause of extinction of the Irish elk may well have been the adaptations for mineral metabolism that were beneficial to Irish elk until vegetation changed, at which time these adaptations became a double-edged sword which contributed to its extinction.

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REFERENCES

Agricultural Research Council. 1980. *The Nutrient Requirements on Ruminant Livestock*. Slough, UK: Commonwealth Agricultural Bureau.

Ahlberg, K., Almgren, E., Wright, H.E., Ito, E. and Hobbie, S. 1996. Oxygen isotope record of late glacial climatic change in western Ireland. *Boreas*, **25**: 257–267.

Banks, W.J., Epling, G.P., Kainer, R.A. and Davis, R.W. 1968. Antler growth and osteoporosis. II. Gravimetric and chemical changes in the coastal compacta during the antler growth cycle. *Anatomical Record*, **162**: 399–405.

Barnosky, A.D. 1985. Taphonomy and herd structure of the extinct Irish elk, *Megaloceros giganteus*. *Science*, **228**: 340–344.

Barnosky, A.D. 1986. Big game extinction caused by late Pleistocene climatic change: Irish elk (*Megaloceros giganteus*) in Ireland. *Quat. Res.*, **25**: 128–135.

Berger, A.L. 1978. Long-term variations of caloric solar radiation resulting from the earth's orbital elements. *Quat. Res.*, **9**: 139–167.

Berger, A.L. 1992. Astronomical theory of paleoclimates and the last glacial–interglacial cycle. *Quat. Sci. Rev.*, **11**: 571–581.

Bergerud, A.T. 1976. The annual antler cycle in Newfoundland caribou. *Can. Field Nat.*, **90**: 449–463.

Braithwaite, G.D. 1983. Calcium and phosphorus requirements of the ewe during pregnancy and lactation. I. Calcium. *Br. J. Nutr.*, **50**: 711–722.

Bubenik, A.B. 1998. Evolution, taxonomy, and morphophysiology. In *Ecology and Management of the North American Moose* (A.W. Franzmann and C.C. Schwartz, eds), pp. 77–123. Washington, DC: Smithsonian Institution Press.

Buckwalter, J.A., Glimcher, M.J., Cooper, R.R. and Recker, R. 1995. Bone biology: Part II. Formation, form, modeling, remodeling and regulation of cell function. *J. Bone Joint Surg.*, **77A**: 1256–1289.

Chapin, F.S., III. 1980. The mineral nutrition of wild plants. *Ann. Rev. Ecol. Syst.*, **11**: 233–260.

Chapin, F.S., III, Shaver, G.R. and Kedrowski, R.A. 1986. Environmental controls over carbon, nitrogen, and phosphorus fractions in *Eriophorum vaginatum* in Alaskan tussock tundra. *J. Ecol.*, **74**: 167–195.

Chapman, D.I. 1975. Antlers – bones of contention. *Mammal Rev.*, **5**: 121–172.

Chase, L.A., Studier, E.H. and Thorisson, S. 1994. Aspects of nitrogen and mineral nutrition in Icelandic reindeer, *Rangifer tarandus*. *Comp. Biochem. Physiol.*, **109B**: 63–73.

Clutton-Brock, T.H. 1982. The functions of antlers. *Behaviour*, **79**: 108–125.

Clutton-Brock, T.H. and Albon, D.S. 1980. Antlers, body size and breeding group size in the Cervidae. *Nature*, **285**: 565–567.

Coope, G.R. 1973. The ancient world of '*Megaceros*'. *Deer*, **2**: 974–977.

Franzmann, A.W., LeResche, R.E., Rausch, R.A. and Oldemeyer, J.L. 1978. Alaskan moose measurements and weights and measurement–weight relationships. *Can. J. Zool.*, **56**: 298–306.

Geist, V. 1987. On the evolution of optical signals in deer: A preliminary analysis. In *Biology and Management of the Cervidae* (C.M. Wemmer, ed.), pp. 235–255. Washington, DC: Smithsonian Institution Press.

Gillingham, M.P. and Bunnell, F.L. 1985. Foraging behaviour: Dynamics of dining out. In *Bioenergetics of Wild Herbivores* (R.J. Hudson and R.G. White, eds), pp. 53–79. Boca Raton, FL: CRC Press.

Goss, R.J. 1983. *Deer Antlers: Regeneration, Function, and Evolution*. New York: Academic Press.

Goss, R.J. 1995. Future directions in antler research. *Anatomical Record*, **241**: 291–302.

Gould, S.J. 1974. The origin and function of 'bizarre' structures: Antler size and skull size in the 'Irish elk', *Megaloceros giganteus*. *Evolution*, **28**: 191–220.

Grasman, B.T. and Hellgren, E.C. 1993. Phosphorus nutrition in white-tailed deer: Nutrient balance, physiological responses, and antler growth. *Ecology*, **74**: 2279–2296.

Guthrie, R.D. 1984. Alaskan megabucks, megabulls, and megarams: The issue of Pleistocene gigantism. In *Contributions in Quaternary Vertebrate Paleontology: A Volume in Memorial to John E. Guilday* (H.H. Genoways and M.R. Dawson, eds), pp. 482–510. Special Publication No. 8. Pittsburgh, PA: Carnegie Museum of Natural History.

Heaney, R.P. 1990. Calcium. In *Calcium Metabolism*, Vol. 4 (J.A. Kanis, ed.), pp. 28–54. Basel: Karger.

Hudson, R.J. and White, R.G. 1985. *Bioenergetics of Wild Herbivores*. Boca Raton, FL: CRC Press.

Jefferies, R.L., Klein, D.R. and Shaver, G.R. 1994. Vertebrate herbivores and northern plant communities: Reciprocal influences and responses. *Oikos*, **71**: 193–206.

Kitchener, A. 1987. Fighting behaviour of the extinct Irish elk. *Mod. Geol.*, **11**: 1–28.

Kitchener, A.C., Bacon, G.E. and Vincent, J.F.V. 1994. Orientation in antler bone and the expected stress distribution, studied by neutron diffraction. *Biometrics*, **2**: 297–307.

Kubota, J. 1974. Mineral composition of browse plants for moose. *Nat. Can.*, **101**: 291–305.

Lister, A.M. 1994. The evolution of the giant deer, *Megaloceros giganteus* (Blumenbach). *Zool. J. Linn. Soc.*, **112**: 65–100.

Mitchell, G.F. and Parkes, H.M. 1949. The giant deer in Ireland. *Proc. Roy. Irish Acad.*, **52B**: 291–314.

Moen, A.N. 1978. Seasonal changes in heart rates, activity, metabolism, and forage intake of white-tailed deer. *J. Wildl. Manage.*, **42**: 715–738.

Moen, R.A. and DelGuidice, G.D. 1997. Simulating nitrogen metabolism and urinary urea nitrogen: Creatinine ratios in ruminants. *J. Wildl. Manage.*, **61**: 881–894.

Moen, R.A. and Pastor, J. 1998a. A model to predict nutritional requirements for antler growth in moose. *Alces*, **34**: 59–74.

Moen, R.A. and Pastor, J. 1998b. Simulating antler growth and energy, nitrogen, calcium, and phosphorus metabolism in caribou. *Rangifer Spec. Issue*, **10**: 85–97.

Moen, R.A., Pastor, J. and Cohen, Y. 1997. A spatially explicit model of moose foraging and energetics. *Ecology*, **78**: 505–521.

Muir, P.D., Sykes, A.R. and Barrell, G.K. 1987. Calcium metabolism in red deer (*Cervus elaphus*) offered herbages during antlerogenesis: Kinetic and stable balance studies. *J. Agric. Sci.*, **109**: 357–364.

Oldemeyer, J.L., Franzmann, A.W., Brundage, A.L., Arneson, P.D. and Flynn, A. 1977. Browse quality and the Kenai moose population. *J. Wildl. Manage.*, **41**: 533–542.

Parfitt, A.M. 1981. Integration of skeletal and mineral homeostasis. In *Osteoporosis* (H.F. De Luca, H.M. Frost, W.S.S. Jee, C.C. Johnson Jr. and A.M. Parfitt, eds), pp. 115–126. Baltimore, MD: University Park Press.

Schwartz, C.C., Regelin, W.L. and Franzmann, A.W. 1987. Seasonal weight dynamics of moose. *Swedish Wildl. Res.*, **1** (suppl.): 301–310.

Shaver, G.R. and Chapin, F.S., III. 1991. Production: Biomass relationships and elemental cycling in contrasting Arctic vegetation types. *Ecol. Monogr.*, **61**: 1–31.

Smith D.M., Khairi, M.R.A. and Johnston, C.C., Jr. 1975. The loss of bone mineral with aging and its relationship to risk of fracture. *J. Clin. Invest.*, **56**: 311–318.

Staaland, H. and Saebo, S. 1993. Forage diversity and nutrient supply of reindeer. *Rangifer*, **13**: 169–177.

Staaland, H., Brattbakk, I., Ekern, K. and Kildemo, K. 1983. Chemical composition of reindeer forage plants in Svalbard and Norway. *Holarctic Ecol.*, **6**: 109–122.

Stephenson, D.C. and Brown, R.D. 1984. Calcium kinetics in white-tailed deer. *J. Nutr.*, **114**: 1014–1024.

Stuart, A.W. 1991. Mammalian extinctions in the late Pleistocene of northern Eurasia and North America. *Biol. Rev.*, **66**: 453–562.

Tataruch, F. and Wolfsperger, M. 1995. Chemical analyses of the antlers of prehistoric red deer and giant elk. *Zeitschrift für Jagdwissenschaft*, **41**: 225–228.

Van Ballenberghe, V. 1982. Growth and development of moose antlers in Alaska. In *Antler Development in Cervidae* (R.D. Brown, ed.), pp. 37–48. Kingsville, TX: Caesar Kleberg Wildlife Research Institute.

Woodman, P., McCarthy, M. and Monaghan, N. 1997. The Irish quaternary fauna project. *Quat. Sci. Rev.*, **16**: 129–159.