



Getting to the hart of the matter: did antlers truly cause the extinction of the Irish elk?

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The extinction of the Irish elk *Megaloceros giganteus* has traditionally thought to have been caused in one way or another by the enormous antlers of the males. Recently, a popular hypothesis for the Irish elk extinction has been their inability to cope with the nutritional demands of growing such large antlers during worsening habitat conditions. However, this hypothesis is weakened by several previously unaddressed and biologically unreasonable assumptions. We discuss these assumptions and conclude that, because antler mass is expected to have been evolutionarily labile, nutritionally sensitive, and ontogenetically variable and male mortality is expected to have had limited impact on population growth, the large antlers of Irish elk probably had little to do with the extinction. We focus on the reproductive energetics of females as a possible contributor to extinction, and model the nutritional demands of producing precocial cursorial young. Our model shows the reproductive output of females being reduced by 50% due to changes in the length of the growing season at the end of the Pleistocene when most populations of Irish elk went extinct. The model was validated with parameters from the extant wapiti, which was predicted to maintain high levels of reproduction during the Pleistocene climatic deterioration. Thus, nutritional stress on reproductive females is likely to have contributed more to the Irish elk extinction than nutritional stress on large-antlered males.

For millennia, the antlers of the great Irish elk *Megaloceros giganteus* have inspired admiration. With prime specimens spanning over 3.6 m and weighing almost 40 kg, they are the largest antlers ever grown (Gould 1974). The antlers were depicted in cave paintings, graced the halls of medieval castles, and have been at the forefront in debates about evolution, extinction, allometry and sexual selection (Gould 1974). Almost all discussions of *M. giganteus* postulate that their extinction was a result of the antlers of the stags being too large, with recent papers suggesting that the stags were unable to deal with the deteriorating climate at the end of the Pleistocene due to the nutritional requirements of rapid antler growth (Barnosky 1986, Moen et al. 1999, Pastor and Moen 2004). The idea that immense antlers caused the extinction of the Irish elk is prevalent in both scientific and popular circles (Stuart 1991, Caro et al. 2003, Kokko and Brooks 2003, Stuart et al. 2004); however, it ignores the role females play in population dynamics (Geist 1998). We argue that the assumptions underlying the hypothesis that Irish elk went extinct because of large antlers are biologically frail and build a model to examine the role female Irish elk reproductive energetics may have played in the extinction.

Weaknesses of the antler-extinction hypothesis

The total range of the Irish elk encompassed Ireland in the west, Lake Baikal in the east, and a broad swath of Eurasia in between (Lister 1994). The portion of this range that was occupied at any given time appears to have been primarily determined by the extent of the grass-shrub and woodland vegetation preferred by the Irish elk. For example, during the Last Glacial Maximum, shrubby woodland habitats shrunk in extent resulting in a corresponding reduction in the range of the Irish elk (Stuart et al. 2004). An exception to this general pattern, however, occurred during the early Last Glacial Interstadial when southern Europe was reinvaded by shrubby woodland vegetation without being reinvaded by the Irish elk, possibly due to relatively high densities of humans in southern Europe (Stuart et al. 2004).

A similar sharp reduction in diverse nutrient-rich shrubby woodland habitats and an increase in more open habits occurred during the large climatic fluctuations at the end of the Pleistocene (Stuart 1991). The loss of most populations of Irish elk at this time, as well as the close association of the earlier Irish elk range with such habitats, supports the idea that habitat change was likely a main driver behind the extinction of the Irish elk. High nutrient

intake at certain times of the year is necessary to support the maximal growth of antlers (Moen et al. 1999); hence the current hypothesis that excessive antler size led to the extinction of the Irish elk. However, this hypothesis has four intrinsic weaknesses that have not been addressed thus far in the literature.

The first weakness is an assumption that the Irish elk could not evolve smaller antlers fast enough to avoid extinction. Sexually selected traits, however, are generally highly variable (Darwin 1859), have higher additive genetic variation than other traits (Pomiankowski and Møller 1995) and appear to be evolutionarily labile (Hegyi et al. 2006) with losses being common (Weins 2001). Gould's (1974) data show that the antlers of Irish elk were consistent with this general pattern, as antler measurements of mature adults have higher coefficients of variation (mean = 14.69, range: 8.39–31.46) than non-sexual skull measurements (mean = 2.93, range: 2.62–3.23), with age-dependent characters (height of the second molar and pedicel height) having intermediate coefficients of variation (mean = 9.38, range: 7.20–11.38).

A large part of this variation in antler measurements was probably genetic. Extant deer species have high coefficients of additive genetic variation (CV_A) for antler mass (red deer: 15.1 (Kruuk et al. 2002); white-tailed deer: 18.6 (Pomiankowski and Møller 1995)), consistent with an increased mean CV_A for sexually selected traits in a taxonomically diverse selection of animals (sexually selected traits: 16.9; non-sexually selected traits: 4.8 Pomiankowski and Møller 1995). Therefore, Irish elk populations in nutritionally poor conditions may have been able to respond relatively quickly to selection for smaller antlers.

The apparent inability of red deer *Cervus elaphus* to respond to selection for larger antler size found by Kruuk et al. (2002) does not imply an inability of that trait to evolve smaller sizes. Kruuk et al. (2002) concluded that their findings were possibly due to an environmental covariance between antler size and an unmeasured trait that was under selective pressure. In other words, antler size only appeared to be related to fitness because the expression of antler size was increased or decreased by environmental conditions in a similar way to that of the unmeasured trait that was actually related to fitness. If this is the case for the system of Kruuk et al. (2002) at the time of their study, it does not imply that antlers are generally free from selection as antler loss has important reproductive consequences (Lincoln 1992). Furthermore, the presence of large and expensive secondary sexual characteristics must be maintained by selection. With selection for increased size in a character, eventually the limit to what is possible will be reached given metabolic, nutritional, and ecological costs. The inability to evolve a larger trait in the face of these costs is not surprising. However, the inability to evolve a reduced trait given genetic variation and increased costs would be surprising, especially when the benefits of a trait are determined not by absolute size but by size relative to that of competitors.

Lister (1989) describes a population of red deer that experienced rapid evolution of extremely reduced body size when their formerly continental range became a predator-free island. Linear measures of body size (limb bone diameters) were reduced to 56% of that of their mainland contemporaries, indicating that insular body mass dropped

to 1/6th of the mainland body mass. A linear measure of antler size (basal circumference), however, was reduced even further to 41% of the mainland mean. Because basal circumference is highly correlated with other linear measures of antler size (Bartoš and Bahbouh 2006), such a decrease indicates that insular antler mass dropped to 1/14th of the mainland antler mass. This reduction in antler mass is 2.7 times more extreme than expected given the allometric relationship between antler and body masses in red deer (Gould 1974) and demonstrates a rapid evolution of smaller antlers. A similar change in a typical Irish elk population with prime stags having 35 kg antlers (Barnosky 1986) would result in antler weights of 13 kg or less in worsening climatic conditions. This estimate is within the range of extant wapiti/red deer (*Cervus* spp.) antler weights (Geist 1998). It has been noted that Irish elk stags in more adverse environments had smaller bodies and relatively even smaller antlers (Barnosky 1985, Moen et al. 1999), but proponents of the antler-extinction hypothesis have not addressed the possibility of rapid evolutionary reduction in antler size. We expect that the antlers of the Irish elk should have been able to evolve rapidly in the face of selection for smaller and less expensive sizes. This conclusion is supported by the great diversity of Irish elk antler forms found among different populations at different times, including compact upright orientations possibly from populations inhabiting more heavily wooded environments (Lister 1994) suggesting the evolutionary malleability of Irish elk antlers.

The second implicit weakness of the antler-extinction hypothesis is an assumption that the antlers were not phenotypically plastic enough to avoid extinction. Cervid antlers are tissues of low growth priority and are therefore sensitive to nutritional status (Bubenik 1982, Gore 1982, Jacobson and Griffin 1982, Suttie and Kay 1982, Ullrey 1982, Verme and Ullrey 1984). Clutton-Brock et al. (1985) reported antler mass of mature red deer stags decreasing 29% in response to an increase in population density and a corresponding decrease in habitat quality. In a different population of red deer, supplementary feeding doubled the antler weight of the stags (Putnam and Staines 2004). Because antlers are regrown yearly, the rate of response to worsening conditions due to phenotypic plasticity is expected to be faster than that of traits that are grown once in an individual's lifetime.

If the Irish elk responded to nutritional restriction as red deer do, a huge and well-fed stag with 40 kg antlers (the near maximal size; Gould 1974, Moen et al. 1999) would have had 20 to 28 kg antlers under poor conditions. These estimates are within the range of extant moose *Alces alces* antlers (Geist 1998). More typical prime stags with 35 kg antlers (Barnosky 1986) would have had 18 to 25 kg antlers in times of nutritional stress. These estimates overlap the range of antler weights of extant wapiti/red deer (*Cervus* spp.) (Geist 1998). While it is recognized that Irish elk stags in unfavorable environments had smaller bodies and relatively even smaller antlers (Barnosky 1985, Moen et al. 1999) (whether due to evolution or plasticity), the ramifications of phenotypic plasticity for the antler-extinction hypothesis have not been addressed. Because it is likely that Irish elk antlers shared the nutritional sensitivity of antlers of extant species, poor habitat quality would likely

have resulted in Irish elk stags with stunted antlers rather than males committing physiological suicide with unsustainable antler growth.

A third weakness of the antler-extinction hypothesis is the assumption that nutritional restriction would affect all males equally. Young cervids, however, grow small antlers, while older cervids grow larger antlers (Kruuk et al. 2002) (Fig. 1). Thus, even if the Irish elk stags were unable to respond to worsening conditions through either evolution or phenotypic plasticity, or prime stags experienced severe winterkill from the sudden onset of an unusually brutal season, many males would still have been available for breeding as antler size increases ontogenetically. If every stag with antlers above a sustainable size had perished, younger stags, normally excluded from breeding by more mature males, would likely have been available.

Though the mating system of the Irish elk is unknown, the extreme development of sexual dimorphism via the antlers implies that large mating congregations, polygyny, and a combination of female-choice and male-hierarchy with inter- and intra-sexual displays and intra-sexual combat were important for male success (Lister 1994). In such a system, few males actually succeed in breeding and a low male/female ratio is not a barrier to population growth or stability – instead it is often the norm (Georgiadis 1985). Thus, even if it is assumed that all stags with large antlers died in poor habitats, it is probable that the presence of only a few stags with smaller antlers (due to genetics, poor nutrition or age) would have been adequate to fill the mating vacuum left by the deaths of the dominant stags.

A fourth weakness of the antler-extinction hypothesis is that the mechanisms through which increased male mortality could have caused extinction have not been addressed. Increased adult male mortality may indeed have impacts on population growth in some systems. In populations with an extreme male sex bias, males may not be able to produce enough sperm to successfully fertilize all females, especially if most males are juveniles (Myserud et al. 2002).

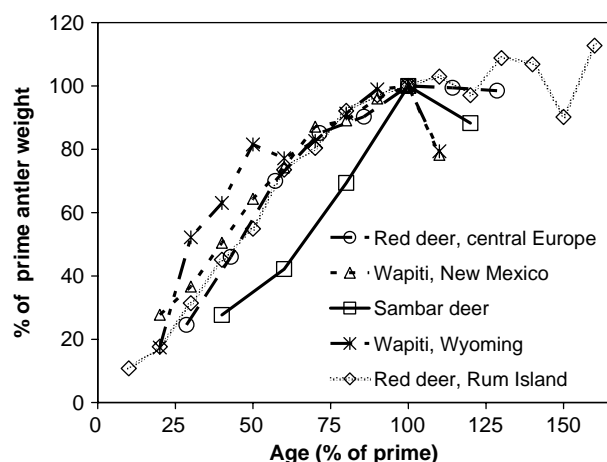


Figure 1. Ontogenetic increases in antler weight of various deer species. 'Prime' is defined as age at highest reproductive success (Rum Island red deer) or, when that was unavailable, age at greatest antler weight (all others). The data are derived from Geist (1998) (red deer, central Europe), Wolfe (1982) (wapiti, New Mexico), Davis (1982) (Sambar deer), Smith (1998) (wapiti, Wyoming) and Kruuk et al. (2002) (red deer, Rum Island).

Additionally, decreased birth synchrony or delayed calving dates, caused by possible dependence of the timing of oestrus or female receptivity on stimulation by multiple or dominant males, may increase the risk of predation and winter-kill (Milner et al. 2007). However, the effect of increased male mortality on population growth is expected to be small in polygynous species, unless mortality is extremely severe (Myserud et al. 2002). This can be seen in the insensitivity of female Saiga antelope fecundity to the proportion of males in rut over a wide range of values until a threshold is met and female fecundity begins to drop (Milner-Gulland et al. 2003). The threshold appears to occur between 0.009 and 0.025 males/female, or about ten times more extreme than found in normal Saiga antelope populations (Milner-Gulland et al. 2003). The severity of this case is due to intense poaching of males and is an artifact of uncontrolled market hunting. Generally, the demographic effects of extremely high male mortality are subtle, evidence of their occurrence is 'somewhat equivocal' and they appear to be unimportant when compared to increased female mortality (Milner et al. 2007).

The potential importance of male mortality on population growth has been suggested in the specific context of trophy or market hunting of males, which increases male mortality only (Myserud et al. 2002, Milner et al. 2007). However, habitat deterioration should affect both males and females. Toigo and Gaillard (2003) have shown that the larger size of males in dimorphic species increases male mortality in poor environmental conditions compared to females. This finding is not unexpected as larger individuals have more mass to maintain and thus higher total metabolic needs. However, mortality is only one side of the coin. In dimorphic cervid species, the smaller females have lower energy and protein needs, while non-reproductive, than males, but have higher demands during gestation and lactation (Barboza and Bowyer 2000). Because of their smaller size, females cannot digest roughage as well as the males and should be more sensitive to a reduction in forage digestibility. Thus, females are likely to respond to deteriorating forage quality by reduced reproductive output before male mortality increases, which in turn should occur before female mortality increases.

The relatively weak effect of male mortality on population growth in cervids can be seen with the modern management tactic of hunting males only. High male mortality has little impact on deer population growth, so male-only hunting often results in overpopulation and nutritional stress (Matschke et al. 1984). Hunting pressure on females, on the other hand, has a greater impact on population viability and can quickly reduce a population below its carrying capacity, as evidenced by improved nutritional status (Mattfeld 1984, Jacobson 1992). Thus, when extant deer population dynamics are modeled, recruitment is generally assumed to depend on female numbers and fecundity, but the male segment of the population is ignored (Albon et al. 1992, Csányi 1992, Nixon and Hansen 1992).

Focusing solely on antler size ignores more likely causes of extinction, as well as the Pleistocene extinctions of most European mammals over 200 kg (Stuart 1991). The Irish elk were unusual in growing such extreme antlers but they were not unusual in going extinct near the end of the

Pleistocene. The antler-extinction hypothesis implies that the Irish elk was particularly vulnerable to extinction because of its antlers. Thus, this hypothesis is further weakened by the observation that *M. giganteus* was one of the last species of the Pleistocene megafauna to go extinct, surviving into the Holocene in one geographic area (Stuart et al. 2004). The sum of these weaknesses encouraged us to look elsewhere for more likely causes of the Irish elk extinction.

Female reproductive strategy

Geist (1998) has shown through analysis of limb proportions and cost of male ornaments that Irish elk were probably the most cursorial of the deer species. Geist (1991) has further linked cursorial lifestyles with the need to produce well-developed and/or well-provisioned young that are able to follow the herd almost immediately. A cursorial strategy implies that female Irish elk needed high-quality forage to produce large precocial young as well as the rich milk needed for their rapid growth and development. During worsening habitat conditions, females would be limited in their ability to produce or maintain young large and healthy enough to keep up with the herd and escape predators (Geist 1991). In extant cervids, ability to produce and nurse living young is strongly tied to the female's nutritional status (Verme and Ullrey 1984, Heydon et al. 1992).

Because of the weaknesses in the antler-driven extinction hypothesis, and the possibility that the high costs of producing cursorial young contributed to the extinction, we modeled the effect of worsening habitat quality on female Irish elk reproductive energetics and success.

Methods

Model description

Our model of Irish elk energetics explores how degraded habitat quality influences the number of offspring a female can produce in her lifetime. We based our simulation of female Irish elk on a model of wapiti *Cervus canadensis* foraging (Turner et al. 1994), but expanded the basic model to include seasonal variation in forage intake (Weber and Thompson 1998), reproduction, and lactation (Moen et al. 1997). We based our model on wapiti foraging because Irish elk probably had a cursorial life-style and diet (Stuart 1991) similar to wapiti; however, the parameters for the Irish elk in our model were estimated allometrically from extant deer species or ecological analogs (Supplementary material Appendix 1). We simulated the daily foraging intake of a single Irish elk female over a reproductive lifespan of 22 years (below). Females were assumed to have a reproductive lifespan of 22 years because males had a total lifespan of around 20 years (Barnosky 1985), and female cervids have longer total lifespans than males (Carranza et al. 2004), including several non-reproductive years near birth and death (Wright et al. 2006).

We focused on climate changes at the end of the Pleistocene when almost all Irish elk populations went extinct, however our hypothesis applies equally well to any

habitat degradation, such as the subtler changes in the Holocene that may have contributed to the extinction of the last remnant population (Stuart et al. 2004). Due to climate change, the growing season decreased considerably at the end of the Pleistocene. During the Allerød interstadial (11 000–12 000 years ago), the plant growing season was approximately 150 days in length, but during the Younger Dryas (11 000 years ago), the growing season was approximately 120 days in length (Moen et al. 1999). The digestibility of plants consumed by deer varies with season, being highest in the early spring, decreasing during the remainder of the plant growing season, and being lowest in the non-growing season (Geist 1998, Moen et al. 1999). Thus, plant digestibility probably played an important role in the yearly energy budget of female Irish elk. The non-growing season, when plant digestibility was at its lowest, was approximately 30 days longer in the Younger Dryas (225 days) than in the Allerød (195 days). We assume a 10 day transitional period at the beginning and end of each growing season in the model. The current length of the non-growing season in moose habitats is about 200–205 days (Moen et al. 1997). We use the low end of the range in the interpretation of the model results because current moose habitats are slightly higher in latitude than Irish elk and current wapiti habitats.

We ran the same model parameterized for extant wapiti (Supplementary material Appendix 1) to compare our Irish elk results with results for a species that survived the Younger Dryas. The reproductive lifespan of wapiti females was defined as the 18 years in which more than 10% of the females reproduced out of a total lifespan of 24 years (Wright et al. 2006).

The need for precocial young and the production of rich milk implies that twins were probably as rare or rarer for the Irish elk as they are in the less cursorial wapiti. Friedel and Hudson (1994) report a ratio of one multiple birth to 271 singletons in farmed wapiti. Thus, we ignored the possibility of twinning in our model.

Model details

The daily forage intake by a female in kilograms (Turner et al. 1993, 1994), I , is equal to the maximum daily foraging rate, FGB , multiplied by the initial female body mass, BM_i , and a feedback term, FB , based on seasonal variation in ungulate foraging (Weber and Thompson 1998). The feedback term was defined as $FB = a + b[\sin(D/58 - c)]$, where a , b and c determine the shape of the function and D is the day of the year (Weber and Thompson 1998). The energy balance, $E_{balance}$, of a female is computed at the end of each simulation day by subtracting energy cost, E_{cost} , from energy gain, E_{gain} . E_{gain} is equal to I times the energy content in forage consumed that day, $ENPK$, which is in turn equal to gross energy in forage, GE , multiplied by in vitro dry matter digestibility, $IVDM$, multiplied by a metabolizable energy coefficient, MC . $IVDM$ varies by season; $IVDM$ therefore differs between the Allerød and the Younger Dryas, and is modeled as in Moen et al. (1999). E_{cost} is equal to the metabolizable energy needed for a zero energy balance, E_{maint} , plus the energy cost of travel, E_{travel} (Turner et al. 1994). E_{maint} is equal to: $E_{maint} =$

$ME(BM^{0.75})$, where ME is the metabolizable energy needed per kilogram of body mass and BM is the current body mass of the female. The cost of travel is calculated as: $E_{\text{travel}} = 2.97(BM^{-0.34})(BM)(S)$. Here, S is the distance traveled. E_{balance} is used to calculate the change in female body mass, BM_{change} , at the end of each simulation day, and is calculated as: $BM_{\text{change}} = [RFATL(E_{\text{balance}}/FATEN)] + [RLBWL(GWP)(E_{\text{balance}}/LEAN)]$. Here, RFATL is the proportion of energy catabolized or anabolized from fat, RLBWL is the proportion catabolized or anabolized from protein, FATEN is the kilojoules per kilogram of fat, LEAN is the kilojoules per kilogram of protein, and GWP is the mass of water per unit mass of protein.

A female mates in a given year if $BM > H(BM_{\text{lean}})$ and reproduces at the beginning of the growing season if $BM > H(BM_{\text{lean}}) + BM_{\text{fetus}}$; where BM_{lean} is the body mass of the female without any fat reserves, BM_{fetus} is the body mass of the offspring, and H is the decision threshold for reproduction. H was calibrated for each species independently so that females would only reproduce if they could do so without dying. If a female does reproduce, her body mass is reduced by BM_{fetus} . Lactating females produce milk according to the equations in Moen et al. (1997). The cost of producing milk, E_{milk} , is added to E_{balance} , and used in calculating BM_{change} . The offspring is assumed to die if producing milk causes the female's body mass to fall below $(0.8)BM_{\text{lean}}$. See Supplementary material Appendix 1 for parameter values and means of estimation.

We performed an uncertainty analysis by running the model 1000 times, randomly choosing each parameter value at the start of each run of the model from a uniform distribution bounded by $+/-10\%$ of the nominal value of the parameter. We then removed unrealistic parameter sets (i.e. the Irish elk or wapiti female either reproduced every year or not at all in both the non-growing season lengths of 185 (10 days shorter than in the Allerød) and 235 days (10 days longer than in the Younger Dryas)). We compared the average number of offspring produced under Allerød and Younger Dryas conditions for both the Irish elk and wapiti.

Results

The decrease in energy intake with increasing non-growing season clearly influenced the lifetime reproductive output of Irish elk females in our model. The average gross energy consumed by a female over the course of a year decreased nearly linearly in our models, corresponding to the decrease in the growing season (Fig. 2a). However the number of offspring produced declined in a step-wise fashion with a decreasing growing season (Fig. 2b). The maximum number of offspring produced by a female Irish elk in our model under Younger Dryas conditions was only 11 compared to 22 offspring in the Allerød.

This contrasts sharply with the results for wapiti parameters. The average gross energy consumed by a female again decreased almost linearly, but less steeply than the average energy intake for the Irish elk (Fig. 2a). The lifetime number of offspring produced remained a constant 18 between the Allerød and the Younger Dryas, dropping off

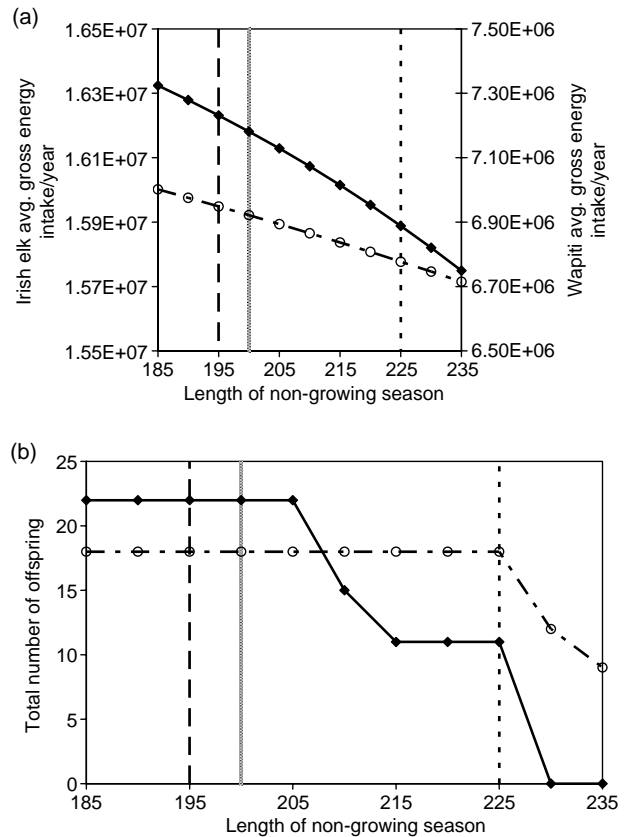


Figure 2. Model results. The length of the non-growing season is indicated by vertical lines: dashed for the Allerød, shaded for the present day, and dotted for the Younger Dryas. Results for Irish elk are indicated by black diamonds with solid lines. Results for wapiti are indicated by empty circles and dashed lines. (a) Average gross energy intake per year in kJ as a function of the length of the non-growing season for both Irish elk and wapiti. (b) Total number of offspring produced by a female during her lifetime as a function of the length of the non-growing season for both Irish elk and wapiti.

only in conditions worse than those of the Younger Dryas (Fig. 2b).

After the unrealistic parameter sets were removed, the sensitivity analysis showed that Irish elk females produced fewer offspring under Younger Dryas than Allerød conditions 73% of the time, and never produced more offspring under Younger Dryas than Allerød conditions. Examining all the realistic parameter sets, an Irish elk female produced an average of 7.2 fewer offspring during her lifetime under Younger Dryas than Allerød conditions. Wapiti females produced fewer offspring under Younger Dryas conditions 64% of the time, but wapiti females produced on average only 3.6 fewer offspring during their lifetime under Younger Dryas conditions.

Discussion

Although the exact length of the growing season in the Allerød and Younger Dryas is not known, our model suggests that Irish elk population growth rates declined

steeply with decreasing length of the growing season. The results therefore support our hypothesis that changing climate and deteriorating habitat could have had enough of an impact on female reproduction to have driven the Irish elk extinct. Yet the wapiti, a smaller species with a similar reproductive strategy (although not as extreme), is shown in our model to be unaffected by a wide range of growing season lengths. These results suggest that nutritional limitation of the females could have led to the extinction of the Irish elk, but smaller body size and less extreme reproductive costs allowed the wapiti to survive the Younger Dryas. It is interesting to note that under current conditions (200 day-long non-growing season) the Irish elk is predicted to have as high a reproductive rate as in the Allerød, even if the Irish elk range is shifted northward to the current moose range (205 day-long non-growing season).

Our model does not incorporate increasing fertility with maturity in young animals, nor does it account for decreasing fertility with senescence. Thus our model extends the prime reproductive rate throughout the reproductive lifetime of a female, and the predicted lifetime number of offspring is higher than should be expected for a real animal even under ideal conditions. However, the use of prime reproductive rates allows comparison with those used by Johnson (2002) to predict Late Quaternary extinction probability. We assumed that Irish elk would not twin but could produce one calf each year under good conditions. Johnson's (2002) derived prime reproductive rate for Irish elk based on extant cervids is nearly identical (1.01 offspring year⁻¹). In the Younger Dryas, our predicted prime reproductive rate dropped to 11 with the females reproducing only every other year. This prime reproductive rate of 0.5 offspring year⁻¹ is far below the threshold of 0.98 offspring year⁻¹ Johnson (2002) found for a 50% extinction probability. Our model thus suggests that the Irish elk could have declined towards extinction because of reproductive rates lowered by female nutritional stresses.

The uncertainty analysis shows the Irish elk having decreased reproduction more often and with a greater average reduction in number of offspring than the wapiti. These reductions result in both species having similar estimated numbers of offspring in the Younger Dryas (14.8 for Irish elk and 14.4 for wapiti). Although these estimates are similar over a female's lifetime, Irish elk reproduce over a longer period than wapiti resulting in prime reproductive rates of 0.67 offspring year⁻¹ and 0.8 offspring year⁻¹, respectively. Thus, though the uncertainty analysis results in a less extreme reduction in reproductive potential for the Irish elk and a reduction in the reproductive potential of wapiti compared with the model run with the best-estimate parameters, the prime reproductive rate of the Irish elk still drops below that of the wapiti, indicating a greater vulnerability to extinction for the Irish elk.

Our model conservatively depicts worsening habitat conditions because it only includes one aspect of the habitat deterioration that occurred in the Younger Dryas, a reduction in the length of the growing season. However, other forms of habitat deterioration may also have been important (e.g. the loss of nutrient-rich plant species from the community, a reduction in summer primary productivity, lower sustainable grazing levels, or increased thermo-

regulatory costs in a cooling climate). Consequently, our model may be conservative in the effect of habitat deterioration on the Irish elk, with females facing even greater obstacles to reproduction in the Younger Dryas than examined in our model.

In the face of worsening forage conditions, populations often respond in ways that mitigate the effects of lowered nutritional status. Upper size limits of herbivores are thought to be imposed by the quantity and quality of food available during the worst season (Illius and Gordon 1992). Extending the limiting season should then result in dwarfing. The observation that the Jersey Island red deer evolved dwarfed sizes quickly enough to avoid extinction when their range was cut off from the continent (Lister 1989) begs the question of what prevented the Irish elk from doing the same in Ireland when their habitats became less able to support their large body size. Raia and Meiri (2006) found that insular dwarfing in ungulates is prevented by the presence of competitors and predators. When Jersey was cut off from the continent, it was free from the predators and competitors of red deer while Ireland had wolves, brown bears, and reindeer during the Younger Dryas (Woodman et al. 1997). Because smaller ungulates are more susceptible to predation by a wider range of predators (Sinclair et al. 2003), large size presumably enabled the Irish elk to escape predation by conferring greater speed and strength and by reducing the number of predators to which they were vulnerable. Additionally, the females had to be massive enough to produce large well-developed young that could escape from predators soon after birth. Thus, the Irish elk were likely trapped between worsening habitat conditions requiring smaller body sizes and predation/competitive pressures requiring large body sizes. Even more limitations would be found in the continental range of the Irish elk because of greater numbers of competitor and predator species. However, it should be noted that habitat productivity driven body size differences have been found among historic hartebeest species and subspecies even in the presence of predators and competitors (Capellini and Gosling 2007).

The habitat deterioration probably did cause nutritional stress on the males, but for a species to be driven extinct by the secondary sexual characteristics of males, it is expected that the costs must be borne by the females (e.g. if males excluded females from a needed resource) (Kokko and Brooks 2003). This is an unrealistic scenario given the sexual segregation in preferred habitat suggested by the fossil record (Barnosky 1985) and typical for dimorphic ungulates, particularly cervids (Barboza and Bowyer 2000). This habitat segregation was presumably the result of the differing needs of males and females. The males are thought to have needed foods rich in minerals to support rapid antler growth, often found in more closed habitats near water, while the females and their young needed the security conferred to cursors by more open upland habitats (Geist 1998). Thus it is unlikely that mineral-starved males specializing in one habitat overexploited the food sources of the females specializing in an entirely different habitat.

Unrelenting increases in male mortality can reduce population viability once extremely low male densities are

reached. However, even if low male densities are reached, the effects of male mortality on population stability are moderated by the impact low male densities have on intrasexual competition. At low male densities, subordinate males are less likely to meet and be suppressed by dominant males and thus are more likely to breed. This increases the proportion of breeding males and buffers the effective sex-ratio from male mortality (Kokko and Rankin 2006). A greater proportion of males breeding also results in relaxed sexual selection (due to reduced suppression of less-ornamented males and reduced opportunity for female choosiness) (Kokko and Rankin 2006), which should allow quicker evolution of antlers as dominance becomes less important to breeding success. This same process should also occur if the densities of both sexes are reduced (Kokko and Rankin 2006), lessening the potential impact Irish elk antlers could have had on their extinction.

As habitat conditions worsened for both sexes and a given home range was able to support fewer individuals, a reduction in overall population density would also have hastened the evolution of smaller antler sizes by weakened sexual selection. In this situation, it is likely that average female herd size decreased and home ranges increased. If herd size decreased and home range increased, at any given population level, the number of herds would increase and herd density would decrease. It seems likely that the reproductive strategy of dominant males was harem herding or lekking (Geist 1998) depending on local conditions and densities. In conditions demanding smaller, more widely scattered herds, harem herding would be favored (Deutsch 1994) and the reproductive payoff to dominant males would be lowered while subordinate males would have greater opportunities to find unguarded females. Both these consequences would relax sexual selection and result in evolution of smaller antler sizes independently of increasing costs of antler growth.

Nutritional stresses may not have been the sole cause of the Irish elk extinction over its entire range. Hunting by humans has been implicated in the Pleistocene extinctions around the globe (Koch and Barnosky 2006). However, hunting alone cannot adequately explain the extinction of the Irish elk. The most well studied Irish elk population, that on Ireland, went extinct during a time of climate and habitat deterioration, but prior to human arrival. Before extinction, body size and relative antler size had declined, indicating a population under nutritional stress (Barnosky 1986). Nevertheless, the fate of the Irish population does not rule out hunting as a factor contributing to extinction in other areas. Stuart et al. (2004) imply that humans may have contributed to the extinction by preventing Irish elk from expanding from refugia once the climate became more favorable. However, the risk of extinction during this period has been linked to reproductive rates (Johnson 2002). Not surprisingly, species with lower reproductive rates were more likely to go extinct. Johnson (2002) also found that certain ecological traits allowed species with low reproductive rates to survive. These traits all reduce the likelihood of encounter with and detection by human hunters (inhabiting high latitude, altitude, or closed habitats, or nocturnal or arboreal habits) and none were presumably shared by the Irish elk, making it vulnerable to hunting pressure. In worsening habitat conditions, when Irish elk prime repro-

ductive rates dropped, as indicated by our model, even low levels of hunting pressure may have been unsustainable. The vast majority of extant species with prime reproductive rates near or below 0.5 offspring year⁻¹ live in refuge habitats (high latitude, high altitude, or closed cover) where they have some protection from being hunted by humans (Johnson 2002). Consequently, hunting may have contributed to the extinction of the Irish elk, but it was probably mediated through the reduction in reproductive output by females in nutritionally poor environments. Thus, the nutritional stress on the females, combined with the need to produce large cursorial young, likely had much more influence on the extinction of the Irish elk than the antlers of the males. Small underdeveloped young have greater significance for the viability of a population than small underdeveloped antlers.

Conclusions

Overall, in areas without humans, it is fairly clear that nutrient stress was the primary cause of population extinctions. In areas with humans, the additional hunting mortality, combined with reduced reproductive rates, probably drove the Irish elk extinct. The importance of nutrient limitation in the extinction of the Irish elk is evidenced by a reduction in body size that accompanied the drop in abundance leading up to the extinction across Eurasia (Koch and Barnosky 2006), but the magnificent antlers of the males need not be invoked.

It seems that the case of the Irish elk exemplifies the natural human tendency to fixate on the most stunning and unique character while ignoring the mundane but potentially important. The antlers of the Irish elk probably had at most a minor role in driving the species to extinction, as only extreme reductions in male–female ratios reduce population viability in polygynous species. Such extremes are unlikely in the case of the Irish elk because worsening climatic conditions would have impacted the nutritional status of both males and females, and decreases in female reproductive ability directly impact a population's growth rate. A decline in reproductive success due to nutritional stress on pregnant and lactating females would not be limited to the Irish elk (unlike the antler-extinction hypothesis), and may have contributed to the extinction of many other species around the end of the Pleistocene. The Irish elk extinction may serve as a valuable example of the potential dangers facing many of the world's remaining megafauna in a time of rapid climate change. Due to anthropogenic habitat reduction and fragmentation, and the subsequent decline in opportunities for dispersal and range shifts as responses to climate change, the ability of large mammals to adjust to changing habitat conditions in situ and often in the face of poorly managed hunting may be fundamental to their continued survival. By looking past their antlers, Irish elk may serve as an important model of how climate change can lead to extinction, and may thus help in identifying extant species of special concern before dire population declines make conservation efforts difficult if not impossible.

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Supplementary material (available online as Appendix O16608 at <www.ekol.lu.se/Appendix>). Appendix 1.