QUATERNARY RESEARCH 25, 128–135 (1986)

"Big Game" Extinction Caused by Late Pleistocene Climatic Change: Irish Elk (*Megaloceros giganteus*) in Ireland

ANTHONY D. BARNOSKY

Section of Vertebrate Fossils, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213

Received May 16, 1985

Megaloceros giganteus, the largest Eurasian deer, inhabited Ireland from ca. 12,000 yr B.P. to the time of its extinction ca. 10,600 yr B.P. The archaeologic record documents that people arrived on the island no earlier than 9000 yr B.P., so they could not have caused the extinction in Ireland. Close stratigraphic association of the geologically youngest elk fossils with sediments indicating the onset of the Nahanagan Stadial (approximately = Younger Dryas) implicates climatic change as the exterminator. Palynologic data support the idea that extinction probably resulted when forage quantity and quality along with length of the spring green-up decreased during the Nahanagan Stadial. For *M. giganteus*, this meant that the energy intake required to sustain large bodies, grow enormous antlers, and build fat reserves for winter was increasingly difficult to maintain, until deaths, primarily by winterkill, outnumbered births. © 1986 University of Washington.

INTRODUCTION

Hunting by prehistoric humans, termed Pleistocene overkill, and climate change are the two leading contenders for causing the extinction of many large mammals near the end of the Pleistocene (Martin and Klein, 1984; Martin and Wright, 1967). It is very hard to decide which of these causes was more important because, despite the fact that many species can be shown to disappear at about the time humans arrived in an area, in most cases the same area was also affected by widespread changes in climate (see, for example, Gruhn and Bryan, 1984; Haynes, 1984; Mead and Meltzer, 1984; Meltzer and Mead, 1983; Martin, 1984). One clear way to determine whether either cause by itself could have decimated the megafauna is to examine extinctions in areas where human arrival did not coincide with climate change. Such methods suggest that humans contributed to extinctions during the late Holocene in at least New Zealand (Trotter and McColloch, 1984; Anderson, 1984; Battistini and Verin, 1967), Europe, and South America (Diamond, 1984). The extinction in Ireland of the giant Irish elk, *Megaloceros giganteus*, provides a contasting example. Archaeologic evidence and ^{14}C dates place the arrival of humans in Ireland at about 9000 yr B.P. (Mitchell, 1976, pp. 98–101; Woodman, 1977; Ryan, 1980, 1981), but abundant pollen, plant macrofossil, insect, and geologic data point to major climate changes earlier, at about 10,000–11,000 yr B.P. (Mitchell, 1976, p. 77; Watts, 1977, and references therein). The evidence presented below strongly suggests that climatic change annihilated Irish elk.

Megaloceros giganteus, family Cervidae, subfamily Cervinae, is technically a deer although Molyneaux (1697) bestowed the common name Irish "elk" (Reynolds, 1929). *Megaloceros* Brooks 1828 is the preferred generic name because it has priority over *Megaceros* Owen 1844. The males were characterized by large bodies and correspondingly large antlers. Prime specimens stood about 1.8 m high at the shoulder and sported ±35-kg antlers measuring up to 4 m from tip to tip. Besides roaming Ireland, *M. giganteus* is known to have ranged through England, Scotland, Denmark, Sweden, France, Germany, Austria, Hun-

0033-5894/86 $3.00

gary, Russia, northern Africa, and northern Asia between <350,000 (Hoxnian Interglacial) and 10,000 yr B.P. (Reynolds, 1929; Mitchell and Parkes, 1949; Kurtén, 1968; Stuart, 1982, p. 56; Mitchell, 1976, p. 75). Unconfirmed reports claim the species survived as late as 2500 yr B.P. in Syria and southern Russia (Kurtén, 1968; Sizer, 1962).

STRATIGRAPHIC FRAMEWORK

This analysis is confined to Ireland because only there are abundant elk fossils well correlated with the paleoecologic and geologic data pertinent to interpreting megafaunal extinction. Nowhere is that better illustrated than at Ballybetagh Bog, located 15 km south-southeast of Dublin, where over 100 Irish elk skulls and many postcranial bones have been examined taphonomically and are associated with lithologic records, fossil plants and pollen, and fossil insects that allow detailed environmental reconstructions. Excavations and sediment cores at Ballybetagh reveal the following four lithologic layers, listed from oldest to youngest, which cumulatively are thickest in the center of a narrow, steep-sided valley (Fig. 1) (see also detailed maps and sections in Jessen and Farrington, 1938; Watts, 1977; Barnosky, 1985).

Layer 1. Facies near the valley sides are gray glaciofluvial gravel and solifluction deposits. Toward the center of the basin these grade into gray inorganic lake clay, which gives way upward into very dark brown gyttja.

Layer 2. Brown lake deposits consist of pebble-bearing silt at the valley sides, but clay or gyttja in the valley center. Irish elk bones are confined to the upper half of this layer, concentrated at the margins of what was a Pleistocene lake.

Layer 3. Near the valley sides these gravels are very like layer 1, except for fewer boulders. Correlative deposits in the center of the valley are dark brown silt changing upward into dark gray silt and sand.

Layer 4. Gray-brown lake deposits composed of clay and gyttja are thinnest at the valley sides. They grade upward into peat, which makes the present surface of the bog.

These four generalized layers characterized most Irish late-glacial lake deposits. Where Irish elk bones are present, they always occur in the upper part of Layer 2 (Mitchell and Parkes, 1949; Mitchell, 1976, p. 73).

Climatic Implications

The widespread occurrence of the four lithologic layers combined with their fossil content suggests they were deposited during four distinct climatic episodes. Layers 1 through 3 represent deposits of the late Midlandian Glacial Stage, which correlates with the late Devensian in British terminology and roughly with the late Wisconsinan of North America (Fig. 1). Layer 1 probably accumulated when late Midlandian glaciers were near their maximum extent in Ireland. At Ballybetagh this is inferred from boulder-sized glacial erratics within the layer, from solifluction deposits, and from the fossil plants and pollen that indicate a landscape sparsely vegetated primarily with grass, *Rumex*-type plants (*R. acetosa*, *R. acetosella*, or *Oxyria digyna*) and *Salix* (probably *S. herbacea*) (Watts, 1977, p. 278). In eastern Ireland, ^{14}C dates from organic lake mud place Layer 1 as older than 12,470 ± 155 yr B.P. (D-109) at Coolteen Lake, 12,235 ± 160 yr B.P. (D-110) at Belle Lake, and 12,470 ± 125 yr B.P. (UB-229F) at Sluggan Lake (Watts, 1977, p. 292). During or slightly before the deposition of Layer 1, all but about one-fifth of Ireland, mostly in the southeast, was presumably covered by ice (Synge, 1969).

Layer 2 records a time of climatic amelioration, the Woodgrange Interstadial (Mitchell, 1976, p. 68), as indicated by its high organic content (up to 60%) and fossil plant remains (Watts, 1977, p. 278; Jessen and Farrington, 1938, pp. 222–225). The Woodgrange Interstadial probably correlates with part of the Alleröd Pollen Zone

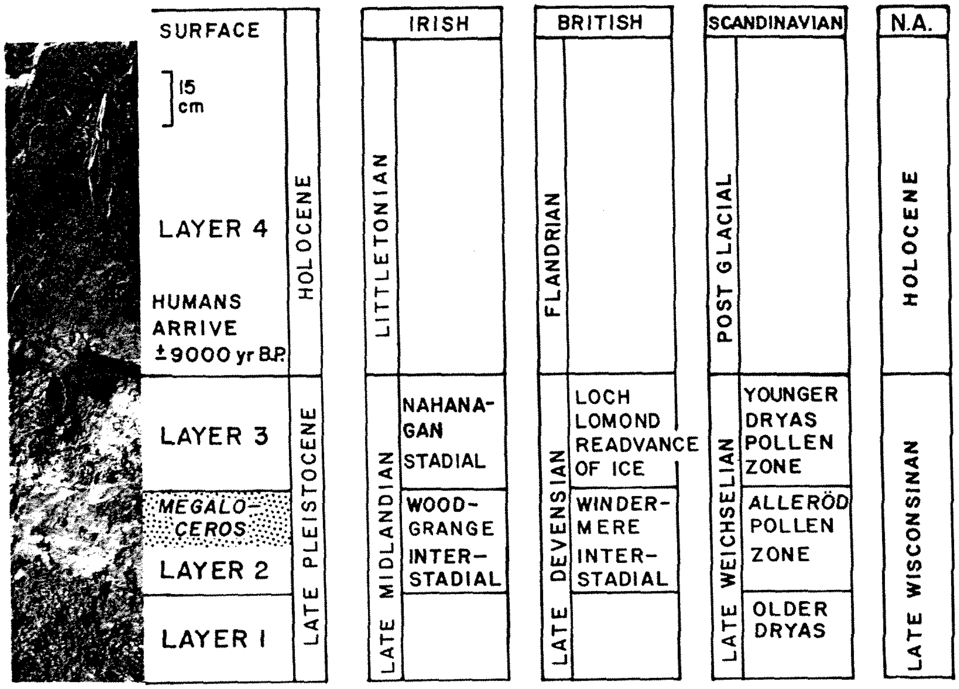

FIG. 1. Late Quaternary stratigraphic section through a typical Irish lake deposit, and general correlation of lithologic units with climatic events. Fossils of *Megaloceros* are confined to the stippled area. The pictured section is at the northwest Ballybetagh bog, located approximately 15 km south-southeast of Dublin's city center (lat 53°13′12″N, long 6°13′00″W). The exact location on an excavation map is shown by Barnosky (1985, p. 341) as the west wall at station S.

of northwestern Europe and with the Windermere Interstadial in Britain (Coope *et al.*, 1979). Pollen assemblages from Ballybetagh, like most sites, show two vegetational phases (Watts, 1977, pp. 278–279). The older phase, represented by the lower half of the layer, is characterized by *Juniperus* (up to 60%) and *Empetrum*. Watts (1977, p. 284) interpreted the upland flora to have been diverse, comprising a dense vegetation cover, and the climate to have been warm in summer with a long growing season. Radiocarbon dates show that the *Juniperus–Empetrum* phase lasted from about 12,470 yr B.P. (D-109) to 12,020 ± 180 yr B.P. (I-5038) (dates on organic mud from Coolteen Lake). In the upper half of Layer 2 the second vegetational phase commences, coeval with the appearance of Irish elk fossils. *Juniperus* pollen decreases and is replaced mostly by that of Gramineae, which contributes up to 50% of the pollen rain. The pollen assemblage and plant macrofossils suggest that vegetation around Ballybetagh changed to predominantly "short grassland with small herbs and shrubs and some stands of *Betula pubescens*" (tree birch) (Watts, 1977, p. 279; Jessen and Farrington, 1938, p. 223). The increase in grass relative to juniper and the failure of tree birch to spread out of isolated stands led Watts (1977, p. 284) to posit that either the growing season shortened as a result of increased windiness and lower annual temperatures, or that tree species were overgrazed by large populations of Irish elk. In either case, the high percentage of *Helianthemum* cf. *canum* pollen and the high organic content of the lake mud throughout the grass phase suggest a climate warmer and more favorable to vegetation than during deposition of Layer 1 or Layer 3. Radiocarbon dates on organic sediments of Layer 2 from Belle Lake place the end of this warm interval near 10,590 ± 185 yr B.P. (D-111) in southeast Ireland (Watts, 1977, and references therein). Radiocarbon dates of lake mud that encloses Irish elk bones at Knocknacran and Shortalstown are 11,300 and 12,150 yr B.P., respectively (lab numbers and errors unreported) (Mitchell, 1976, p. 74). A bone-collagen ^{14}C date from Ballybetagh, which was on a jaw recovered from the contact between Layer 2 and Layer 3, is 10,610 ±495 yr B.P. (UB-2699). (The remainder of the jaw is Carnegie Museum specimen no. 45049.)

Layer 3 represents a return to cold conditions, the Nahanagan Stadial. Evidence at Ballybetagh includes solifluction deposits mildly reworked by streams near the valley side, silt and sand near the valley center, abundant fossil leaves of *Salix herbacea,* and a fossil pollen assemblage that begins with a peak of *Cruciferae* that is followed by high percentages of *Artemisia,* Caryophyllaceae, *Thalictrum, Sedum rosea, Armeria, Koenigia,* and *Polygonum viviparum* (Watts, 1977, p. 279). The crucifer peak signals the deterioration of stable grasslands, possibly from the effects of solifluction, as the climate cooled toward arctic-alpine conditions recorded by the subsequent *Artemisia* phase (Watts, 1977, p. 280). The middle part of the *Artemisia* phase correlates with the advance of mountain glaciers, as shown by pollen assemblages interstratified with moraines at Lough Nahanagan in the Wicklow Mountains of southeast Ireland. The cold period represented by Layer 3 was apparently sudden and of short duration as shown by ^{14}C dates that bracket it between 10,590 ± 185 (D-111) and 10,210 ± 110 yr B.P. (D-108) in southeast Ireland. The dates are on organic sediments in Belle Lake and Coolteen Lake, respectively (Watts, 1977, p. 292).

Layer 4 marks the onset of the Littletonian Warm Stage, which roughly correlates with the British Flandrian and the Holocene (Mitchell *et al.,* 1973). The organic content of sediments increased and pollen types of the *Artemisia* phase are replaced first by dominantly Gramineae and *Rumex,* then *Juniperus* and *Filipendula,* and then *Betula* (tree birch), which was eventually joined by *Corylus, Quercus, Ulmus,* and *Pinus* (Watts, 1977, p. 280). The sequence indicates that climatic warming commenced about 10,200 yr B.P. and culminated in the present temperate conditions.

Fossil beetles collected from Layers 1 through 4 at Ballybetagh (G. R. Coope, personal communication, 1984) and Drumurcher, Co. Monaghan, are in accord with these climatic interpretations (Coope *et al.,* 1979).

EXTINCTION OF IRISH ELK

At Ballybetagh very few Irish elk bones occur at the contact between Layers 2 and 3, and those that do are commonly reworked. Even fewer bones are present within the lowest part of Layer 3. None are present above that level. The same holds true for all *M. giganteus* localities in Ireland where good geologic information is available (Mitchell and Parkes, 1949; Mitchell, 1976, pp. 73–74). The stratigraphic link is strong: Irish elk were present only during the last half of the Woodgrange Interstadial (Layer 2), and they became extinct as the Nahanagan Stadial began (Layer 3).

Humans apparently arrived later, as indicated by the oldest known archaeologic sites in Ireland: the mesolithic habitations at Mt. Sandel, Co. Derry (Woodman, 1977; Mitchell, 1976, pp. 98–101), and Lough Boora, Co. Offaly (Ryan, 1980, 1981). Radiocarbon dates at both sites range from about 9000 to 8500 yr B.P. That people did not cause the extinction is corroborated by the Irish elk fossils themselves. Despite a century of awareness that potential predators of *M. giganteus* may have included humans (Reynolds, 1929, p. 11 and references therein), no tools, marks, or breakage that would indicate hunting and butchering have been discovered in association with any of the hundreds of known Irish specimens. Such evidence for humans was specifically sought at Ballybetagh, but none was found (Barnosky, 1985). Neither was any found in the extensive collection of Irish elk bones at the National Museum of Ireland (Natural History), which includes over 200 skulls and many postcranial elements. The few examples of marks reputed to have been inflicted by humans (Jukes, 1864; Adams, 1881) cannot be distinguished from other kinds of breaks, abrasions, gnaw-marks, or scratches.

What mechanism exterminated Irish elk as the climate cooled and mountain glaciers advanced approximately 10,600 yr B.P.? Paleobotanic and morphologic evidence point to vegetational change and a shortened feeding season, a combination that Guthrie (1984a, 1984b) convincingly argued was detrimental to late Pleistocene megafauna elsewhere. Pollen assemblages and the distribution of Irish elk sites in Ireland suggest that the most beneficial food plants were found where vegetation consisted mainly of short grasses but also included herbs, shrubs, and stands of birch (Watts, 1977; Mitchell and Parkes, 1949). The dental morphology of Irish elk, much like that of *Alces alces* (moose) and *Cervus elaphus* (wapiti, red deer), is characteristic of opportunistic browsers that supplement their diets with large amounts of grass. For example, browse such as twigs and leaves compose more than 75% of the diet of *A. alces*, and commonly more than 90%; grass usually comprises less than 10% (LaResche and Davis, 1973; Knowlton, 1960). *Cervus elaphus* eats more grass, commonly in the range of 60 to 80% of its diet, but nevertheless these deer rely heavily on trees, forbs, and shrubs, particularly in winter when such items average between 30 and 90% of its food (Mitchell *et al.*, 1977; Harper, 1962). At the beginning of the Nahanagan Stadial, browse plants that were common during the preceding interstadial all but disappear in most pollen records (Watts, 1977). For example, at Ballybetagh *Juniperus* and *Empetrum* drop out of the record, and *Betula* decreases in abundance. *Salix herbacea*, a dwarf willow, becomes dominant over *S. aurita* and possibly *S. phylicifolia*, both large plants with stems 1 to 4 m long (Jesson and Farrington, 1938, p. 224). Grass decreases to the benefit of small herbaceous plants, notably Cruciferae, Caryophyllaceae, Rosaceae, *Saxifraga*, *Thalictrum*, and *Artemisia*. Such changes indicate that, compared to the interstadial, fewer nutrient-rich plants were available for fewer weeks in spring and summer, and fewer browse plants were present in winter. Studies of extant artiodactyls (Guthrie, 1984a, 1984b) suggest that the reduction in quantity and quality of vegetation was fatal to Irish elk. Both population size and fitness of individuals likely decreased because the feeding season was too short for ingestion of all the nutrients required to sustain large bodies *and* to add fat for the winter. The energy required to grow antlers would have made the scarcity of nutrients particularly detrimental for males. Assuming antler regeneration took place over the 5 months of April through August, which is a long estimate in comparison with the 3 to 4-month growth times for extant deer, even a small Irish elk antler of 1.3 m would have grown at an average of 8.7 mm/day. As Goss (1983, p. 90) noted, one conceivably could have watched a large antler grow several centimeters per day at the fastest part of the growth cycle. Extinction occurred when such energy drains caused deaths, primarily from winter-kill, to outnumber births.

Taphonomic data are consistent with this conclusion. Attritional age-frequency distributions, presence of antlers, and bone weathering suggest most Irish specimens of *M. giganteus* died from winter-kill. At Ballybetagh, where the narrow stratigraphic interval may preserve a sample of an elk population that lived just prior to the extinction event—that is, around 10,610 ± 495 yr B.P. (UB-2699)—the overrepresentation of young adults 6 and 9 yr old indicates death by malnutrition during winter.

Ballybetagh animals on average died younger, were smaller, and had abnormally small antlers as compared to Irish elk from other localities (Barnosky, 1985). Younger age at death, small body size, and small antlers are characteristic of modern cervids raised on poor or overstocked rangeland (Mitchell *et al.*, 1977, pp. 44–45; Clutton-Brock *et al.*, 1982, pp. 270–272; Goss, 1983, pp. 260–262 and references therein).

These observations support Mitchell's (1976, p. 73) and Coope's (1973, p. 977) idea that a deteriorating climate expelled Irish elk from Ireland. An alternative extinction mechanism, the development of woodland through which large-antlered animals could not freely travel (Gould, 1974, p. 216), seems less plausible. Pollen records suggest tree cover decreased, not increased, at the time populations of Irish elk waned.

Citing a shortened feeding season as the cause of extinction of Irish elk may answer an additional perplexing question: Why did *M. giganteus* not reinhabit Ireland when the Holocene began and their preferred food plants were once again plentiful? The obvious response, that the Irish Sea prohibited colonization, is not entirely satisfactory because *M. giganteus* was unable to survive *anywhere* by the early Holocene. By 10,000 yr B.P. summer insolation at latitude 50°N already was beginning to decrease toward present values (Wright, 1984, p. 103). Despite the presence of suitable plants, the spring "green-up," when plants contain their maximum nutrients and thereby accelerate growth of cervid bodies and antlers, may have remained short relative to the late Pleistocene season. The length of the green-up seems to be particularly important to large artiodactyls with large antlers for maintaining fitness (Guthrie, 1984a, p. 282, 1984b). It is probably no coincidence that *M. giganteus'* presence in Ireland, as well as its maximum abundance in Britain, corresponds so closely with the time of maximum summer and minimum winter insolation, ca. 12,000 to 10,000 yr B.P.

DISCUSSION AND CONCLUSIONS

Climate stands out clearly as the cause of the extinction of Irish *M. giganteus* primarily because nature so simplified the experiment: Ireland is an island; Irish elk were the only abundant large herbivores; humans were absent at the time of extinction; and the deterioration of climate was synchronous with the elks' disappearance. Deciphering causes of Pleistocene extinction on a scale that includes all of Europe or North America is more complex. Over such large land areas, multiple herbivores competed and otherwise interacted. Humans did hunt the herbivores. And in principle animals could have migrated to suitable refugia if climate changed for the worse. Nevertheless, the Irish example is important in showing that climate change—even the onset of a stadial event—by itself can trigger the extinction of a "big game" species. Equally important, it was not Holocene warming, but a brief cold spell just before warming that eliminated *M. giganteus* from Ireland. This is in direct contrast to the climatic amelioration that apparently coincided with other megafaunal extinctions in North America and elsewhere in Europe. The contrast suggests that the sum of many local causes of extinction led to the total demise of the late Pleistocene megafauna. With continued studies of individual species from restricted geographic areas, it may yet be possible to convict either climate or man as the principal culprit.

ACKNOWLEDGMENTS

I thank N. Monaghan for providing access to collections at the National Museum of Ireland; W. A. Watts and C. H. Holland for facilities at the Trinity College Dublin Geology Department; G. W. Pearson of Queen's University, Belfast, for ^{14}C analysis of Ballybetagh bones; G. Frank Mitchell for stimulating discussion; C. W. Barnosky, H. E. Wright, G. R. Coope, M. Ryan, P. Woodman, W. A. Watts, and two anonymous reviewers for criticizing the manuscript; and the Leverhulme Foundation and Trinity College for funding.

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