

Taphonomy and Herd Structure of the Extinct

Irish Elk, *Megaloceros giganteus*

Abstract. *Fossils of the late Pleistocene elk Megaloceros giganteus from Ballybetagh bog, near Dublin, Ireland, indicate that males segregated from females during winters. The segregation implies seasonal rutting and polygynous mating and is consistent with the idea that large antlers functioned for social display. Within male groups, winterkill was the chief cause of death and was highest among juveniles and small adults with small antlers. There is no evidence to support the popular conception that heavy antlers caused animals to drown or become mired.*

The late Pleistocene Irish elk, *Megaloceros giganteus*, is famous for antlers that spanned up to 4 m and weighed 35 kg or more (1). As in other cervines, the antlers were carried only by males and were allometrically in proportion to body size (2, 3). These facts, the shape and orientation of the antlers, the hypertrophied cervical vertebrae, and antler function in extant deer suggest that the antlers were displays for attraction of females and dominance of rival males (2–6). Nevertheless, the usual explanation for the abundance of male *M. giganteus* fossils in Irish lake sediments is that the animals became mired in the mud or were drowned, in part because their antlers were so cumbersome (4, 7–11). New taphonomic data from Ballybetagh bog, Ireland, help to resolve the conflict between the claim that the large antlers functioned advantageously and the claim that the antlers were responsible for frequent deaths.

Ballybetagh bog (Fig. 1A) has yielded over 100 skulls and many postcranial bones—far more than any of the other localities, which are most common in Ireland but are spread throughout Eurasia. The study area includes the northwest bog, which was partially excavated for this research, and the southeast bog, in the bottom of a valley 0.9 km long (12). The valley bottom (altitude, ~230 m) is narrow, measuring less than 100 m across in most places, and the steep sides slope upward 15° to 30° for at least 100 m. From approximately 10,590 to 12,390 years ago, during the Woodgrange Interstadial (10, 13), the study site was covered by a lake in which up to 1.5 m of brown organic silty clay was deposited. The Irish elk fossils are confined to the upper half of this clay (Fig. 1B), as is typical throughout Ireland (14). Besides the Irish elk, the only fossils known from Ballybetagh are three *Rangifer* skulls (15) and perhaps *Cervus elaphus* excavated from the southeast bog and one rodent vertebra, one rodent incisor, and one fish vertebra screened from the northwest bog.

Evidence required to accept the miring-drowning model should include (i)

overrepresentation of males; (ii) abundance of males with relatively large antlers; (iii) frequent articulated skeletons, or at least vertically oriented feet and legs; (iv) sticky clay deposits more than 1 m thick (17); (v) bedding disturbed by trampling; and (vi) water deeper than the height of an Irish elk, about 2.2 m. Points (i) through (iii) apply to both drowning and miring, (iv) and (v) only to miring, and (vi) only to drowning.

1) *Overrepresentation of males.* Males are overrepresented in the death population. The usual explanation, that peat cutters selectively retrieved males, does not apply to Ballybetagh. Natural historians who could recognize males and females and who wanted both were present at Ballybetagh excavations to collect Irish elk in 1846–1847 (15), 1875 (18), 1876–1877 (7), 1914 (16), and 1934 (12). They found more than 100 skulls, probably more than 118, from the southeast bog, and one from the considerably less worked northwest bog. All the skulls were from antlered males.

2) *Large antlers.* The antlers on skulls from Ballybetagh are not abnormally large. In fact, they are relatively small, as compared first to some 70 specimens on display and measured by Gould (3), second to 50 specimens judged unworthy of museum display because they are broken or the antlers appear too small, and third to a lumped sample of the 50 non-display skulls and 25 display skulls (Table 1) (19). The lumped sample probably provides the best estimate of the total population, because display samples are biased toward animals with large antlers. The antlers from Ballybetagh appear smaller than normal even when the relatively small size of the skulls is taken into account.

3) *Articulated skeletons.* The skeletons are neither articulated nor nearly complete at Ballybetagh. Bones apparently lay on the surface for as much as a few years but more commonly for several months before burial, as evidenced by scattering and downslope alignment (Fig. 1C); gnawing by rodents, fox-sized carnivores, and probably Irish elk; missing snouts, antler portions, or other

breakage; and flaking (stages 0 to 2) (20). Moreover, the sturdiest bones are overrepresented; these include skulls, antlers, and mandibles for the entire sample and vertebrae, ribs, and podials for the postcranial sample. For example, the minimum number of individuals (MNI) recorded by cranial fossils from the northwest bog is three, and the MNI recorded by postcranial fossils is one. The southeast bog samples yielded MNI's of 40 (cranial) and 10 (postcranial) for the 1875 study (18) and 22 to 36 (cranial) and 9 (postcranial) for the 1914 study (16). The less robust bones were probably dispersed and destroyed in part by trampling, as indicated by the occurrence of a sharply broken jaw and a shed antler, each with the pieces still side by side (specimens 5 and 11 in Fig. 1C). Trampling of skeletons commonly occurs today near African water holes used by ungulate herds (20, 21).

4) *Clay deposits exceeding 1 m.* The thickness of the bone-bearing clay in the northwest bog ranges from only 6 cm at the west edge of the excavation to 65 cm at the east edge (Fig. 1B). All records from previous excavations show that the bones were stratigraphically separated from firm underlying boulders or gravel by less than 1 m (12, 15, 22).

5) *Disturbance of bedding.* Bioturbation is not evident in the northwest or southeast bog. The contact of the clay with the upper and lower glaciofluvial sediments is sharp, and laminations within the clay are not disturbed.

6) *Water deeper than 2 m.* In the northwest bog the bone-bearing clay becomes progressively thinner westward and pinches out 20 cm west of the excavation. It contains more silt and pebbles from east to west and abundant seeds of *Potamogeton* throughout (12). These patterns and the lake floor topography (Fig. 1C) suggest that the western shore of the lake was near the western edge of the excavation and that water depth there did not frequently exceed 2 m. Previous excavations and sediment cores also suggest that the bones are abundant only at the edges of the ancient lake (7, 12, 13, 16, 18, 22).

Facts (ii) through (vi) do not fit the drowning-miring paradigm. All the points, however, are consistent with a hypothesis, derived from observations of modern cervids, that males visited Ballybetagh bog more often than females did during winters, when unfit animals died and decomposed near the water's edge, in some cases on the ice, and were scavenged and trampled. The fragmented, weathered bones would have fallen into the lake as they were washed,

pushed, or kicked downslope from the adjacent shore or as they dropped through the melting ice.

Data from Ballybetagh satisfy other predictions of the winterkill hypothesis, namely that there should be (i) evidence for seasonal death; (ii) an age-frequency distribution that indicates attritional mortality, that is, juveniles and animals in the last half of the estimated maximum life-span should be overrepresented in the death population relative to their assumed frequency in the living population; (iii) signs that individuals were in poor physical condition; and (iv) suitable modern analogs.

1) *Seasonal death.* The basal rose ("coronet" or "burr") of the antler was completely developed on 34 of 35 skulls, signifying a fully grown antler. Fully grown antlers are present only in the autumn and winter, and some years into late spring, in most living temperate-latitude cervines, including the fallow deer *Dama dama*, to which *M. giganteus* is considered taxonomically closest (6, 23). The antler cycle is apparently triggered by seasonal changes in day length (6, 24), which would not have varied

significantly in the past 13,000 years. Heads without antlers have not been found at Ballybetagh, suggesting that few animals died during middle or late spring. Elk did occupy the site then, as numerous shed antlers attest. Only one specimen died in the late summer or early autumn; its full-sized antlers lacked the basal rose.

2) *Attritional mortality.* Age categories were estimated by measuring the height of the pedicle and crown height at the protocone of the second upper molar (M2), as well as by Klein's algorithm (25). The age-frequency distribution of the living Irish elk population was assumed to resemble those of extant cervids. Attritional mortality is clearly indicated at Ballybetagh and elsewhere in Ireland for the adult age categories (Fig. 2A). Juveniles are probably underrepresented in the diagrams, as in nearly all fossil accumulations, because of their low preservation potential (21, 25). Fragments of three juvenile skulls and one pelvis verify their presence. However, juveniles younger than 1 year would also be underrepresented if, as in modern deer, they spent most of their time with

their mothers, wintering away from the stags. An attritional assemblage is consistent with the maximum time spanned by the bone-bearing bed, approximately 900 years, which is within the range for other attritional deposits (13, 26).

3) *Poor physical condition.* At Ballybetagh young adults between pedicle ages 4 and 10 seemed to die most frequently when they were 6 or 9 years old; only one died at the age of 8 (Fig. 2A). A very similar age distribution is evident for modern young adult moose that died from malnutrition (Fig. 2B) (27, 28).

The basal length of the skull accurately predicts body size in cervids (2, 3). Comparisons of this measurement show that dead adults from Ballybetagh were significantly smaller than average for Irish elk (Table 1). It is unclear whether the death assemblage was drawn from a live population of smaller than average elk or whether only small elk died at Ballybetagh. In either case the limited size of adults could have resulted from some combination of limited resources, malnutrition, or disease during fetal or postnatal growth. In modern cervids such small adults are more vulnerable to

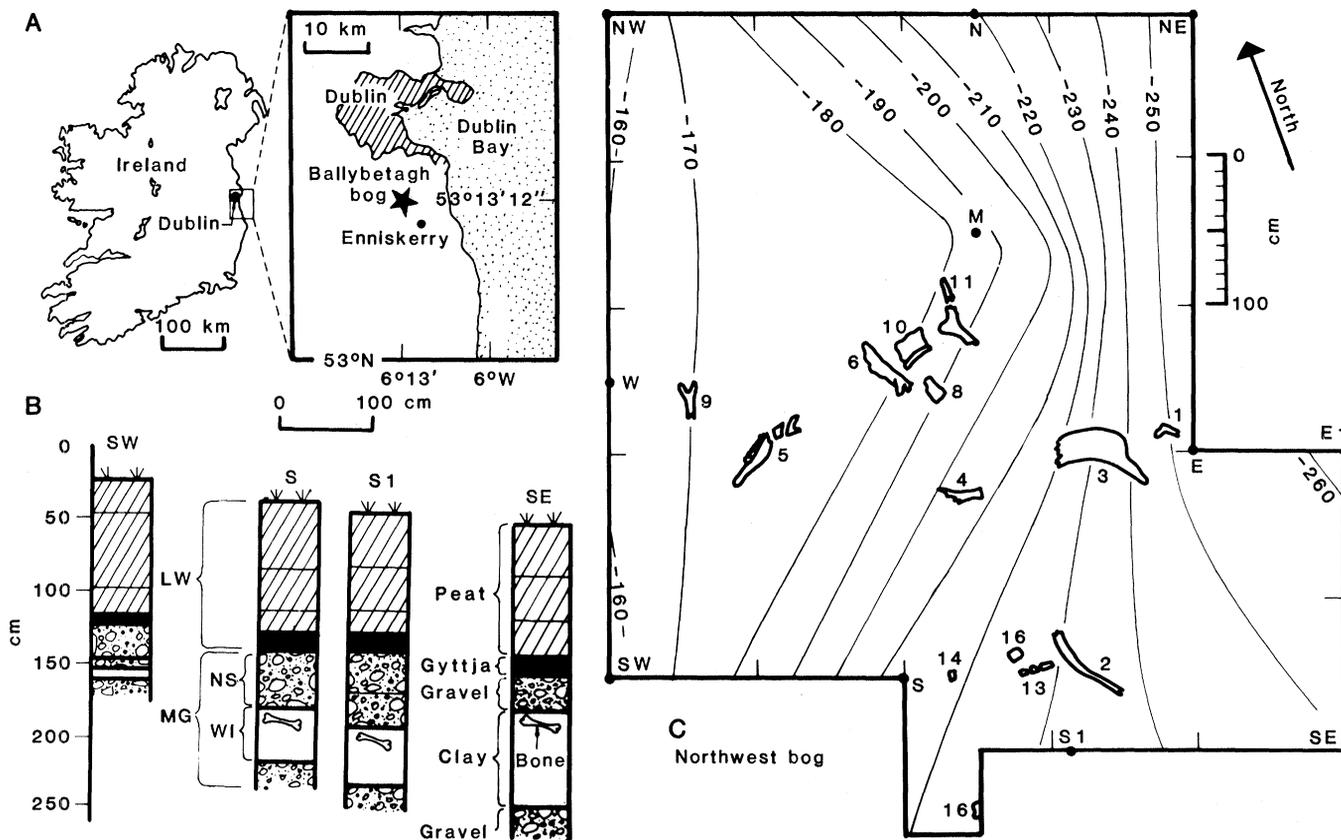


Fig. 1. (A) Locality map. (B) Stratigraphic sections at stations labeled in (C). Lithologic units roughly correspond to four geologic-climatic units: the Littletonian Warm Stage (LW; 0 to 10,000 years ago), the Late Midlandian Glacial Stage (MG; 10,000 to 26,000 years ago), the Nahanagan Stadial (NS; 10,000 to 10,590 years ago); and the Woodgrange Interstadial (WI; 10,590 to 12,390 years ago) (10, 13). (C) Position of bones in the northwest bog excavation. Contours show the approximate topography of the ancient lake floor at the contact between bone-bearing clay and underlying gravel, measured down from a datum located 20 cm above station NW. Bones identified are rib fragments (1 and 2); antler fragments (3, 6 to 11, and 16); distal scapula (4); mandible (5); caudal vertebrae (13); and podial (14). Antlered skull and separate antlers were recovered within 5 m south of the south wall of the pit (12).

predation and starvation than adults whose healthy early years allow them to attain average or larger size (27).

Small body size cannot fully explain

the small antlers in Ballybetagh elk (Table 1). For example, the linear relation between rose diameter and basal length of the skull is very weak for the compar-

ative sample and insignificant for the Ballybetagh sample (Fig. 2C). Beam circumference also shows a weak linear relation with basal length. Furthermore,

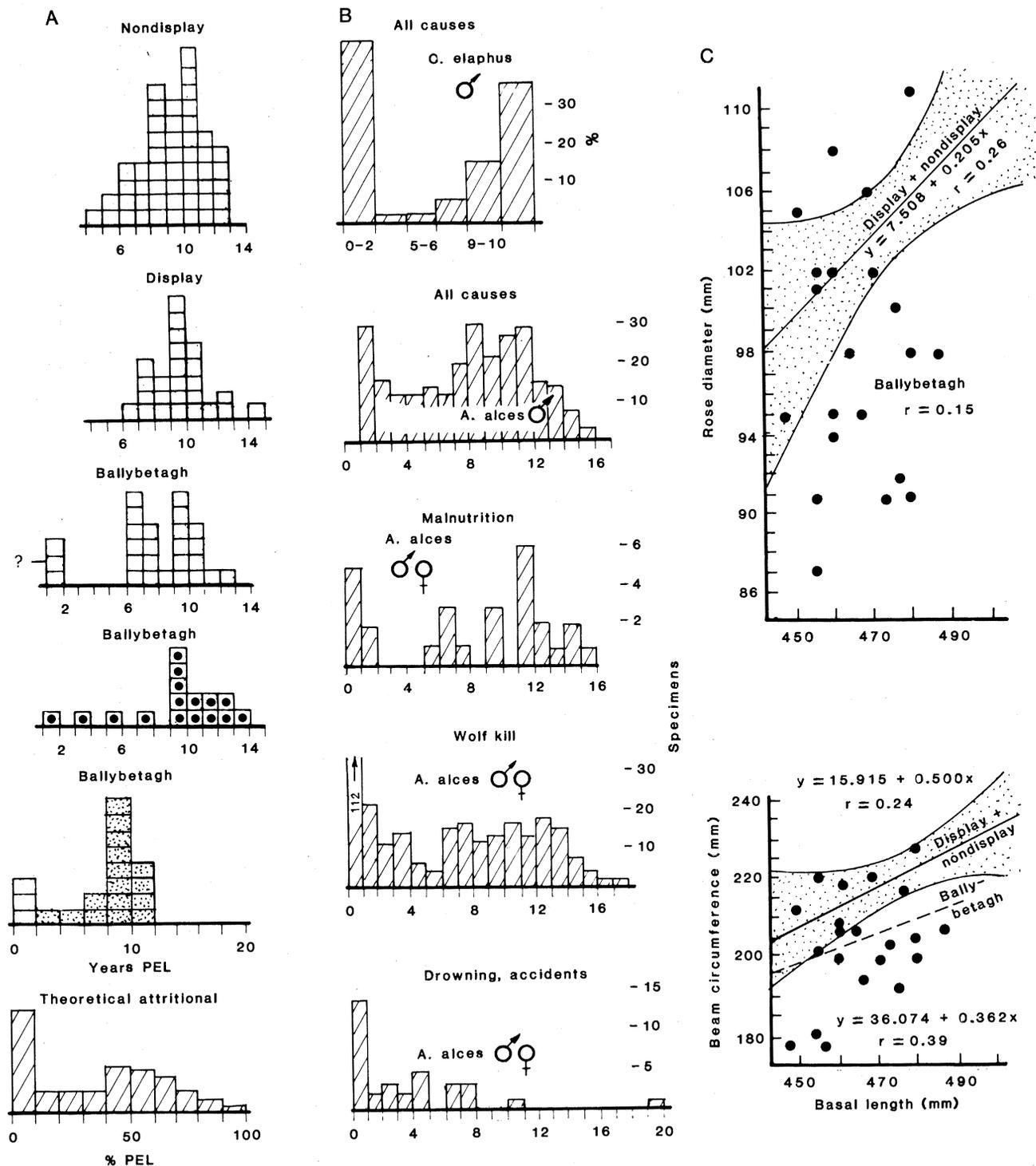


Fig. 2. (A) Age-frequency distributions for *M. giganteus* death populations (25). Each box represents one specimen. Open boxes are estimates derived by (pedicle height)/(basal skull length) and boxes containing filled circles are estimates derived by (protocone height)/(length \times width) of M2. Ages in years on horizontal scales were estimated from M2 protocone height by Klein's algorithm (shaded boxes) (25), assuming potential ecological longevity (PEL) of 20 years, eruption of M2 at 1.5 to 2 years, and an unworn M2 protocone height of 300 mm. (B) Age-frequency distributions for attritional death populations of extant cervids. Data are lacking for deer older than 12 in the top diagram (5); other data are from Peterson (27). (C) Bivariate plots and least-squares regressions of basal skull length (horizontal axis) against proximal measurements of antlers in Ballybetagh samples (plotted points and dotted line) and lumped display and nondisplay comparative samples (solid line; $n = 73$ for upper diagram and 72 for lower) (3, 19). The shaded areas represent 95 percent forecast intervals. In the upper diagram only the lumped sample shows significant correlation and the slope exceeds 0 ($P = 0.012$, t -test). In the lower diagram the slopes do not differ significantly, being 0.500 ± 0.240 for the lumped sample and 0.362 ± 0.191 for Ballybetagh; the probability that the slopes do not exceed 0 is 0.019 and 0.035, respectively (t -test). Measurements for the smallest Ballybetagh skull are not plotted (basal length, 420 mm; rose diameter, 93 mm; and beam circumference, 193 mm).

when beam circumference is regressed against basal length, the least-squares line for Ballybetagh falls significantly below that forecasted from the comparative sample (Fig. 2C). Likewise, the index "antler size" (3) was smaller than predicted when regressed against basal length for the only two Ballybetagh specimens complete enough for computation. Neither can age entirely account for the diminutive antlers. Juveniles (which were excluded in Table 1) and very old individuals commonly grow smaller-than-average antlers (2, 3, 6), but the mean pedicle age class for fully grown adults at Ballybetagh, 8.72 years (Fig. 2A), approximates the age, 7 to 8 years, at which *C. elaphus* stags of Rhum, Scotland, hold the largest number of does in their harems and are therefore likely to have their best antlers. The means of the comparative *M. giganteus* samples, 9.66 years for display and 9.42 years for nondisplay, fall closer to the end of the reproductive range of 4 to 11 years for Rhum stags (5). Elsewhere, antlers of *C. elaphus* usually attain maximum weight on animals 9 to 12 years old (29, 30). Of 12 Ballybetagh animals estimated to be in this age range, at least six had beams and roses smaller than expected from the comparative sample regressions. Abnormally small antlers in living cervines are grown by sick animals and in years of scarce resources when the deer begin winter with depleted fat reserves (5, 6, 29, 30).

4) *Modern analogs.* Most extant temperate-latitude cervines (such as fallow, red, sika, and white-tailed deer) segregate into sexually separate groups for most of the year, in part because the different physiologies of males and females require them to eat different plants (5, 23, 30). Winterkill accounts for most deaths in such cervines and in the moose *Alces alces* (5, 23, 27, 30). Malnutrition during the colder months starves animals to death or generally weakens them, which increases their vulnerability to predation, disease, and accidents. Male mortality is greater than female mortality during winter, apparently because males, unlike females, eat little during the fall rut and enter the winter in poor condition (5, 27, 30). Furthermore, male red deer seek shelter and occupy valley bottoms more frequently than females do during winter (5, 30), that is, they prefer the kind of topography that Ballybetagh offers. Many winter-killed cervids die near lake shores because they need water and because they are easy prey on ice (27, 31).

The data imply that Irish elk herds segregated into male and female groups

for the winter and early spring and that consequently the elk bred seasonally. Such segregation supports assertions that Irish elk were polygynous and that the giant antlers functioned as displays during rutting (2-6). In winter males sought the sheltered lowland with water at Ballybetagh. Malnutrition then culled mainly animals younger than 3 years and small adults, many with antlers smaller than their skull size would predict. The males apparently stayed at Ballybetagh through the spring, when they shed their antlers. They either moved elsewhere in the early and middle summer or died so infrequently then that bones were not preserved. There is no evidence that Irish elk drowned or were mired at Ballybetagh; the sample seems little diluted by deaths from causes besides winterkill.

Winter's hardships probably led to most of the deaths recorded by other *M.*

Table 1. Antler and skull measurements from different samples of *M. giganteus* (3, 19). Breakage of nondisplay specimens precludes their inclusion in the last five comparisons. All Ballybetagh, nondisplay, and display + nondisplay skulls, and 90 percent of display skulls, are from fully grown adults; S.D., standard deviation.

Sample	Measurement (mm)		n*
	Mean	S.D.	
<i>Right rose diameter</i>			
Ballybetagh	97.59	7.63	29
Display	107.38†	12.01	73
Nondisplay	103.20†	9.73	50
Display + nondisplay	104.75†	9.87	75
<i>Right beam circumference</i>			
Ballybetagh	204.61	14.64	28
Display	229.32†	28.32	74
Nondisplay	215.73†	24.25	48
Display + nondisplay	221.00†	25.86	72
<i>Basal length of skull</i>			
Ballybetagh	465.16	14.80	25
Display	475.70†	12.93	64
Nondisplay	472.46†	12.23	50
Display + nondisplay	474.31†	12.42	75
<i>Left brow tine length</i>			
Ballybetagh	183.50	58.36	6
Display	242.51†	32.82	61
<i>Left back tine length</i>			
Ballybetagh	83.33	20.82	3
Display	326.91†	110.90	56
<i>Right second tine length</i>			
Ballybetagh	154.00	78.22	6
Display	322.31†	87.02	52
<i>Left antler length</i>			
Ballybetagh	950.00	28.28	2
Display	1433.91†	238.18	46
<i>Left palm length</i>			
Ballybetagh	368.67	451.52	3
Display	1177.87†	150.63	61

*Number of specimens per group. †Significantly different from the corresponding value for the Ballybetagh sample ($P < 0.05$, *t*-test).

giganteus fossils in Ireland, as suggested by the scavenged, weathered condition of the skulls, the presence of antlers, and the attritional age-frequency distribution of the display and nondisplay skulls (allowing for poor preservation potential of juveniles). However, a minority of Irish elk undoubtedly did die from other causes, which would explain the similarity of the age-frequency distributions for the display and nondisplay samples (Fig. 2A) to the distributions for all causes of death in modern cervids (Fig. 2B).

There are at least three possible explanations for the small body size, small antlers, and younger adults found at Ballybetagh bog. The first is that the temporal interval represented at Ballybetagh is short and samples a time when most elk had smaller bodies, antlers, and a shorter life-span than earlier in the Woodgrange Interstadial. In this case the traits of the Ballybetagh animals would imply selection against large bodies and antlers just before the Nahanagan Stadial, a cold phase when the Irish elk became extinct. The second is that the temporal and geographic ranges of animals at Ballybetagh resemble those for the comparative fossil populations, but the sample is biased toward small, slightly younger adults with small antlers because poor nutritional history predisposed those animals to winterkill. A corollary is that large animals with large antlers survived winters more frequently, that is, that selection favored those traits. The third possibility is that the Ballybetagh animals belonged to a population that randomly drifted to small body and antler size and was isolated from other populations by the Wicklow Mountains and Irish Sea or by territorial behavior of herds. Taphonomic and stratigraphic studies at more sites should help to distinguish between these intriguing possibilities.

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References and Notes

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13. W. A. Watts [*Philos. Trans. R. Soc. London Ser. B* 280, 273 (1977)] lists ¹⁴C dates that bracket the Woodgrange Interstadial between 10,590 ± 185 and 12,390 ± 160 years before present in southeast Ireland. Therefore the upper half of the lake clays at Ballybetagh probably spans less than 900 years. The Woodgrange Interstadial is approximately correlated with the Alleröd pollen zone.
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19. The Ballybetagh skull sample consists of 31 heads from the 1875 excavation (18), two found in 1914, and two in 1934. My measurements of 25 display skulls did not differ significantly ($P = 0.05$, *t*-test) from Gould's (3) measurements of about 70 adults and 9 juveniles. All comparative skulls are from Irish localities other than Ballybetagh, except for one Russian specimen. Six of the comparative skulls are in the Carnegie Museum of Natural History (Nos. 45,000 to 45,005); ten in the British Museum (Natural History); one in Trinity College, Dublin (No. 17,378); and the rest in the National Museum of Ireland (Natural History). Ballybetagh material excavated from the northwest bog for this study is stored at the Carnegie Museum of Natural History (Nos. 45,049 to 45,073).
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28. The Ballybetagh sample differs from the display sample of Irish elk because more young adults died before reaching age 7, and it differs from the nondisplay sample because fewer died when age 8. The probability of no association of age at death with locality is less than 0.05, as determined by chi-square tests for Model II 2 × 2 contingency tables that, for two given localities (Ballybetagh or other), compare the proportion of animals in two different age categories between 4 and 10 (for example, the proportion of animals 4 to 7 to animals older than 7 but younger than 10).
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32. This research was initiated at the Department of Geology, Trinity College, Dublin. I am grateful to C. H. Holland and W. A. Watts for providing

facilities; N. Monaghan and A. J. Sutcliffe for allowing access to museum collections; P. Jackson, M. Deasy, and C. Barnosky for fieldwork; G. F. Mitchell, W. A. Watts, H. E. Wright, D. Palmer, and two anonymous reviewers for criticizing the manuscript; E. Cullen for drafting; and the Leverhulme Foundation and Trinity College for funding.

12 October 1984; accepted 7 December 1984

Functional Properties of Individual Neuronal Branches Isolated in Situ by Laser Photoinactivation

Abstract. *The functional properties of an isolated dendritic branch of an identified sensory interneuron in the cricket were studied. The branch responded to wind stimuli directed at the animal and displayed a distinct directional sensitivity to those stimuli. A technique was used that allows a neuron to be specifically lesioned in a semi-intact preparation during intracellular recording. Lesioning was achieved by dye-sensitized photoinactivation with a laser epi-illumination stereomicroscope.*

The function of a neuron depends on the structure of its dendritic and axonal branches in two important respects. First, the location of a neuron's branches in the nervous system determines the subset of other cells with which it may interact. Second, the fine structure of the branches determines how synaptic inputs and endogenously generated currents are integrated and transformed into "meaningful" output to other cells. The relations between neuronal structure and

function have been studied extensively by experimental and theoretical neurobiologists over the past three decades. However, there has been no way to test directly how the structure of a cell affects its integrative properties, since such a test would require changing the structure of the cell in situ during physiological recording.

We report here a technique for ablating specific regions of individual neurons during intracellular recording. Using the technique, which involves dye-sensitized photodynamic inactivation, we isolated a single dendritic branch of an identified sensory interneuron and determined the response properties of that branch to sensory stimuli.

When a neuron is filled with a fluorescent dye and illuminated with intense light of the appropriate wavelength, the cell becomes functionally inactivated (1). Neither the illumination nor the dye alone harms the tissue; it is the interaction between the two that results in photooxidative damage (2). Studies have shown that the axon of a single neuron can be selectively inactivated by filling the entire cell with dye but irradiating only the nerve containing the axon (1, 3). The illuminated section of the axon is killed and the rest of the cell remains intact. For the present study this technique was substantially refined so that single dendrites of dye-filled neurons could be inactivated during physiological recording. To allow the placement of microelectrodes into neurons in a semi-intact preparation, it was necessary to use a dissecting stereomicroscope. In order to project a light beam small enough to illuminate single dendritic branches, we developed a laser epi-illuminator attachment for the microscope. With dichroic mirrors and filters the

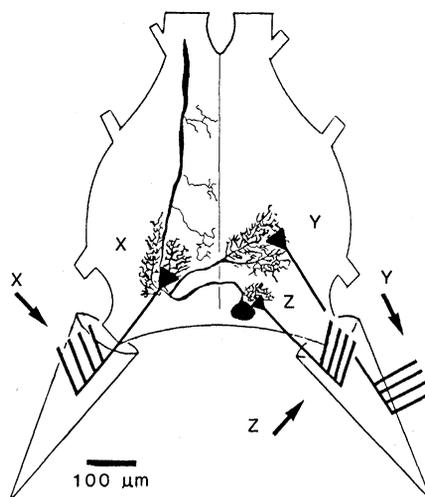


Fig. 1. Interneuron 10-3 and its presumed excitatory inputs (camera lucida drawing of a whole-mount preparation of this neuron stained with cobalt and intensified with silver). Each of the three dendritic regions has been labeled with a letter (X, Y, or Z). The three classes of afferents presumed to provide excitatory input to 10-3 are shown on the cerci (represented as cones). Afferents that overlap with dendrite X respond best to wind stimuli directed at the lateral face of the left cercus. Wind directed at the medial face of the right cercus activates afferents that overlap with dendrite Z and wind directed at the right front of the animal activates afferents that overlap with dendrite Y.