

Antler conformation in red deer of the Mesola Wood, northern Italy

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Red deer *Cervus elaphus* Linnaeus, 1758 stags from the Mesola Wood (northern Italy) are known for the very simplified structure of their antlers. An analysis was made of 180 sets of cranial appendages on 41 different individuals observed over 10 years. Considering only stags 5 years and older, the mean number of tines per antler pair was 5.36. The maximum number of tines per beam was invariably 4: the bez tine and the crown were always absent. Yearlings and subadults exhibited scarcely developed cranial appendages, with a high incidence of knobbers and spikers respectively. While the poor performance of young classes may be mainly due to malnutrition, in adult stags a genetic component may prevail over dietary factors: selective shooting, inbreeding and genetic drift could have fixed the already simple design of their antlers.

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Introduction

The only native red deer *Cervus elaphus* Linnaeus, 1758 of the Italian peninsula live in the "Gran Bosco della Mesola" Natural Reserve; this population, isolated for centuries, was protected from persecutions by the neighbouring large marshes (Mattioli 1990). Local stags are known for their simple antler design (Castelli 1941, Perco 1984, Mattioli 1990). Cervid antlers are particularly sensitive to external and internal influences, but the relative importance of diet and heredity remains speculative (Goss 1983). Here I provide qualitative and quantitative data on the morphology of the cranial appendages of Mesola stags and discuss on the origin of their peculiarly poor quality, evaluating the potential role of nutritional and genetic factors.

Study area and methods

The Gran Bosco della Mesola is situated in northern Italy, in the Po delta area (44°51'N, 12°15'E). Of its 1058 ha (110 inaccessible to ungulates), woods account for 87%, with *Quercus ilex* predominant (Piccoli *et al.* 1983). The soil is sandy. Annual rainfall averages about 650 mm. The majority of red deer live in the fenced area of Elciola (97 ha, including 68% of woodland and 16.5% of grassland). I

analysed the characteristics of 180 sets of frontal appendages belonging to 41 different individuals from the Elciola enclosure. An annual population of 15 – 25 stags ≥ 1 year old was followed from 1982 to 1989. During the 1990 – 1991 period, after the translocation of some adults, monitoring was continued for 6 – 7 animals aged 1 – 4 years. The cranial appendages were documented by photos and sketches, noting the number and type of points ≥ 2 cm (tines). Animals allowed observers to approach by car as close as 10 – 15 m. The age was determined exactly for those stags marked as calves ($n = 10$); for other individuals ($n = 31$) only an estimate of age was possible, based mainly on tooth eruption, replacement and wear patterns observed during capture (Wagenknecht 1984). Ageing live animals is necessarily approximate, so stags > 1 year old were then mostly pooled into 3 age classes (subadults 2 – 4 years old, adults 5 – 9 years old and adults 10 years and older). Besides ear tags and ear notches, individual recognition was also based on skin scars and coat colour patterns. Four sets of abnormal antlers were excluded.

One-way ANOVA was used to test for differences among years in number of antler tines: the raw data were square-root transformed (Sokal and Rohlf 1981). Differences between other means were examined using Student's *t*-test.

Results

In antlered stags ≥ 2 years old from 1982 to 1989, the mean number of tines per antler pair was 5.01 ($n = 143$). Considering only stags 5 years and older, the mean number of tines was 5.36 ($n = 124$; Table 1). No differences were found among years for number of tines ($F_{7,116} = 1.68$, $p = 0.12$). Mean values for stags 5 – 9 and ≥ 10 years old were respectively 4.59 ($n = 56$) and 5.99 ($n = 68$) tines per antler pair; the difference between these age classes was highly significant ($t = 5.82$, $df = 122$, $p < 0.001$). In adult stags beams with three tines prevailed, with an incidence of 41.5%; but sometimes simple unbranched spikes were also present, with a frequency of 10.7% in stags 5 – 9 years old (Fig. 1). The maximum number of tines per beam was never more than 4: the brow tine, the trez tine and the terminal fork. The bez tine and the crown were always missing. The fork did not occur before 10 years of age and then only infrequently: in stags 10 years and

Table 1. Mean number of points per antler pair in adult red deer stags ≥ 5 years old from the Mesola Wood in period 1982 – 1989.

Year	\bar{x}	SD	<i>n</i>
1982	4.94	1.06	16
1983	5.77	1.25	17
1984	5.17	1.04	18
1985	6.00	1.62	17
1986	4.67	1.68	18
1987	5.07	1.67	15
1988	5.75	1.91	12
1989	5.73	1.35	11
Total	5.36	1.49	124

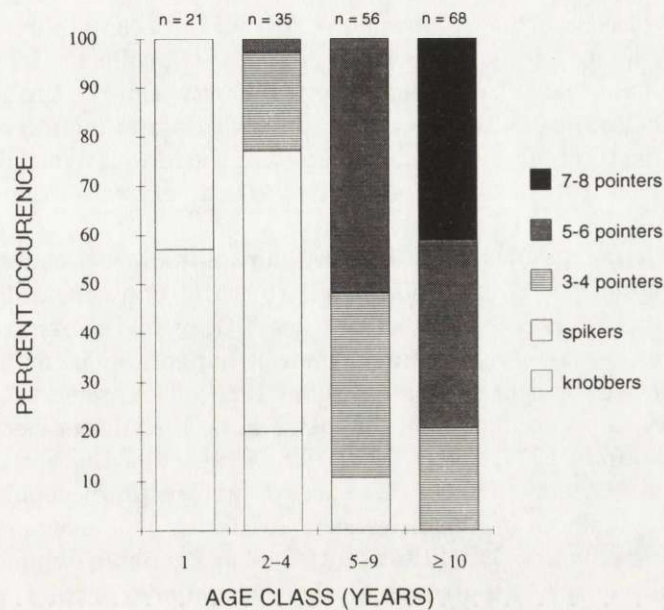


Fig. 1. Red deer stags classified according to point and age classes from the Mesola Wood in period 1982 – 1991.

older only 28.7% of beams had 4 tines and only 16.2% of antler pairs had 8 total tines. Only 4 different individuals were able to bear a total of 8 tines at least once in the study period (see Mattioli 1990 for representative antler types).

The first set of true antlers occurred at 1 – 4 years of age. During the 10-year study, of 44 stags 1 – 3 years old, 19 (43.2%) were antlerless. Of 21 yearlings, 12 (57.1%) failed to develop antlers; these stags normally delayed the growth of the pedicle until 14 – 16 months; in two cases the pedicles did not begin to develop until 20 months. When antlered, yearlings had two very short spikers, the pedicles being visible at 11 – 13 months of age. Of 15 stags 2 years old, 5 were knobbers, only with fur-covered pedicles or with pedicles and tiny bone buttons. Of 9 stags 3 years old, 2 were knobbers with buttons. 'Hummels', i.e. antlerless adults with under-developed pedicles, did not occur.

Discussion

This very simplified antler structure was not an exclusive characteristic of the Elciola population during the years of study. The other sub-population of stags (about 15 individuals), in the same period, had roughly the same antler configuration, with a predominance of 5 – 6 pointers among adults. Also, the only stag reared in captivity had antlers with two and three tine beams as an adult (1980 – 1989). According to reserve personnel, the present antler conformation

has invariably occurred for at least 30 – 35 years: the only partial exception is represented by a basal fragment of beam just cast-off, collected in 1981, that had a short stump (snag) about 1 cm long above the brow tine, in the typical position of the bez tine. Antlers with a bez tine, and with a rudimentary three-pointed crown, were sometimes observed and collected in the Mesola Wood during the first decades of the century (Castelli 1941: 311); the last very rare examples date back to the 50s.

The complete lack of antlers with crown during the last decades is surprising, practically unique: the multi-pointed cup-like crown is a constant characteristic of all the European populations of red deer. Only in the Asiatic and North-American forms is it very uncommon (maral, hangul, shou) or absent (wapiti) (Geist 1971, Groves and Grubb 1987, Dolan 1988). The crown originated in the early Middle Pleistocene and since the late Middle Pleistocene became a regular antler trait (Beninde 1937, Lister 1987). The absence of the bez tine is equally peculiar; it is an exclusive tine of this species, present in all populations, though not in all individuals or in all antler sets. According to Isakovic (1969) the bez tine was missing only in 5.5% of the adult stags in Pannonia, while it was lacking in 28.5% of cases in the Carpathians. In the German area of the Harz Mountains, which is sufficiently representative of the Central Europe condition, the bez tine occurred in about half the stags 8 – 14 years old during the 80s (H. Drechsler, pers. comm. 1989).

Typically, a fully mature European stag has antlers with 10 – 12 total tines (Drechsler 1980, Langvatn 1986). The three-tined beam already occurs at 2 years of age and the four tine condition is typical of stags 4 years old (Reulecke 1987). Even the modest antlers of deer from the Scottish Highlands and Sardinia are on average less simplified and more variable than those of the Mesola Wood (Lowe 1971, Mitchell *et al.* 1986; Beccu 1989, S. Mattioli, pers. obs. 1990). And yet, the Scottish and Sardinian red deer are quite similar to the Mesola deer in body size. At Glenfeshie (Scotland) adult stags sampled had a mean live weight of 115 kg, a mean antler mass of 1.2 kg, and a mean tine number of 6.6 (range 0 – 14) (Mitchell *et al.* 1986). Adult stags shot at Rhum (Scotland) in 1957 – 1965 had the same mean body weight, with an antler mass averaging about 1.35 kg; they were mainly 8 – 9 pointers, but tine number ranged from 0 to 16 (V. P. W. Lowe, pers. comm. 1986). In Sardinia adult stags weigh 100 – 120 kg and have a number of antler tines ranging from 0 to 12 (Beccu 1989). Adult stags from Mesola weigh on average about 110 kg, are typically 5 or 6 pointers bearing antlers of 0.9 kg; at 10 or more years of age, they reach a body weight of about 120 – 125 kg, are on average 6 pointers, and have a mean antler mass of 1.25 kg (SD = 0.36, $n = 23$) (Mattioli 1990 and unpubl.).

Only the antlers of the extinct Corsican red deer may have had an equally simplified construction (Vigne and Marival-Vigne 1988): but this may be an artifact due to the limited sample available, as suggested by a comparison with the similar Sardinian red deer antlers (S. Mattioli, pers. obs. 1990).

Antlers, like other secondary sexual characters, have low growth priority and are strongly affected by ecological factors: their growth and dimensions are influenced by food quality and availability (Vogt 1947, Goss 1983, Brown 1990). Antler size varies in response to periodic environmental fluctuations (Anderson 1981, Rasmussen 1985, Schmid 1990). Colonizing populations in high quality habitats ('dispersal phenotypes', *sensu* Geist 1987) display rapid body growth, but also relatively large antlers (McCorquodale *et al.* 1989). Resource-restricted populations in environments with poor forage and/or at high density ('maintenance phenotypes' of Geist 1987), show, together with a low reproductive performance and modest body size, scarcely developed antlers (e.g. Scotland, Sardinia and North Africa). Antler dimensions are often used as a 'condition index' of cervid populations (Anderson and Medin 1969, Rasmussen 1985, McCorquodale *et al.* 1989, Brown 1990).

High population density tends to delay antler development, resulting in a high proportion of knobbers among yearlings (Clutton-Brock *et al.* 1982, Mitchell *et al.* 1986). Pedicle initiation is associated with a threshold body weight and the development of the first antler set is only possible when the pedicle reaches a critical length (Suttie and Kay 1983, Fennessy and Suttie 1985). Dietary deficiencies during foetal growth or early life can condition the maturation of the endocrine system, with marked effects on pedicle and antler development of young stags ('retarded' deer of Bubenik 1983). Stags characterized by delayed maturation are occasionally unable to compensate in adult age for initial disadvantages: the 'hummel' phenomenon, occurring in marginal and impoverished habitats, seems to be a case (Lincoln and Fletcher 1984). The poorly developed cranial appendages of yearlings and subadults from the Mesola Wood may be primarily due to undernutrition. During the study period, this red deer population clearly suffered the effects of high density and inter-specific competition (around 6,700 – 10,200 kg of ungulate biomass per sq km), with reduced body weights, attenuated sexual dimorphism, delayed puberty, low calving rate and post-winter recruitment (Mattioli 1990, 1993). But as noted above, the current antler design has been present in the Mesola Wood for decades, even when the density was much lower (1950 – 1970: perhaps 1 – 4 red deer plus 0 – 21 fallow deer per sq km, equivalent to about 70 – 1,200 kg of biomass per sq km). This suggests a possible role for genetic factors, which in adult stags could prevail over nutritional effects. Body size and antler characters have been related to genetic variability; high levels of heterozygosity in white-tailed deer *Odocoileus virginianus* from Savannah River Plant corresponded to greater body mass, antler length and number of tines (Scribner *et al.* 1989, Scribner and Smith 1990). Hartl *et al.* (1991) failed to detect any association between heterozygosity and antler features in red deer, but they found a relationship between certain genotypes and morphological characters of antlers; they also documented an influence of selective hunting on allele frequencies at genes associated with physical traits used as selection criteria.

Hunting (legal until the 1940s) and poaching, deliberately removing the best 'trophy' stags from Mesola Wood (Castelli 1941: 312), may have affected the gene pool of the small population of red deer. Moreover this relict nucleus of animals is heavily inbred; in 1945 – 1947 perhaps only 10 survived and the sub-population of the Elciola enclosure originated in 1972 from probably 12 founders. The founder principle has been proposed to explain the simple antler shape in two different populations of sika deer *Cervus nippon* (Feldhamer *et al.* 1985, Kaji *et al.* 1988); the same effect was suggested for high quality antlers of white-tailed deer from George Reserve (McCullough 1982). The Mesola red deer, segregated for centuries in a restricted and relatively unproductive area, probably has been represented for long periods by maintenance phenotypes, with animals of reduced stature and poorly antlered stags; 'trophy'-oriented shooting, genetic bottlenecks and inbreeding may have 'crystallized' the already simple antler architecture. In order to fully understand the potential of the Mesola red deer and verify to what extent the current antler traits are reversible, it is essential to remove as far as possible the present disturbing factors (lowering density, eliminating other ungulates and improving the quality of pasture) and to start a genetical screening and controlled breeding programs.

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