

## On the habitat and diet of *Cervus Elaphus*

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### INTRODUCTION

By whatever quantitative measure employed, *Cervus elaphus* was the most important animal species hunted for food by Upper Paleolithic and Mesolithic inhabitants of Cantabria/Vascongadas. Red deer remains are present in all archeological deposits excavated to date, and numerically predominate in all levels, except for those of a few sites which, by dint of their location in or near areas with steep, rocky slopes, served at some or all times as specialized ibex hunting stations (e. g. Ermitia, Ekain, Bolinkoba, Rascaño, Collubil and certain levels at La Riera). (Reindeer slightly surpasses red deer in only one Basque site level: Urtiaga I, where all faunal remains are very scarce [Altuna 1972: 173, 330, 416].) Red deer obviously thrived in the Würm Upper Pleniglacial and Tardiglacial environments of Vasco-Cantabrian Spain, as evidenced not only by their overwhelming numerical superiority in prehistoric game bags, but also by their often very large size—far larger than that of modern Iberian *Cervus* (Vega del Sella 1930:85; Altuna 1972:328-30, 407; Fuentes & Meijide 1975:64).

The clear importance of red deer to the diet of prehistoric inhabitants on the region—beginning particularly in the Solutrean and Lower Magdalenian—has been discussed by many recent authors (Altuna 1972; González Echegaray 1972-73; Freeman 1973; Straus 1977). Many characterizations of preferred

*Cervus* habitat have stressed that this cervid is a woodland species (Freeman 1973:II; Straus 1977:55; Madariaga 1966:76-77, but see also Madariaga 1978). The presence of high percentages of red deer remains in archeological levels has been commonly taken as an indicator of forested conditions (see for example González Echegaray 1966: 4, 6, 9). However, the constant abundance of *Cervus* throughout the Last Glacial and early Holocene posed a problem to its use as an environmental indicator. González Echegaray (1972-73:171), following Vega del Sella (1930:85), argued that there were two Würm subspecies: one, large and adapted to rigorous climates and the other, smaller and adapted to forested, more temperate and humid conditions. There is as yet no indication that such was the case in Cantabria.

### VASCO-CANTABRIAN RED DEER

#### HABITATS OF THE LATE WÜRM

The application of pollen analysis to the study of several Cantabrian sites in recent years (e.g. Leroi-Gourhan 1966, 1971, n.d.; Boyer-Klein 1976) has produced direct evidence for Last Glacial vegetation types, obviating the need to rely on the highly imprecise use of large mammals for such purposes. These palynological results immediately call into question the existence of a woodland habitat for *Cervus*, especially during glacial maxima in Cantabria. A brief comparison of percentages of red deer remains and percentages of arboreal pollen grains from the same archeologi-

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Site	Level	Period	% <i>Cervus</i> Remains	% Arboreal Pollen
La Riera	9	Solutrean	80.7	4.0
»	10	»	83.0	0.25
»	11	»	90.4	4.0
»	12	»	82.6	3.25
»	13	»	76.6	5.5
»	14	»	79.7	2.75 (av.)
»	15	»	80.0	1.5
»	16	»	79.1	6.0 (av.)
»	17	»	80.7	3.5
»	18	Lower Magdalenian	82.0	2.0
»	19	» »	77.6	11.0
»	20	» »	81.1	4.75
»	21/23	Upper Magdalenian	84.3	5-11 (av.=8.3)
Cueva Morín	3	Solutrean	76.1	10.0
» »	2	Upper Magdalenian	81.1	2.0
» »	1	Azilian	86.6	3.0
Tito Bustillo	1c	Upper Magdalenian	85.2	0-18 (av.=8.7)
» »	1b	Upper Magdalenian	79.3	7.0

cal levels serves to illustrate this point. Selected for presentation are levels with very high percentages of deer remains and very low AP. Sources are Altuna (1971, 1976, n.d.), Leroi-Gourhan (1971, n.d.) and Boyer-Klein (1976).

In addition, in the Terminal Magdalenian/Azilian of El Otero, with a great majority of red deer remains (number unspecified) (Madariaga 1966), there are only 3.5-4.5 % arboreal pollen (Leroi-Gourhan 1966). For a species supposedly with woodland preferences, *Cervus elaphus* was consistently the main game animal in cold late Würm environments which included few if any trees-many or most of which were pines. In contrast, early Holocene pollen samples indicate the presence of fairly dense forests (with many thermophile deciduous species of trees): 53 % AP in the La Riera Asturian *conchero* (Leroi-Gourhan n.d.); 42.4% AP in the Asturian Level (1) of Liencres (Clark and Menéndez-Amor 1975). Red deer was the dominant Asturian game species too, although there were by then also significant numbers of roe deer and boar.

### CERVUS ELAPHUS HABITAT

The question posed by this apparently contradictory information concerns the diet of *Cervus elaphus*, as diet is the key element in

determining the habitat of an animal species. To maintain that red deer is fundamentally a forest animal is to suggest a diet which is first and foremost based on browsing as opposed to grazing. This note is an exploration of that proposition, using data on the habitats and eating habits of Eurasian red deer and North American wapiti (or elk) - both now generally acknowledged to be members of one Holarctic species, *Cervus elaphus* (see Flerov 1960; Altuna 1976b; preface and various papers in Boyce & Hayden-Wing 1979).

It is true that in the present day, *Cervus elaphus* tends to be associated with wooded areas of Eurasia and North America (Corbet 1966; Hainard 1949; Henrich 1961; Page 1964; Van den Brink 1968; Walker 1968). However, Darling's (1963) classic study of red deer behavior (*A Herd of Red Deer* - first published in 1937) was conducted in the open moors of the western Scottish Highlands (ca. 58° N), where trees (mostly pines) are limited to relatively small groves. Nonetheless, the density of red deer in this largely open habitat is high: about one deer per 40 acres. On the nearby Island of Jura, which is essentially treeless, the figure is a very high 1 deer per 15.5 acres (Page 1964); on the Island of Rhum, also off the western Highlands, there is a similar density of 1 per 15.3 acres, with home rangers of 400-

500 acres (Lowe 1966). In contrast, the figure is about one deer per 100-120 acres under heavily wooded conditions in Bohemia and England (Leopold 1933; Page 1964). More recently determined density figures from American forests are highly variable (depending in part upon method of determination), but the point is that red deer abundance on the open Scottish moors is high and the animals seem to thrive, Flerov (1960:136) argues, in fact, that red deer are mostly found in hilly or mountainous areas today due to displacement from the plains by man, and that the confinement of most red deer to densely forested areas is likewise an artifact of pressure from humans. He believes that *Cervus* was originally a creature of forest-steppe or open forest, for which reason it still prefers forests with grassy meadows. Murie (1951:53), writing on the North American elk, which was once distributed from the Atlantic to the Pacific in both open plains and wooded mountains, believes that the elk of the plains were simply exterminated or driven to refuge in the mountains by white hunters in the 18th and 19th centuries.

Darling (1963:53) notes that, unlike roe deer (*Capreolus capreolus*), red deer is not a «true woodland creature», pointing out that while roe deer move by bounding (a method useful in undergrowth), red deer trot. In addition, roe deer have a capacity for recognizing detail at short distances in woodland, whereas red deer have much longer sight (useful in the open).

### **CERVUS ELAPHUS DIET: EUROPE**

Despite differences concerning preferred habitats among various authors, many agree that red deer are highly eclectic in their eating habits (Altuna 1976b:193; Borowski & Kossak 1975; Cabrera 1914:340; Corbet 1966; Darling 1963:147 ff., 195; Flerov 1960:137; Hainard 1949; Henrich 1961; Dzieciolowski 1967, 1970 a, b, c; Hobbs et al. 1979; Marcum 1979; Murie 1951:254-5; Pribicevic & Bogovic 1967; Walker 1968; see also Page 1964 and Uloth 1968 for discussion of red deer feeding on seaweed and other aquatic plants, and Darling 1963: 195 and Lowe 1969 for evidence that red deer even rapidly consume the antlers and bones of dead

conspecifics, probably for their calcium phosphate). (In Texas and New Mexico deserts, elk even eat agave [Murie 1951:207].) *Cervus elaphus* not only eats leaves, conifer needles, twigs, nuts, shoots and bark of trees, but also bushes and shrubs, forbs (including many composites), grasses of all sorts, sedges, ferns, mosses, lichens, mushrooms and other fungi. Dietary mix generally depends more or less directly on what plants are available and found in association with one another (see Borowski & Kossak 1975; Kossak 1976). The extent to which *Cervus elaphus* is dependent on grasses and forbs is surprising in light of the supposed woodland adaptation of this cervid. Jensen (1968) found that grasses dominated rumen contents of Danish red deer living in both forested and open dune areas. Grasses, sedges and forbs (and dwarf shrubs such as the heathers) are mainstays of the Scottish Highlands red deer (in the near absence of trees) (Darling 1963:149-52). The abundant red deer of Rhum can only graze on grasslands and grass-heaths, as there are no trees (Lowe 1969).

From observations of actual (wild and tame) red deer feeding in lowland Polish (mixed coniferous and mixed deciduous) forests (ca. 52-53° N) with some open areas and various stages of climax, Dzieciolowski (1967) found that the diet included very few grasses or herbs in winter when the deer depended on browse. However in spring, 19 % of the diet came from herbs and 7 % from grasses, sedges and rushes; in summer 36 % and 19 % respectively, and in fall 15 % and 37 % respectively. The importance of grazing even in these dense Polish forests is confirmed by rumen content analyses (Dzieciolowski 1970a). In general, controlled feeding experiments with tame red deer in Poland have found up to 32 % use of grasses, sedges and rushes in coniferous forest, and up to 33 % use of dicotyledonous plants in mixed deciduous forest (Dzieciolowski 1970c).

### **NORTH AMERICA**

Many detailed studies of *Cervus elaphus* habitat and diet have recently been published

in the United States and Canada (especially Boyce & Hayden-Wing 1979), where wapiti were (and, to a lesser extent, are still) distributed over a vast range and diversity of environments. These studies help complement the European studies cited above. In the East, wapiti ranged from Georgia in the south to Québec in the north, and in the Rocky Mountain West, from the Guadalupe Mountains of the New Mexico-Texas-Mexico border area (32° N) north to the border between Alberta and Northwest Territories (60° N) (Murie 1951). This range spans a wide diversity of deciduous, mixed and coniferous forests, grass plains, deserts, lowlands and mountains, and is testimony to the adaptability of *Cervus elaphus* and catholicity of its feeding habits. In his classic study, *The Elk of North America*, Murie (1951:198-9) stresses that grass is the preferred food of elk all year long, and, where available in sufficient quantity, can dominate the diet - especially in winter (in the regions he studied). Sedges are also important to elk diet, as are a wide variety of herbaceous plants (weeds, herbs and other forbs, etc.) (Murie 1951:204-5).

Detailed observations of summer elk feeding in favored high Rocky Mountain meadows in Idaho have revealed a heavy reliance on forbs, sedges and grasses, in descending order of importance. Shrubs (mostly *Salix*) were of far lesser importance (Hayden-Wing 1979a). In high Rocky Mountain pastures of Colorado, Hobbs et al. (1979) found that 60 % of elk winter diet consisted of graminoids (grasses and grass-like plants), while 65 % of summer diet was so composed. Protein content of the grasses (even when these are not snow-covered and thus available to elk) falls in winter, perhaps explaining the elk shift to a greater intake of browse with then higher protein content. Graminoids were found to be important (31 %) in early summer (June) in the Rocky Mountains of western Montana, but then fell off rapidly in dietary importance toward the end of summer (Marcum 1979). The same study showed that forbs provided over half the overall summer elk diet, with browse constituting an average of 36 %, with marked increase in use in late summer. Graminoids once

again became significant in fall, reaching nearly two-thirds of the total diet in October, as forbs decreased in importance and browse remained at about one third of the diet. Marcum's (1979) study area was 93.3 % forested (mostly pines, firs, spruce and larch), yet the elk found plenty of grasses and forbs to graze in clearings, making for a healthy, productive herd.

In the Pauline pasture of the National Bison Range in the Rocky Mountains of northwestern Montana, elk stomach contents were analyzed for a full year feeding cycle by Morris and Schwartz (1975). This mountain valley locality consists mostly of *Agropyron* grassland with limited stands of Douglas fir and Ponderosa pine, as well as some shrubs. Elk ate from 100 to 96 % grasses in all months, except for 90 % in July and 67.5 % in August, when the remaining 32.5 % of the contents were forbs. In this environment, elk ate far more grass than did deer (*Odocoileus*), which browsed and ate forbs to a much greater degree than elk in all seasons. In the Elk Island National Park near Edmonton, Alberta (Canada), an area of mixed boreal forest with stands of aspen, willow and birch, sedge meadows and grasslands, both elk and bison graze extensively. Bison eat 100 % grasses, sedges and forbs in spring-summer, and elk eat 95 %; in winter bison eat 99 % grasses and sedges while elk eat 36 %. In winter the elk browsed primarily willow and aspen for the remainder of their food (Telfer and Cairns 1979).

On the northwest coast of California, in lowland redwood forest with grassland clearings, as well as shrubs and forbs, Harper (1962) observed natural feeding of elk. Grasses made up 75.9 % of their diet in winter, 61.1 % in spring, 57.6 % in summer and 56.5 % in fall. Forbs were only significant in summer (20.2 %) and fall (22.5 %), with browse constituting about 20 % in all seasons except spring (33.6 %).

Mackie (1970), cited by Spiess (1979:255) found that *Cervus*, in an area of the Upper Missouri valley with 45 % *Pinus-Juniperus* parkland and 55 % grassland with *Artemesia*, more resembled cattle in its preference for

grass than its browsing cervid relative, *Odocoileus*. Only in summer do *Bos* and *Cervus* diets diverge somewhat, with the former eating more grass and the latter more forbs.

In a very different environment (hardwood forest of the Allegheny Plateau in southeastern Pennsylvania) elk also have been found to eat large amounts of herbaceous vegetation, particularly in summer-early fall (Devlin and George 1979). Browse is an important source of winter elk food in this area, but in these forests (as is usually the case) open areas with young growth are preferred by the elk. Dense stands of aspen are not usually browsed (Hunter *et al.* 1979).

These examples, drawn from the European and North American literature, show that while often restricted to forest areas today, *Cervus elaphus* is a highly eclectic feeder, depending for a major proportion of its diet on the grazing of grasses (including sedges and other graminoids) and forbs (including *Compositae* and *Ericaceae*). The extent of such dependence varies with season and habitat type. It is of note that this cervid species seeks open feeding areas when dwelling in a generally forested environment, and can thrive in almost totally open environments as well (heath moors, prairie grasslands, etc.). *Cervus elaphus* is unlike other deer found commonly in forests (e.g. *Capreolus*, *Odocoileus*) in its heavy use of grass and much lesser general dependence upon browse.

### CERVUS ELAPHUS IN WINTER

If they are not a universally essential dietary resource for *Cervus elaphus*, trees are nonetheless useful especially as starvation food, particularly in areas of deep/crusted winter snow. Where the red deer live in forested areas, as in Poland (or Pennsylvania), browse can provide a major portion of their winter food (Dzieciolowski 1967; Hunter *et al.* 1979). In the Polish forests, *Pinus sylvestris* browse can make up a fifth of the winter diet of red deer, but it is probably mostly hunger food, due to the unavailability of preferred foods (Borowski & Kossak 1975:500-1). In the Jackson Hole - Yellowstone Parks of Wyoming where Murie (1951:242) conducted most of his

studies, the elk turn to browsing Douglas fir and lodgepole pine extensively only in February. In bad winters and in some areas, their diet may be 100 % browse if the grasses, sedges and forbs have either been consumed earlier or are covered with deep, crusted snow (see also McNamara 1979). But Murie (1951:243) notes that such desperation browsing is a sign of an overstocked elk range: «Where the animals are less numerous, they have a much easier time (in winter).» Knight (1970), cited by Spiess (1979:255-6), found that while elk may enter forested areas of the Rocky Mountain foothills of Montana in winter, they still primarily rely on grasses for food, although this dependence varies with weather conditions. Very extensive winter dependence upon browse is, therefore, not necessarily a characteristic of *Cervus elaphus* at all times and places; in fact the Scottish Highland red deer do largely without.

Trees may be very important to red deer/elk in winter, however, as shelter from storms. Yarding is a notable characteristic of *Cervus elaphus* (Henrich 1961; Flerov 1960; 137-8; Murie 1951: 49,61,263), although Darling (1963: 53) cautions against overemphasizing even this aspect of the relationship between trees and *Cervus*. In the absence of fens, red deer seek shelter from winter winds and precipitation behind natural topographic features, as on the Island of Rhum (Lowe 1966). The concentration and aggregation of *Cervus elaphus* in «yards» is in part due to the effect of snow (see Hayden-Wing 1979b; Eveland *et al.* 1979; Telfer & Cairns 1979; Olmsted 1979). Deep (60-80 cm.) and/or crusted snow definitely hinders or practically stops the movement of *Cervus elaphus* (Borowski & Kossak 1975; Hayden-Wing 1979b) - making snow, incidentally, a very useful tool in hunting this and many other ungulate species. Smaller cervids (e.g. *Capreolus*, *Odocoileus*) are hindered by much less deep snowfalls, although, being lighter than *Cervus*, they can often walk atop crusted snow. Obviously, aggregation allows *Cervus* to dig collectively through the snow to reach dry grasses and forbs, although winter aggregations may occur in wind blown, snowless areas or in thickets with browse as well as shelter.

## CONCLUSIONS

The purpose of this note has been to show that *Cervus elaphus* is neither necessarily a forest dweller nor necessarily a forest feeder. Worldwide the species is notably adaptable to a very wide range of climatic, topographic and vegetational conditions. One remarkable characteristic of red deer/wapiti/elk is its extensive (sometimes nearly exclusive) and successful use of grasses and forbs for food—seasonally or year-round—particularly in areas which are either treeless or which have extensive meadows. In short, *Cervus elaphus* is to a very great extent a grazer, although it can make use of browse when circumstances (e.g. a fairly densely forested habitat; deep/crusted snow) require.

Returning to the evidence from Late Würm Cantabria, then, the presence/dominance of *Cervus elaphus* in often essentially treeless habitats dominated by grasses, composites and, sometimes, heaths, is not surprising in light of the modern evidence of red deer habitats from Eurasia and North America. Up to 70 % of the pollen in red deer-dominated level 1 b of Tito Bustillo are of *Graminae*; well over half (ca. 65 %) of the pollen in level 1c are of *Ericaceae* (Boyer-Klein 1976). Heaths (*Erica*, *Calluna*, etc.) make up very nearly 100 % of the pollen in some heavily red deer-dominated levels (especially level 15) at La Riera and over 50 % in several other levels, while grasses can constitute up to 20-30 % and composites 40-60 % in others where *Cervus* remains constitute 80 % of the fauna (or more) (Leroi-Gourhan n.d.). Very high percentages of composites characterize the pollen spectra from the Solutrean, Magdalenian and (Tardiglacial) Azilian of Cueva Morin (Leroi-Gourhan 1971). *Cervus elaphus* today can and obviously did in the late Pleistocene thrive in such open environments, presumably seeking shelter from winds and snow in localized thickets or on low, south-facing slopes of the numerous small valleys of the coastal zone. The generally large size of late Pleistocene red deer from Cantabria compared with the very small average size of modern Iberian red deer is an indication of the optimal nature of the Würm

habitats (as well as perhaps the operation of Bergman's law [Altuna 1976b:187 fn. 1]).

In trying to explain the abrupt difference between the reindeer-dominated archeological faunas of extreme southwestern France and the red deer-dominated ones of north-central Spain, Altuna (1972:416; 1976a:162; 1979) argues that the latter region served as a less than optimal «refuge» for *Cervus elaphus*, blocked in its attempt to move even further south during periods of great cold by the Cantabrian Cordillera. Yet Altuna (1979) himself notes that the range of this species today extends into areas of Europe with severe winter temperatures (to about 65° N in Scandinavia), and that at times Cantabria lacked the trees he argues were another differentia between *Cervus* and *Rangifer* habitats. It seems clear that another factor besides diet and habitat—that of competition between the two species—needs to be investigated. Perhaps reindeer (with its specially constructed hooves) had the competitive edge in snow (Banfield 1951:30; Kelsall 1968:34), for example, while red deer had it in the more broken terrain of Cantabria. A comparative study of the diets of these two large cervids—both very broad in their feeding behavior—would obviously also be most useful. Despite the scarcity or lack of trees, Vasco-Cantabrian Iberia was rich in grasses, composites and heaths, and had adequate shelter and water to allow red deer to not only survive, but to thrive—much to the benefit of Upper Paleolithic hunters.

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