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THE FUNCTIONS OF ANTLERS

by

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(With 2 Plates)

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> "When the males are provided with weapons which in the females are absent, there can hardly be a doubt that these serve for fighting with other males; and that they were acquired through sexual selection, and were transmitted to the male sex alone."
>
> DARWIN, 1871. p. 502

INTRODUCTION

Like the curving tusks of the babirusa, the spiral spears of male narwhals and the ornate horns of the lamellicorn beetles, the spectacular antlers of male cervids pose a fascinating problem to evolutionary biologists. The heavy energetic costs of annual antler renewal (GOSS, 1970) indicate that if antlers did not afford their possessors some important advantage, selection would quickly suppress them. Moreover, the common argument that non-functional traits may be retained through phylogenetic inertia (see WILSON, 1975; GOULD, 1979) is untenable in this case since antler-less phenotypes (hummels) occur regularly though rarely in many cervid species (*e.g.* LYDEKKER, 1898; MITCHELL & PARISH, 1970).

What are the functions of antlers? Although antlers are one of the most commonly cited examples of sexual selection, their adaptive significance is widely disputed (GEIST, 1966a, b, 1971a, b, 1978; HENSHAW, 1968, 1969; STONEHOUSE, 1968). While many possible functions have been suggested (see GEIST, 1966a; GEIST & BROMLEY, 1978), ranging from the removal of excess minerals in the diet (KRIEG, 1937 in BENINDE, 1937) to assistance in erotic stimulation (DARLING, 1937; PRUITT, 1960), five plausible reasons why antlers might be maintained are current in the

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literature: (1) because they act as weapons in intra-specific combat, (2) because they provide a defence against predators, (3) because they serve as heat radiators during their period of growth, (4) because they display the dominance or fighting ability of their possessor and allow competing males to assess each other without fighting, (5) because they reflect the genetic quality of the male and are maintained by female choice and epigamic selection.

A necessary preliminary to any attempt to evaluate different functional explanations for a trait is to be clear about the meaning of the term function. It is taken here to refer to those consequences of a trait through which natural selection acts to spread or retain the trait in a population (see HINDE, 1976; CLUTTON-BROCK & HARVEY, 1979). Thus evidence that an animal uses an appendage in a particular context need not imply that this use is a function or that it contributes to the maintenance of the trait. For example, males of many primate species will display their penises in aggressive interactions with their rivals (*e.g.* BALDWIN, 1968) but this does not mean that this use necessarily explains why they possess penises or even that it generates selection pressures which modify penis shape or size.

This paper critically reviews evidence for each of the five hypotheses concerning the functions of antlers and concludes that the only one for which there is compelling evidence is their use in fighting. Of course, evidence for a particular function does not necessarily indicate that others are not involved, nor does the absence of evidence for an effect necessarily indicate that it is unimportant. Nevertheless, the absence of unequivocal support for the importance of antlers in defence against predators, in heat regulation, in assessment between rivals and in selection by females leaves open the possibility that, despite their bizarre appearance, antlers evolved as weapons and are retained because of their functions in intra-specific combat.

ANTLERS AND INTRA-SPECIFIC COMBAT

(1) *Antlers are weapons adapted for use in intra-specific combat* (DARWIN, 1871; GEIST, 1966a, 1971b; LINCOLN, 1972; CLUTTON-BROCK, ALBON, GIBSON & GUINNESS, 1979).

There is plentiful evidence to support the use of antlers in fights between stags. Even in small deer with short and simple antlers, they are used to parry the opponent's blows (BARRETTE, 1977) while, in large-antlered species where fighting males lock antlers, they are used to damage opponents, protect their possessors and, in some cases, to allow stags to grip their opponents firmly in head to head pushing contests (see Fig. 1). Natural breakage or experimental amputation of substantial parts of the antler beam have been shown to have a pronounced effect on fighting ability and dominance (ESPMARK, 1964; LINCOLN, 1972; CLUTTON-BROCK *et al.*, 1979). The occurrence of antlers in males and their absence in females (who do not have to fight for access to mating partners) is in accordance with the theory that they evolved as weapons. So, too, is the tendency for antlers to be most highly developed in species where individual males can monopolize breeding access to considerable numbers of females and variance in their reproductive success is likely to be correspondingly high (CLUTTON-BROCK, ALBON & HARVEY, 1980; CLUTTON-BROCK, GUINNESS & ALBON, in press).

Three principal objections to the theory that antlers evolved as weapons are found in the literature. First, it is argued that fights are too rare to justify the heavy energetic expenditure of growing antlers (DARLING, 1937; STONEHOUSE, 1968). This criticism ignores the fact that, even if fighting were uncommon, the evolution of elaborate weaponry might be favoured if the outcome of fights had an important influence on an individual's reproductive success — as appears to be the case in many polygynous mammals (LEBOEUF, 1974; CLUTTON-BROCK, ALBON, GIBSON & GUINNESS, 1979). However, contrary to some suggestions (DARLING, 1937; STONEHOUSE, 1968; GOULD, 1974), systematic observation of rutting males in the larger deer species shows that fights are *not* rare and that males are *commonly* injured. In two samples of Russian red deer, rutting mortality accounted for 13% and 29% of all adult male deaths respectively (HEPTNER, NASIMOVITSCH & BANNIKOV, 1961, quoted in GEIST, 1971b) while on the Isle of Rhum as many as 6% of rutting stags are permanently injured each year and some 25% show some sign of damage (including antler breakage) each rut (CLUTTON-BROCK *et al.*, 1979). In an expanding population of European moose in Poland (PIELOWSKI, 1969) the mean proportion of bulls killed in rutting fights each year was 4% while in a sample of 21 mature mule deer bucks observed during a single season by GEIST (1974), 19% were wounded and subsequent inspection of tanned hides suggests that the proportion of animals that are woulded may be even higher (GEIST, pers. comm.). In reindeer, BERGERUD (1973, 1974) estimated that rutting mortality was the commonest cause of death in adult males. If males rut for several years, even a relatively low chance of being severely injured *per season* can represent a high chance of injury at some stage in the individual's lifespan: to quote GEIST's (1971b) example, if only 4% of bull moose are killed in fights per year and surviving bulls rut for 10 years, over 30% of individuals will be killed at some point in their rutting life and almost all will be injured at some stage. Since even slightly injured individuals probably run a considerably higher risk of predation by large carnivores (KRUUK, 1972; SCHALLER, 1971) the advantages of possessing antlers that minimize the risk of injury are likely to be strong.

The second criticism of the idea that antlers are functional weapons is based on the suggestion that hummels are more successful in competition for females than antlered stags (LYDEKKER, 1898; WHITEHEAD, 1972; MCNALLY, 1975). DARLING (1937, p. 158) discussing Scottish red deer (*Cervus elaphus*) is emphatic on this point. ''A hard dunt in the ribs from the polled head of a hummel seems to upset his opponent more than a sharp jab from the points of an antler. Were it possible to take a count of services by each stag in a large population, I think it would be found that hummel stags would have covered individually a larger number of hinds than each of their antlered fellows... Lack of antlers would appear to be a biological advantage in Scottish red deer.''

If this were really the case, it would be surprising that selection has not suppressed antler growth in Scottish red deer many years ago and that hummels are so rare: DARLING estimated that only one in a hundred Scottish stags is a hummel while WHITEHEAD suggests that the figure is closer to one in 300 (WHITEHEAD, 1972). In fact, no study has yet collected the information necessary to compare either fighting ability or reproductive success between hummels and antlered stags and there is no definite evidence that hummels are generally more successful in rutting competition: observations that hummels occasionally win fights against antlered stags (*e.g.* MCNALLY, 1975) provide no firm basis for thinking that they are generally more successful. Moreover, experiments with red deer involving antler removal (see LINCOLN, 1972) suggest that hummels are likely to receive more challenges than antlered stags and are less well equipped to meet them. It is conceivable (and is commonly argued) that the suppression of antler growth in hummels permits them to grow larger than antlered stags and that this helps to compensate for the absence of antlers. However, despite the fact that the majority of stalkers avoid shooting the largest antlered stags but selectively shoot hummels, irrespective of size and condition, the only published comparison of the weights of hummels versus antlered stags found little difference between them (MITCHELL & PARISH, 1970). In fact, the correct question to ask may not be why hummels are so rare — but why they exist at all. Controlled breeding of the progeny of one red deer hummel showed that the trait was not under simple genetic control (Lincoln & Fletcher, 1977) and suggested that hummelling may be caused by adverse environmental conditions during early growth. Studies of several ungulate species have shown that in populations dependent on scarce food resources, both breeding competition between males and sexual dimorphism in body size is reduced (Clutton-Brock *et al.*, in press) and it is conceivable that, under these circumstances, selection may sometimes favour the suppression of antlers.

The third common objection to the suggestion that antlers are effective weapons is based on their shape and size. For example, the colossal, palmate antlers of the extinct giant Irish elk (*Megaceros giganteus*), with their backward-directed points, so impressed Gould that he affirmed that he would prefer to argue that they were a non-adaptive by-product of selection for increased body size (see Huxley, 1932) than that they were adapted to combat (1974, p. 212). Current knowledge of fighting behaviour is inadequate to judge the efficiency of antler conformation in many species. However, in red deer, for which detailed studies of fighting behaviour are available (Butzler, 1974; Clutton-Brock *et al.*, 1979), the numerous points assist both in gripping opponents, so that they can be twisted into a disadvantageous position, and in attempts to horn the opponent in parrying direct thrusts (Clutton-Brock *et al.*, 1979). The common argument that a single, forward-pointing spike would be more dangerous to the opponent (Darwin, 1871) may have some substance but a weapon of this kind would fail to protect its carrier's head and neck and would not provide a firm mechanism for gripping an opponent. Since a stag must win many fights in the course of its lifetime in order to breed successfully (see above), the effectiveness of antlers in defence in probably as important as their effectiveness in attack and their shape reflects this. The palmated antlers of fallow deer still present a problem. However, unlike red deer, which lock antlers base to base, fallow typically lock only the top points of their antlers (F. Alvarez, pers. comm.) and it is conceivable that the palmation of the upper points stiffens and strengthens them against breakage — a detailed analysis of the structure of antlers is long overdue. Though we shall never know how *Megaceros* used its gigantic antlers, it is not inconceivable that they were effective weapons, their great breadth providing leverage in attempts to twist the opponent sideways (see Clutton-Brock *et al.*, 1979) and the palmations of the upper antler reinforcing the long top points. That the latter curved upwards and backwards does not indicate that they could not have been used

Fig. 1. Mature red deer (*Cervus elaphus*) stags fighting on the Isle of Rhum (Scotland).

against a rival for most heavily antlered deer fight with their foreheads at an acute angle to the ground. In fact, DARWIN himself (1871) quotes a case where a wapiti stag when avoiding attempts to restrain it "kept his face almost flat on the ground, with his nose nearly between his fore feet". In this position, tines which are directed upwards and backwards when the animal is standing, point forward, forming an effective defence. Tines on the rear of the antler, which point backwards when the head is erect are also found in reindeer and fallow deer and may either assist in antler locking or may help to prevent any attempt by an opponent to lunge forward over the top of lowered antlers.

ANTLERS AND DEFENCE AGAINST PREDATORS

(2) *Antlers provide important weapons of defence against predators* (DARWIN, 1871; DARLING, 1937).

It seems unlikely that antlers are principally an adaptation to defence against predators: although larger species of deer will occasionally use their antlers against predators, they more commonly use their feet, while smaller deer rely on flight rather than defence (MECH, 1966; GOULD, 1974). Moreover, the absence of antlers in females of most species and the fact that several cast their antlers at the time of year when they are most susceptible to predation (WHITEHEAD, 1972; GEIST & BROMLEY, 1978) argues against this explanation though it is possible that the use of antlers in defence may contribute to selection pressures favouring their retention.

ANTLERS AND TEMPERATURE REGULATION

(3) *Antlers act as heat radiators during their period of growth* (STONEHOUSE, 1968).

In support of this argument STONEHOUSE points to the highly vascular nature of the integument of growing antlers, the lack of sub-dermal fat and the presence of shunts, permitting a rapid flow of blood through the major vessels without capillary intervention; to the branching formation of antlers, giving a large surface area: weight ratio; to the lesser development of antlers in small species with high surface area: volume ratios and reduced problems of heat loss; and to the fact that antlers are grown during the hottest months of the year. He counters the obvious objection that antlers are only present among males with the argument that, unlike females who are lactating, males gain weight rapidly during the summer and have larger subcutaneous fat reserves and more acute problems of temperature regulation than females.

However, the anatomical peculiarities of antlers can equally well be attributed to the necessity for very rapid growth, their form and size to their use in fighting (see above), and the fact that in most (thought not all) deer species they are grown in summer to the advantages of synchronising antler growth with the period of maximum food availability and the timing of the reproductive cycle. As GEIST (1971a, b) and HENSHAW (1969) have pointed out, a thermoregulatory explanation for antlers is unlikely for a variety of reasons. Not all deer species grow their antlers during the hottest months of the year — for example, roe deer (*Capreolus capreolus*) grow them during the winter (WHITEHEAD, 1972) while in tropical cervids there is no close association between antler growth and temperature (SCHALLER, 1967). In temperate species, like red deer and moose (*Alces alces*), males are fattest and temperatures are still comparatively high in late summer after antler cleaning has occurred (PETERSON, 1955; MITCHELL, STAINES & WELCH, 1977; CLUTTON-BROCK *et al.*, in press). Though the fat reserves of young and non-lactating females are typically as great (relative to their body weight) as those of stags (see MITCHELL, MCCOWAN & NICHOLSON, 1976; CLUTTON-BROCK *et al.*, in press) they show no obvious signs of heat stress during the summer months. Moreover, in most temperate species, fat is localized and would not provide a major impediment to heat loss (see POND, 1978). Finally, contrary to the predictions of STONEHOUSE's theory, the antlers of temperate deer species tend to be larger, relative to their body size, than those of tropical species (see WHITEHEAD, 1972).

ANTLERS AND ASSESSMENT

(4) *Antlers advertise an individual's fighting ability or dominance and allow competing males to assess each other without fighting* (BENINDE, 1937; GEIST, 1966, 1968, 1971a, b, 1978; BUBENIK, 1968; HENSHAW, 1968, 1969; LINCOLN, 1972; TOPINSKI, 1974; GOULD, 1974; BARRETTE, 1977).

Since fights between male cervids can be damaging to the winner as well as the loser, a trait which allowed males to assess each other's fighting ability and to settle contests without resorting to contact could be strongly favoured by natural selection (GEIST, 1971b; MAYNARD SMITH & PRICE, 1973; PARKER, 1974; CLUTTON-BROCK & ALBON, 1979). Three lines of evidence are commonly cited to support the suggestion that antlers have developed or been retained because they allow competitors to assess each other:

(a) evidence that antlers are used in aggressive displays (Beninde, 1937; Bubenik, 1968);
(b) evidence that loss of large parts of the antler affects fighting ability and dominance rank and increases the probability that an individual will be challenged (Lincoln *et al.*, 1970; Lincoln, 1972);
(c) evidence that antler size is correlated with dominance or fighting ability and that individuals react subordinately to animals with larger antlers (Beninde, 1937; Henshaw, 1969; Topinski, 1974).

However, the available evidence falls some way short of providing a clear indication that antlers are important in assessment, and can be explained on other grounds. Below we examine each of the lines of evidence in turn.

(a) As we have already argued, evidence that a trait is used in a particular context does not necessarily indicate that this use contributes to selection pressures maintaining the trait in its present form. Threats commonly contain elements of intention movements (Hinde, 1970) and it is unsurprising that these should involve the conspicuous presentation of the animal's principal weapons. That they do so, need not indicate that opponents assess each other by the form or size of their weapons, or that this use leads to selection pressures which modify the form of the weapons.

(b) Although experiments with red deer and reindeer provide firm evidence that amputation of substantial parts of the antler beam affects an individual's fighting ability and dominance rank (Espmark, 1964; Lincoln *et al.*, 1970; Lincoln, 1972) this does not show that natural variation in antler *size* affects an animal's fighting ability or is used in assessment procedures. If antlers are a stag's principal weapons, it would be surprising if rivals were not quick to attack a disarmed opponent.

(c) Despite frequent citations, there is little good evidence that antler size is closely correlated with fighting ability or dominance in natural populations and none that it has a direct effect on an individual's success in contests. Many of the studies that claim to demonstrate a correlation between antler size and fighting ability or dominance in cervids have included animals of very disparate ages, and this could account for the associations (see Clutton-Brock *et al.*, 1979). An extreme example is Topinski's (1974) study of a penned group of red deer, including one two-year-old male and three three-year-old stags, of which two had been castrated. Observing that dominance rank across these animals was correlated with antler mass, TOPINSKI concluded that the size of antlers was an important factor in the establishment of the hierarchy but — as differences in antler size were confounded with variation in age, body size and sexual status, it is possible that any of these three variables may have accounted for the relationship he observed. In reindeer, HENSHAW (1969) claimed that animals with larger antlers almost always dominated individuals with smaller ones, irrespective of age or sex, referrring both to his own previous work (HENSHAW, 1968) and to ESPMARK's (1964) study. However, neither study provides quantitative evidence of any relationship between antler size and dominance among animals of similar ages and ESPMARK (1964, p. 422) concludes that "with few exceptions, the relations of dominance were dependent on age and size of individuals".

Several recent studies of red deer have demonstrated associations between some measures of antler size or weight and estimates of fighting ability or dominance when age effects have been taken into account. In a group of fourteen red deer stage of between seven and ten years old on Rhum, CLUTTON-BROCK *et al.* found that the number of points on the antler was weakly correlated with fighting ability ($r_s = .466$, $n = 13$, $p \simeq 0.1$) while in one sample of stags over five years old (but not in another) APPLEBY (1981) found a positive correlation between antler weight and winter dominance ($r_s = 0.68$, $n = 19$, $p < .01$). In another study of fourteen four and five-year-old stags maintained in an enclosure, SUTTIE found a correlation between social dominance and antler weight ($r = 0.60$, $n = 14$, $p < .02$), (SUTTIE, 1979) but neither this study nor the previous one found any relationship between dominance rank and other more (visually) obvious measures of antler size, such as length and point number. In a group of 27 red deer stags in the Zehusice game reserve in Czechoslovakia, BARTOS found that antler weight and length were more closely related to an animal's dominance rank than age (BARTOS & HYANEK, 1981).

However, it is obviously unsafe to assume that any of these correlations indicate that there is a causal relationship between point number or antler weight and fighting ability or dominance. Point number and antler weight increase with a stag's body weight (HUXLEY, 1926, 1931; HYVARINEN, KAY & HAMILTON, 1977) and, since body weight apparently influences fighting success in red deer (CLUTTON-BROCK *et al.*, 1979, in press), as in many other vertebrates that fight by pushing (SCHEIN & FOHRMAN, 1955; BOUISSOU, 1972; ESPMARK, 1964; BERGERUD, 1972; DAVIES & HALLIDAY, 1977), the simplest explanation is that these relationships are a consequence of a correlation between body size and antler size. So far, no study has been able to examine correlations between antler size and dominance, controlling for the effects of variation in body size. It is relevant to note that when SUTTIE removed the antlers of all members of the group of stags that he observed, this had no effect on their dominance rank (SUTTIE, 1979), while in contests between mature red deer stags on Rhum, there is no consistent tendency for stags to avoid fighting individuals with larger antlers or, when they do so, for the stag with the larger antlers to win (CLUTTON-BROCK *et al.*, 1979, in press; APPLEBY, 1981), and similar results are reported for *Odocoileus* (GEIST, pers. comm.).

Since firm evidence that antler size plays an important part in assessment will necessarily be difficult to collect, it is worth asking whether individuals that did assess their opponents by their antler size would commonly make the right decisions. Since antler size is correlated with body size which is related to dominance rank and fighting ability, antler size must give some indication of an opponent's prowess. However, the correlations between antler size and fighting ability or dominance are not particularly close — for example, none of those described account for more than 50% of the variance in dominance rank — and, as we have already emphasized, it is not the most obvious aspects of antler size that are most closely correlated with fighting performance and dominance rank. Moreover, any stag that assessed its rivals principally on their antler size would make many inaccurate decisions because an individual's fighting ability changes during the course of the rut whereas his antler size remain constant. A more sensitive measure of a rival's prowess is provided by his behaviour in the roaring contests and parallel walks that precede fights which, unlike antler size, change as body condition deteriorates during the rut (CLUTTON-BROCK & ALBON, 1979).

If there is no conclusive evidence that deer assess their rivals by the size of their antlers, what evidence is there that other ungulates use their horns as a basis for assessment? The most widely cited evidence for assessment by antler or horn size is provided by the careful studies of mountain sheep by GEIST (1966b, 1971b). It is intrinsically more likely that horn size in sheep is related to fighting ability for, in contrast to deer, the horns are used as sledgehammers and an increase in their weight generates a multiple in force during the downward strike when rivals clash their horns (GEIST, 1971b; pers. comm.). Nevertheless, GEIST's study of mountain sheep does not provide unequivocal evidence that horn size is related to fighting ability when variation in age and size are taken into account. GEIST allocated rams over 26 months old to four horn-size categories (I-IV): the first three categories represented age grades and differed markedly in body weight, while Clas IV rams overlapped Class III in age, though they tended to be older and somewhat heavier (GEIST, 1971b, p. 57). Quantitative comparisons showed that, on average, Class IV rams were dominant to those belonging to the other three categories and had the highest reproductive success; that rams tended to interact with members of the same horn-size category; and that Class III rams behaved subordinately to Class IV rams even if they had not met before. However, GEIST provided no quantitative evidence for a relationship between dominance and horn size *within* these categories (though he cited two cases where a young ram dominated an older individual only when it has surpassed it on horn size) and his published data are open to the alternative interpretation that the dominance of rams was principally determined by their age and body size and the correlation between horn size and dominance was a consequence of a common dependance on body size (CLUTTON-BROCK & HARVEY, 1979). GEIST himself, was careful to point this out, concluding (1971b, p. 179) that "the demonstration that horn size of rams is more closely related than age to dominance is as yet outstanding" but the point is often ignored (see MAYNARD SMITH, 1979).

ANTLER SIZE AND FEMALE CHOICE

(5) *That relative antler size reflects the genetic quality of the stag, and that females mate preferentially with males possessing relatively large antlers* (BRUHIN, 1953; GEIST, 1971b; GOULD, 1974; ZAHAVI, 1975, 1977a, b; TRIVERS, 1976).

The suggestion that antlers serve as ornaments and may help to attract females dates back to DARWIN (1871): "If, then, the horns, like the accoutrements of the knights of old, add to the noble appearance of stags and antelopes, they may have been modified partly for this purpose, though mainly for actual service in battle; but I have no evidence in favour of this belief".

Unfortunately, there have been few attempts to study female choice in cervids and little quantitative evidence is yet available. In red deer, hinds avoid mating with young stags of less than five years old but this is probably due to the fact that the latter are unable to defend hinds effectively and their harems are regularly disrupted (CLUTTON-BROCK *et al.*, in press). Variation in reproductive success among stags of seven to ten years old is correlated with the number of points on their antlers, though not with antler length (CLUTTON-BROCK *et al.*, 1979). However, like the association between antler size and fighting ability, the simplest explanation of this association is that body weight is correlated both with point number and fighting ability and the latter affects reproductive success (ibid). There is little evidence in red deer that different hinds show similar (or even consistent) preferences for particular categories of stags (GIBSON, 1978): investigation of the comparative frequency with which hinds that left harems moved to different stags showed that they moved as frequently to the harem of a stag with smaller antlers as to one with larger antlers (CLUTTON-BROCK *et al.*, in press). Evidence of mate choice is again suggested by GEIST's study of mountain sheep (GEIST, 1971b): both in bighorn and in Stone's sheep GEIST found a (non-significant) correlation for females in oestrus to accept a higher proportion of mounts from Class IV males than from Class III. However, as in red deer, this could represent a tendency for females to avoid mating with younger and smaller males rather than any preference for individuals with large horns.

DISCUSSION

Thus, there is no conclusive evidence for any function of the antlers of male cervids other than their use as weapons in intra-specific combat and their occasional use against predators. This does not, of course, indicate that antlers are *not* used in assessment procedures between rivals or that females do not choose males according to their antler size — though in red deer, the cervid whose behaviour has been most intensively studied, stags apparently use other means to assess each other and there is no evidence that hinds selectively mate with stags on the basis of their antler size. Further studies of fighting behaviour and mate choice in other species are badly needed, though they will need to distinguish carefully between any effects of antler size and those of body size and age.

In several other groups of animals that possess bizarre weaponry, recent field studies have shown that the weapons are in fact effective in fights and elaborate functional explanations are unnecessary. Like antlers, the horns of lamellicorn beetles have been regarded as ornaments on the grounds that they do not appear well adapted to fighting and fights are seldom observed (Darwin, 1871; BEEBE, 1944). However, more detailed studies have revealed that males do fight regularly and that their horns *are* well adapted as offensive and defensive weapons (EBERHARD, 1979). In addition, horns occur in species where females have little opportunity to assess their mates by visual cues (OTTE & STAYMAN, 1979). The huge curving upper tusks that sprout from the forehead of the babirusa (Suidae) and which Wallace thought might serve as an eyeshield against spiny vines, apparently play an important part in protecting the face from the sharp lower tusks of rival males, and both upper and lower tusks are not infrequently fractured and chipped by blows (Mackinnon, 1981). Similarly, while many ingenious functions have been proposed for the tusk of the narhwal (*Monodon monoceros*), including its use as an ice augur and as a sound transmitter, observation of narwhals and the high incidence of broken tusks in adult males indicate that tusks are used as weapons in fights between males (Silverman & Dunbar, 1980).

But if, as I suggest, their use as weapons in intraspecific combat is the principal function of the antlers of male cervids, why do females habitually develop antlers in reindeer and caribou? No firm answer is yet possible but, among the cervids, reindeer and caribou are unusual in several ways which might favour the development of antlers. During much of the winter, both males and females dig craters in the snow to gain access to the lichens that are their main food supply (Pruitt, 1959, 1960; Leader-Williams, 1980). Food sources are thus more highly localised than is the case for most other cervids and social rank plays an important part in gaining and maintaining access to feeding craters. Moreover, unlike most cervids, females and males occur in the same herds during the winter so that females must compete both with each other and with the larger males. Consequently, weaponry that can be used in disputes may be important to female reindeer and may help them to gain access to adequate food supplies both for themselves and for their calves (Espmark, 1964). It is relevant that in primates, where canine teeth are the principal weapons, females have relatively larger canines in species where they have to compete frequently with males for food (Harvey, Kavanagh & Clutton-Brock, 1978).

A third difference between reindeer and most other cervids is that calves are remarkably precocious and follow their mothers from the day of birth (Lent, 1974; Espmark, 1971). Among African antelope, females tend to have horns in species where calves are precocious, perhaps because they need to defend their young against predators and conspecifics (Packer, in prep.) and this, too, could help to explain the incidence of antlers in female reindeer.

SUMMARY

1. This paper reviews evidence for five functional explanations of the evolution of antlers in male cervids: that they are used as weapons in fights; that they allow individuals to defend themselves against predators; that they act as heat radiators during their period of growth; that they advertise an individual's fighting ability and allow males to assess each other without fighting; and that they increase the chances that a male will be selected as a mate by females.

2. There is extensive evidence that antlers are used in fights between competing males. Contrary to some suggestions in the literature, fights are regular during the breeding season and can be damaging. In species where fighting behaviour has been studied in detail, antlers have proved to be effective weapons of defence and offense, and there is no systematic evidence to support the suggestion that antler-less males (hummels) are more successful in competition for females than antlered stags.

3. Though male deer sometimes use their antlers in defence against predators, the absence of antlers in females of most species suggests that this is not their principal function. Nor does it seem likely that antlers evolved as heat-regulating mechanisms — in some species, they are grown during the winter months and there is no tendency for them to be larger in tropical species than in temperate ones.

4. Despite many suggestions, there is no conclusive evidence that males assess each other by their relative antler size and most measures of antler size and shape are not closely correlated with dominance or fighting ability. Nor is there firm evidence that females selectively mate with large-antlered males.

5. The absence of unequivocal support for the importance of antlers in defence against predators, in heat regulation, in assessment between rivals and in attracting mates leaves open the possibility that, despite their bizarre appearance, antlers evolved as weapons and are retained by selection because of their function in intra-specific combat.

REFERENCE

Appleby, M. C. (1981). Social dominance: functional aspects in red deer stags. — Ph.D. thesis, Univ. of Cambridge.

Baldwin, J. D. (1968). The social behavior of adult male squirrel monkeys (*Saimiri sciureus*) in a seminatural environment. — Folia primatologica 9, 281-314.

Bartos, L. & Hyanek, J. (1981). The relationship between developed antlers and rank order in the red deer stag. — Abstract in 'International Symposium of Antler Development in Cervidae' Caesar Kleberg. Wildlife Res. Inst. Texas.

Barrette, C. (1977). Fighting behaviour of muntjac and the evolution of antlers. — Evolution 31, p. 169-176.

Beebe, W. (1944). The function of secondary sexual characters in two species of Dynstidae (Coleoptera). — Zoologica 29, p. 86-93.

Beninde, J. (1937). Zur Naturgeschichte des Rothirsches. — Monographie Wildsäugetiere. Bd. IV. Leipzig. P. Schops.

Bergerud, A. T. (1971). The population dynamics of Newfoundland caribou. — Wildl. Monogr. 25, p. 1-55.

—— (1973). Movement and rutting behaviour of caribou (*Rangifer tarandus*) at Mount Alberta, Quebec. — Can. Field Nat. 87, p. 357-369.

—— (1974). Rutting behaviour of Newfoundland caribou. — In: The behaviour of ungulates and its relation to management (Geist, V. & Walther, E., eds) IUCN, Morges, Switzerland, p. 395-435.

Bouissou, M. F. (1972). Influence of body weight and presence of horns on social rank in domestic cattle. — Anim. Behav. 20, 474-477.

BRUHIN, H. (1953). Zur Biologie der Stirnaufsätze bei Huftieren. — Physiol. Comp. et Eocol. 3, p. 63-127.

BUBENIK, A. B. (1968). The significance of antlers in the social life of the Cervidae. — Deer 1, p. 208-214.

BÜTZLER, W. (1974). Kampf und Paarungsverhalten, soziale Rangordnung und Aktivitätsperiodik beim Rothirsch (*Cervus elaphus* L.). — Z. Tierpsychol. Suppl. 16, p. 1-80.

CLUTTON-BROCK, T. H. & ALBON, S. D. (1979). The roaring of red deer and the evolution of honest advertisement. — Behaviour 69, p. 145-170.

——, ALBON, S. D., GIBSON, R. M. & GUINNESS, F. E. (1979). The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). — Anim. Behav. 27, p. 211-225.

——, —— & HARVEY, P. H. (1980). Antlers, body size and breeding systems in the Cervidae. — Nature 285, p. 565-567.

——, GUINNESS, F. E. & ALBON, S. D. (in press). Red deer: the behaviour and ecology of two sexes. — Chicago Univ. Press, Chicago.

—— & HARVEY, P. H. (1979). Comparison and adaptation. — Proc. R. Soc. Lond. B 205, p. 547-565.

DARLING, F. F. (1937). A herd of red deer. — O.U.P., London.

DARWIN, C. (1871). The descent of man and selection in relation to sex. Edition 1888. — John Murray, London.

DAVIES, N. B. & HALLIDAY, T. R. (1977). Optimal mate selection in the toad, *Bufo bufo*. — Nature 269, p. 56-58.

EBERHARD, W. G. (1979). The function of horns in *Podischnus agenov* (Dynastinae) and other beetles. — In: Sexual selection and reproductive competition (BLUM, K. & BLUM, R., eds). Academic Press pp. 231-258.

ESPMARK, Y. (1964). Studies in dominance-subordination relationship in a group of semi-domesic reindeer (*Rangifer tarandus* L.). — Anim. Behav. 12, p. 420-425.

—— (1971). Mother-young relationship and ontogeny of behaviour in reindeer (*Rangifer tarandus* L.). — Z. f. Tierpsychol. 29, p. 42-81.

GEIST, V. (1966a). The evolution of horn-like organs. — Behaviour 27, p. 175-214.

—— (1966b). The evolutionary significance of mountain sheep horns. — Evolution 20, p. 558-566.

—— (1968). On the interrelation of external appearance, social behaviour and social structure of mountain sheep. — Z. Tierpsychol. 25, p. 199-215.

—— (1971a). The relation of social evolution and dispersal in ungulates during the Pleistocene, with emphasis on the old world deer and the genus *Bison*. — Quart. Res. 1, p. 283-315.

—— (1971b). Mountain sheep: a study in behavior and evolution. — Chicago Univ. Press, Chicago.

—— (1974). On fighting strategies in animal combat. — Nature, Lond. 250, p. 354.

—— (1978). On weapons, combat and ecology. — In: Aggression, dominance and individual spacing (KRAMER, L., PLINER, P. & ALLOWAY, T., eds) Plenum, New York.

—— & BROMLEY, P. T. (1978). Why deer shed antlers. — Z. Säugetierkunde 43, p. 223-231.

GIBSON, R. M. (1978). Behavioural factors affecting reproductive success in red deer stags. — D.Phil. thesis, University of Sussex.

GOSS, R. J. (1970). Problems of antlerogenesis. — Clinical Orthopaedics 69, p. 227-238.

GOULD, S. J. (1974). The origin and function of 'bizarre' structures: antler size and skull size in the "Irish elk", *Megaloceros giganteus*. — Evolution 28, p. 191-220.

—— (1979). The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. — Proc. R. Soc. Lond. B. 205, 581-598.

Harvey, P. H., Kavanagh, M. J. & Clutton-Brock, T. H. (1978). Sexual dimorphism in primate teeth. — J. Zool. 186, p. 475-485.

Henshaw, J. (1968). A theory for the occurrence of antlers in females of the genus *Rangifer*. — Deer 1, p. 222-226.

—— (1969). Antlers - the bones of contention. - Nature 224, p. 1036-1037.

Heptner, W. A., Nasimovitsch, A. A. & Bannikov, A. G. (1961). Mammals of the Soviet Union. — Fisher-Verlag, Jena.

Hinde, R. A. (1970). Animal behaviour: a synthesis of ethology and comparative psychology. — McGraw Hill, New York and London.

—— (1976). The concept of function. In: Function and evolution of behaviour (Baerends, G. P., Beer, C. & Manning, A., eds). — Clarendon Press, Oxford. pp. 3-15.

Huxley, J. S. (1926). The annual increment of the antlers of the red deer (*Cervus elaphus*). — Proc. Zool. Soc. Lond. 67, p. 1021-1036.

—— (1931). The relative size of antlers in deer. — Proc. Zool. Soc. Lond. 19, p. 819-864.

—— (1932). Problems of relative growth. — MacVeagh, London.

Hyvarinen, H., Kay, R. N. B. & Hamilton, W. J. (1977). Variation in the weight, specific gravity and composition of the antlers of red deer (*Cervus elaphus* L.). — Br. J. Nutr. 38, p. 301-311.

Kruuk, H. (1972). The spotted hyena. — Chicago University Press, Chicago.

LeBoeuf, B. J. (1974). Male-male competition and reproductive success in elephant seals. — Amer. Zool. 14, p. 163-176.

Lent, P. C. (1974). Mother-infant relationships in ungulates. In: Behaviour of ungulates and its relation to management (Geist, V. & Walther, F., eds). — I.U.C.N., Morges.

Lincoln, G. A. (1972). The role of antlers in the behaviour of red deer. — J. Exp. Zool. 182, p. 233-250.

—— & Fletcher, J. (1977). History of a hummel. 5. Offspring from father/daughter matings. — Deer 4, p. 86-87.

——, Youngson, R. W. & Short, R. V. (1970). The social and sexual behaviour of the red deer stag. — J. Reprod. Fert. Suppl. 11, p. 71-103.

Lydekker, R. (1898). The deer of all lands. — Ward, London.

Mackinnon, J. (1981). The structure and function of the tusks of babirusa. — Mammal. Rev. 11, p. 37-40.

McNally, L. (1975). The year of the red deer. — Dent, London.

Maynard Smith, J. (1979). Game theory and the evolution of behaviour. — Proc. R. Soc. Lond. B. 205, p. 475-488.

—— & Price, G. R. (1973). The logic of animal conflict. — Nature 246, p. 15-18.

Mech, L. D. (1966). The wolves of Isle Royale. — U.S. National Park Fauna Series No. 7, 210 pp.

Mitchell, B. & Parish, T. (1970). Are hummels bigger than stags with normal antlers? — Deer 2, p. 521-522.

——, McCowan, D. & Nicholson, I. A. (1976). Annual cycles of body weight and condition in Scottish red deer, *Cervus elaphus*. — J. Zool. Lond., 180, p. 107-127.

——, Staines, B. W. & Welch, D. (1977). Ecology of red deer: a research review relevant to their management. — Institute of Terrestrial Ecology, Cambridge.

Otte, D. & Stayman, K. (1979). Beetle horns: some patterns in functional morphology. — In: Sexual selection and reproductive competition (Blum, K. & Blum, R., eds). Academic Press, New York.

Parker, G. A. (1974). Assessment strategy and the evolution of fighting behaviour. — J. Theor. Biol. 47, p. 223-243.

Peterson, R. L. (1955). North American moose. — University of Toronto Press, Toronto.

Pielowski, Z. (1969). Die Wiedereinbürgerung des Elches *Alces alces* (L.) im Kampinos - Nationalpark in Polen. — Z. Jagdwirtschaft 15, p. 6-17.
Pond, M. (1978). Morphological aspects and the ecological and mechanical consequences of fat deposition in wild vertebrates. — Ann. Rev. Ecol. Syst. 9, p. 519-570.
Pruitt, W. O. (1960). Behavior of the barren-ground caribou. — Biol. Papers University of Alaska 3, p. 1-43.
Schaller, G. B. (1967). The deer and the tiger. — University of Chicago Press, Chicago.
—— (1971). The Serengeti lion. — University of Chicago Press, Chicago.
Schein, M. W. & Fohrman, M. H. (1955). Social dominance relationships in a herd of dairy cattle. — Br. J. Anim. Behav. 3, p. 45-55.
Silverman, H. B. & Dunbar, M. J. (1980). Aggressive tusk use by the narwhal (*Monodon monoceros* L.). — Nature, 284, 57-58.
Stonehouse, B. (1968). Thermoregulatory function of growing antlers. — Nature 218, p. 870-872.
Suttie, J. M. (1979). The effect of antler removal on dominance and fighting behaviour in farmed fed deer stags. — J. Zool. 190, p. 217-224.
Topinski, P. (1974). The role of antlers in establishment of the red deer herd hierarchy. — Acta Theriologica 19, p. 509-514.
Trivers, R. L. (1976). Sexual selection and resource-accruing abilities in *Anolis garmani*. — Evolution 30, p. 253-269.
Whitehead, G. K. (1972). Deer of the world. — Constance, London.
Wilson, E. O. (1975). Sociobiology: the new synthesis. — Harvard, Belknap Press.
Zahavi, A. (1975). Mate selection - a selection for a handicap. — J. theor. Biol. 53, p. 205-214.
—— (1977a). The cost of honesty. — J. theor. Biol. 67, p. 603-605.
—— (1977b). Reliability in communication systems and the evolution of altruism. — In: Evolutionary ecology (Stonehouse, B. & Perrins, C. M., eds). MacMillan, London, p. 253-259.

ZUSAMMENFASSUNG

1. Dieser Artikel gibt einen Überblick über die Anhaltspunkte zu fünf funktionalen Erklärungen zur Evolution von Geweihen bei männlichen Hirschartigen: nämlich, daß sie als Waffen in Kämpfen benutzt werden; daß sie es Individuen ermöglichen, sich gegen Raubfeinde zu verteidigen; daß sie als Hitzeregulatoren während der Wachstumsperiode dienen; daß sie die Kampffähigkeit eines Individuums anzeigen und es den Männchen gestatten einander einzuschätzen, ohne zu kämpfen; und daß sie die Chancen eines Männchens von Weibchen als Partner ausgesucht zu werden, erhöhen.

2. Es gibt zahlreiche Beweise dafür, daß Geweihe während des Kampfes zwischen rivalisierenden Männchen eingesetzt werden. Im Gegensatz zu einigen Mutmaßungen in der Literatur kommt es während der Aufzucht der Jungen regelmäßig zu Kämpfen, die beschädigend sein können. Bei den Arten, bei denen Kampfverhalten im Detail untersucht wurde, erwiesen sich Geweihe als wirksame Angriffs- und Verteidigungswaffen, und es gibt keine systematischen Anhaltspunkte für die Aufrechterhaltung de These, daß geweihlose Männchen erfolgreicher im Konkurrenzkampf um Weibchen seien als solche mit Geweih.

3. Obwohl Hirsche ihre Geweihe manchmal zur Verteidigung gegenüber Raubfeinden einsetzen, deutet das Fehlen von Geweihen bei den Weibchen der meisten Arten darauf hin, daß dies nicht ihre Hauptfunktion ist. Es erscheint auch nicht warhscheinlich, daß Geweihe sich als hitzeregulierende Mechanismen entwickelten — bei einigen Arten wachsen sie während der Wintermonate, und es besteht auch keinerlei Tendenz bei tropischen Arten, größere Geweihe auszubilden als bei Arten im gemäßigten Klima.

4. Trotz vieler Mutmaßungen gibt es keine schlüssigen Anhaltspunkte für ein gegenseitiges Einschätzen der Männchen nach ihrer relativen Geweihgröße; und die meisten Maße betreffs Größe und Gestalt der Geweihe sind nicht eng mit Dominanz oder Kampffähigkeit korreliert. Auch gibt es keine festen Beweise dafür, daß Weibchen Männchen mit großen Geweihen zur Paarung bevorzugen.

5. Des Fehlen eindeutiger Beweise für die Wichtigkeit der Geweihe als Verteidigung gegen Raubfeinde, als Hitzeregulierung, als Einschätzung von Rivalen und als Anziehung von Partnern, läßt die Möglichkeit offen, daß Geweihe sich trotz ihrer bizarren Erscheinung als Waffen entwickelten und wegen ihrer Funktion im intraspezifischen Kampf während der natürlichen Selektion beibehalten wurden.