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The effect of antler removal on dominance and fighting behaviour in farmed Red deer stags

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(With 3 figures in the text)

This study was carried out on farmed Red deer stags prior to and immediately after the sexual phase of the annual reproductive cycle. The dominance hierarchy was established after the stags cleaned their antlers of velvet and both before and after antler removal. Each stag was weighed live and the antlers weighed and measured after removal.

Antler weight and live weight were correlated significantly with dominance order. The removal of antlers only slightly altered the dominance hierarchy. An examination of fighting behaviour allows Geist's theories of antler function to be tested.

Contents

Introduction

Red deer stags (*Cervus elaphus* L.) are seasonally breeding mammals which show a marked dichotomy between social and sexual behaviour enabling social behaviour to be studied at times of the year when overt sexual behaviour is not manifest. During which time stags remain in groups separate from hinds. These groups have been shown to have a well marked social dominance hierarchy in Red deer (Darling, 1937; Lincoln, Youngson & Short, 1970; Lincoln, 1972).

The importance of antlers in the social and sexual life of deer has been pointed out by several authors (Darling, 1937; Espmark, 1964; Schaller, 1967; Bubenik, 1968; Lincoln *et al.*, 1970; Lincoln, 1972) and Geist (1966) suggests antlers function as weapons, shields, binding organs and display organs. But other characters, such as live weight, are also known to affect dominance behaviour (Espmark, 1964; Schaller, 1967). Fighting behaviour has been studied previously by Darling (1937), Schaller (1967), Barrette (1977) and Lincoln (1972). In all these studies the presence, absence or relative size of antlers has been stressed as the most significant character determining the outcome of conflicts. It thus appears

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that antlers are of fundamental importance in deer behaviour. The aims of this study were (1) to discover the dominance hierarchy while the stags were in hard horn (2) to repeat this after antler removal and as far as possible after the rut (3) to evaluate the importance of live weight and antler characteristics in determining dominance (4) to determine the effects of antler removal on fighting behaviour.

Materials and methods

The study area and animals

The study area was the experimental deer farm run by the Hill Farming Research Organization and the Rowett Research Institute at Glensaugh Research Station (Blaxter, Kay, Sharman, Cunningham & Hamilton, 1974). The breeding stags are not usually maintained as a single group, but for the purpose of this study 15 were kept in one large paddock (53 acres); these were the oldest and largest stags on the farm, comprising five 5-year-olds and ten 4-year-olds.

Behavioural methods

The heads of the stags were all drawn accurately and from the drawings a dichotomous key was drawn up. This was used to identify each stag until after several days individuals were recognized at a glance by antler configuration, coat colour, shape and any specific behavioural characteristic such as a peculiar way of walking or of carrying the head. The stags were attracted twice a day at 08.00 and 16.00 to a feeding area where 8–12 piles of pelleted barley and oats were laid out in a line approximately a metre apart. Observations were recorded, using a tape recorder, of the outcome of any interactions between animals while competing for food, and any other fighting behaviour. A stag was said to be dominant over another if it displaced it from a feeding pile on two or more occasions and was not displaced itself. The tameness of the animals made it possible to observe them from a point five metres away from the food piles without their behaviour being influenced by the observer.

On 14 September the antlers were sawn off each animal. A stump of 2 cm remained in each case. The animals were then fed, as before, and a second dominance hierarchy was drawn up, after each stag had interacted with all of his fellows.

In November, the stags were observed meeting for the first time after the rut. The ensuing struggle was usually violent and the winner was said to be dominant over the loser.

Tabulation of results

After all the animals had cleaned their antlers and the results were tabulated a dominance hierarchy was produced. It was drawn as follows: the stag numbers were set down in a list with the stag dominating most of his fellows at the top (17), and the stag dominating least of his fellows at the bottom. However, a stag which was below another because it dominated fewer stags nevertheless could dominate one above it, for example 24 and 17. So an arrow was drawn linking the two, outside the main line of the hierarchy.

The strength of hierarchy was calculated using Landau's (1951) equation

$$h = \frac{12}{n^3 - n} \sum_{a=1}^{n} \left(V_a - \frac{n-1}{2} \right)^2 \text{ before and after antler removal}$$

where h = strength of hierarchy on a scale of 1–0
n = the number of animals in the group
and V_a = the number of group members that the ath animal dominates.

Measuring methods

The live weights of the stags were measured after antler removal in a weighing crate (Blaxter *et al.*, 1974). The antlers were weighed the day after removal using a spring balance. Antler lengths and lengths of each tine were also measured and Fig. 1 shows the dimensions used, the measuring tape following the contours along the outside of the antler for each length.

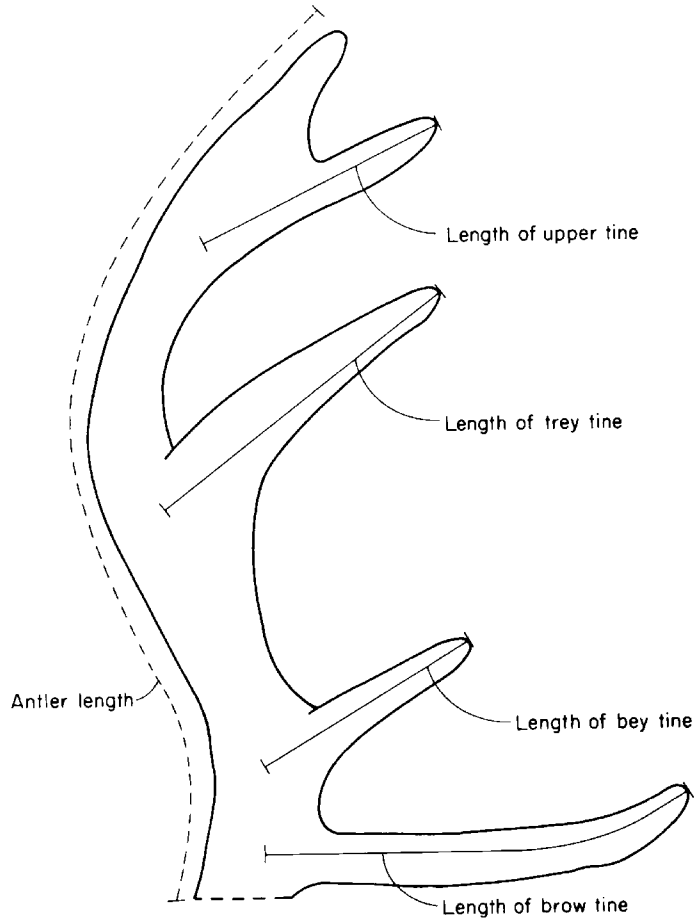

FIG. 1. Left antler of 18 showing dimensions measured.

Results

Social dominance hierarchy prior to antler removal

Figure 2(a) represents the dominance hierarchy before antler removal. All stags were in hard horn when these observations were made. No. 57 remained a "loner", apart from all stags at all times when they were being observed. He did not come to the feeding place and hence did not figure in the dominance hierarchy. His measurements are thus not included in analysis of dominance.

Methods of displacing fellows from the feed piles varied considerably depending on dominance relationships. A dominant animal would react very aggressively to a fellow dominant; and stags would display to each other as follows: the upper lips would be raised and the lower lips lowered on one side of the mouth thus showing teeth, the tongue might also be protruded from the mouth to cover the black spot on the lower lip. At all

times a grinding sound would be made by the molar teeth and both eyes would be rolled, although the position of head and ears would not be altered. If the rival did not submit by walking or running away, then the contest would progress to a more intense form of aggression. The head would be raised, chin held high with ears well back while at the same time displaying all characters mentioned above in the lower intensity form of aggression. A fight ensued usually with heads lowered and antlers locked but sometimes the antlers were not locked and the dominant animal then charged his opponent in the flanks with his antlers.

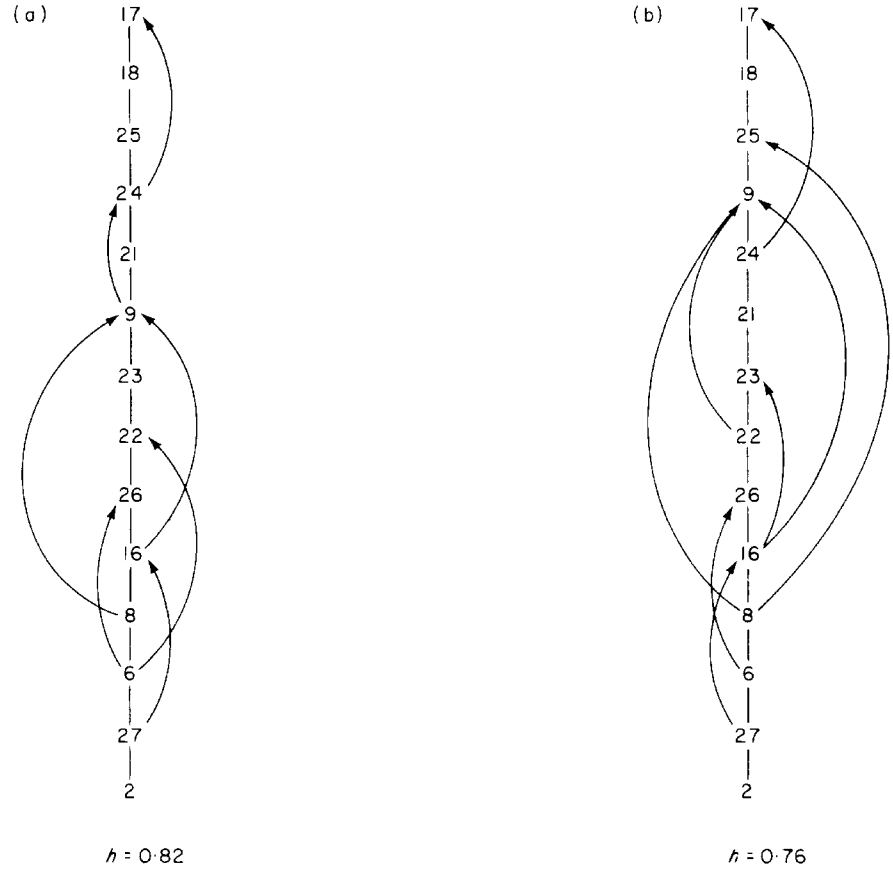

FIG. 2. Dominance hierarchy (a) before antler removal and (b) after antler removal. h=strength of hierarchy. Arrows represent triangular relationships of dominance.

A dominant animal could displace a junior subordinate by walking toward him or by dipping his head (and thus antlers) towards him. This had the effect of turning the subordinate away. More persuasive threats were seldom required in this type of situation. However, very high ranking stags, often tolerated very low ranking stags, even allowing them to share their feed piles, but these low ranking stags were always very wary and fled at the slightest threat by a dominant. Subordinate animals rarely showed signs of aggression to fellow subordinates even in displacing them from feed piles, which they frequently shared.

Social dominance hierarchy after antler removal

Immediately after antler removal very junior stags were observed challenging and fighting dominant animals. Behaviour of this kind was not observed before antler removal. Animals fought by rubbing stumps of antlers together and pushing hard as if antlers had been present. These unusual challenges continued for only a few hours after antler removal. A stable hierarchy was then established and was discovered using the same methods as before (Fig. 2(b)).

Social dominance hierarchy after the rut

Complete observations could not be made since several stags were still rutting, and the herd was divided with four stags on one part of the farm and seven on another. The balance of the study group were culled prior to the rut. Such results as were obtained are shown in Fig. 3. The challenges observed were different from before the rut in that the stags were not competing for food, but were aiming to establish themselves in the hierarchy. A typical challenge was as follows. Two stags who had previously been in separate paddocks were allowed to mingle by opening a gate. They did not charge straight at each other, instead they slowly approached until they were 50 metres apart and then began to walk steadily, with stiff legs, towards each other. When they were about 3 metres apart, they walked a few paces parallel to one another, all the time displaying the high intensity form of aggression described above. The heads were turned away from each other, in such a way that would have shown off their antlers (if they were present) and neck girth to best advantage. When the heads had moved to about $1\frac{1}{2}$ metres apart, they suddenly crashed together and a pushing match ensued. The one that gained higher ground and pushed down on his adversary was always the winner. Frequently the winner took the opportunity to strike the loser on the undefended flanks with his head as it was momentarily off balance. Fights observed lasted between 7 and 50 seconds; there was always a clear winner and the loser was never observed to return for a second challenge. Occasionally no fight occurred at all, the subordinate merely walking away when the dominant walked purposefully towards him, thus avoiding the challenge altogether.

No. 57, hitherto a loner, was seen to interact with other stags for the first time and was thus included in the dominance hierarchy.

Correlations

A measure of antler complexity is the sum of the lengths of both antlers and the lengths

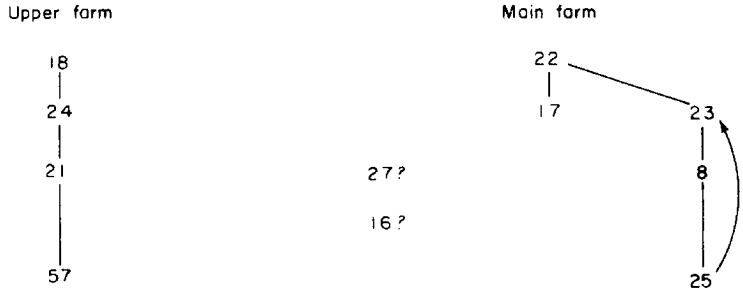

FIG. 3. Dominance hierarchy after the rut. Question marks indicate which stags were not observed to interact with their fellows.

of each tine divided by two. Relative antler weight is the total weight in grams of both antlers divided by the weight of the animal in kilograms.

In order to discover which features analyzed might affect dominance, antler weight, live weight, antler length, antler complexity and relative antler weight were all plotted against number of stags dominated (Table I). Live weight and antler weight, the characters found to be correlated significantly with dominance, were tested with each other for a correlation ($r = 0{\cdot}28$, $n = 14$ not significant). Live weight does not, therefore, correlate with antler weight in this study.

TABLE I

Correlations between dimensions measured and number of stags dominated

	n	r	Significance
Live weight before antler removal (kg)	14	0·82	$P < 0{\cdot}001$
Live weight after antler removal (kg)	14	0·83	$P < 0{\cdot}001$
Antler weight (g)	14	0·60	$P < 0{\cdot}02$
Antler length (cm)	14	0·05	n.s.
Antler complexity (cm)	14	0·39	n.s.
Relative antler weight (g/kg)	14	0·25	n.s.

Discussion

During this study the stags had a fixed dominance hierarchy whilst in hard horn. Before antler removal a value of $h = 0{\cdot}82$ on Landau's scale of 0–1 indicates a strong relationship of dominance (Landau, 1951). However several triangular relationships were observed. Lincoln (1972) working with older (6–14 years) wild stags found a more linear hierarchy. Espmark (1964), however, found such triangular relationships in reindeer not at all anomalous, but his observations were partly confounded by the presence of antlered females.

After antler removal the strength of hierarchy, $h = 0{\cdot}76$ decreased but this does not indicate an important alteration in strength of dominance hierarchy. The dominance order is unaffected by antler removal. These results are similar to those obtained by Woodbury (1941) who observed no alteration in the dominance hierarchy after polling all cows in a dairy herd. However in studies where only a few individuals had antlers removed at one time profound effects were noted (Lincoln *et al.*, 1970; Lincoln, 1972; Espmark, 1964).

To discover which factors determine dominance, several characters were measured. Live weight and antler weight correlated positively and significantly with dominance order but not antler length, antler complexity or relative antler weight. After antler removal there was no increase in significance of the correlation between live weight and dominance. Live weight and antler weight were not significantly inter-correlated, thus they exert independent effects on dominance. As live weight shows a higher correlation with dominance it is concluded that it exerts a larger effect than antler weight on dominance. Schaller (1967) found antler length to be correlated with rank in Chital (*Axis axis*), but no correlation exists with Red deer. Relative antler weight is influenced by nutrition and tends to be a constant for year classes (Hyvarinen, Kay & Hamilton, 1977). In

studies by Schein & Fohrman (1955) on dairy cattle (*Bos taurus*) and by Espmark (1964) on reindeer (*Rangifer tarandus*), live weight has also been found to correlate with dominance. In the latter example correlation coefficient $r = 0{\cdot}92$, $P < 0{\cdot}001$; this indicates a highly significant correlation between live weight and dominance. Schaller (1967) observed that dominance hierarchies among Gaur (*Bos gaurus*) were largely based on size.

This study has shown that a group of antlerless stags kept from antlered competitors can fight, maintain a stable dominance hierarchy and breed like normal stags. It is interesting to speculate why this is so.

Geist (1966) has suggested that "horns" in ungulates evolved to function as weapons, defence organs, binding organs and display organs, and the present study throws further light on these functions. It is assumed that each stag immediately after antler removal is unaware of his own mutilation, only that of his fellows. A stag on seeing a fellow without antlers, irrespective of former dominance relationships displays a high intensity, head up frontero-lateral form of aggressive behaviour. However his opponent is aware of his adversary's loss and displays in the same way. The loss of the opponent's display organ and weapon is apparent to both and each behaves as if he had gained an advantage over the other without realising his own loss. As organs of offence are not present, organs of defence are not required, so the loss of antlers is not serious for the latter. When the fight begins with lowered heads, there is no binding organ to hold the heads together, but deer can push with their heads almost as efficiently as if the antlers were present. However the ability to wrestle is impaired and the heads tend to slip if moved laterally and this enables one stag to deliberately hit the other in the undefended flank if it is off balance. The skill of stags in maintaining an opponent in front of its shields is remarkable, but during fighting the strategy of an attacker is to hit the opponent in the flank. Antlers act as a shield whereby such an attack can be intercepted and neutralized. Branched antlers in particular are very effective at this, together with circling movements to keep the vulnerable flank behind the shield. Thus pushing matches may be seen as attempts by the adversaries to get the opponent off balance so a blow to undefended flanks may be delivered. The rarity of this occurrence recorded in the literature testifies to the effectiveness of the branched antlers as defence and binding organs, and the loss of this function is probably the most serious consequence of polling.

In conclusion it was found that a dominance hierarchy existed among the stags. Antler weight and live weight correlated significantly with dominance. Loss of antlers by all stags does not affect dominance relations but competition with antlered rivals would have been severely affected due mainly to loss of defensive binding functions of the antlers.

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