Dominance and Aggression in Various Sized Groups of Red Deer Stags

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The influence of group size on agonistic behaviour of "white" red deer stags (Cervus elaphus L.) of different ranks in the hierarchy was examined during artificial feeding. Size of the social group was dependent on the season in the year and on age and general rank within the whole bachelor group inhabiting the enclosure of the stags. Group size differentially affected the behaviour of the stags according to the rank of the individual in the particular groups. Increased group size resulted in increased agonistic activity in top-ranking stags. The number of attacks directed towards bottom-ranking stags by other group members was also elevated. Stags of intermediate rank position showed a decrease in the number of interactions involved and a suppression of agonistic activity.

Key words: red deer, stag, social group, agonistic activity, aggression, rank

INTRODUCTION

In our previous study on "white" red deer (Cervus elaphus L.), a relationship was found between the dominance hierarchy and timing of the stag antler cycles (Bartoš, 1980) and between position in the hierarchy during the velvet period and antler growth (Bartoš and Hyánek, 1982). It appeared that the phenomenon of antler cycle timing is based on the aggressive behaviour of the individual (Bartoš, 1985b; Bartoš, in preparation). It was found that the order of antler casting corresponded closely to the position of the stag in the general dominance hierarchy, as did the order of velvet shedding. It is suggested that this is based on differential composition of the bachelor group during the preceding time. The period preceding velvet shedding is characterised by disintegration of the main group of stags into smaller, non-stable groups (Bartoš and Perner, 1985). Distinct conditions appeared necessary for agonistic behaviour in individual stags. In the population of red deer on the island of Rhum, Scotland, the rate at which deer threatened other individuals increased with group

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size (Clutton-Brock et al., 1982). The aim of the present study was to assess the influence of group size on agonistic behaviour of stags of different ranks in the group hierarchy.

METHODS

The study was performed on a “white” red deer population living in the Game Reserve in Žehušice, Central Bohemia, Czechoslovakia, during 1982 and 1983. Observations were carried out in the main penned area of the reserve (1.26-square-km), which was inhabited in 1982 by 36 red deer, of which 13 were stags, and in 1983 by 37 deer of which 14 were stags. Only animals of 2 years or older were observed. During the period of observation one stag was killed during an agonistic encounter with others of the herd. On the whole, the same 12 stags were observed throughout the study; in 1983 they were joined by two more of age 2 years (yearlings in the previous year).

Appleby (1980) reported a similar dominance relationship among stags grazing under natural conditions on Rhum and among animals congregating at artificial feeding sites. A similar situation was observed in the Žehušice population of stags (Bartoš, 1982). Hence all the observations in the present study were made during artificial feeding, which was performed throughout the year as described earlier (Bartoš, 1982). The amount of food provided was dependent on group size.

As in the previous studies (Bartoš, 1980, 1982; Bartoš and Hýánek, 1982; Bartoš, 1985b), observations of these semi-tame deer were made at a distance of 20–30 m by an observer seated on a tractor. The number of dominance interactions and the results of these interactions were recorded for each stag. Only agonistic activities which involved display by one individual and resulted in some evasive action being taken by a second individual were considered. During the 2 years of study, 18 periods of observation were carried out. However, as differences in the composition of the bachelor group occurred around the time of the velvet period (Bartoš, 1985b; Bartoš and Perner, 1985), the periods of observation were not evenly distributed throughout the season (three periods of observation in February, two in March, two in April, two in May, four in June, one in July, one in August, two in September, and one in October). Observations therefore covered both the velvet period, hard antler period and time of antler casting (March). Age of the subjects were known as each stag had been identified at birth.

Size of the social group and number of agonistic interactions each stag in that group was involved in was analysed statistically. A value for the “dominance activity index” (DAI) (Bartoš, 1985b) was calculated for each member of a group using the following equation:

$$DAI = \log \left\{ \frac{(P + 0.1)^2}{N + 0.1} \right\} + 1$$

where \(P\) = sum of all dominance interactions exhibited by a given individual and \(N\) = sum of all the submissive interactions exhibited by the same individual. If \(P = 0\) then \(N\) is negative.

Three classes of stags were recognised, namely, “the top-ranking stag” (highest ranked animal within a given group with the mean ± S.E. 1.69 ± 0.62), “the
intermediate stag" (a stag of median rank with the mean of 6.75 ± 0.49) and finally "the bottom-ranking stag" (the lowest ranking animal in the group with the mean rank of 10.94 ± 0.65). These three types of stags differed from each other significantly (ANOVA, F(2,45) = 61.09, P < 0.001).

The same population was observed throughout the entire study period. However, individual groups of stags could potentially differ in several aspects such as stage in the antler cycle, season, year, age, and general rank within the whole bachelor group of stags inhabiting the penned area that was tested by one way analysis of variance. The possible influence of each individual was not tested as the stags were by chance of different ages; therefore age testing was simultaneously testing the influence of individual subjects.

The original plan was to have 60 minutes as a standard observation period. However, on some occasions, deer left the feeding site after less than 60 minutes had elapsed. The mean length (± standard error) for a single observation period was 55.28 ± 2.63 minutes. For the purpose of analysis, all data was standardized to a 60 minute period.

RESULTS

During the 18 periods of observation, 3,804 interactions were recorded between stags, with a mean of 211.33 ± 31.73 (mean ± standard error) interactions per observation period. Top-ranking stags were involved in 69.00 ± 12.12 interaction period, intermediate stags in 39.65 ± 4.75 interactions and subordinate stags were involved in only 11.06 ± 2.85 interactions per observation period. The differences in the mean number of interactions between top-ranking and bottom-ranking, top-ranking and intermediate, intermediate and bottom-ranking stags were significant (Wilcoxon test, T = 0, N = 17, P < 0.001; T = 8, N = 17, P < 0.001; T = 3, N = 18, P < 0.001). The group size ranged from two to 13 stags with a mean of 9.44 ± 0.83 individuals. All agonistic interactions in which top-ranking stags initiated the interactions were of "dominant" character (given as "P" in the previous equation) and all interactions involving a bottom-ranking stag were of a submissive nature (given as "N" in the equation). But the intermediate type stags exhibited both dominant and submissive gestures.

**Dominance Activity Index (DAI), Number of Interactions and Rank**

The nature of the general dominance hierarchy was estimated as in previous studies on the results of encounters between all stags within the whole bachelor group inhabiting the area. General dominance hierarchy was very stable the whole year round (Bartoš, 1980; Bartoš and Hyáněk, 1982). A DAI value was calculated for each stag for each period of observation. Spearman rank correlation analysis was carried out between social position in the given group (expressed in the rank order based on the encounters of single stags with each animal of the group) and value of the DAI for each period of observation. The coefficient of correlation per period of observation ranged from \( r_s = 0.770 \) to \( r_s = 1.000 \) with a mean of \( r_s = 0.9996 \), \( P < 0.001 \) (after "z" transformation used as in Weber, 1972). The values of the correlation coefficients tended to be higher as group size decreased (\( r_s = -0.510 \), \( P < 0.05 \)). High-ranking stags showed the highest DAI values \( 4.33 ± 0.18 \), intermediate stags showed a mean value of \( 1.22 ± 0.06 \), while bottom-ranking stags showed a mean
DAI value of \(-0.004 \pm 0.004\). The difference in mean DAI values between top-ranking and intermediate stags, top-ranking and bottom-ranking stags, and intermediate and bottom-ranking stags were significant (Wilcoxon test, \(T = 0, N = 18, P < 0.001; T = 0, N = 18, P < 0.001; T = 0, N = 18, P < 0.001\)).

**Factors Affecting Group Size, Number of Interactions and DAI**

The data were divided to test the influence of separate factors as illustrated in simplified form in Figure 1. Table I indicates the results of ANOVA carried out on this data. The stage a top-ranking stag is at in the antler cycle causes a significant difference in the number of interactions in which he is involved. Detailed analysis using the Kramer test (Scheffé, 1959) indicated that the data recorded during antler casting differed significantly from the data collected during the velvet period (\(P < 0.001\)). The difference between data collected in the hard antler phase was also significantly different to that from the casting phase (\(P < 0.001\)). However, data collected in the velvet period and hard antler period did not differ significantly. As only two periods of observation were performed during the time of antler casting (March), the data collected at this time were omitted from further analysis. Season, age, and general rank of the stag within the whole bachelor group inhabiting the enclosure also significantly influenced its behaviour but agonistic activity actually did not differ significantly between calendar years.

The three stag types differed in age; top-ranking stags were a mean age of \(5.39 \pm 0.31\) years old, intermediate stags a mean age of \(4.82 \pm 0.21\) years, and bottom-ranking stags only \(3.17 \pm 0.19\) years old. The difference in age between top-ranking and bottom-ranking animals and between intermediate and bottom-ranking stags was significant (\(t\)-test, \(t = 7.88, P < 0.001; t = 6.06, P < 0.001\)). But the difference in mean age between top-ranking and intermediate stags was not significant (\(t\)-test, \(t = 1.84, NS\)).

**Group Size, Number of Interactions and DAI**

According to the results shown in Table I, group sizes, numbers of interactions, and values of DAI were adjusted for age of subject (median age for the intermediate stags), rank position (median rank achieved by intermediate stags), and season of the year by the linear regression method described by Snedecor and Cocharan (1965). The adjusted means for group size were correlated with the adjusted data for DAI and number of interactions. For top-ranking type stags, the coefficient of correlation for group size and DAI was \(r = 0.700, P < 0.01\) and for group size and number of interactions \(r = 0.292, NS\). For intermediate type stags the coefficient for group size and DAI was \(r = -0.411, NS (t_{14} = 1.69, for P = 0.05 \ t_{14} = 2.14)\) and for group size and number of interactions \(r = -0.580, P < 0.02\). Bottom-ranking stags were also analysed and the coefficient of correlation for group size and DAI was \(r = 0.980, P < 0.001\) and for group size and number of interactions \(r = 0.920, P < 0.001\).

**DISCUSSION**

The DAI value appeared a good indicator of position within a small group dominance hierarchy in “white” red deer stags. The DAI reflected an individual’s “aggressivity” but not in bottom-ranking animals, where it was based on the number of
Fig. 1. The division of data with aspects considered separately. Only the data that showed significant variation are presented. For vertical scale: A, top-ranking stags; B, intermediate stags; C, bottom-ranking stags. Open columns, number of agonistic interactions; black columns, size of a group. For stage in antler cycle: 1, hard antler period; 2, period of antler casting; 3, velvet period. For season: Sp, spring; Su, summer; A, autumn; W, winter. For age and rank: − means "and less"; + means "and more." All the data are presented as means ± S.E.
<table>
<thead>
<tr>
<th>Factor</th>
<th>Top-ranking stag</th>
<th></th>
<th>Intermediate stag</th>
<th></th>
<th>Bottom-ranking stag</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>d.f.</td>
<td>Size of group</td>
<td>Interactions (number)</td>
<td>DA1</td>
<td>d.f.</td>
<td>Size of group</td>
</tr>
<tr>
<td>Stage in antler cycle</td>
<td>2,15</td>
<td>1.18</td>
<td>9.12**</td>
<td>2.40</td>
<td>2,15</td>
<td>1.18</td>
</tr>
<tr>
<td>Season</td>
<td>3,12</td>
<td>3.56*</td>
<td>0.96</td>
<td>1.02</td>
<td>3,12</td>
<td>3.56*</td>
</tr>
<tr>
<td>Calendar year</td>
<td>1,16</td>
<td>0.31</td>
<td>0.87</td>
<td>0.73</td>
<td>1,16</td>
<td>0.31</td>
</tr>
<tr>
<td>Age</td>
<td>2,15</td>
<td>0.57</td>
<td>1.30</td>
<td>0.08</td>
<td>1,16</td>
<td>9.82**</td>
</tr>
<tr>
<td>General rank</td>
<td>1,16</td>
<td>1.63</td>
<td>0.62</td>
<td>0.24</td>
<td>4,13</td>
<td>4.59*</td>
</tr>
</tbody>
</table>

*P < 0.05.

**P < 0.01.
threats and/or attacks received. Hence the higher the number of threats received by a subordinate stag, the higher the DAI value, thus identifying the socially active subordinate stags. The results show a clear and close correlation between rank of a stag and agonistic activity. High ranking animals exhibit the greatest amount of agonistic behaviour (compare with Lincoln, 1972; Bartoš, 1985b).

Artificial feeding does not usually alter dominance relationship in Ungulates, but it affects the frequency of interactions (Clutton-Brock et al, 1976). From this point of view the analysis indicated the differential influence of group size on red deer stags of different ranks at least during artificial feeding. Increased group size resulted in increased agonistic activity by top-ranking stags. The number of agonistic interactions was highly elevated by increased group size and hence the number of attacks directed towards bottom-ranking stags by other group members. The intermediate type stags occupy the middle range position in the hierarchy and showed a decrease in number of agonistic interactions when group size increased. In conclusion, increasing the size of a social group affects animals at the two extremes of the hierarchy (the alphas and omegas). Increased group size elicited agonistic activity in the former and suppressed it in the latter.

Group size was dependent on the season of the year, on age of the members of the group and on rank of the individuals in the population. The animals tended to aggregate into larger groups during periods of food shortage (Appleby, 1980; Bartoš, 1985b). “White” red deer stags of similar age and rank tend to associate in groups (Bartoš and Perner, 1985) as was reported by Bützler (1974), Appleby (1983), and Clutton-Brock et al (1982).

Rank and age are usually closely associated in red deer up to the age of 5 years (Appleby, 1980; Bartoš and Hyánek, 1982). The mean age in the population observed in the present study was less than 5 years and it appeared that rank influenced the group size to the same extent as age in this situation.

The number of interactions an intermediate stag was involved in was dependent on stage in the antler cycle, the number of interactions being highest during antler casting. Casting is the period in which temporal changes occur in rank of the dominant animals in the hierarchy due to the loss of the most potent weapon, namely the antlers (Lincoln et al, 1970; Bützler, 1974; Clutton-Brock et al, 1982). The frequency of rank change in “white” red deer is much lower than in other populations (perhaps due to limited space), which induced a stability that lasted over an entire year (Bartoš, 1985a). However, there are still definite periods of increased social friction in the “white” red deer during casting.

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REFERENCES

and social hierarchy relationships in the red deer stag. Behavioural Processes 5:293–301.


