

## The implications of social structure for dominance hierarchies in red deer, *Cervus elaphus* L.

LINTON C. FREEMAN, SUE C. FREEMAN & A. KIMBALL ROMNEY  
*School of Social Sciences, University of California, Irvine, CA 92717, U.S.A.*

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**Abstract.** A recent paper by Iverson & Sade (*J. quant. Anthropol.*, 1990, **2**, 61–83) suggests that red deer stags that are high in a dominance ranking are equally likely to defeat those lower in the ranking, regardless of how different they are in their relative positions. Their result contradicts the common observation that stags find it easier to defeat those far below them in the hierarchy than those close to them in the hierarchy. This paper demonstrates that the apparent contradiction can be eliminated by considering two questions about the structure of agonistic encounters: ‘Who fights with whom?’ and ‘Who fights at all?’

Iverson & Sade (1990) examined a probability-based model for dominance in animal societies. Their model is based on the ratio  $r_{ij}/n_{ij}$ , where  $r_{ij}$  is the observed number of occasions on which animal  $i$  won a fight with animal  $j$  and  $n_{ij}$  is the number of occasions in which  $i$  and  $j$  fought.

Iverson & Sade specified the null hypothesis that any observed pattern of dominance is a chance variation from a situation in which no hierarchical structure is present. Under that null hypothesis, the ratio  $r_{ij}/n_{ij} = 1/2$ , and any animal would be equally likely to win an encounter with any other. They explored this null model against an explicit alternative model of hierarchy that they called EQ. The EQ model embodies a structure in which animals are arranged in a hierarchy in terms of the number of opponents that each can defeat with a probability greater than  $1/2$ . Then, given an encounter between a pair of animals, the EQ model specifies that the more dominant of the two will win with some constant probability ( $\Theta > 1/2$ ).

They tested the EQ model on data reflecting the outcomes of agonistic encounters among conspecifics in red deer, olive baboons, *Papio cynocephalus anubis*, and rhesus monkeys, *Macaca mulatta*. Their results were impressive, and they concluded that the model corresponded quite closely to the data for all three species. The remarkable thing about this result is that the EQ model predicts that, in any pairwise encounter, the more dominant of the two animals will win the fight with a constant probability, regardless of the other animal involved. This suggests that the most dominant ani-

mal would have just as much trouble (or ease) dominating the least dominant animal as he/she would have dominating the animal in the second position in the hierarchy.

This result seems to contradict the widely reported observation that individual traits like ‘size, strength, weaponry and experience’ typically determine an animal’s potential to win an encounter with another (Parker 1974). It also suggests that ‘the implicitly accepted notion of dominance hierarchies as rankings of ability or merit is cast into doubt’ (Iverson & Sade 1990).

We show here that, at least with respect to red deer stags, the contradiction between Iverson & Sade’s result and the commonly accepted notion of dominance hierarchies as rankings of ability is more ‘apparent’ than ‘real’. The aim of the present paper is to extend Iverson & Sade’s analysis by exploring how the dominance patterns they uncovered are tied into the broader structure of social linkages. We will focus on the patterning of agonistic contact, and in particular, on the question of which pairs of deer get embroiled in fights and which pairs do not.

We confine our attention to one species, red deer, because we suspect that the patterning of agonistic interaction is likely to differ from species to species. Among many primates, for example, sets of individuals develop patterns of long-term alliance (Cheney & Seyfarth 1990). Thus, when a pair of individuals meet in an agonistic encounter, one or both are often supported by their allies. Red deer, in contrast, seem to limit their agonistic interaction to

**Table I.** The outcome/number of pairwise agonistic encounters among seven 3-year-old red deer stags (from Appleby 1983)

Winner	Loser						
	A	B	C	D	E	F	G
A	—	8/9	5/9	6/8	6/11	4/4	1/1
B		—	1/1	11/12	15/17	0/0	1/1
C			—	0/0	2/3	0/0	0/0
D				—	0/0	2/2	0/0
E					—	0/0	5/5
F						—	0/0
G							—

pairwise conflicts (Clutton-Brock et al. 1982). It would be difficult to imagine, therefore, that dominance patterns would have the same relation to patterns of agonistic encounters in all the species originally studied by Iverson & Sade.

## METHODS

In their analysis, Iverson & Sade (1990) used data that had been recorded by Appleby (1983). Appleby tallied the number of fights occurring between each pair of stags in a population of red deer, along with a notation of which stag was the victor in each case. The data are shown in Table I.

The aim of Iverson & Sade's analysis was to determine dominance patterns by examining the ratios shown in Table I. Any stag that won the majority of his encounters with another individual was considered to be dominant over that stag. The problem was to find an ordering that embodied the patterns of wins and losses and arranged the individuals from the most to the least dominant.

There is a more or less standard procedure for defining dominance given the kind of data shown in Table I. The typical approach considers each pair of animals, *i* and *j*. Then any animal *i* in the *ij* pair is defined as dominant in that pair if and only if *i* beats *j* more often than *j* beats *i*. This induces a dominance relation on the data.

The question, then, is whether the observed dominance relation yields a hierarchical order. For a given set of dominance data to be considered hierarchical they must exhibit at least a partial order, that is, the dominance relation must be transitive. The hope in every case is to find a total order, one that is not only transitive but where for

every *ij* pair, either *i* dominates *j* or *j* dominates *i*. But, in any case, observing intransitive triples (where *i* dominates *j*, *j* dominates *k* and *k* dominates *i*) would indicate that ordering was impossible.

Dominance data on red deer stags seldom display any appreciable number of intransitive triples (Appleby 1983). Red deer consistently form some sort of hierarchical order. But, in most cases, available data are insufficient for the task of demonstrating a total, or even a partial, order. Typically, there are several pairs of animals that are simply never observed fighting with each other. For these pairs, then, it is impossible to specify a clear dominance pattern.

In practice, many of these apparent gaps in the data are handled by the simple expedient of assuming transitivity whenever it is not inconsistent with the data. Thus, in cases where some stag *i* dominates another *j*, *j* dominates a third *k* and *k* and *i* never fight, it is assumed that *i* dominates *k*.

In cases where there are no intransitive triples, the assumption of transitivity yields at least a partial order. In the specific case of the data of Table I, for example, stags B and F did not fight. But, since stag D dominated F and B dominated D, it is reasonable to assume that if B and F did fight, B would dominate. Even this assumption, however, is often not enough to produce the desired total order. Consider the CDF triple. Although D dominates F, there are no fights between either D and C or F and C, and therefore, no way to determine whether C falls above D, between D and F, or below F in the hierarchy. Thus, it is often impossible, even with the assumption of transitivity, to extract a total order from the data in a case like this. Instead, the best we can do is to use the assumption of transitivity to uncover the partial order shown in Fig. 1.

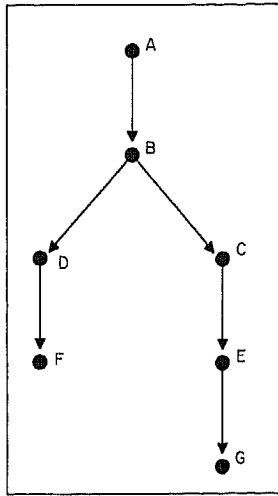


Figure 1. Hasse diagram of the partial order of the data in Table I.

The partial order shown in Fig. 1 is consistent with 10 total orders. An investigator who is interested in the dominance hierarchy of these stags typically seeks a way to choose among them, to find the total order that best describes the hierarchical structure. Various procedures for choosing the best total order on the basis of available information have been proposed (Brantas 1968; Richards 1974; Syme 1974; Clutton-Brock et al. 1979). Clutton-Brock et al. (1979) suggested a procedure for determining the position of each stag in a dominance hierarchy. Any stag, its position in the hierarchy is determined by a ratio. The numerator contains the number of other stags  $i$  beat plus the number that those other stags beat plus 1. And the denominator is the number of other stags that beat  $i$  plus the number that beat them plus 1.

Clutton-Brock et al. ran their index against a number of other measures and showed that it correlated highly ( $r \geq 0.929$ ) with the others. Because all of these procedures produce essentially the same total order, we can choose any one of them to order the data of Table I.

We used the procedure defined by Clutton-Brock et al. (1979) on the data of Table I. That procedure ordered these stags alphabetically, with A as the most dominant stag and G as the least. But this, or any of the other ordering procedures, leaves open the question of whether such a hierarchical ordering is a real structural phenomenon or is merely an artefact of chance (Appleby 1983). This is the

Table II. The number of pairwise agonistic encounters among seven 3-year-old red deer stags (from Appleby 1983)

Winner	Loser							$\Sigma$
	A	B	C	D	E	F	G	
A	—	9	9	8	11	4	1	42
B		—	1	12	17	0	1	40
C			—	0	3	0	0	13
D				—	0	2	0	22
E					—	0	5	36
F						—	0	6
G							—	7

problem that was addressed by Iverson & Sade (1990).

## RESULTS

For the present analysis, we wanted to go beyond the question of winning and losing as such. Rather, we focused on the problem of the patterning of agonistic encounters. We were concerned, therefore, not with the ratios shown in Table I, but instead with the denominators of those ratios. We considered the question of who fights whom among these stags. The data of interest are those shown in Table II.

Romney & Faust (1982) called attention to two sources of variability that must be recognized in attempting to model the frequencies in Table II. The first source resides in the variability in the marginal totals. In the present case this variability may be interpreted as individual variation among the stags in the tendency to get involved in fights. Stag A, for example, engages in 42 agonistic encounters while stag F engages in only six. The second source of variability resides in differential interaction among pairs of stags. In the present case this variability may be interpreted as a 'preferential' pattern where some pairs of individuals seem to 'seek one another out' for conflict (or to avoid conflict with each other) at rates above (or below) those suggested by the overall encounter rates of the individuals involved.

Our model takes these two sources of variation into account by addressing two questions. (1) To what extent does the number of agonistic encounters between two individuals simply reflect differences in their individual propensities to fight? (2) Beyond that, is there any evidence that

stags show any systematic pattern of choosing opponents for fights?

We began by asking whether red deer stags vary in their individual tendencies to get involved in fights. The answer, of course, is yes. A quick glance at Table I shows a great deal of variation in the marginal totals. In all, there were 83 encounters between pairs of stags. Because it takes two to fight, 166 individuals were involved in these encounters. Of these, stag A was involved in 42, B in 40, C in 13, D in 22, E in 36, F in 6 and G in 7. If we assume that each of these seven stags was equally likely to get involved in fights, then the expected number of involvements for each is  $166/7 = 23.71$  ( $\chi^2 = 206.25$ ,  $df = 6$ ), and the notion that these deer are equal in their willingness to fight may be rejected at any reasonable level of significance.

Given that these red deer stags vary, as individuals, in terms of their tendency to get involved in fights, fighting between any two stags could depend only on their individual tendencies to get involved. If that were the case, then the probability of a fight between any two stags would simply be the product of their individual probabilities of fighting.

This question can be addressed by using a variation of the approach employed in the chi-squared test of independence. To the degree that a confrontation between two stags,  $i$  and  $j$ , reflects no more than the independent tendencies of stag  $i$  and stag  $j$  to get involved in fights, then the probability of a fight between  $i$  and  $j$  is simply the product of  $i$ 's probability of fighting and  $j$ 's probability of fighting. This is the chi-squared model.

In this kind of case, however, we are faced with a situation in which certain cells in the data table are undefined. As a stag cannot fight with himself, the cells along the main diagonal of the matrix in Table II, must contain zeros, and the expectations produced by the chi-squared independence test would be inappropriate.

There is, however, an iterative log-linear procedure for testing quasi-independence (Bishop et al. 1975). Testing quasi-independence permits us to eliminate these structural, or logical, zeros, and to calculate expected cell values on the assumption that the diagonal cells in the table must remain at zero. Non-diagonal cells with zero entries are not constrained; they will depart from zero as the iterations proceed. This procedure was used on the data shown in Table II and yielded the expectations, based on quasi-independence, shown in Table III. Those expectations depart noticeably

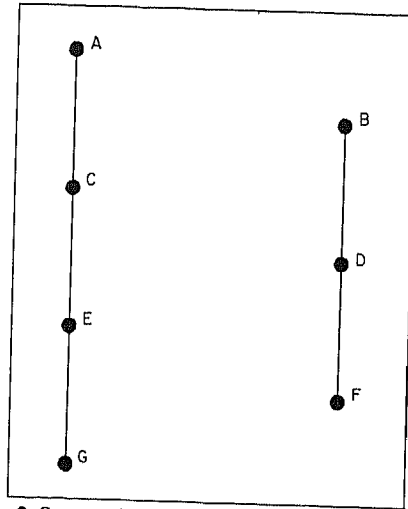


Figure 2. Symmetrical preference structure for agonistic encounters.

from the observations shown in Table II ( $\chi^2 = 88.43$ ,  $G^2 = 100.21$ ,  $df = (6 \times 6) - 7 = 29$ ). At face value, then, it would seem that the values of the cells in Table II are not solely determined by the magnitudes of the marginals; the likelihood of a fight between two stags is not simply a function of their individual tendencies to get involved in fights.

These large values of  $\chi^2$  and  $G^2$ , however, must be interpreted with caution. A large proportion of the expectations shown in Table III are small ( $< 5$ ). This suggests that the results of significance tests based on statistics calculated from Table III would be doubtful.

Even though the results suggest that the cells of Table II are not 'determined' by the marginals, the marginals do have considerable impact on cell values. To some degree, the frequencies of observed conflicts between pairs of stags do reflect variations in the tendencies of individuals to engage in conflict. In fact, the Pearsonian product-moment correlation between the 21 cells of Table II and the 21 cells of Table III is 0.80 ( $P < 0.001$ ).

It would seem, therefore, that despite the departure from independence, slightly more than 60% of the variance in who fights whom among these stags is simply a consequence of the fact that stags that fight tend to fight with others who themselves fight often. What about the other 40% of the variance? It is possible that much of the variance could be accounted for in terms of some regular patterning of encounters (i.e. the stags may exhibit preferences

**Table III.** The expected number of pairwise agonistic encounters among the seven stags under the quasi-independence model

Winner	Loser						
	A	B	C	D	E	F	G
A	—	14.83	3.84	6.89	12.73	1.71	2.00
B		—	3.56	6.38	11.79	1.58	1.85
C			—	1.65	3.05	0.41	0.48
D				—	5.48	0.73	0.86
E					—	1.36	1.59
F						—	0.21
G							—

**Table IV.** The results of iterative dual normalization of the data on encounters among the seven stags

Winner	Loser						
	A	B	C	D	E	F	G
A	—	8.94	39.46	12.50	7.89	24.14	7.07
B		—	10.92	37.99	24.76	2.91	14.48
C			—	3.42	20.58	12.83	12.78
D				—	0.56	40.99	4.54
E					—	2.11	44.10
F						—	17.02
G							—

to fight with, or to avoid, specific others). To address this problem we need a method of examining the patterning of the encounters among the stags in a way that frees us from the marginal effects demonstrated above. We want to be able to visualize the data in a way that assumes each stag has exactly the same number of agonistic encounters as any other stag.

The standard use of iterative proportional fitting (Bishop et al. 1975) provides such a description. By setting the marginal totals to 100 for each stag, we can iterate the frequencies of encounters to what we would expect if each stag had 100 encounters. Thus, each cell is based on the proportion of encounters between two stags and represents the number of encounters they would have had if all the marginal totals were equal. All pairwise cross-product ratios, and related measures of association such as gamma, are invariant under iterative proportional fitting. As Bishop et al. (1975) suggest, 'fitting homogeneous margins to a simple two-way table brings out features of the interaction pattern that are not easily discernible in the raw data'.

The iteratively normalized red deer data are shown in Table IV. The diagonal values were fixed at zero since they are structural. Other zeros were treated as arising from insufficient sampling. To eliminate them, therefore, a constant of 0.25 was added to all non-diagonal zero cells.

One structural feature of the table is immediately apparent. With only one exception, the largest entries in each row and column of the table are two steps off the diagonal. Stag A's preferred opponent, for example, is stag C, and C's most frequent choices are A and E. The only exception to this pattern is that stag E slightly prefers B, who is three steps off, to C, who is two steps off. The overall pattern, however, suggests that these stags prefer to fight with those that are separated by exactly two ranks in the dominance hierarchy.

We can examine the question of just how closely this characterization corresponds to the data of Table IV by constructing a simple model and evaluating its fit using quadratic assignment (Hubert & Schultz 1976). Our model is simply that stags fight with those that are two steps away in

**Table V.** A simple model for the structure of agonistic encounters among the seven stags

Winner	Loser						
	A	B	C	D	E	F	G
A	—	0	1	0	0	0	0
B		—	0	1	0	0	0
C			—	0	1	0	0
D				—	0	1	0
E					—	0	1
F						—	0
G							—

the dominance hierarchy and that they do not fight with those in other positions. This preference structure is embodied in the graph of Fig. 2 and the adjacency matrix of Table V.

Quadratic assignment is based on matrix permutation. It provides a method, for calculating the probability that the large and small entries in two matrices are in the same order. Thus, it provides a way to evaluate the goodness-of-fit between a data matrix like Table IV and a model structure matrix like that shown in Table V. In practice, normal approximations are usually substituted for the calculations of exact probabilities, and that is what we have done here.

Quadratic assignment compares two matrices and yields a similarity index,  $\Gamma$ , that is normally distributed. In this case,  $\Gamma = 366.27$ . Under the null hypothesis that the large and small entries in these two matrices are independent, the expected mean ( $\pm$ SE) value is  $166.67 \pm 60.97$  ( $Z = 3.27$ ,  $P < 0.001$ ).

More evidence of the similarity between these two matrices can be obtained by unfolding each of them into a vector and calculating Pearson's product-moment correlation between the vectors. For the present data, the value of  $r$  is 0.83. This suggests that 69%, or over two-thirds, of the variance in the data matrix is accounted for by the simple model of Table V.

## DISCUSSION

In one of the earliest accounts of the social life of red deer, Darling (1937) reported that, 'only stags of almost equal merit fight each other'. The observation has been repeated again and again over the years as more data on red deer have been acquired.

In one recent study of 26 stags, Clutton-Brock et al. (1982) showed that fights between stags, whose positions in the hierarchy were more than two steps apart, occurred less frequently than one might expect by chance ( $\chi^2 = 18.2$ ,  $df = 1$ ,  $P < 0.001$ ).

The results of our analysis of Appleby's (1983) data are consistent with that result. Our analysis shows that fights between stags that are more than two steps apart in the dominance hierarchy are uncommon. But our analysis also suggests that fights between stags that are only one step apart also are uncommon. Our results indicate that fights typically occur between animals that are separated by exactly two steps in the dominance hierarchy.

We commented above on the difficulty of accepting Iverson & Sade's (1990) conclusion that a more dominant animal will, with a constant probability, win a fight with a less dominant animal, regardless of how far apart they are in the dominance hierarchy. But if we consider Iverson & Sade's conclusion in the light of our present results, perhaps we can clarify the situation.

We define three types of pairings among stags: (1) pairs of stags that are adjacent in the dominance hierarchy, (2) pairs that are two steps apart and (3) pairs that are more than two steps apart. We then consider these pairings in terms of the differences in resource-holding potentials and differences in possible pay-offs for the stags involved (Maynard Smith & Parker 1976). Consider first a type (3) pairing. If we assume, with Clutton-Brock et al. (1979), that animals that are widely separated on the dominance hierarchy will have markedly different access to resources, we might guess that the less dominant of such a pair might have much to gain in a fight. But, because the less dominant animal will almost certainly lose, he should tend to avoid a conflict.

Now consider a type (1) pairing. Here the animals are almost evenly matched, both in terms of access to resources and with respect to fighting ability. The less dominant animal might win in such an encounter, with a probability approaching 0.5, but since he would stand to gain very little, he should again avoid conflict.

However, in a type (2) pairing, the less dominant animal could be expected to have noticeably less access to resources, but at the same time he might be close enough to the dominant animal with respect to fighting ability (given his potential gain) to risk a fight. In any case, the results of the present analysis of fighting frequency show that fights involving

type (2) pairings are considerably over-represented as compared to a chance model, and that fights involving type (1) and type (3) pairings are under-represented.

It is reasonable to suppose that, among the type (2) pairings, in which stags are separated by exactly two steps in the hierarchy, the probability of victory by the dominant animal will be more or less constant. And, since fights of this sort are greatly over-represented, they can be expected to be the major contributors to the constant probability of victory by the dominant animal reported by Iverson & Sade (1990). Thus, the results of the present analysis of fighting frequency, help to explain the constant probability found by Iverson & Sade (1990). To the extent that fights between stags occur disproportionately among opponents that are separated by exactly two steps in the dominance hierarchy, we would expect the dominant animal to win with a constant probability.

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