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SHORT COMMUNICATIONS

A model of coalition formation among male baboons with fighting ability as the crucial parameter

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In savanna baboons, *Papio cynocephalus* spp., middle ranking and, to a lesser extent, low ranking adult males frequently form coalitions, while coalitions of high ranking males are relatively rare (review in Noë 1992). In two groups of average size (six to eight adult males) as well as in a much larger group (14–17 adult males) the highest frequencies were found for males ranking directly below the two or three top males (Noë 1990, 1992; Noë & Sluijter 1990, in press). Three explanations have been given for this phenomenon (for references see Noë 1992). (1) The formation of coalitions involves complex behaviour and requires a long learning process (the experience or age hypothesis). (2) Coalitions are limited to pairs that had enough opportunity to learn to act in a coordinated way (the friendship or familiarity hypothesis). (3) Coalitions are most frequently formed by males of intermediate strength, while the most dominant males are strong enough to win conflicts without the help of others, and the lowest ranking males are too weak to contribute significantly to the success of a coalition (the fighting ability hypothesis). The third hypothesis was empirically supported by Bercovitch (1988) and Noë & Sluijter (in press). In both studies it was concluded that the apparent relationship with other parameters such as male age and familiarity between allies, can be explained by the strong correlation of rank with both age and the duration of group membership. The conclusion was based on the relative plausibility of the three explanations, however, since the close correlation between the relevant parameters makes it hard to prove unequivocally that one hypothesis explains the data better than the others.

Here I show that it is theoretically possible to generate frequency distributions similar to the ones observed, using a simple model in which the relative fighting ability of coalitions and their targets is the pivotal parameter. The model applies to coalitions formed between adult males, which are usually immigrants that are not closely related to each other. Other group members tend to have little influence on the conflicts within this sub-group. I list the basic assumptions of the model first and then discuss some modifications.

Assumption 1: fighting ability and age have a bell-shaped relationship. Few will doubt that long-lived mammals go through an optimum in vigour during their lifetime. For male baboons I consider a negatively skewed bell shape to be likely; a relatively fast increase from 0 to about 7 years of age, an optimum reached between 7 and 10 years, and a gradual decrease thereafter (cf. Altmann et al. 1981).

Assumption 2: the distribution of fighting abilities in a group corresponds to the age–fighting ability relationship. The distribution of relative fighting abilities among immigrant males can be derived from the age–fighting ability relationship, if (1) the age–fighting ability relationship is similar for all males, (2) males immigrate at the same age, and (3) males immigrate at regular intervals. The rank–fighting ability curve for immigrant males corresponds to the right-hand tail of the age–fighting ability curve, since most males leave their natal group around the time they attain their maximal prowess (Altmann et al. 1988). Second and further migrations do not disturb the picture, if on average

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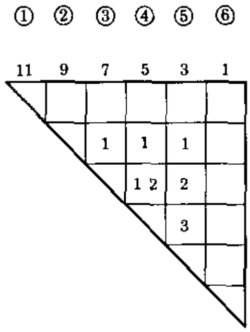

Fighting ability	Rank	N Partners	N Targets	N Combinations
11	①	0	0	0
9	②	3	1	3
7	③	3	2	4
5	④	3	3	4
3	⑤	3	3	3
1	⑥	0	0	0

Figure 1. Example of the calculation of the number of partner–target combinations for a simple linear relationship between rank and fighting ability. The figures in the cells of the matrix indicate the rank of the target that can be beaten by a coalition of the row and the column male. The fighting ability of a coalition is found by adding the values for each partner.

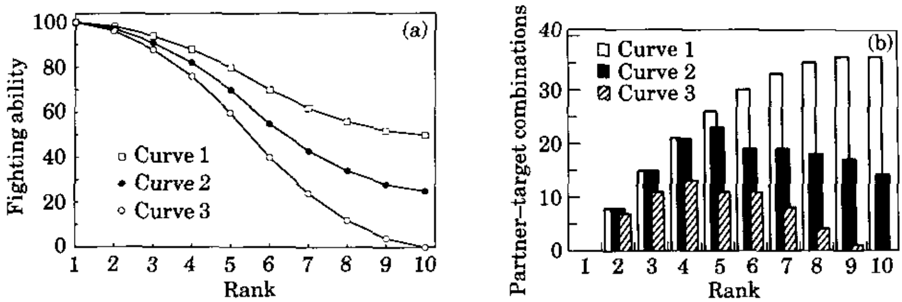

Figure 2. (a) Three hypothetical relationships between rank and fighting ability. (b) The corresponding distributions of partner–target combinations.

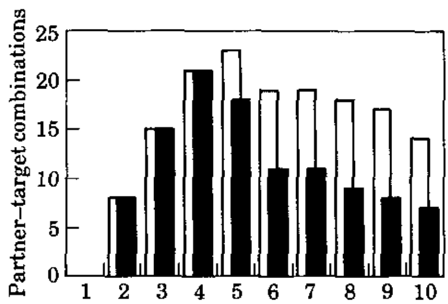

Figure 3. The effect of a modification of the assumption of equal distribution of coalitions over all targets. □: Distribution of partner–target combinations for curve 2 in Fig. 2b; ■: the distribution under the assumption that coalitions are formed only against the males on ranks 1 to 3.

males of the same age are exchanged between groups.

In a stable population with a pyramid-shaped demographic distribution the age gaps between the older, lower ranking immigrants will on average be larger than between the younger, higher ranking immigrants. Compared with the age–fighting ability curve the right-hand tail of the rank–fighting ability curve will therefore fall off a bit faster.

Assumption 3: the fighting ability (F) of a coalition can be calculated from the fighting ability of its members according to the formula $F_{coalition} = c(F_{partner1} + F_{partner2})$. It is difficult to say what would be a realistic value for the multiplication factor c. A synergistic effect ($c > 1$) is likely when the partners attack in a very coordinated manner. In the majority of cases, however, we had the impression that at least one of the partners did not pull his weight ($c < 1$). In the examples $c = 1$ has been used.

Assumption 4: only two-male coalitions against single targets are formed. This excludes combinations of more than two males and 'counter-coalitions'.

Assumption 5: any two males can form successful coalitions against any target with a fighting ability lower than their combined fighting ability.

Assumption 6: no male forms a coalition against a male with a lower fighting ability. A male that can win a conflict single-handedly has little to gain from coalition formation. This is notably the case if the coalition is formed to gain access to resources of which the partner would want his share.

Assumption 7: a male forms coalitions with a frequency proportional to the number of combinations of one partner and one target possible under the restrictions posed by assumptions 4, 5 and 6.

One can calculate the number of potential partner–target combinations for each male for any distribution of fighting abilities and any value of the multiplication factor *c*. An example is given in Fig. 1. There is no simple and obvious way to construct a hypothetical rank–fighting ability relationship, since many parameters play a role, some of which are difficult to measure. For the present purpose I constructed a number of examples of the shape hypothesized under assumption (2) with a maximum fighting ability of 100 and a minimum of 0 (Fig. 2). A male with zero fighting ability contributes nothing in a coalition with an adult male partner against an adult male target.

Curve 1 applies to a group in which the male on rank 1 is twice as strong as the male on rank 10. This means that each pair of males could form a successful coalition against any adult male in the group. Curve 3 illustrates a case in which the fighting ability declines relatively fast with age, or a group in which the age intervals between the males are large. The male on rank 10, for example, would have no impact in any coalition. With very steep curves (not illustrated) no pair would be strong enough to defeat the male ranking immediately above them and no coalitions would be possible. Curve 2 depicts a group in which the male on rank 1 is four times as strong as the male on rank 10, which is fairly realistic. In savanna baboons it is not unusual to see a high ranking male defeating several low-ranking males simultaneously.

So far I have assumed that the number of coalitions formed is proportional to the number of partner–target combinations (assumption 7). It is unlikely, however, that males would form coalitions against all potential targets equally often. The higher in rank a male is, the more he is able to monopolize resources, and the more he will be the target of coalitions. For example, high ranking males are in consort with oestrous females at the start of the day much more often than middle and low ranking males and coalitions against them are most frequently formed by the males of middle rank (Noë & Sluijter 1990, and references therein). Figure 3 illustrates the difference in distribution if the assumption is added that only the high ranking males are targeted by coalitions. The resulting distribution reasonably reflects observed data as presented in Noë (1990, 1992) and Noë & Sluijter (1990, in press).

Assumption (7) further implies that the number of coalitions a male forms against a target depends on the number of his potential partners. This would not be true if coalition formation is a purely goal-oriented behaviour aimed at the defeat of a certain target under certain circumstances. I have the impression, however, that coalitions are frequently formed opportunistically when a suitable partner is at hand.

It is unlikely that all males that could potentially form coalitions on the basis of their combined fighting ability would indeed do so (Noë 1992). The fighting ability model gives only the constraints within which coalition formation is possible, and therefore discrepancies between data on single groups and the predicted distributions are to be expected. The fighting ability hypothesis should be rejected, however, if the data on many groups combined also fail to show the predicted pattern.

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