

Committee V
The Emotions: Focus on Inter-Male
Aggression and Dominance Systems
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SOME BASIC BIOLOGICAL TERMS AND CONCEPTS OF PRIMATE
AGGRESSION

by

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1. Introduction

In discussing inter-male aggression and dominance in primates there is a need to define the terms used and their underlying concepts. This paper attempts to offer such basic clarification. Though the focus will be on macaques, the definitions and most of the concepts are meant to be applicable for all primates, including man. Here only a few important topics will be treated in short. For a systematical, more detailed and more complete analysis see ANGST 1980.

2. Aggression

A real definition of the term 'aggression' seems rather impossible. But this is no excuse for using the word vaguely and with changing meaning. A consensus of various disciplines should be possible over the following determination:

As 'aggression' there is labelled a behaviour which is directed at inducing a detrimental effect on the integrity of a partner or oneself.

'Aggressiveness' on the other hand means the readiness for aggressive behaviour, which is exclusively dependent on internal variables.

The word 'fight' should be limited to interactions, in which both partners engage in physical aggression against each other. For all kinds of disruptive interactions, covering all kinds of aggression, flight and their combinations, we have the term 'agonistic behaviour' (SCOTT 1972).

3. Dominance and inferiority as components of personal relationships

The observation of any established primate group shows that

types of interaction, their durations, frequencies and inter-relations differ among various dyads of individuals. This leads to the conclusion, that primates maintain personal relationships, which are based on mutual recognition and experience. HINDE (1975) and HINDE and STEVENSON (1976) have thus defined social relationships as the content, quality and patterning of interactions.

A component of such a relationship is the patterning of agonistic interactions. In a comparable way as affiliative and sexual interactions e.g. are patterned, agonistic interactions are. In a dyadic relationship we call the one who regularly wins in a conflict the 'dominant' individual, the one who regularly loses the 'inferior' individual. This component of the relationship is the 'dominance relationship' (ANGST 1975). The term 'dominance' therefore should be reserved for established relationships, correspondingly 'dominant' should not be substituted for stronger, more aggressive and the like, concerning individuals which have not yet established a relationship.

The system of dyadic dominance relationships in a group results in the social hierarchy, which is a component of the group's social structure.

Of course in many primate species we find dominance relationships on the inter-group level as well.

The maintenance of dominance relationships as a result of earlier experience helps all individuals involved to avoid risks of being wounded as well as spending time and energy unnecessarily. So not aggression is, as often stated, an organizing and advantageous factor of a group, but rather the establishment and maintenance of personal relationships, including dominance relationships.

4. Reassurance and appeasement

Most primates have signals which enhance friendly contact. Some of these signals, like grooming and lip-smacking in many macaques, are used by any individual towards any other, irrespective of dominance relationships. Others of these signals are correlated with the dominance relationship. So e.g. in *Macaca fascicularis* only inferior individuals perform the grimace and the teeth-chattering face.

The friendly - and often also fearful - behaviour of an inferior individual towards a dominant one, by which the dominant's aggression is reduced or (and) his friendliness enhanced, is called submissive or appeasing. The friendly behaviour of a dominant individual towards an inferior one, by which the inferior's flight (fear) is reduced and (or) his friendliness enhanced, is called reassuring.

Appeasement and reassurance have both in common a friendly component in motivation, and a reduction of tension as well as an enhancement of friendly contact as effect.

5. Contexts of aggression

MOYER (1968) produced a pioneering list of eight different contexts of aggression. But because this list was based mainly on rodents in a laboratory situation and included also predation, it cannot be transferred to primates. However, using MOYER's list as point of departure, ANGST (1980) has made a preliminary list of aggression-contexts for non-human primates:

1. Competition for food.
2. Sexual competition.
3. Territoriality (competition for living space).
4. Competition for a place (to rest or pass through).
5. Competition for dominance.
6. Encounters with outgroup individuals (including inter-group competition).
7. Take-over of alpha-male position (leading to infanticide in several species).
8. Receiving aggression (leading to defence or redirected aggression).
9. Social facilitation of aggression (joining in).
10. Preferred partner receiving aggression (leading to protective aggression, e.g. mother - infant).
11. Unaccepted proximity of a partner.
12. Non-sexual competition for proximity with a partner.

Besides these twelve widespread and common contexts there are a number of rarer ones, most of which being confined to a few species. Here three examples:

13. Sexual frustration.
14. Female of harem is too far away (male triggers its return by threatening it).
15. Rape (Orang-Utan).

All these contexts hold true for male aggression, numbers 7, 14 and 15 even exclusively so.

6. Aggression and the concept of evolutionarily stable strategy

As was shown above, aggression serves as a means of attaining advantage at the cost of another in a wide range of contexts, but

in the frame of interindividual competition within a species. Selection, as one of the principal factors promoting evolution, superficially also occurs on the level of interindividual competition in terms of differential reproductive success. According to the modern sociobiological theories however, there are rather the competing alleles. i.e. the different versions of a given gene, which are selected and thus differentially propagated.

It is not difficult to understand, that in primates alleles which make possible an efficient and variable use of aggression are selected positively against alleles which lead to a weak or rigid strategy of aggression. However, it is less obvious, why unlimited, lethal aggression strategies do not evolve.

Using game theory and population genetics PARKER (1974), MAYNARD-SMITH (1976) and MAYNARD-SMITH and PARKER (1976) could show, that extreme strategies of aggression cannot evolve, because they would not be evolutionarily stable. In competition with other strategies or even identical ones they would disappear. Furthermore it was shown, that single strategies of aggression can principally not be evolutionarily stable, only mixed strategies can be so.

Mixed strategies means that either any individual uses different strategies or different individuals use different strategies.

So may e.g. a macaque male in its prime of age rely on actual fighting, because its chance to win is relatively high, while a weaker (younger or older) individual specialises in bluff, display and enlisting support, and rather avoids actual fighting.

So convincing the theory is, it must be born in mind, that there is still a huge gap between the simplicity of the theory and the complexity of observed behaviour.

7. Kin selection and coalitions

In the above chapter aggression turned out to be a paradigm of selfish behaviour. But what about aggressive support and protection?

Generally aggressive coalitions in non-human primates are characterized by the following rule: Besides some opportunistic coalitions, aggressive support and protection are limited to kins and sex-partners. Kins share a part of their gene set, according to the degree of relatedness. The closer related they are, the more they share of their gene set (e.g. mother - offspring 50 percent), and the more they tend to support each other. Thereby they act indirectly selfishly, because ^{they} help select their own genes. The same holds true for supporting a sex-partner.

8. Conclusion

Only a few points could be raised here and these had to be much simplified. However, they are of great importance in discussing and for understanding aggression in non-human primates. In addition to that, it seems worthwhile to check the biological bases of human aggression along these lines.

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