A coalition of two adult males against a third adult male. The immediate cause of this conflict was meat (note the Thompson gazelle fawn carried by the right most male).

After Packer (1977) confirmed an earlier suggestion of Trivers (1971) that baboon allies are reciprocal altruists, this view gained the status of textbook truth. Packer’s conclusions were not challenged for more than a decade. Two recent studies, however, have questioned the validity of the reciprocal altruism theory for baboon alliances. I start this review with a synopsis of this critique. Thereafter I list the phenomena that should be accounted for by a model of alliance formation. This list is based on observations of coalitions and alliances made in a large number of baboon groups at various study sites. Finally I give an overview of my own efforts to formulate such a model. I compare coalition formation to interactions on a marketplace, where supply and demand determine which deals are closed and how profits are allocated. Paradigms for this kind of processes are provided by coalition games, N-player games in which bargaining among the participants plays an essential role. My first concern, however, is to identify the males that qualify as players in the game. I approach this problem by asking two questions: which males would gain by coalition formation, and which males would be able to form successful coalitions?

The study of baboon coalitions: a historical overview

The first extensive descriptions of alliances among male savanna baboons were given by Hall and DeVore (1965). They described the existence of what they called ‘central hierarchies’ in two groups of olive baboons (Papio cynocephalus anubis). Hall and DeVore wrote about one of their study groups:

It became clear that certain of the adult males constantly associated with each other and tended to support each other in aggressive interactions with other males. Some of
these males associated so closely that they were scarcely ever observed acting independently in such episodes, and on this basis three of them came to be designated a 'central hierarchy'. (Hall and DeVore 1965, pp. 59-60).

Following Hall and DeVore's publications (see de Waal and Harcourt this volume pp. 9-27 for more detail), data on coalitions and alliances among the adult male members of the several subspecies of the savanna baboon (Papio cynocephalus) have been gathered at a large number of sites in an even larger number of groups. These observations taken together now form the largest data set available on alliance formation among unrelated primates.

Hall and DeVore's pioneering work also influenced the subsequent study of alliance formation in a more indirect way. Inspired by a visit to their study site, Trivers mentioned baboon coalitions as a possible example of 'reciprocal altruism' in his seminal paper published in 1971. Alliances among male baboons became one of the textbook examples of reciprocal altruism after Packer (1977) confirmed Trivers' conjecture on the basis of field data. The power and appeal of Trivers' theory apparently led to a ready acceptance of Packer's conclusions, although one crucial step leading to these conclusions was made on the basis of six observations only (see Bercovitch 1988; Noé 1990). Further data on coalition formation were presented in studies of various aspects of the social organization and mating system of savanna baboons (Bercovitch 1985, 1986, 1987; Collins 1981; Noé 1986; Packer 1979a, b; Rasmussen 1980; Smuts 1985). The reciprocal altruism interpretation of baboon alliances was challenged in none of these publications. Then, in a paper on the use of coalitions as a tactic to improve reproductive success published in 1988, Bercovitch cast doubt on the applicability of the reciprocal altruism model. Finally, after a study especially devoted to coalition formation, I too concluded that the reciprocal altruism model was not valid and proposed an alternative approach (Noé 1989, 1990).

PROBLEMS WITH RECIPROCAL ALTRUISM AND THE PRISONER'S DILEMMA

In view of the close connection between the prisoner's dilemma model and the reciprocal altruism theory the statement that baboons are reciprocal altruists almost automatically implies that the prisoner's dilemma is a valid paradigm for baboon coalition formation. Casting doubt therefore on the validity of reciprocal altruism also casts doubt on the use of the prisoner's dilemma. Since there has been some discussion about the validity of the prisoner's dilemma paradigm in the case of reciprocal altruism, I briefly deal with this problem. My conclusion is that the prisoner's dilemma model is consistent with reciprocal altruism in most important features. Since the prisoner's dilemma model more explicit than the original reciprocal altruism theory, I phrase my criticism as much as possible in terms of the former. One assumption specific to the reciprocal altruism approach is that coalitions between male baboons are interactions in which one male acts as an altruist. I discuss this assumption separately.

Although a general discussion of the prisoner's dilemma model is beyond the scope of this review, I devote a separate section to its general relevance.

Is one of the participants in a coalition an altruist?

Few people will have doubts about the collaborative character of baboon coalitions, i.e. the total benefit to both participants combined will on average be larger than the total cost they both suffer. The question is whether the coalitions are altruistic in character, which according to the biological meaning of the term implies that in each interaction one participant gains, while the other loses. The alternative is that coalitions are cooperative in character, i.e. both participants normally obtain a net gain. It is also possible that alliances are a mosaic of both types of interaction.

As mentioned above, Trivers (1971) suggested and Packer (1977) appeared to confirm that coalitions are altruistic acts. On what grounds did they think so? Packer concentrated on coalitions formed to obtain access to females. Since females are indivisible entities, only one participant can end up with the female. Thus, when both invest in coalitions, such coalitions will inevitably be altruistic in character. This fact is not enough, however, to make these coalitions an interesting case for the study of the evolution of altruism. For that purpose each participant should a priori know which role he is going to play, in other words, which male is going to end up consorting the female, when the coalition proves to be successful. The theory of reciprocal altruism says something about the decision to act altruistically. I refer to a strategic decision here, of course, not to a conscious decision. The decision to help an unrelated individual, so the theory goes, is taken on the grounds of the chances that aid will be received from the beneficiary in the future. The theory of reciprocal altruism is not needed to explain the occurrence of coalitions, when both participants stand a fair chance (which does not have to be an equal chance) of gaining the female after each successful interaction, and when each of the males has a net gain over a longer series of interactions (see also Bercovitch 1988). Whether or not a male will have a net gain over a series of coalitions with a particular partner will depend on (1) the cost of taking part in a coalition; (2) the success rate of the coalitions; (3) the chance to obtain the consort after a successful coalition; and (4) the benefit of obtaining a consort.

It is thus crucial to the reciprocal altruism argument that it is clear from the onset of the formation of each coalition, which of the two males will gain access to the female. This is what Packer (1977) argued to be the case. He found that in all cases he observed only one of the males asked for support (using a behavioural element called 'head-flagging') and that this male always
obtained the consort. Unfortunately Packer saw this connection between head-flagging and obtaining the consort in only six cases. Bercovitch (1988) used data presented in Rasmussen (1980) and his own data to show that the initiator of the coalition was as likely as his partner to become the new consort male. He therefore concluded that baboon allies are not reciprocal altruists. I found that in some cases it was not even clear which of the males took the initiative to form the coalition, and that often both showed the head-flagging simultaneously (Noé 1989). Neither Bercovitch (1988) nor I could observe an indication at the start of a coalition as to who would profit from a successful take-over. On the contrary, in most cases it seemed to be a matter of chance. Once the close proximity between the female and the consorting male is broken, a race between the partners towards the female may take place. Reaching the female first normally suffices to make a male the undisputed owner for some time (Bercovitch 1988; own observations). This phenomenon could be based on a respect for ‘ownership’ reminiscent of hamadryas baboons (cf. Kummer et al. 1974). The new owner may even be a male that did not take part in the battle over the female. Often the male that lost the female will go on fighting one of his opponents for some time, while the other sneaks out to the female. One could say, therefore, that in such cases the previous owner largely determines which coalition partner gets the female.

Bercovitch (1988) concluded that both partners in a coalition have a chance to obtain the resource, and thus are in fact cooperating. Other coalitions, notably interferences against strong opponents, may nevertheless be altruistic interactions. It is, however, also plausible that such interferences at least partly serve the interest of the interferer: he may seize the opportunity to settle his own affairs with the target of the coalition, or his main goal may be to prevent damage to his partner, who is instrumental in getting access to certain resources (cf. Kummer 1979).

Once could argue that the question of whether altruism or cooperation is involved is bound to remain academic, since we are not, and probably never will be, able to measure the cost/benefit budgets involved. How important is it to be able to tell the difference? Historically the theory of reciprocal altruism was an answer to the challenge to explain the occurrence of altruism among unrelated animals. At the time altruism was a central problem in the debate about individual selection vs. group selection. Strong emphasis was laid on the significance of the time lag between investment and return in reciprocal altruism. The time lag would make it difficult to recognize ‘cheating’ by a partner. This emphasis probably exaggerated the difference between cooperation and reciprocity. At a later stage Axelrod and Hamilton (1981) proposed the iterated prisoner’s dilemma as a paradigm for both cooperation and reciprocal altruism among unrelated animals and implicitly pointed out the resemblance between cooperation and reciprocity: the individuals involved have to guard themselves against exploitation by the partners in both cases. Axelrod and Hamilton’s proposal implies the validity of the iterated prisoner’s dilemma game as a paradigm for coalition formation among baboons. In the following sections I examine the usefulness of this approach.

**Is the prisoner’s dilemma game a valid paradigm for reciprocal altruism?**

There has been some discussion whether the prisoner’s dilemma model indeed applies to reciprocal altruism (see Packer 1986). In an iterated prisoner’s dilemma each player makes a choice between ‘cooperation’ and ‘defection’ in each round. Two reciprocal altruists make these decisions one after the other. If one were to take two such decisions, one by each player, to be comparable to a single round in the game, then there would be one player in each such round that would not be faced with the dilemma so typical for the game, since he would already know the other player’s decision. It is essential, however, that reciprocal altruists are not informed about the next decision of their partner. Therefore it is likely that a game can be constructed for reciprocal altruism, which resembles the prisoner’s dilemma in essential features. Boyd (1988) indicated how the prisoner’s dilemma can be adjusted to make it compatible with reciprocal altruism.

**Is the prisoner’s dilemma a valid paradigm for coalition formation in baboons?**

In order to qualify as an example supporting the prisoner’s dilemma model the following statements about baboon coalition formation should hold:

1. The formation of coalitions depends on the behaviour of two individuals only, since the model is based on the two-player iterated version of the game.
2. The (potential) costs and benefits concur with the pay-off configuration of the prisoner’s dilemma.
3. Communication between the partners does not influence the decision to participate in coalitions.

The confirmation of the following statement would support the prisoner’s dilemma model, although its refutation would not necessarily imply the rejection of the model:

4. The behaviour of baboon allies is consistent with playing a tit-for-tat strategy.
1. Is a two-player game suited as a paradigm for baboon alliance formation?

The two-player prisoner's dilemma is not suited as the basis of a model that takes into account the possibility to weigh one potential partner against another. The use of the two-player version of the game implies that each individual regulates its collaboration with each of its partners separately. Strategic decisions in interactions with a certain partner are supposed to be influenced only by past interactions and/or expectations about future interactions with that same partner.

Male baboons switch over to another partner, not so much because the old partner refuses collaboration, but rather because the new partner is a more effective member of the coalition (Noë 1986, 1989) (see Fig. 11.1(a) (b)). This makes sense, because a male that can reach a goal only through collaboration with one other male, and that has several potential partners, should select the best to do the job. This can be the most effective partner in one case and the least demanding in another. Two phenomena are thus crucial to the understanding of this kind of collaboration: (1) partnerships form through a process of selection from several potential partners; (2) a possibility of switching partners remains after partnerships have formed. This coin has another side as well: when the number of potential partners is limited, competition over valuable partners can be expected.

A game theoretic model that accounts for this kind of dynamics should be based on an $N$-player game. For those not familiar with game theory it might seem that the $N$-player variant of the prisoner's dilemma, best known from Hardin's (1968) explanation of the 'tragedy of the commons', could be the proper base for such a model. This is not true, however. The pay-offs for players in an $N$-players prisoner's dilemma game depend on the behaviour of all players involved, e.g. all members of a social unit. Collaboration does not pay if not all players, or at least a large proportion, decide to 'cooperate'. In an $N$-player prisoner's dilemma all others, defectors and fellow cooperators alike, profit from the decision of a player to cooperate. The paradigm can be applied to cases of collective collaboration, e.g. to the problem of vigilance in flocks of birds. The type of collaboration considered here is distinctly different. Individuals can increase their fitness by forming small collaborating subunits, with a neutral or disadvantageous effect on the fitness of other individuals involved.

2. Is the cost/benefit budget of coalition formation in agreement with the prisoner's dilemma's pay-off configuration?

I have already mentioned that gaining access to receptive females is an important goal of coalitions among male baboons. In these, and other coalitions that yield indivisible resources, only one partner can gain a positive benefit. Thus one possible outcome of the prisoner's dilemma, the one in

Fig. 11.1. Two scenes of a single conflict. The males at the right threaten (raised eye brow) the screaming male on the left. The conflict is unusually tense, possibly because it was one of the first conflicts in which the male on the foreground/right sided with the male in the background instead of with the other male. Both males were his allies throughout the study period, but he changed preference between them coinciding with a drop in rank of the disfavoured ally.
which both players gain the 'reward for cooperation', is fundamentally impossible. This problem is analogous to the problem of applying the prisoner's dilemma model to reciprocal altruism discussed in the previous section, and can be solved in the same way. An apparent solution would be to assume that there always is a small benefit for the less lucky partner. This would imply the assumption that the decision to take part in the coalition is based on the chance to obtain this small benefit. By invoking such undemonstrable benefits one could make all cost/benefit budgets consistent with any model; a rather fruitless procedure.

A more serious problem is that the 'temptation to defect' (T) in baboon coalition formation is not likely to be greater than the 'reward for cooperation' (R) (see PD-matrix in Boyd, this volume pp. 473–89). A high value of T implies that a 'defecting' baboon could reap the benefits of the effort of a 'cooperating' partner; in other words, the goals collaborating baboon males strive for could in principle be reached through the effort of one male alone. In most types of coalition this is not likely to be the case. Moreover, the 'cheated' partner would be able to react to the defection by breaking off the interaction at the start of the formation of the coalition in most cases, although it may be difficult to react to subtle forms of cheating in that manner. I thus consider baboon coalitions to be a form of 'synergistic cooperation' (Maynard Smith 1983) for which the trust game, in which R > T, would be a more appropriate paradigm than the prisoner's dilemma (see Liebrand 1983 for a classification of the social dilemma games). One could try to evade this problem and state that one of the partners could 'defect' by appropriating the resource gained after the successful collaboration. This option would, however, only be open to the strongest or most dominant individual, which is at variance with the assumption of the prisoner's dilemma model that both partners must have the option to defect unilaterally.

I mentioned above the possibility that baboon males would interfere in agonistic interactions to the advantage of their partners in order to prevent damage, which could make the partner less useful in the future. Lima's (1989) analysis shows that the pay-off configuration of coalitions would no longer be consistent with the pay-offs used in Axelrod and Hamilton's (1981) model, if indeed the future value of the partner plays a role in the decision to form coalitions.

3. *Is the decision to participate in coalitions independent of communication between the males involved?*

The prisoner's dilemma model is based on non-cooperative game theory, and thus explicitly excludes the possibility that negotiations influence the decision to collaborate. The argument is as follows: communication about intentions cannot be honest, because it would pay to signal willingness to cooperate and to defect as soon as the other decided to cooperate. Given the prisoner's dilemma's pay-off configuration this is a correct conclusion; not so, however, when coalition formation is indeed a form of synergistic cooperation. When both participants stand to gain by cooperation, while neither can reap direct benefits from defection, honest communication and negotiation become realistic possibilities.

Before and during coalitions baboons show extensive communication (Noë 1989). It would be rather unlikely for such behaviour to evolve if it did not have a positive influence on the behaviour of the partner. I refer to this communication more extensively in my discussion of 'bargaining', which forms an essential part of my alternative model.

4. *Do baboon males play tit-for-tat?*

On the basis of a number of computer tournaments, Axelrod and Hamilton concluded that tit-for-tat is an evolutionary stable strategy (ESS) of the iterated prisoner's dilemma (Axelrod 1984; Axelrod and Hamilton 1981). Although this conclusion had to be weakened in the light of later work (Boyd and Lorberbaum 1987; Selten and Hammerstein 1984) one can still assume that tit-for-tat (or strategies with similar properties, see Axelrod 1984; Boyd this volume pp. 473–89) are likely to be played in all situations for which the iterated prisoner's dilemma is a valid paradigm. It is thus worthwhile to examine whether baboons play tit-for-tat or a similar strategy. It should be noted, however, that refuting tit-for-tat does not necessarily invalidate the iterated prisoner's dilemma as a paradigm. On the other hand observing tit-for-tat does not prove that an iterated prisoner's dilemma is being played, since this strategy can also be a good strategy in other games. For example the strategy 'retaliator' in the hawk–dove game (Maynard Smith and Price 1973; this game is also known as the 'game of chicken') is identical to tit-for-tat (Rapoport 1975).

Two observations make it unlikely that baboon males play tit-for-tat. Firstly, some males participated in coalitions over consorts again and again, although they almost never gained the main prize, the oestrous female (Collins 1981; Noë 1990). Secondly a number of alliances did not fall apart, even after one ally repeatedly refused to collaborate by not responding to solicitations to do so (Bercovitch 1988; Collins 1981; Noë 1989). Tit-for-tat is not a likely strategy, when only few potential partners are available. Individuals using this rule basically select their partners by trial-and-error, rejecting those that do not collaborate properly. The tit-for-tat rule in a strict sense is very sensitive to the occurrence of an occasional mistake, misunderstanding or inability to effectuate a decision to cooperate. Such events can very easily lead to an echo effect of repeated defections. With few partners available this can soon lead to the rejection of all potential partners. Boyd (1989) proposed a solution for the problem of mistakes, based on a modified version of tit-for-tat. Boyd's solution assumes, however, that (1) the defector-by-mistake would 'know' that he had made a mistake and that (2) animals on occasion would also make the reverse mistake and
cooperate when they should have defected (but see Boyd this volume pp. 473–89). I do not know how to translate the latter assumption in terms of baboon behaviour. It therefore remains to be shown that tit-for-tat-like rules can survive in populations split up in relatively small social units when mistakes occur regularly.

**Is the prisoner's dilemma a useful paradigm for other forms of collaboration?**

My conclusion is that the prisoner’s dilemma model does not apply when animals have a choice among partners. In those cases the dynamics of coalition formation play a role. These dynamics cannot be modelled using the prisoner’s dilemma (cf. Colman 1982). This excludes the use of the prisoner’s dilemma in virtually all cases of collaboration between members of the same social unit, except for those forms of collaborative behaviour which benefit the whole unit. In the latter case the $N$-player version of the game could be useful. Coalition formation does not play a role in social units, when for some reason each individual that could gain by collaboration has only one possible partner. In that case the proper paradigm is the trust game ($R > T > P > S$), when the collaboration is synergistic, and the prisoner’s dilemma ($T > R > P > S$), when the collaboration is inessential (see section above, question 2).

This should not be taken to mean that there are no useful applications of the prisoner’s dilemma paradigm. Good examples are conflicts between ‘dear enemies’ (Getty 1987; Whitehead 1987) and gamete exchanges in some simultaneous hermaphrodites (Fischer 1980, 1988; Leonard and Lukowiak 1984; Sella 1985). In both cases the animals involved are condemned to collaborate with the given partner and a choice among partners plays no role. Dear enemies are basically competitors that can reduce the costs of competition by some form of collaboration. The hermaphrodites figuring in the studies mentioned normally have no simultaneous choice between partners, while finding an alternative partner incurs a high cost. A mechanism to guarantee this high cost can be part of the strategies played (see Fischer 1980).

I know of one game-theoretic development that could lead to a compromise between the prisoner’s dilemma model and my desire to involve the dynamics of coalition formation: the possibility of forming ‘implicit coalitions’ in three-player prisoner’s dilemmas as studied by Fader and Hauser (1988). The problem is, however, that in Fader and Hauser’s version of the game the players can opt for actions that are relatively fine-tuned intermediates between the prisoner’s dilemma’s ‘cooperation’ and ‘defection’. In the case of baboon coalition formation I do not see the real world equivalent of such a continuous range of options.

**The need for a new model of coalition formation in baboons**

The conclusion from the above is that the prisoner’s dilemma model, and thus implicitly the reciprocal altruism theory, is not satisfactory in the case of coalition formation in male baboons. The model is at variance with a number of observations and falls short in capturing important features of coalition formation: (1) the possibility to switch between partners, or at least to threaten with such a switch; (2) the competition over preferred partners; (3) the role played by communication. I am convinced that these shortcomings are not confined to the case of baboon coalition formation, but are typical for all cases in which members of social units can form collaborative subsets of varying composition (this view is further developed in Noë et al. 1991). I limit myself here to an alternative model of alliance formation among adult male baboons, but before presenting this model I give an overview of the relevant features of the coalitions and alliances formed by these males.

**THE BIOLOGY OF ALLIANCES AMONG MALE BABOONS**

**A short description of coalitions**

Coalitions can start in several ways: a male may interfere in an ongoing conflict; two males may attack a third individual simultaneously, or two males may defend themselves against aggression directed at both of them. In many cases the formation of a coalition is preceded by some spatial manoeuvring, by the exchange of side-directed behaviour (term coined by de Waal and Van Hooff 1981), like ‘head flagging’ and ‘staccato grunting’, and by pseudo-sexual behaviour between the participants.

Coalitions among males are formed for a variety of (apparent) reasons and against opponents of virtually all age–sex classes, apart from very young infants. The probably most frequent, and certainly best-studied, immediate cause is competition over receptive females. Typically, two or more adult males challenge a male in consort with an estrous female. Almost invariably the challenged male is dominant to each of the coalition partners. Baboon consorts are exclusive in character, i.e. a male cannot normally mate with an estrous female that is in consort with another male. The consorts can thus be seen as the entities over which males compete. Roughly one-quarter to one-third of all coalitions formed by adult males are formed to obtain or defend a consort (Noë 1989). In other words, competition over consorts is by no means the only reason to form coalitions. Other recognizable immediate causes are: (1) disputes over food (notably meat); (2) the defence of third parties (notably infants) against aggression of other group members; and (3) the redirection of mutual tension on bystanders. A considerable number of coalitions, however, have no recognizable immediate cause.
Coalition partners and their targets

Important clues to the mechanism of coalition formation are given by the attributes of coalition partners and their targets. Table 11.1 summarizes the findings of a number of studies. Note that my own study of three different groups, is the only study that concentrated on all coalitions formed. Most other studies give data on coalitions formed in the context of sexual competition only. General conclusions can therefore be drawn only for the latter type of coalitions. In all alliances I observed that a minority of the coalitions were over consorts, but this type of coalition certainly formed an important segment. If a general pattern can be recognized for the formation of coalitions over consorts, this pattern may be valid for other types of coalitions as well.

Which general pattern can be recognized? From Table 11.1 one can see that the targets of coalitions are almost invariably young, high-ranking immatures before their growth spurt and only later rise in rank in their new group. With the passing of time the immigrants drop in rank as new males arrive. This situation is reflected in a simplified form in Fig. 11.2.

Apart from idiosyncratic cases, there are a number of systematic exceptions to this pattern. (1) Males that migrate at a later time in life, usually for the second or third time, will be in the group for a shorter period than other males of comparable rank and age. (2) Some males stay in their natal group after they became sexually active adults. My impression is that such is the case especially in large groups, such as those studied in Gilgil (Bercovitch 1985, 1986, 1987; Noé 1989; Smuts 1985). My speculation is that while natal males in small groups are excluded from mating with most females due to incest-avoidance mechanisms, natal males in large groups have enough potential mates in spite of such mechanisms. (3) A few males migrate as immatures before their growth spurt and only later rise in rank in their new group.

Young, high-ranking males have an advantage in locations where conflicts tend to remain dyadic, like sleeping trees or sleeping cliffs. These males are usually in consort in the early morning as a result. Later in the day, however, the circumstances enhance the chances of a coalition (Bercovitch 1988; Noé and Sluijter 1990; Popp 1978; Rasmussen 1980; Smuts 1985).

Because of the close correlation between the main characteristics of males,
### Table 11.1: Attributes of coalition partners and their targets.

<table>
<thead>
<tr>
<th>Sub-species</th>
<th>Site</th>
<th>Period</th>
<th>Group</th>
<th>Number of adult males</th>
<th>Number of coalitions observed</th>
</tr>
</thead>
<tbody>
<tr>
<td>anubis</td>
<td>Nairobi NP, Kenya</td>
<td>3.5 months (1959)</td>
<td>aSR</td>
<td>28</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>6 months (1959)</td>
<td>bSV</td>
<td>40</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>cA, B, and C</td>
<td>26–51</td>
<td>3–11</td>
</tr>
<tr>
<td></td>
<td>Gombe NP, Tanzania</td>
<td>8 months+</td>
<td>A, B, and C</td>
<td>20</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>Gilgil, Kenya, Tanzania</td>
<td>12 months (1972–74)</td>
<td>dPumphouse</td>
<td>78–90</td>
<td>4–8</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>eEburr u Cliffs</td>
<td>120</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>'Eburr u Cliffs</td>
<td>95–114</td>
<td>14–17</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Viramba</td>
<td>102–120</td>
<td>34</td>
</tr>
<tr>
<td></td>
<td>Mikumi NP, Tanzania</td>
<td>10 months (1976)</td>
<td>hMembe</td>
<td>70–72</td>
<td>7–8</td>
</tr>
<tr>
<td></td>
<td>Ruaha NP, Tanzania</td>
<td>5 months</td>
<td>Alto</td>
<td>50–55</td>
<td>6–9</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>W</td>
<td>77</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Honnet NR, South Africa</td>
<td>6 months (1968)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Long-lasting alliances?**

<table>
<thead>
<tr>
<th>Rank</th>
<th>Age</th>
<th>Residence status</th>
<th>Attributes of targets</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>yes</em></td>
<td>all</td>
<td>late prime, old, very old</td>
<td>high rank</td>
<td>Hall and Devore (1965)¹</td>
</tr>
<tr>
<td><em>yes</em></td>
<td>high middle, low 'older'</td>
<td>newcomer, resident</td>
<td>high rank</td>
<td>Packer (1977, 1979a, b)²</td>
</tr>
<tr>
<td><em>no?</em></td>
<td>high middle, low 'older'</td>
<td>newcomer, long time resident</td>
<td>high rank</td>
<td>Bercovitch (1986)</td>
</tr>
<tr>
<td><em>yes</em></td>
<td>middle, low 'older'</td>
<td>immigrant of long residence</td>
<td>high rank</td>
<td>Smuts (1985) 'study 2'³</td>
</tr>
<tr>
<td><em>yes?</em></td>
<td>middle, low 'older'</td>
<td>young, prime, natal, newcomer, long time resident</td>
<td>high rank</td>
<td>Noë (1989)</td>
</tr>
<tr>
<td><em>yes</em></td>
<td>middle, low prime, aging, aged</td>
<td>long time resident</td>
<td>high rank</td>
<td>Rasmussen (1980)</td>
</tr>
<tr>
<td><em>yes</em></td>
<td>middle, low 'older'</td>
<td>immigrant of long residence</td>
<td>high rank</td>
<td>Collins (1981)</td>
</tr>
<tr>
<td><em>yes</em></td>
<td>middle, low 'older'</td>
<td>immigrant of long residence</td>
<td>high rank</td>
<td>Noë (1989)</td>
</tr>
<tr>
<td><em>yes</em></td>
<td>middle, low prime, old</td>
<td></td>
<td>high rank</td>
<td>(idem)</td>
</tr>
</tbody>
</table>

¹ Ranking not based on naturally occurring dyadic conflicts and thus not comparable to other studies.
² Data of 12 different males in three different groups combined.
³ One alliance started in 1977 (Smuts' Study 1) and lasted most likely till the death of one ally during Noë’s study in 1984.
⁴ In addition consorts were defended successfully 14 times.
⁵ In addition consorts were defended successfully five times.
Table 11.2. Proportion of consort change-overs effectuated through coalitions. The table attempts to give an impression of the order of magnitude of the impact of coalition formation on male reproductive success. The criteria for consorts, agonism, and coalitions varied considerably between studies. Note that the data are biased in favour of coalitionary take-overs (explanation in text). The data of Noé and Sluijter differ from the others in that the mode of defence of a coalition (alone or with help of others) was substituted when the start of the consort was not seen. This method reduces the bias in favour of coalitionary take-overs.

<table>
<thead>
<tr>
<th>Source</th>
<th>Observed consort take-overs</th>
<th>Observed agonistic take-overs</th>
<th>Percentage of all take-overs</th>
<th>Percentage of agonistic take-overs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rasmussen (1980) (Fig. 7.13)</td>
<td>23</td>
<td>91.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Collins (1981) (Table 8.VIII)</td>
<td>16</td>
<td>64.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bercovitch (1988) (Fig. 1)</td>
<td>15</td>
<td>61.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Smuts (1985) (p. 135ff.)</td>
<td>18</td>
<td>37.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Noé and Sluijter (1990) (Table XII)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Group A</td>
<td>80</td>
<td>20.3</td>
<td>32.5</td>
<td></td>
</tr>
<tr>
<td>Group H</td>
<td>83</td>
<td>16.8</td>
<td>25.3</td>
<td></td>
</tr>
</tbody>
</table>

The impact of the mating success of males that lost their consorts due to coalitions formed by others is harder to estimate. In the first place the number of consorts they had was not affected and in the second place it is impossible to know how long they would have had their consorts without take-overs through coalitions. The proportion of consorts thus lost can be considerable: in a number of groups studied the high-ranking males lost one-third to over one-half of their consorts due to coalitions (Collins 1981; Noé and Sluijter unpublished data).

The division of pay-offs

Little information exists about the division of pay-offs between allies. One only gets an idea who benefits when tangible resources are at stake, notably food and receptive females. Other potential benefits, like improvement of status, prevention of injury, defence of kin, etc. are almost impossible to quantify, let alone the question of whether or not receiving benefit A can be compensated by receiving benefit B. A statistical analysis of the division of pay-offs can only be attempted for the few alliances in which the successful take-over of at least six tangible resources of comparable value (read consorts) has been observed. One such alliance was observed by Bercovitch (1988). Of 20 successful coalitions four involved a third male. In the remaining 16 cases the consorts were fairly symmetrically divided (7–9). In Amboseli we observed one pair of males with eight such successful coalitions; one male obtained the female in all eight cases (Noé 1990). The asymmetry in this alliance is even more remarkable, when the three-male
Coalitions and 'provocations' in which these males were involved are considered too (Table 11.3). A comparable asymmetry was observed by Collins (1981) in the most successful alliance in his group: one of the males obtained the female after seven of eight successful take-overs. For the model presented below it is important to know the number of potential partners each ally had. An indication for this number is the total number of adult males present during coalition formation in each group. For the three cases mentioned above these numbers were: Bercovitch: four adult males (personal communication); Collins: 7-8 males; Noe: 6-7 males. One should keep in mind that these data reflect observations on one type of benefit from coalitions only. Other benefits accruing from the same alliances may have been very differently distributed and thus have shifted the balance.

Table 11.3. Results of conflicts with coalitions (bold) or provocations over consortships between alliances of low-ranking males and single high-ranking males. H5, H6, and H7 were the three lowest-ranking of seven adult males in Hook's Group. 'Provocations' are interactions in which the allies provoke a conflict with a consortship male, without forming a coalition (from Noe 1990).

<table>
<thead>
<tr>
<th>Alliance</th>
<th>Conflicts with coalitions</th>
<th>Successful coalitions</th>
<th>Provocations</th>
<th>Male in consort after conflict</th>
</tr>
</thead>
<tbody>
<tr>
<td>H5-H6</td>
<td>12</td>
<td>8</td>
<td>3</td>
<td>8+3 0+0</td>
</tr>
<tr>
<td>H5-H7</td>
<td>5</td>
<td>4</td>
<td>3</td>
<td>4+2 0+1</td>
</tr>
<tr>
<td>H6-H7</td>
<td>6</td>
<td>1</td>
<td>1</td>
<td>1+1 0+0</td>
</tr>
<tr>
<td>H5-H6-H7</td>
<td>5</td>
<td>5</td>
<td>2</td>
<td>5+2 0+0</td>
</tr>
<tr>
<td>Total</td>
<td>28</td>
<td>18</td>
<td>9</td>
<td>17+7 1+1 0+1</td>
</tr>
</tbody>
</table>

**Phenomena to be explained**

It is now possible to summarize the features that should be accounted for by a model of alliance formation.

1. Coalitions are formed by a limited set of males. Rank largely determines which males combine. In small groups these are middle- and lower-ranking males with a relatively strong participation of the middle-ranking males.

2. All kinds of divisions of benefits can be found, from quite symmetrical to extremely asymmetrical.

3. Some alliances are quite stable and coalitions continue to occur, despite occasional lack of response to the partner's appeals to form coalitions.

I present three separate *post hoc* models that form the building blocks of a theory of alliance formation. The purpose is to explain why certain males form alliances and others do not, and why they arrive at certain divisions of pay-offs. The first model makes clear that coalitions are only formed by males below a certain rank, because only these males gain by doing so. With the help of the second model I show that the number of males likely to be involved in coalitions is further limited, because not all pairs of males can form coalitions strong enough to be successful. What is then left to be explained in the third model is why only some of the potential combinations actually develop into alliances and why some of these coalitions can be remarkably stable, even when the pay-offs are asymmetrically divided between the allies. A major problem that will arise in this part is the question whether such animals as baboons are able to bargain about the formation of coalitions and about pay-off distributions. A fourth section is devoted to this question.

**Who would benefit from coalition formation?**

I first approach the problem of who will form coalitions by asking who would gain a net profit by doing so. As discussed before, costs and benefits remain elusive quantities for the most part. We have some more grip, however, on the coalitions over consortships. Noe and Sluijter (1990) calculate at what rank a male should switch over from trying to obtain consortships on his own to trying to obtain consortships with the help of others. I give a brief account of our findings here.

Our starting point was S. A. Altmann's (1962) priority-of-access model as applied to baboons by Hausfater (1975). According to that model the mating success of a male depends on his rank and on the number of receptive females available. The male highest in rank obtains the first female, the second in rank the next and so on, till the number of available females is exhausted. It is assumed that the males can be ranked in a linear rank order, the female after seven of eight successful take-overs. For the model presented above these numbers were: Bercovitch: four adult males (personal communication); Collins: 7-8 males; Noe: 6-7 males. One should keep in mind that these data reflect observations on one type of benefit from coalitions only. Other benefits accruing from the same alliances may have been very differently distributed and thus have shifted the balance.

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<tr>
<td>H6-H7</td>
<td>6</td>
<td>1</td>
<td>1</td>
<td>1+1 0+0</td>
</tr>
<tr>
<td>H5-H6-H7</td>
<td>5</td>
<td>5</td>
<td>2</td>
<td>5+2 0+0</td>
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<td>28</td>
<td>18</td>
<td>9</td>
<td>17+7 1+1 0+1</td>
</tr>
</tbody>
</table>
more extreme conditions, like severe droughts (data on Gilgil population: Bercovitch personal communication; Noé and Sluijter unpublished). The calculation also asks for a precise indication of the days of the menstrual cycle that are of interest. Menstrual cycles are variable, however, for individual females and between individuals.

We therefore preferred to use a short-cut, which we think gives more relevant results. Since there were always more sexually mature males around than receptive females, we assumed that each female of interest to the males would be consorted. Our estimate of females available per day was thus directly based on the number of females consorted. This number follows a Poisson distribution, as shown in Fig. 11.4. On the basis of this distribution one can calculate the mating success of a male for each rank, under the assumption that the priority-of-access model is correct.

Hausfater (1975) found that the data are not in agreement with the model on one point: males had a much lower mating success than predicted by the model during the time they occupied rank 1. This result was corroborated by our findings. As explained above, the males on rank 1 are usually young, recent immigrants. Such males are often rather peripheral in the group and have difficulty forming relationships with especially the older and higher-ranking females (see also Smuts 1985). One of our groups had newcomers on rank 1 and 2 at the same time and both had a lower-than-expected success. Hausfater (1975) did not observe the formation of coalitions and thus did not incorporate the effect of coalition formation in his calculations. We, however, tried to calculate at what rank it would benefit a male to start to form coalitions, under a number of assumptions. A first assumption is that two coalition partners divide the consorts obtained equally among themselves, and a second that every coalition is successful. From these assumptions it follows that it is worthwhile to form coalitions as soon as the success in obtaining consorts on an individual basis is less than half of the maximum number obtainable, which is the number the male on rank 1 would have according to the priority-of-access model. We did not consider the possibility of 'counter-coalitions', i.e. coalitions formed by a high-ranking male to counteract the effect of the coalitions formed by males of lower rank, since such coalitions rarely occurred. To see for which rank it would pay to form coalitions an additional factor has to be added: the number of females that become available after they have been voluntarily abandoned by the consort-male. We found that about one-third of the consorts is given up voluntarily and used this figure in our model, but even higher proportions have been reported (Bercovitch 1988).

The result of our calculations is presented in Fig. 11.5. The figure shows that in both our study groups it would pay to form coalitions for a male on rank 3 or lower. The rank thus found is of course dependent on the size of the group. Our study groups were in the medium size range (33-55, with 6-8 adult male immigrants).

Thus by taking the effect of coalitions into account the priority-of-access model can be modified to fit the data much better than Altmann's original version, but some discrepancies between data and model remain. The first, the relatively low success of high-ranking newcomers, has been discussed above. A second discrepancy we found was that both groups had a male with low mating success ranking between the successful males of high rank and the highest-ranking male that successfully used coalitions. The third deviation we found was that some middle-ranking males used coalition formation with more success than the low-ranking males. This success was the result of more frequent participation in coalitions against consort-males, of a higher success rate of these coalitions and, in some cases, of an asymmetry in the chances to obtain the consort. The second and third deviation from our modified priority-of-access model can be understood, if one considers the dynamics of coalition formation among a small number of potential participants, as I explain below. We considered all three discrepancies as systematic deviations from the basic model and incorporated them in our descriptive model as given in Fig. 11.6.
Which males could potentially form coalitions?

There is one hidden assumption in the above model: each combination of two adult males would be able to beat each adult male member of the group. Any observer of baboons would hesitate to use this assumption. The next approach to the problem of who forms coalitions should thus be: who is able to form coalitions successfully against whom? The following model is based on differences in fighting ability between males. Perhaps I should speak of a thought experiment, rather than a model, since I have no way of estimating the most crucial parameter, (relative) fighting ability. We are not completely ignorant about the relative fighting abilities in a subgroup of adult male baboons, however.

Firstly, the rank order is usually linear at any given time. The apparent exception described by Strum (1982) is probably an artifact. Strum constructed a single rank order over a 14-month period. In the course of such a long period many changes in the rank order can be expected (cf. Bercovitch 1986; Hausfater 1975), especially in a group the size of her study group. Among the adult males, rank reversals may regularly interrupt longer periods in which rank orders are stable. When rank orders are constructed for each of these stable periods, they are likely to be linear (see for instance Bercovitch 1986). Moreover, instability in rank orders should not be confused with instability in individual dominance relationships. In the vast majority of relationships between adult males the periods of uncertain dominance are very short compared to the periods of clear-cut dominance.

Secondly, the impression is that the rank orders among adult males are rather steep, i.e. the difference in fighting ability between two males of adjacent rank can be large. This impression is based on frequent observations of high ranking males that were able to defeat several low-ranking males simultaneously. The average difference between two males of adjacent rank is less in large groups than in small groups, if the assumption is correct that rank is largely correlated with physical parameters with absolute minimal and maximal values. I see no way of quantifying relative or absolute differences, however. The ‘cardinal rank’ method proposed by Boyd and Silk (1983) does not work for baboons, because dominant males tend consistently to win fights, without the occasional losses needed for that method. If the relation of fighting ability to age follows roughly the same inverted U-shape (Packer 1979a) for all males, the estimate of relative fighting abilities can be further improved on the basis of age estimates.

For the present purpose a simplified picture will suffice. Imagine a group in which the differences in fighting ability between each pair of males of
adjacent rank can be expressed as a simple ratio. An example is given in the diagonal cells of the matrix in Fig. 11.7. In this example the fighting ability of the lowest-ranking male is taken as unity and each other male is 1.3 times as strong as the male ranking below him. Such a group could result if males with equal fighting ability curves all immigrated at the same age and at regular intervals.

The possible alliances that can be formed in such a group can now be deduced, given the following assumptions: (1) Only two-male coalitions are formed. (2) A male will not form a coalition against a male weaker than himself (i.e. no counter-coalitions are possible). (3) A coalition will be successful when the combined fighting ability of two males exceeds the fighting ability of their opponent. I assumed simple additivity, which is perhaps more acceptable when the "ability to contribute to a coalition" (which encompasses specific tactical skills) would be used as a parameter instead of "fighting ability". I suppose that the two parameters are closely related, however. (4) Coalition formation does not influence dyadic dominance relationships.

![Matrix](image)

**Fig. 11.7.** The distribution of potential alliances. The matrix is based on an imaginary group of 10 males in which the fighting ability of the lowest ranking male is set to unity and each of the other males is 1.3 times stronger than the male ranking directly below him. The non-diagonal cells of the matrix show the number of higher ranking males that could potentially be defeated by the combination of the male at the top and the male at the right. The figures in the right-hand column give the number of options each male has, i.e. the number of combinations of one specific partner and one specific opponent.

**Fig. 11.8.** The relationship between relative fighting ability and the distribution of potential alliances. The graph shows the relationship between the 'steepness' of the male hierarchy (expressed as the ratio between the fighting abilities of two males of adjacent rank) and the number of options each male has. The numbers for the ratio 1.3 are the same as in Fig. 11.7, right-hand column.
The dynamics of coalition formation

The assumption that two collaborating animals are equally powerful (in a game-theoretical sense) and will thus most likely divide costs and benefits equally, is implicit, or even explicit (Lombardo 1985; Whitehead 1987) in several publications on reciprocal altruism and the prisoner's dilemma model. This prediction is explicitly given in neither model, however, although Trivers (1971) hinted at it (p. 37: '... roughly equivalent benefits ... at roughly equivalent costs'). The prediction of symmetrical division also agrees with one's intuitive expectations about the outcome of a symmetrical game like the prisoner's dilemma, at least when played by two adult male baboons that strive to obtain the same resources. Some baboon allies divide the spoils rather asymmetrically, however (Collins 1981; Noe 1990), which could point at an asymmetry in power. I use the model described in the section above as a basis to show that the options of two allies are often unequal, which can explain such an asymmetry in power. How this power asymmetry is translated into an asymmetrical division of pay-offs is a problem to be discussed in the next section.

Some examples of possible configurations of the potential combinations between four males, who combine forces against two males ranking above them, are given in Fig. 11.9. Figure 11.9(a) reflects an extreme case in which one individual belongs to any successful combination that can possibly be formed. Such individuals are in a so-called veto position: they can demand high pay-offs, because they can play off their potential partners against each other. A simple example of a veto player is a salesman in possession of a right shoe, dealing with two colleagues who each possess a left shoe. If only a pair of shoes can be sold and bargaining is possible, then it is clear that the right-shoe salesman can ask a lion's share of the profit (see Kahan and Rapoport 1984; Murnighan 1978 for reviews of the research on veto games).

![Fig. 11.9. Patterns of coalition formation. The figure shows some configurations of potential combinations of four low-ranking males (C–F) against two high ranking males (A and B). In (a), male C has a veto position: he is a member of all possible combinations against B. In (b), the males D and E have an alternative against B, but to beat A male D has no other choice but C. Since C is dependent on D too, D has much more leverage over C in configuration (b) than in configuration (a).](image)

Although I actually found a case (Noe 1990), a veto player is bound to be rather rare among baboons seeking to form alliances. The effect of differences in options between partners, dubbed the market effect by Noe et al. (1991), may well be present in a weaker form in many alliances. No two allies are likely to have exactly the same options, which may result in a difference in leverage from the one over the other. One can expect a virtual symmetry in power, and thus in pay-offs, when both partners have a large number of options. Real symmetry is expected, if two males have only one option, namely each other. The symmetrical alliance formed by the two lowest ranking of four males observed by Bercovitch (see personal communication cited above) is probably an example. Symmetrical alliances can thus be expected in very large and very small groups. In large groups low frequencies of coalition formation per alliance can be expected, combined with frequent partner switches, in small groups high frequencies per alliance are likely. This expectation is consistent with data presently available (Bercovitch 1988 and personal communication; Noe 1989).

From power to pay-off: do baboons bargain?

The key assumption in the above story is that an asymmetry in power will be translated into an asymmetry in pay-off. I assume that some kind of bargaining will play a role in this translation process. The question whether bargaining plays a role in the collaboration among animals like baboons, can be split into four parts.

1. Are baboons able to convey information about their desire to collaborate?
2. Are baboons able to convey information about the level of costs and benefits they are willing to accept?
3. Is collaboration on the basis of communication possible in spite of temptations to convey 'dishonest' information?
4. Are baboons able to keep each other to agreements?

Are baboons able to signal their desire to collaborate?

The answer to this question is relatively straightforward: yes, they can. At first individuals willing to form a coalition have to show their desire to do so, point out with whom they would like to form a coalition, and agree about the timing of the event. Offers to form a coalition and the acceptance of such offers is made clear by baboons through special gestures and vocalizations, like 'head-flagging' and 'staccato grunting'. These behaviour patterns with their typical rhythmic and repeated character are addressed at the (potential) partner before and during coalitions. Synchronization can be achieved through the use of external cues, which will often be the behaviour of the opponent, through synchronization of locomotion, or with the help of pseudo-sexual greeting rituals (see description in Smuts and Watanabe 1990).
Are baboons able to convey information about the desired pay-off division?

In many cases the division of benefits poses no problem, because it is given by the nature of the goal reached by forming a successful alliance: e.g. status improvement, the support for an infant, etc. Cooperation that takes the form of an exchange of (indivisible) commodities likewise poses no problems. An example from a rather different species is the exchange of shells between hermit crabs (Hazlett 1983). Problems arise when costs and/or benefits can be divided in many different ways. I do not expect baboons to show exchanges such as ‘I settle for 60 per cent, but not for 55 per cent’. It can be much simpler than that, provided the interaction is repeated. Suppose two animals repeatedly have to split up a divisible food source they obtain through cooperation. They can start out by any division, e.g. determined by speed of consumption, or by splitting in halves. Each animal can show discontent with the original division. A strong show of discontent is a refusal to collaborate on the next occasion. As mentioned above, observations show that blunt refusals do not necessarily lead to an end of the alliance. An adjustment of the pay-off distribution may also be reached by using some signal that conveys a threat to refuse in the near future. The behavioural repertoire of baboons contains enough signs of discontent, in a graded form if necessary, that can be used to this end.

Is the information conveyed dishonest?

Clearly, when animals communicate about levels of costs and benefits they are willing to accept, there is a temptation to ask for more than the minimum. This temptation may endanger the collaboration. Game theorists studying the theory of animal conflicts have encountered a similar problem. A number of authors concluded that animals would not convey honest information about their strength and intentions during combat (Caryl 1979; Dawkins and Krebs 1978; Maynard Smith 1982a, b). Empirical studies seem to suggest that animals in conflict tend to give honest information (see Hinde 1981). Various suggestions have been made about the circumstances in which animals would be expected to give honest signals during conflicts (Bond 1989; Gardner and Morris 1989; van Rhijn 1980; van Rhijn and Vodegel 1980). Bond (1989) argued that animals interested in winning a conflict, but at the same time interested in avoiding escalation, are likely to show some bluff (dishonest information), but that most of their message is likely to be honest.

Markl (1985) makes clear that the existence of honest information is much less of a problem in the case of cooperation. If two animals both stand to gain by the cooperation, and neither can obtain an immediate gain by refusing to cooperate (synergistic cooperation), both are likely to be honest if they signal their willingness to cooperate. In correspondence to the possibility of slight bluff in conflicts (Bond 1989), it should be possible to get away with some exaggeration of demands without jeopardizing the deal itself, when costs and/or benefits can be varied gradually. It is a prerequisite of bargaining that one asks for a bit more than strictly needed.

One can speak of a ‘bargaining zone’ when the costs and/or benefits can be divided in several small discrete steps or along a continuum in such a way that all divisions satisfy the minimum demands of both participants (Davies and Houston 1984; Noe et al. 1991). Collaboration is likely to be unstable when the bargaining zone is large, because the division of pay-offs can oscillate wildly, increasing the chance that once in a while the minimal demands of one partner are not fulfilled. Collaboration will be more stable when there is a point of attraction, or saddlepoint, on which the division of pay-offs tends to converge. Such a saddlepoint is more likely to occur when the collaborating animals differ in power than when they have equal power. For example, an animal in a veto position with two potential partners is able to push the pay-off distribution to his favour till one of the partners drops out, because his minimally acceptable pay-off is reached. In more general terms: in any case in which a threat to seek an alternative partner cannot be met with an effective counter-threat the division of pay-offs will stabilize on a level that just satisfies the minimal demand of the weakest partner but one. Likewise a saddlepoint can be expected when the maximum demand of the most powerful player falls within the bargaining zone, e.g. when he is satiated before a divisible food source is exhausted completely.

The proposition that animals bargain is likely to be met with a sceptical attitude. I should like to challenge the sceptics with the following question. Suppose one finds animals that are clearly engaged in collaboration with a variable pay-off division. Can one imagine a mechanism by which they converge on a certain division of costs and benefits other than through bargaining, and can one demonstrate the existence of this mechanism?

Do baboons conclude binding agreements?

The last problem to be discussed in this section is that of the existence of binding agreements, or contracts. Among humans the conclusion of (written) contracts about the division of costs and benefits before any party makes an investment is typical for one-off deals. In such cases each partner is kept to the contract by a threat that has little to do with the collaborative interaction itself. Such policed agreements are less necessary when the collaboration is continuous or often repeated, because then the necessary threat can be contained in the collaborative interactions themselves. It is not unusual for a dealer to send goods ordered by telephone to a regular customer without receiving a written confirmation of the order and before any payment is made.

In continuous or repeated collaboration among animals bargaining and forcing the other to accept certain pay-off divisions by threats can be one and
the same process. Bargaining implies threats that the relationship will not be continued, unless a more favourable division of pay-offs is agreed upon. The other side of the same coin is that extremely high demands are not made, as long as the threat to lose future gains from it suffices to suppress the temptation to try to win high immediate gains. The analogy to Trivers' (1971) and Axelrod and Hamilton's (1981) reasoning will be obvious. Yet there is a crucial difference: I expect the 'future gains' to enter the equation as the difference between the future gains from the present collaborative relationship and the future gains from alternative relationships. The dealer in the above example has to send the goods in order to prevent the customer to do business with a competitor, who is less anxious and therefore delivers faster.

COALITION FORMATION IN BABOONS AS PARADIGM FOR OTHER FORMS OF COLLABORATION

Formation of partnerships in other social systems

The idea that competition over partners and differences in options to form partnerships determine the way in which individuals collaborate for a large part, applies to many forms of collaboration among animals. Noë et al. (1991) formulate this 'market' theory in a more general form, and widen its scope to collaboration among unrelated group-living animals in general. The restriction to unrelated individuals is theoretically not necessary, but it is likely that market effects will be swamped by effects of kin selection and thus will be hard to demonstrate. The restriction to collaboration among members of the same social unit is important, however. The impact of the market effect is dependent on the option to choose among potential partners, but when both partners have a virtually unlimited number of alternative partners, the impact will be minimal.

The use of coalition games as paradigms

Coalition games have been developed as paradigms for many aspects of human behaviour. Extensive theoretical and empirical work has been done in the fields of social psychology, political science, and economics. Only a small part of this vast body of knowledge is useful for biologists, however. Theories that do not assume individual rationality, i.e., the aspiration to maximize the individual pay-off, are of little use to us (cf. Parker and Hammerstein 1985). 'Social norms', 'reputation', and 'conscience' may influence the behaviour of some species, notably primates, but it would do little good to seek parallels with models from the social sciences that incorporate these phenomena. Coalition games would be easier to handle if they could be described in the normal form, i.e., using the strategic matrices biologists are familiar with through the hawk–dove game and the prisoner's dilemma. Whether the coalition games can be transformed to a matrix notation is a point of dispute (Kahan and Rapoport 1981; Michener and Potter 1981).

There are more shortcomings in the theoretical developments around coalition games. In the first place, relatively little work has been done on iterated games with the same players. In the second place, most theories about solutions for these games, i.e., predictions about the coalitions that will be formed and the pay-off configurations that will be agreed on, are deterministic in character. The theories predict a specific outcome or a set of outcomes, rather than calculating the chance of occurrence of each outcome. None of the existing theories is strongly supported by empirical data, and as a result there is no single, dominating theory (Kahan and Rapoport 1984; Parker and Hammerstein 1985). The solution could be found in the development of more stochastically oriented theories (Van der Linden and Verbeek 1985). An example of a development of such a stochastic theory for an iterated game is given by Laing and Morrison (1974).

The players and their tactics

The use of coalition games as paradigms implies that the equivalents of the players in the theoretical games are the individual animals, and not some kind of uniform vehicles for certain strategies. Publications on ESS theory and the use of the prisoner's dilemma leave the impression that the proximate tactics of animals and ESSs are one and the same thing. One could say that the strategies themselves play against each other. In such a framework it is preferable to use the mathematically more rigorously formulated form of game theory, non-cooperative theory, in which such things like bargaining and binding agreements play no role. When, however, animals are found to use communication between each other to arrive at certain decisions, one is almost forced to use the language of cooperative theory, which is generally used in the analysis of coalition games. If one does not accept that, then one is forced to postulate very complicated conditional strategies to account for the reactions of animals to the information they get from their partners. Moreover, non-cooperative game theory is ill suited to cope with phenomena like coalition formation, choice among partners, and competition over partners. The choice, unfortunately, is between realistic paradigms with sloppy theory and unrealistic theory based on sound mathematics.

Obviously players that rely on processing ad hoc information cannot do completely without innate capabilities and basic strategies to play the game well. Basic rules of thumb could be: (1) Break off any collaboration with a long-term negative pay-off. (2) Compare partners and seek the most profitable one(s). (3) Force any partner to yield the highest attainable pay-off. To live up to these rules of thumb players should be capable of remembering the yield of interactions with various partners and of comparing these yields.
They should also be able to signal their demands and to interpret any signals received correctly. Interesting possibilities arise with increased cognitive abilities. If animals are able to place themselves in the position of their potential partners and assess the alternatives these partners have, a much more sophisticated way of playing the game may result. This calls for one remark, although it should be superfluous: the fact that we recognize the resemblance between a certain social interaction and a certain theoretical game does not mean that the animals (or humans) involved perceive the interaction at that level.

The predictive power of models based on coalition games

Rarely will all parameters involved be so well understood that precise predictions can be made about which alliances will be formed and how pay-offs will be distributed. A comparable problem would be to predict the positions of all pieces in a game of chess after 40 moves. This is an impossible task, although one knows all the rules and the starting positions of all the pieces. It is, however, possible to predict the direction of changes in the distributions of pay-offs and the likelihood of recombinations of alliances after changes in the structure of a social unit. Such predictions also provide the opportunity to test the coalition game models.

SUMMARY

1. Coalition formation among unrelated adult male savanna baboons has been observed in a large number of groups, belonging to three different subspecies.
2. The theory of reciprocal altruism does not apply to alliances among male baboons. Although one can a posteriori recognize a male with a net loss and another with a net gain in several coalitions, it cannot be shown that one of the participants in a coalition a priori opts for an altruistic role. Moreover, alliances continue in spite of repeated refusals to collaborate by one of the allies.
3. The prisoner’s dilemma game is neither a suitable paradigm for baboon alliances, nor for most other forms of collaboration among group living animals. The prisoner’s dilemma model seems to apply, however, to basically competitive situations which can be mitigated by cooperation and to cooperation in situations in which alternative partners are hard to find.
4. The most frequent immediate causes for the formation of coalitions by male baboons are competition over resources, notably oestrous females and meat, defence against aggression and defence of infants. Many coalitions lack a recognizable immediate cause, however. Alliances are usually multi-purpose.
5. The most frequent participants in coalitions are males of middle and lower rank. These males are usually past their prime and resident in the group for a relatively long time. The latter findings can be explained by the correlation of age and of the period of residence with rank.
6. Young newcomers of high rank are frequently the targets of coalitions.
7. The division of benefits between allies can range from symmetrical to very asymmetrical.
8. A modified priority-of-access model can be used to make plausible that in a group of average size males of rank 3 or lower potentially gain from coalitions over consorts.
9. Males of middle rank have most options to form coalitions, under the assumption that relative fighting ability is the crucial parameter that determines which pairs are able to form coalitions successfully.
10. A number of features of coalition formation among baboons can be understood with the help of the theory of N-player coalition games. One of these games, the veto game, was shown to be a suitable paradigm in a particular case. The most relevant features of coalition games are: (1) The players compete with one another over suitable partners. (2) The relative power of the players depends on the options each of the players has to form alternative coalitions. (3) Which coalitions are formed and how pay-offs are allocated is determined by bargaining.
11. Bargaining is considered to be crucial for the translation of the power balance between allies into a corresponding distribution of pay-offs. The fact that coalitions are a form of ‘synergistic cooperation’ and the fact that the same individuals interact repeatedly, limits the likelihood of a disruption of the collaboration due to ‘dishonest’ information.
12. An agreement over a pay-off distribution is not hard to reach, if the allotment of costs and benefits is inherent to the cooperative interaction, as e.g. in an exchange of indivisible items. The distribution of variable pay-offs is relatively straightforward, if one ally is more powerful than the other.

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REFERENCES


Alliance formation among male baboons

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