

A Veto game played by baboons: a challenge to the use of the Prisoner's Dilemma as a paradigm for reciprocity and cooperation

RONALD NOË*

Laboratory of Comparative Physiology, University of Utrecht, Jan van Galenstr. 40, NL-3572 LA Utrecht, The Netherlands

Abstract. According to a widely accepted paradigm, cooperation among animals resembles an iterated, two-player Prisoner's Dilemma game. In this symmetrical game the two players have equivalent strategic options. Decisions are based only on information obtained in similar interactions with the same player in the past. The Prisoner's Dilemma model ignores the social organization within which cooperation occurs. This paper advocates a set of alternative models based on *N*-player coalition games that apply especially to collaboration (that is, cooperation and reciprocity) within social groups. The model takes into account the effect of competition for the favours of suitable partners. In Coalition games negotiations are possible and the strategic options of the players can be unequal. An example of a Coalition game, the Veto game, is illustrated by patterns of coalition formation among adult males in a group of wild baboons *Papio c. cynocephalus*.

Over the past two decades theorists as well as empiricists have devoted considerable effort to the study of collaboration between unrelated animals. Most attention has been given to cases in which two individuals repeatedly interact with each other. Two major modes of collaboration can be distinguished: (1) both participants obtain a net benefit from each single interaction in the series (serial cooperation); and (2) each interaction has a net loser and a net winner, but over the series of interactions both benefit (reciprocity). Trivers (1971) was the first to present a plausible model of strategies, selected at the individual level, that can lead to reciprocity among unrelated animals: the Reciprocal Altruism model. Unfortunately the original formulation of the model by Trivers (1971) was rather vague. Several authors (Bertram 1982; Wrangham 1982 among others) have tried to formulate more precisely what is meant by reciprocal altruism and have tried to indicate limits to the kind of situations to which it should apply, but much uncertainty remains (cf. Packer 1986). The following definition reflects my own notion of reciprocal altruism. First, in each interaction one individual has a net cost, while the other has a net benefit. Second, over a finite series of interactions, each individual has a net benefit. It is not essential that the costs per act of the altruist are lower than

the benefits to the receiver, as is often stated in definitions of reciprocal altruism (see for example Seyfarth & Cheney 1984). Third, each individual alternately plays the role of altruist and beneficiary. It is not essential that the roles are alternated in a strict sense, but the roles should reverse frequently during a series of interactions. Fourth, different types of altruistic acts can be part of a single reciprocal altruistic chain of events.

A new milestone was reached when Axelrod & Hamilton (1981), elaborating on an earlier suggestion by Hamilton (personal communication, cited in Trivers 1971; Hamilton 1971a), presented the Prisoner's Dilemma game (Fig. 1) as a model that could provide insight into the strategies leading to both serial cooperation and reciprocity. Both the reciprocal altruism model and the Prisoner's Dilemma model assume that collaboration is the best solution for both participants in the long run, while non-collaboration is the best solution for at least one participant in the short run. The dilemma between short-run benefits and long-run benefits is thought to make collaborative relationships unstable. Collaboration is therefore thought to be possible only when individuals interact often and are able to detect cheating by the partner and react to it. An obvious reaction is to end the collaborative relationship.

* Present address: Ethologie und Wildforschung, Universität Zürich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland.

The Current Models

Although Axelrod & Hamilton (1981) claimed

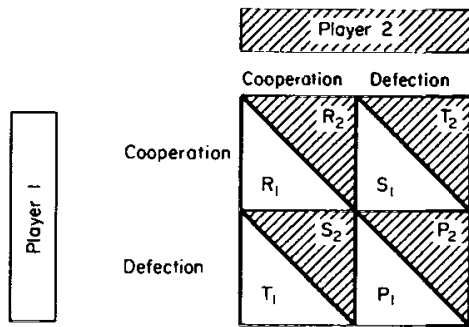


Figure 1. The Prisoner's Dilemma game. The two players have to choose simultaneously and without communication between two options: cooperation or defection. The possible payoffs to the players are: T, Temptation to defect; R, Reward for cooperation; P, Punishment for simultaneous defection; and S, Sucker's payoff. The relative values of the payoffs are such that for each player the two following conditions are fulfilled: $T > R > P > S$ and $2R > T + S$.

that the Prisoner's Dilemma game was a suitable model for both reciprocity and serial cooperation, it is, strictly speaking, only suited as a model of serial cooperation. To date there is no game theoretical model specifically suited for reciprocity, but such a 'reciprocity game' would be similar in character to the Prisoner's Dilemma game (P. Hammerstein, personal communication). The Prisoner's Dilemma itself can be used to describe reciprocity when the second condition of the game (Fig. 1; twice the reward for cooperation is greater than the sum of the temptation to defect and the sucker's pay off) is removed. An altruistic act corresponds to a move in which one player 'cooperates', while the other 'defects'. Reciprocity corresponds to a series of such moves in which the players alternate their roles (cf. Michod & Sanderson 1985). This is not a dominant strategy in the normal version of the Prisoner's Dilemma. Some principal differences between reciprocity and serial cooperation remain, which make it unlikely that the optimal strategies of the two games are the same. In a move in the Prisoner's Dilemma each player can potentially reap immediate benefits by defecting, while in a move in a reciprocity game only one of the players can obtain an immediate benefit by defecting. A second difference between both games is that in a Prisoner's Dilemma the conduct of the partner can be monitored in each

move, while in a reciprocity game there is a delay between investment and control.

In practice the question which kind of game is being played, a Prisoner's Dilemma game or a reciprocity game, is bound to remain academic, because it is usually impossible to distinguish between 'altruistic', 'cooperative' and 'selfish' acts. For example, in Seyfarth & Cheney's (1984) study on reciprocal altruism in vervet monkeys, *Cercopithecus aethiops*, the influence of grooming on the probability of receiving support in agonistic interactions was investigated. This is a valid example of reciprocity, however, only when it can be made plausible that grooming as well as support are altruistic acts and that the costs of support can be compensated by the benefits of being groomed. Such problems are bound to remain unsolved, however. In specific cases the nature of the resources at stake may exclude the applicability of one of the two models. Male baboons, *Papio cynocephalus* spp., that form coalitions to obtain access to oestrous females (Packer 1977; this study), are an example of animals that collaborate in order to get an indivisible resource. Such a resource excludes the use of the Prisoner's Dilemma, because the players a priori cannot obtain a reward simultaneously.

Because of the theoretical similarities and the practical problems mentioned, I will hereafter not distinguish between the reciprocal altruism model and the Prisoner's Dilemma model. I assume remarks on the Prisoner's Dilemma model to apply to both models.

Theoretical Problems

A major problem with the Prisoner's Dilemma model is its limited scope. The game of collaboration has three sub-games: the formation of pairs (or other small subsets) of animals which may collaborate, the process in which each individual decides to collaborate or continue to collaborate, and the division of the yield of the collaboration. The Prisoner's Dilemma applies to the second sub-game only, with a further restriction that this sub-game is assumed to be played by not more than two players. In cases in which as a rule small subsets (e.g. pairs) of a larger set (e.g. a social group) collaborate, the Prisoner's Dilemma model does not predict which subsets are formed and by what mechanism. Yet, the way in which the pairs are

formed can have a fundamental influence on the dynamics of the cooperation within the pair.

The Prisoner's Dilemma game does not predict how two players will divide the resources they gain by collaborating. Intuitively one would expect that players in such a symmetrical game would share equally when they derive comparable benefits from a resource, have comparable costs when collaborating and use collaboration to obtain resources from the same pool. This assumption is formulated explicitly by several authors (Trivers 1971; Lombardo 1985; Whitehead 1987). Theoretically, however, the Prisoner's Dilemma has a continuum of possible solutions (P. Hammerstein, personal communication), so no prediction about the division of the yield of collaboration can be made on the basis of the Prisoner's Dilemma model. Thus the validity of the model cannot be tested by observations of the division of benefits between two collaborating animals. Nevertheless, consistent observations of strong asymmetries would make the model implausible.

Another problem is that the use of a 'non-cooperative' game (unfortunately the jargon for a game without communication) implies that communication between collaborating animals cannot form an essential part of their tactics. The root of this problem is that, at present, ultimate strategies and proximate tactics are assumed to be identical. When one assumes that the frequency of strategies in the 'strategy-pool' is determined solely by games among the strategies and not by games among the users of the strategies, then it is correct to employ games without communication, as strategies do not communicate. To my mind, however, real-life players can use information based on communication, when available and reliable, to improve their strategic choices.

Whether or not players in a Prisoner's Dilemma communicate makes little difference, because they cannot conclude enforceable agreements (Colman 1982). The only reliable way to obtain information about another player in a Prisoner's Dilemma is to monitor his actual choices. Communication about intentions and negotiation about payoff divisions cannot be used by the players, because there is no guarantee that the information obtained is correct. If the Prisoner's Dilemma were a correct paradigm for collaboration among animals, collaborating animals should not change their behaviour under the influence of communicative behaviour of the other party. Consequently, there would be selec-

tion against a reaction to any signal from a potential partner and thus one would not expect the communication itself to evolve. Therefore the use of the Prisoner's Dilemma implies that one does not expect collaborating animals to communicate, or that communication during collaboration has nothing to do with the collaboration and does not influence the interaction.

Lack of Empirical Support

Few data supporting either reciprocal altruism or the Prisoner's Dilemma have been published so far, and these data have not been very convincing. Packer's (1977) example of reciprocal altruism among male baboons has become a classic example, but a close look at the data presented casts doubt on the conclusions drawn. I shall consider this example in some detail because my own example also concerns male baboons who form coalitions to gain access to oestrous females. The behavioural element that Packer showed to be reciprocated is 'head-flagging'. This behaviour, which occurs in a similar form in macaques, *Macaca* spp. (De Waal et al. 1976), is interpreted by Packer and several other authors as 'soliciting-for-aid' (references in De Waal & Van Hooff 1981). That interpretation refers only to the appeal contained in the message, however, not to the offer to form a coalition. If one assumes that head-flagging has the function of asking support, it seems odd to consider reciprocation of such utterly selfish behaviour as proof for reciprocal altruism. Packer emphasized, however, the link between head-flagging and coalition formation. He showed that, in coalitions formed to obtain oestrous females, the head-flagging individual always got the female. Packer reasoned that the reciprocation of head-flagging implied that partners took turns in obtaining a consort partner. Unfortunately Packer observed only six coalitions in which one of the two partners obtained an oestrous female. Moreover his observations were spread over 18 males in three groups.

Smuts (1985) repeated Packer's claim that male baboons are reciprocal altruists. Her data (Table 7.4, page 137) are more detailed than Packer's, but she did not observe more than five successful coalitions in a single pair, which is not enough to show an alternating pattern with statistical methods. Bercovitch (1988) concluded that the reciprocal altruism model does not apply to coalitions of

male baboons, because such coalitions should be considered as cooperative.

Other examples given in support of either model in the literature also suffer from various flaws. Very weak are those examples in which animals are assumed to reciprocate because they refrain from some type of behaviour damaging to the partner, which the observer inferred they should have performed (e.g. Lombardo 1985; cf. Koenig cited in Packer 1986). It is simply impossible to count the number of cases in which an animal does not perform a certain act. Furthermore, examples are convincing only when kin selection can be ruled out. This is not the case in, for example, Wilkinson's (1984) example of food sharing in vampire bats, *Desmodus rotundus*. The behaviour of the sticklebacks, *Gasterosteus aculeatus*, in Milinski's study (1987) can be understood satisfactorily as a selfish herd effect (Hamilton 1971b).

The most crucial element of both models, the detection of and retaliation against cheating, proved to be very hard to detect in real-life systems. This does not mean that cheating never occurs, because it may be controlled so effectively that it cannot be observed. Moreover, situations resembling the Prisoner's Dilemma may be commonplace, but 'always defect' may be the strategy that has emerged in most cases (P. Hammerstein, personal communication).

Coalition Formation in Social Groups

In many cases collaboration takes place between members of social groups. Usually only part of a group will take part in certain forms of collaboration and the actual interactions will often involve only two or three individuals. How are participation in collaborative interactions and the allocation of costs and benefits determined? When the number of potential participants is limited, dynamics come into play that resemble the processes characterizing coalition games, which are cooperative games in which subsets of players can combine forces (see Murnighan 1978; Kahan & Rapoport 1984 for reviews). Situations in which unrelated members of (small) social groups potentially benefit from collaboration have the following features in common with coalition games: (1) there is competition over partners, as a result of the limitation of the number of potential partners; (2) there are differences in power of the participating

individuals, as a result of differences in options to form combinations; and (3) 'negotiations' lead to a distribution of benefits that corresponds with the power balance. Games of this type proved to be useful in the study of human behaviour, notably in social psychology, economics and political science.

I give the coalition formation among the adult males of a baboon group as an example of the use of one particular coalition game: the Veto game. The Veto game is a relatively simple game with one strong player and several weak players (Murnighan & Roth 1977, 1980; Murnighan 1978; Murnighan & Sz wajkowski 1979; Kahan & Rapoport 1984). The game has the following properties. (1) Coalitions have to be formed to reach a certain goal. (2) No successful coalition can be formed without the so-called veto player. (3) The veto player can form a successful coalition with any other player. The veto player is able to 'play off' his potential partners against each other and is consequently able to claim the lion's share. The following situation is a classical example of a Veto game. A salesman possesses a right shoe while two other salesmen each possess a left shoe. Single shoes have no value since only a pair consisting of a right and a left shoe can be sold. The owner of the right shoe has a veto position; he can demand a disproportionately large share of the profit gained by selling the pair of shoes.

In Fig. 2 a fictitious example is given in which the individuals involved can be ranked, like male baboons, in a linear order. The strongest individual, the opponent, can be defeated only by a number of combinations of the weaker individuals, the actual players in the coalition game. One of the players holds a veto position because his participation is essential to make a combination stronger than the opponent. The power of a veto player may also be based on a unique skill, possession of a unique resource, etc. Note that 'power' refers to the player's leverage over others due to his strategic position in the game, not to leverage based on dominance or fighting ability.

Playing off of two partners against each other has been described for male chimpanzees, *Pan troglodytes*, in captivity (De Waal 1982) and in the wild (Nishida 1983). Wrangham (1982) has alluded to the theoretical possibility of similar effects for coalition formation among related animals.

In this paper I want to propose the theory of coalition games in general, not a particular coalition game, as the basis of a model of coalition

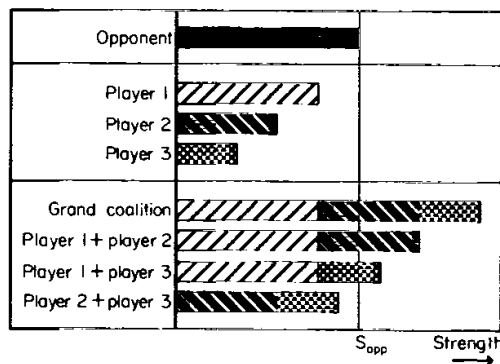


Figure 2. An example of a Veto game. The length of the bars reflects the strength of each individual, respectively in the coalition. The players have to form a coalition that is stronger than the 'opponent', thus the combined strength has to be greater than S_{opp} (simple additivity is assumed). Player 1 is a veto player, because no coalition strong enough to beat an opponent of strength S_{opp} can be formed without him.

formation among adult male baboons. I recognized the resemblance to a Veto game in the data on coalition formation among the males of one of the three groups I studied. I chose to use these data to back up my more general claim for three reasons. (1) A Veto game-like situation can be recognized relatively easily, due to the extreme difference in power between the players. (2) These data are more clearly at variance with the reciprocal altruism and Prisoner's Dilemma models than data on males with less extreme power differences. (3) Although the coalition formation process described in this paper is probably exceptional for baboons, the Veto game may prove to be particularly relevant to a number of other social systems.

The following features of baboon males and their coalitions are of interest here. First, typically, a medium-sized baboon group (40–70 individuals) has five to eight adult males. Coalitions are usually formed by middle- and low-ranking males against higher ranking males. Individuals of other age–sex classes cannot contribute significantly to a coalition in conflict with a high-rankin adult male. Thus the number of potential players is about three to six. Second, coalition formation is an important means of gaining access to fertile females for the middle- and low-ranking males (Smuts 1985;

Bercovitch 1988). Third, the most important resources gained by coalition formation, oestrous females, are indivisible. This implies that, for each coalition formed, only one participant can obtain a major benefit.

I first present data that lead me to investigate the Veto game. Then I formulate hypotheses that follow from the assumption that the allies in my study group resembled players in such a game. Finally, I present evidence for the validity of the paradigm.

METHODS

Study Group and Observations

A group of yellow baboons, *Papio c. cynocephalus*, was studied in Amboseli National Park, Kenya, from December 1981 until November 1982. The group (Hook's Group) had been under study with interruptions since 1976. For a description of the site see Hausfater (1975), Altmann (1980) and Altmann et al. (1985).

B. Sluijter and I observed the group on foot for 211 h spread over 73 days. Additional information on demographic changes and menstrual cycles was gathered by other observers on intermediate days. Data on agonistic and sexual interactions were obtained by ad libitum sampling (Altmann 1974). Group size and observational conditions were such that almost all multi-male conflicts could be observed in sufficient detail.

The codes used for the individual males indicate their group (Hook) and the agonistic rank they occupied in an average rank order over the whole year of the study. When a male occupied several ranks during the study period he was assigned an average of these ranks, whereby the periods over which he kept the rank were weighted according to the number of consorts observed in each period, not according to its duration. The real rank orders and their changes over time are indicated in Fig. 3. Dominance relationships were inferred from the occurrence of six submissive behavioural elements observed during dyadic conflicts. The direction of these elements within pairs was highly consistent over time and they also showed a high mutual correspondence in direction (Noë, unpublished data). In baboons dominance among immigrant males is closely correlated with how long a male has been in the group. In this group within each pair, the male that arrived most recently was dominant

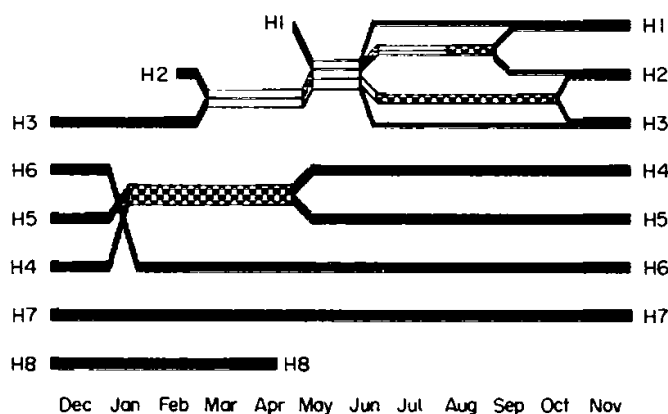


Figure 3. Rank orders and rank reversals during the study. The rank orders are based on the occurrence of six submissive elements in dyadic conflicts among the males. Black: only one male showed submission; white: period without conflicts; chequered: both showed submission. For example H1–H2–H3 in July: H1 dominant over H3, no conflicts observed between H1 and H2, and H2 and H3 both showed submissive behaviour towards each other.

Table I. The adult males of the study group

Code	Name	Birth	Immigration	Emigration
H1	Ozzie	4 January 1975*	8 May 1982	
H2	Leonard		19 February 1982	
H3	Styx		1 October 1981	
H4	Kong		25 April 1981	
H5	Stu	~1969*	26 June 1980	
H6	Warlock		11 June 1980	
H7	Slik		~1 December 1977	
H8	Harvey		< October 1977	26 April 1982 (to Alto)

* Born in another study group ('Alto's Group').

(see Table I). H1 and H2 were seen as subadults in other groups shortly before they immigrated; H3 and H4 were young adults; H5, H7 and H8 were considerably older. H6's age was hard to estimate, but he was probably older than H3 and H4 (Table I). Close kinship between males that formed alliances often (H5, H6 and H7) is considered unlikely.

Consorts

A consort is defined as any period of persistent close proximity and attuned locomotion of an adult male and a female with a swollen perineal skin, lasting longer than 30 min. Close proximity was established subjectively, relative to the distance

between the female and other adult males. Consort pairs at the periphery of the group could be several metres apart. Undisturbed copulations during consorts shorter than 30 min were rare. To gain access to a consorted female a male must first break up the existing consort. The number of consorts missed during observations is considered to be negligible.

Coalitions, Alliances and Provocations

Two or more individuals form a coalition when they direct aggressive behaviour towards a common opponent simultaneously or within 5 s of each other. Either one of the partners can start a coalition by interfering in an ongoing conflict, or both partners can form a coalition simultaneously.

Table II. Coalitions formed by H5, H6 and H7; opponents and immediate causes

Alliance	Opponent	Immediate cause				Total
		Consort	Support of third	Meat	None observed	
H5-H6	High ♂	12	2	—	11	25
	H7	—	2	—	4	6
	Low ♂	—	—	—	2	2
	Adult ♀ or immature group member	—	3	—	8	11
Total for alliance						44
H5-H7	High ♂	5	1	—	2	8
	Low ♂	—	1	—	1	2
	Adult ♀ or immature group member	—	1	—	1	2
Total for alliance						12
H6-H7	High ♂	6	4	2	5	17
	Low ♂	—	1	—	3	4
	Adult ♀ or immature group member	—	3	—	2	5
Total for alliance						26
H5-H6-H7	High ♂	5	1	—	2	8
	Low ♂	—	1	1	1	3
	Adult ♀ or immature group member	—	—	—	—	—
Total for alliance						11
Total		28	20	3	42	93

High ♂: H1, H2, H3 or H4; Low ♂: H8, or one of two subadults.

An alliance is a pair of individuals who form coalitions frequently.

In some cases a consorting male was provoked to start a conflict. Such provocations usually took place when two or more males, 'followers', trailed the consort-pair. Provocations sometimes lead to a transfer of the consort without the formation of a genuine coalition. In such cases the new owner is assumed to have obtained the consort partly due to the presence of his fellow followers. Note, however, that the definition of a provocation is based on the behaviour of the consorting male and the outcome of the conflict. In contrast to coalitions it is therefore not possible to speak of 'unsuccessful provocations'.

RESULTS AND DISCUSSION

The Asymmetric Division of Gains

Three males (H5, H6 and H7) accounted for 93 coalitions, 84% of all coalitions observed among the eight adult males (Table II). Fifty-eight of these

93 coalitions were formed during conflicts against a high-ranking male, and 28 of these were conflicts over consorts. I will concentrate on these consort coalitions because they have some unique properties: (1) they are not likely to be chance combinations because conflicts over consorts can be foreseen (by the observers and thus presumably by the males involved); (2) they can be classified unambiguously as successful or unsuccessful; (3) one principal beneficiary can be identified; and (4) such coalitions may have an immediate effect on the reproductive success of the beneficiary. H5 benefited much more from these coalitions over consorts than his two partners (Table III). Table III also shows the asymmetric allocation of benefits from the provocations.

Discussion

It is clear that benefits from coalitions over oestrous females were very asymmetrically distributed among the allies in this study group. Coalitions over oestrous females, however, formed about one-third of all coalitions observed. Was the

Table III. Results of conflicts with coalitions or provocations over consorts between alliances of low-ranking males and single high-ranking males

Alliance	Conflicts with coalitions	Successful coalitions	Provocations	Male in consort after conflict		
				H5	H6	H7
H5-H6	12	8	3	8+3	0+0	—
H5-H7	5	4	3	4+2	—	0+1
H6-H7	6	1	1	—	1+1	0+0
H5-H6-H7	5	5	2	5+2	0+0	0+0
Total	28	18	9	17+7	1+1	0+1

asymmetry to the advantage of H5 in the consort coalitions compensated by an asymmetry to the advantage of H6 and H7 in coalitions of another type? Here one runs into the problem of having to add values that cannot be reduced to a common currency in a straightforward way.

In spite of the methodological problems I shall try to investigate the likelihood that the asymmetry found for the coalitions over consorts was compensated in other coalitions. The coalitions formed by the three males H5, H6 and H7 can be divided into three categories, each representing roughly one-third of the total number: (1) coalitions over consorts against high-ranking males; (2) coalitions against high-ranking males with other immediate causes; and (3) coalitions formed against lower ranking individuals, mostly adult females and immature group members (see Table II). Operationally, coalitions can be divided into 'interference coalitions' (formed after the interference of one partner in an ongoing conflict in which the other partner was involved) and 'parallel coalitions' (formed when the two partners simultaneously came into conflict with the same opponent). In parallel coalitions there are usually no grounds to assume appreciable asymmetries in costs and benefits. These coalitions were often formed when the partners reacted simultaneously to the same cue, for example the scream of an infant. The high potential costs in a parallel coalition against a strong opponent make it important that the partners act simultaneously, but when they do it is not likely that their costs and benefits differ considerably. Similar coalitions formed against weak opponents ask for little coordination and need not, in fact, be explained by a model of collaboration. Interferences against weak opponents are not very costly, while the supported

partner has little benefit. Due to the large size dimorphism, an adult male baboon can easily win a fight against one or more members of any other age-sex class.

The major potential source of compensation for the asymmetry found for the consort coalitions are the interference coalitions against high-ranking males. Interferences in ongoing conflicts are often described as 'support' or 'aid-in-conflict' for the opponent of the individual that is attacked by the interferer, suggesting that an interference is an altruistic act. Of course, a male avoids costs by not interfering, but an ongoing conflict is also a good opportunity to try to defeat a higher ranking male. It is possible, therefore, that many interferences are beneficial for both the interferer and the supported animal. Note that the interferer can form such a coalition without any risk of cheating by the partner.

Another aspect is that once an alliance is established the ally becomes an important instrument in reaching certain goals; in other words, the ally becomes a resource in itself (Kummer 1979). The interfering male can prevent the reduction of vigour of the partner that could result from serious wounding, or from the experience of losing a fight.

In conclusion it is unlikely that there is an appreciable compensation for males that receive a low share from coalitions over oestrous females, as a result of other coalitions. Moreover, no benefit of coalition formation is likely to contribute as much to individual fitness as gaining access to a fertile female. It is therefore highly unlikely that the benefits over all coalitions are distributed more or less symmetrically over the allies, although I am unable to provide conclusive evidence. A strong asymmetry does not imply, however, that H6 and H7 had no net benefit from their alliance with H5.

THE VETO GAME HYPOTHESIS

Questions Following from the Hypothesis

The asymmetry found led to the hypothesis that the mechanisms involved in the alliance formation between H5, H6 and H7 were comparable to the mechanisms that operate in a Veto game. I analysed the data further to answer the following questions. (1) Was H5 more effective than H6 and H7 in conflicts against the higher ranking males? (2) Were coalitions including H5 successful while those without him (i.e. between H6 and H7) were unsuccessful? One might also expect that coalitions of H6 and H7 would never form, if they had a very low chance of being successful. H6 and H7 did form only six consort coalitions, but this was not fewer than those formed by H5 and H7 (Table II). (3) Did the males communicate during the formation of coalitions and could 'negotiation' processes be recognized?

Test of the Hypothesis

(1) Was H5 more effective in conflicts against the high-ranking males than H6 and H7? To answer this question I examined dyadic conflicts between these three males and H1, H2, H3 and H4. H5, H6 and H7 all lost the majority of these conflicts, but even in lost conflicts they sometimes behaved aggressively. Over the whole observation period H5 showed aggression in 17.4% ($N=144$), H6 in 13.6% ($N=169$) and H7 in 8.1% ($N=135$) of cases. The difference between H5 and each of the other two males is significant, but the difference between H6 and H7 is not (448 conflicts in total, one-tailed t -tests with pooled estimate of variance and the high-ranking males as four test-cases. H5-H6: $P=0.043$; H5-H7: $P=0.017$; H6-H7: $P=0.183$. The data were not biased towards more conflicts of H5 with the lower ranking of the opponents). In conclusion, H5 indeed put up significantly more resistance than H6 and H7 in conflicts with high-ranking males.

(2) Were coalitions including H5 significantly more often successful in conflicts over oestrous females than coalitions without him? Only the two-male coalitions were analysed since the success of three-male coalitions could have reflected merely the number of participants. Twelve coalitions in which H5 took part were successful and five failed; H6 and H7 had one successful coalition while five failed (Table III). Thus the two-male coalitions

with H5 were more successful than those without him (Fisher exact probability = 0.035, one-tailed. The result is conservative since the average rank of the opponents was the lowest for the H6-H7 coalitions). The success rate of provocations could not be analysed because 'unsuccessful provocations' were not defined.

(3) Did the males communicate during the formation of coalitions and could 'negotiation' processes be recognized? This question can be answered only qualitatively. The frequent exchange of 'side-directed behaviour' (De Waal & Van Hooff 1981) and 'sexual greeting' (Smuts 1985) shortly before and during coalitions suggests that communication took place at the level of single coalitions. Sexual greetings often directly preceded synchronized attacks. Exchange of information about willingness to maintain the long-term relationship probably took place mainly through the coalition themselves. In this light the formation of seemingly unnecessary coalitions against weak opponents also makes sense. These coalitions may have served the alliance itself by cementing the bond much as grooming may have done for Seyfarth & Cheney's (1984) vervet monkeys. Male baboons do not show forms of affiliative behaviour like grooming, with the exception of pseudo-sexual behaviour.

One way to bargain about the cost-benefit balance in an alliance is to refuse to form a coalition when the ally is asking for it. We have seen such refusals several times. In the H5-H6 alliance, for example, H6 refused a few times to join H5 in a coalition against a consorting male; H5 several times refused to support H6, when H6 was attacked by one of the higher ranking males. The asking male could show strong signs of distress in such cases, such as standing bipedally and looking in the direction of the ally while screaming. This usually happened after the normal side-directed behaviour (head-flagging and staccato grunting) was ignored by the ally.

Discussion

A methodological problem is that the predictions based on the Veto game hypothesis were tested with the same data that generated the predictions. The specific analyses were made, however, after the hypothesis was formulated.

The Veto game model assumes that animals negotiate about collaboration and, like the Pri-

soner's Dilemma model, it assumes that important information is conveyed during the collaborative acts themselves. In addition it assumes direct communication about intentions. While the existence of true negotiation between animals is hard to demonstrate, it is certainly possible to recognize behaviour patterns of baboons that could play a role in direct negotiations over the formation of single coalitions. Coalition partners frequently communicated before and during coalitions and their communication seemed more intensive when coalitions were more risky. Compared with humans, baboons have limited means of communication and, consequently, of negotiation. In Veto games among human players, restriction of the possibility to communicate leads to higher payoffs to the Veto player (Murnighan & Roth 1977).

GENERAL DISCUSSION

Predicted Proximate Tactics

Game theoretical models are normative and therefore cannot be tested directly with empirical data (Colman 1982). Acceptance depends on relative plausibility. What can be tested, however, is the use of decision rules predicted by the models at the proximate level. The coalition game model predicts proximate tactics that differ from the tactics predicted by the Prisoner's Dilemma model. It should be possible to decide which model is the more plausible on the basis of observations about decisions animals take in situations in which collaboration is an obvious option. Decision rules that are apparently successful in the Prisoner's Dilemma are 'reciprocity rules': they prescribe to check the behaviour of the partner by reacting in kind to defections. The best known and most stringent reciprocity rule is Tit-For-Tat, the strategy considered to be evolutionarily stable by Axelrod & Hamilton (1981). A player adhering to the Tit-For-Tat rule in an iterated two-player Prisoner's Dilemma game of uncertain length will cooperate on the first move and will in subsequent moves copy the decision the other player made in the previous move. Two Tit-For-Tat players will thus cooperate till the end of the game, in which case the rule remains indistinguishable from the rule 'always cooperate'. The true nature of Tit-For-Tat is revealed when a Tit-For-Tat player encounters a player who defects. This difference even shows when the other player's tactic differs only slightly

from Tit-For-Tat in that, in each move, there is a small chance that he will defect without being provoked by defections of the other player (cf. the strategy JOSS in Axelrod 1984). The cooperation will break down after the first defection and will never be restored. In theory a rule like JOSS may not be an optimal rule to play in an iterated Prisoner's Dilemma (Axelrod 1984), but it is likely to describe the real-life behaviour of a player that is (genetically) programmed to play Tit-For-Tat. In real life one might expect occasional misunderstandings or the inability to carry out a decision to cooperate (Selten & Hammerstein 1984). Perhaps reciprocity rules can be described that are somewhat more robust under real-life circumstances. The crux of such rules remains, however, that a relationship with a partner that refuses to collaborate a few times is broken off and is never restored.

A reciprocity rule may be useful for an animal that repeatedly has an opportunity to collaborate with an unrelated partner whose availability was determined by some process beyond the animal's control (see example in Whitehead 1987). The costs of foregoing such opportunities depend on the alternatives. One possible alternative is to reach the goal without collaboration, which is, however, not always possible. Another possible alternative is to select a different partner, assuming one is available. The existence of alternative partners implies that there is a choice among potential partners. In that case a rule is needed, to choose among partners. Reciprocity rules could provide a method to find good partners through trial and error. The chance exists, however, that all potential partners are rejected in the process. The trial-and-error process itself should also not be too costly. The main problem facing an animal living in a social group, and in need of a collaborator, is not to check the behaviour of a given partner. The problem is to find the best partner(s) within a limited set and to gain as much as possible from collaboration. Such problems are equivalent to the problems facing a player in a coalition game.

A player in situations resembling coalition games should use a tactic with the following properties.

(1) The player should react to incidental failures or refusals of his partner to collaborate, by making efforts to repair the relationship, not by breaking off the relationship immediately. The investment in these efforts will depend on the player's alternative options and the history of the relationship with the

partner, which can be used as a basis for assessing the nature of the 'defection' (by accident or on purpose) and the probability that it will be repeated.

Rule 1 is rather elastic: the more options a player has, the less 'forgiving' the player should be in case the partner refuses to collaborate. When the number of alternative options is large, a Tit-For-Tat rule is to be expected as the most unforgiving extreme.

(2) When the player collaborates in order to obtain resources in which the partner is also interested, the player should make use of the limited options of the partner to gain as large a share as possible at the expense of the latter.

(3) When the player has several potential partners, which are all interested in the same pool of resources, the player should reduce the burden of competition within the alliance by searching for the weakest partner with whom successful collaboration is still possible. The most likely alliance to form is thus the weakest combination that can still form successful coalitions. This is known as the 'minimum resource theory' (Gamson 1961). When the interests of the partners do not overlap, the player should search for the strongest partner.

(4) The player should switch to another partner when a greater net benefit results from collaborations with the alternative partner. To gauge the difference, the player may have to interact simultaneously or alternately with several partners over some period of time.

Taken together this leads to the following rule: search for the weakest (or strongest, see rule 3), partner available and start a collaborative relationship. Increase the net benefit as much as possible, until the partner refuses to collaborate. At that point yield more to the partner, until the point is reached at which an alternative partner can be found who is willing to collaborate for a competitive price. The net benefit can be increased by decreasing the investment and/or increasing the share claimed from resources of mutual interest. I assume that in most cases gradual adjustments can be made, but in series of collaborative interactions with an all-or-nothing character, adjustments can be made in the number of times investments are made and benefits are reaped. In the latter case the distinction between a coalition game rule and a reciprocity rule can in principle be shown with a runs-test (Sokal & Rohlf 1981) when all occurrences of collaboration are observed within a pair.

A reciprocity rule should lead to very short runs (series of interactions in which the same partner benefits); a coalition game rule can lead to longer runs. The more asymmetric the power balance in the coalition the longer the runs of interactions, in which the more powerful partner is the beneficiary.

There has been little research into the actual decision rules used by animals. Lombardo (1985), Milinski (1987) and Whitehead (1987) reported cases in which animals used the Tit-For-Tat rule. In the introduction, I pointed out problems I see with the studies of Lombardo and Milinski. Whitehead studied a system that differs essentially from the kind of system considered in this paper. His territorial howler monkeys, *Alouatta p. palliata*, were not members of the same social unit; they could not choose their partner. In such a situation the Prisoner's Dilemma seems the appropriate paradigm. Neither Tit-For-Tat, nor another reciprocity rule, was apparently used by the baboons in this study. In another baboon group in Amboseli I observed a rather slow process in which a middle-ranking male exchanged one lower ranking ally for another (Noë 1986, 1989). This process involved several long interactions in which all three males took part. An important observation is that the relationship with the former ally was not ended abruptly.

Some predictions can be made on the basis of the coalition game model about the stability of collaborative relationships. Which pair(s) actually form such relationships is determined by rule 3 above. When several combinations could be formed, mechanisms described by Seyfarth (1977) in his model of the formation of grooming pairs could take effect. A relationship, once established, will not easily be broken off, according to rule 1 above. Keeping a sub-optimal collaboration going is better than no collaboration at all, as long as the collaboration yields a positive result. A further prediction is that the stability of alliances, measured as the frequency with which partners are exchanged, is a function of the number of interchangeable partners in each role. This number will often depend in turn on the size of the group or subgroup. I indeed found less stable alliances among males in a group of baboons that included an average of 14 adult males (Noë 1989).

A theory based on coalition games predicts that the costs and benefits are distributed among the players according to their 'power' in the game. When two players have comparable options, and

are thus equally powerful, one would expect that they share equally. Thus the allocation of costs and benefits may match one's intuitive expectations for the situation in which two players play according to a reciprocity rule. The more alternative options both players have, the more likely they are to have equivalent power.

In my opinion animals collaborate in many cases, because they have a certain chance of benefiting immediately, which they cannot reach without collaboration. In such situations neither player can have high immediate gains by refusing to collaborate. It thus pays to convey honest information about the intention to collaborate, since nothing is accomplished when the other does not join in. The assumption of the Prisoner's Dilemma model that 'defection' always yields a higher immediate benefit often does not hold. The actual outcome of a collaborative interaction influences the assessment of the chance of immediate gain in comparable situations in the future, but when there is a long history of collaboration the influence of a single interaction will be small. When resources are indivisible, the chances of a weak player benefiting immediately may be low, but never so low that the overall benefits do not outweigh the costs. Changes of this chance over time will, however, be hard to assess for weak players.

The Applicability of the Coalition Game Model

The drawback of coalition games is that they do not provide a mathematical instrument in the search for 'stable' or 'dominant' strategies. In cooperative games enforceable agreements, or 'contracts', should be possible (Harsanyi 1982). It is hard to imagine how animals could conclude contracts. However, if the game is iterated and the alternative options are limited, individuals may have sufficient leverage over their partners to keep them to the agreement (see Maynard Smith 1982, for a similar argument concerning reciprocal altruism).

Coalition games are suitable paradigms for situations in which partners seek each other out for profitable collaboration, taking some competition among each other into the bargain. The theory of coalition games seems relevant to a variety of social systems. The Veto game can, for example, be recognized in the collaboration between breeders and their helpers, between territory holders and

their satellites, and between parents and their offspring. The Prisoner's Dilemma remains the best paradigm in cases in which two animals are condemned to cope with each other in a basically competitive situation which they can improve to some extent by cooperation.

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