

male generally has fewer relatives in a matrilineal group than does a female. Although migration or displacement of either sex avoids the risks of inbreeding, there are, in primates for example, only four of thirty primate species (for which data are available) in which the female acts in this way (Wrangham, 1980). The factors that influence male migration are thought to be the increase in mating opportunities and the avoidance of inbreeding (Clutton-Brock and Harvey, 1976; Packer, 1979). There is an equally compelling reason for females not to migrate, which may thus induce the male to do so. In the course of emigrating from her natal group, a female would lose more opportunity than would a male to aid kin and benefit from them. Her certainty of offspring allows her to establish a close knit kin system that would contribute more to the kinship component of her inclusive fitness¹ than would her emigration.

Only when brothers or half-brothers migrate simultaneously, as in lions (Bertram, 1976), are there good prospects for kin selection among males. Such possibilities are largely confined to social carnivores and small mammals that have a number of young per litter. Among the higher primates, with a single young per litter, birth spacing of brothers limits the opportunities for coalitions among related male migrants. In most species, when a male moves to a new group, there is little chance he will meet, or can identify, a close relative (see, however, Lindburg (1969) and Meikle and Vessey (1981)).

It would seem that the greater certainty and availability of kin that a female has will offer her more scope than a male for increasing the kin component of inclusive fitness. Hence on this basis, males, more than females, should focus on the personal component of their inclusive fitness in interactions with others.

SOCIAL STRATEGIES

Competing individuals within a social group can directly or indirectly manipulate their social partners. Some forms of manipulation require more social skill than others and the forms available and their significance to either sex are ex-

amined in this article. Multimale primate groups where males migrate are emphasized because here kin certainty and availability are limited and because one might therefore expect the greatest opportunity and selection for social manipulation, particularly among males.

The limiting resource will tend to be different for each sex, since for males, who have a large variance in reproductive potential, competition will center on access to females (Bateman, 1948); for females, who have a low variance in reproductive potential, it will center on food (Wrangham, 1980).

In this discussion the term tactic means "any skillful method used to gain an end" (Websters, 1956), whereas strategy means a longer term and larger plan incorporating various tactics. Strategies involve behaviors of genotypic or phenotypic origin that increase an individual's inclusive fitness.

During competition an individual can use only three tactics: exploitation, cooperation, or reciprocity, although they may be used in combination. Because these terms are crucial to our argument and have been used in a variety of ways in the literature, we will define them as follows.

1. *Exploitation* involves interactions between individuals where one benefits at the expense of the other. The most common form of exploitation is a dominance system where one individual actively excludes another from resources according to dominance rank (Calhoun, 1962; Hall and DeVore, 1965; Le Boeuf and Peterson, 1969; Geist, 1971). Exploitation through dominance succeeds because the subordinate's costs in contesting the interaction are higher than the potential benefits of the resource. Vehrencamp (1979) treats the issue of exploitation more broadly in her discussion of how much "skew" is possible in a variety of social interactions.
2. *Cooperation* involves interactions between individuals where there is an immediate joint benefit that is greater than if each individual acted alone. The salient feature of cooperation is the lack of time delay in mutual benefits (Clutton-Brock and Harvey, 1978, p. 136). Cooperation is similar to mutualism (Vehrencamp, 1979) and most often occurs in situations of mutual defense or mutual foraging and food-sharing (DeVore, 1965; Klingel, 1965; Bertram, 1976).

¹ Here we use the concept of inclusive fitness (Hamilton, 1964a,b) as modified by West Eberhard (1975), where inclusive fitness includes both a personal and a kinship component.

Sex, Kinship, and the Evolution of Social Manipulation

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In recent years kin selection has been widely used to explain social systems and the evolution of complex social traits. However, because a knowledge of kin is a prerequisite of kin selection theory, and because a male has less certainty of kin and, in many cases, few or none available to him within a social group, he will be unable to favor kin or benefit from them as reliably as will a female. It is predicted, therefore, that social strategies involving unrelated individuals will be more common among males than females and suggested that the greater encephalization among higher mammals, particularly primates, allowed complex nonkin strategies of social manipulation to evolve, realizing its greatest sophistication in human political systems. Finally, the question whether selection for certain types of social strategies in males may not have led to differences from females in assessment and manipulation skills is considered.

Key Words: Kin selection; Reciprocal altruism; Competition; Social strategies; Sex differences.

INTRODUCTION

Differences between males and females in reproductive potential and willingness to invest in offspring are commonly used to explain courtship behavior, mating systems, and their evolution as an outcome of conflicting strategies

between the sexes (Bateman, 1948; Maynard Smith, 1958; Orians, 1969; Trivers, 1972; Emlen and Oring, 1977). While the differences in reproductive strategies have been widely realized, Wrangham (1980) points out that the significance of social groups has been treated implicitly as though it were similar for both sexes and goes on to show that matrilineal primate groups are a female adaptation, based on kin selection, to increase a female's access to food.

This article further explores the consequences of reproductive strategies and considers how the certainty and availability of kin will influence sex-specific efforts to maximize fitness by manipulating social partners within the group.

KIN CERTAINTY

An assumption of our argument is that males are less certain of their offspring and kin than are females (Alexander, 1974). A female's certainty of her offspring begins at their birth when she recognizes them by sight, sound, and smell. By an extension of that knowledge through her descendants and those of her female siblings, she will be very certain of her closer kin because they typically remain in the same group (Crook and Gartlan, 1966; Estes, 1974; Bertram, 1976; Wrangham, 1980). By contrast, because there is always a chance of cuckoldry, even in monogamous pairs (Trivers, 1971; Birdsall and Nash, 1973; Barash, 1976; Erickson and Zanone, 1976), a male can never be absolutely sure of his progeny. Furthermore, among social mammals, a

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3. *Reciprocity* involves cooperative actions between individuals where participants realize benefits at different times. Reciprocity implies at least two sequential interactions, the sum of which provides benefits to both partners that exceed the costs to either (Trivers, 1971). However "benefits are only given when there is a high likelihood of a compensating return to the phenotype of the benefit-giver (but conceivably to the phenotypes of relatives of the benefit giver)" (Alexander 1974, p. 356) (see also Emlen (1980)). Coalitions and alliances are the most frequently cited examples of reciprocity among animals (Wilson, 1975; Cheney, 1977; Packer, 1977), although sequential food sharing may also be included (Reynolds and Reynolds, 1965; Sugiyama, 1969; van Lawick and van Lawick Goodall, 1971; Teleki, 1973; Kuhme, 1965).

Viewed evolutionarily, reciprocity has greater potential than either exploitation or cooperation. Asymmetry limits exploitation because a subordinate will eventually contest domination, as shown in models of aggressive strategies (Maynard Smith and Price, 1973; Parker, 1974; Maynard Smith and Parker, 1976; Popp and DeVore, 1979). Similarly, opportunities limit cooperation because there are few circumstances offering immediate and equal benefits to both partners.

The sequential nature of reciprocity eliminates the restrictions of both cooperation and exploitation. A greater variety of resources can be shared than under conditions of cooperation and the reciprocal sequence ameliorates the cost inequities of exploitation. A simple example illustrates this point. Consider the costs and benefits of exploitation, cooperation, and reciprocity to males competing for estrous females. If one male can dominate another, he can exclude him from reproduction. However, the subordinate will risk injury or even death, at some point, in order to reproduce. The dominant animal may monopolize some females but cannot do so for too long without challenge. By contrast, two males might ally to defeat a dominant male, yet their alliance cannot be based on strict cooperation (mutualism), since only one male can ultimately father the offspring. But if their alliance is reciprocal in nature, then by sequentially sharing females, one male can afford to forego the immediate benefits of reproduction provided the ultimate returns for both males exceed their independent efforts. Packer (1977) states the the-

oretical case as follows:

Natural selection would favor individuals that engaged in reciprocal altruism if they distributed their altruism with respect to the altruistic tendencies of the recipient, preferring individuals that were most likely to reciprocate and excluding nonaltruists from the benefits of further altruism.

THE POTENTIAL FOR RECIPROCITY

If reciprocity does have the greatest potential for evolutionary development of the three tactics discussed above, why are animals so devoid of it, as Wilson (1975) and others contend? We will consider this question further, since it is so germane to our argument.

Two factors may have handicapped the search for cases of reciprocal altruism (reciprocity), one resulting from the theoretical model, the other from practical problems of identifying the phenomenon. Let us consider the theoretical constraints first.

Some disagreement exists about the relationship between kin selection and reciprocal altruism. Kin selection, as formulated by Hamilton (1964) and elaborated by West Eberhard (1975), can operate when

$$K > \frac{1}{r} \text{ [Hamilton]} \quad (1)$$

where K is the benefit to cost ratio and r is the degree of relatedness between partners, or

$$K > \frac{r_{A_y}}{r_{B_y}} \text{ [West Eberhard]} \quad (2)$$

where r_{A_y} is the probability of Ego having, through descent, a gene in common with the young of the donor, and r_{B_y} is the probability of Ego having, through a descent, a gene in common with the young of the beneficiary.

Reciprocal altruism was originally conceived to explain actions outside the realm of kin selection (Trivers, 1971). Since then, reciprocal altruism has been viewed as a subset of kin selection where the degree of relatedness (r) between interactants is equal to zero ("classical reciprocal altruism") (Alexander, 1974). It has also been applied to interactions where the degree of relatedness between actors is relatively low, but not zero (West Eberhard, 1975). Recently, Rothstein (1980) went further, stating

that because altruists must share genes in order for altruism to occur, reciprocal altruism is identical to kin selection.

There is also disagreement about the role of reciprocity in reciprocal altruism. Although Trivers considered reciprocity necessary, others have taken the position either that it is not (Rothstein, 1980), or that sequential acts of kin-altruism satisfy the condition for reciprocity (West Eberhard, 1975) as conceived in Trivers' original definition.

The prevalent view, and the one to which we adhere, is that reciprocal altruism must involve at least two interactions in which altruistic behaviors are "base upon a selfish probabilistic expectation of a reciprocal return of helping in the future" (Emlen, 1980) (see also Alexander (1974) and Axelrod and Hamilton (1981)). Furthermore, it is possible to make the distinction between behaviors that could have evolved by kin selection because they fulfill the conditions of eqs. (1) or (2) and those in which

$$K \leq \frac{r_{A_y}}{r_{B_y}} \quad (3)$$

but $K > r_{A_y}/r_{B_y}$ for the sequence of acts. The latter cases cannot be explained by kin selection but can be explained by reciprocal altruism.

The relationship of kin selection and reciprocal altruism is less critical to our arguments than it is in general, since we are contrasting the strategies available to males and females in multimale primate groups where males migrate. The potential contribution of the kinship component to the inclusive fitness of individuals of the two sexes, under these conditions, will therefore lie at opposing extremes on a continuum of kin selection-reciprocal altruism, regardless of how that continuum might be demarcated.

Trivers (1971) gives the conditions under which reciprocal altruism could evolve and be maintained in a population. These include the frequent occurrence of altruistic situations during the altruist's lifetime, repeated interaction of the small set of individuals, and symmetrical exposure of individuals to situations where roughly equivalent benefits and costs accrue to them. He suggests that the biological circumstances favoring reciprocal altruism are long life, low dispersal rate, mutual dependence, parental care, lack of dominance, and aid in combat. Despite these stringent conditions Trivers states that "although the preconditions for the evolu-

tion of reciprocal altruism are specialized, many species probably meet them and display this type of altruism."

We suggest that many species may well exhibit reciprocal altruism, but that the necessary conditions have been overstated. For example, life history parameters and rates of interaction are related to size and to physiological time (Western, 1979) such that a longer lifespan does not necessarily imply more numerous interactions per lifetime. Short lived species can have the same interaction rate when scaled to lifespan, yet may possess greater mental capacity than larger, longer lived species (compare, for example, a vervet monkey and a rhino). Thus the potential for reciprocal altruism need not relate to lifespan.

Further, while dispersal may play a part, it is individuals with greater dispersal rates that must place more reliance on reciprocity (see below). More species may therefore have the potential for reciprocal altruism than previously assumed and more individuals within a species should consequently experience conditions favorable to its development.

The conditions for reciprocity can also be relaxed, because neither the benefits nor the costs need necessarily be commensurate for the partners, as required by Trivers' model. Provided the benefits exceed the costs for both individuals, each should enjoy an advantage. Such would be the case where benefits are complementary.

The evolution and maintenance of reciprocal altruism is further held to be constrained by the presence of cheaters (Trivers, 1971). However, cheating is less of a problem when reciprocal altruism is considered in the long term rather than in the short term. Under these circumstances, partners in altruism should form a "relationship" in which the short term advantages of cheating would rarely outweigh the long term costs if the cheating was detected (see Wrangham (1982b) for a similar discussion of "mutualism"). Here too, if partners do not have to benefit equally or equivalently from reciprocity, there are fewer constraints on its evolutionary development.

The less restrictive theoretical conditions herein enumerated expand the evolutionary potential for reciprocity to occur in animal societies. Recently, Axelrod and Hamilton (1981) demonstrated the ease with which reciprocity

(or cooperation) can be established in a population with a simple "tit for tat" game plan, even under extremely adverse conditions. Axelrod and Hamilton's attempts are part of a growing trend to consider the evolution of reciprocal altruism as theoretically possible and important.

But there still are, in addition to these theoretical issues, practical problems that have limited our recognition of reciprocal altruism among nonhuman animals. To distinguish between kin altruism and reciprocal altruism, a knowledge of kinship is necessary. This requires long term studies of individually recognized animals, and as yet few of these have been undertaken. Costs and benefits must also be known. In practice these seldom are known because of the difficulty of measuring them directly.

In addition to these problems, and because of Trivers' theoretical premise, the search has concentrated on identical rather than complementary benefits. The situations where such equivalency can occur are, like cooperation, relatively rare.

Finally, reciprocal altruism is difficult to distinguish from other behavior when assumptions made about relatedness or benefits and costs are the very parameters being tested. A good illustration can be found in the interpretation of agonistic buffering among male baboons. These have ranged from arguments based on group selection (Ransom and Ransom, 1971), to kin selection (Popp, 1978; Busse and Hamilton, 1981), to mutualism (Packer, 1980), to reciprocal altruism (Strum, 1982b). Without real measures of the genetic and economic parameters of behavior, conclusions are contingent on the qualifying assumptions.

The rarity of reciprocal altruism among nonhuman animals may therefore be more apparent than real. In fact, under these expanded conditions for reciprocity many social relationships among unrelated individuals are likely to be examples of reciprocal altruism, especially in more complex social systems (Strum, 1982d). We can now return to considering the differences in male and female social strategies with these points in mind.

MALE AND FEMALE STRATEGIES

Social manipulation used during competition includes the tactics of exploitation, cooperation, and reciprocity. Both males and females should

use all three tactics, but the nature of both the tactic and the strategy will be influenced by male-female differences. First, since most stable groups are matrilineal, female strategies will primarily use tactics that have both a personal and kinship component and are under the influence of kin selection, or at least difficult to distinguish from it. In contrast, male strategies, once males leave their natal group, have to rely upon tactics not dependent on biological relatedness.

Second, the sexes also differ in the manner in which they can use exploitation, cooperation, and reciprocity. For example, in circumstances such as competition for limited resources, males can be more exploitative than females because they need not consider the kin component in most of their interactions (see Popp and DeVore (1979) for a parallel argument about the limitations of aggressive competition). By contrast, a female is likely to be related to her social partners and fitness considerations must weigh the personal with (or against) the kinship component (see Vehrencamp (1979) for a general model).

At other times, in order to elicit cooperation or reciprocity from another individual, a male will need to be more cooperative or altruistic² than a female. A female can rely on benefits from kin without having to dispense prior benefits to them, since kin altruism is based on genetic self-interest. Further, in order to engage kin in mutualistic interactions she does not have to cooperate or share as fully as she does when involving unrelated individuals (Hamilton, 1964a,b; West Eberhard, 1975; Wilson, 1975).

We have also suggested that reciprocity has the greatest evolutionary potential of the three tactics. But, here too, males and females differ in the degree to which this potential can be realized. Both sexes benefit from reciprocity and theoretically benefit more from reciprocal altruism with kin than with nonkin (Alexander, 1974; Emlen, 1980; Axelrod and Hamilton, 1981), since in doing so they increase the kin component of their inclusive fitness simultaneously with their personal component. However in matrilineal primate societies, males and females encounter different social circumstances. Thus while a female's reciprocity favors the kinship

² An actor is considered altruistic when he benefits a partner at some net cost to himself.

component of her inclusive fitness, a male's reciprocity will necessarily be directed predominantly at increasing the personal component. Because the availability and certainty of his kin is limited, a male should, to a far greater extent than a female in this context, be prepared to "invest" (see Hinde (1978), Kummer (1978), Seyfarth et al. (1978), and Strum (1982a,b,c)) in nonkin for purposes of reciprocity. A female's willingness to invest in nonkin will be limited by the number of interactions she can undertake and by the greater benefits she derives from investing that same time and effort in nepotistic interactions.

There is some evidence that a female's attempts at reciprocity with nonkin may be constrained by kinship considerations. Cheney's data on chacma baboons (1977) provide a rare and excellent example. Immature baboons in the troop she studied attempted to ally with members of high ranking families (who would bring them the most potential benefit), rather than with closely related individuals, who had adjacent dominance ranks. Despite these efforts, the alliance system among adult females was between related individuals of adjacent rank.

Similarly, Chapais and Schulman (1980) successfully model a primate female dominance system from kin selection theory, alone. This model also shows an exceptional fit with existing data on rhesus macaques.

Since females have limited opportunities for reciprocal altruism with nonkin, we need to consider, when they should enter into a "tit for tat" relationship with kin rather than rely on kin benefits without reciprocation. Theoretically, nepotistic reciprocal altruism should occur when eq. (3) holds. For example, Chapais and Schulman (1980) suggest that reciprocity would aid a female in acquiring rank or preventing outranking. However, even in their model (and their data), there are limited situations where benefits would be dispensed counter to expectations based on kin selection. It may be that female reciprocity with kin has the greatest potential at low degrees of relatedness and/or when reciprocation allows the acquisition of resources that could not be simultaneously shared. If so, these nepotistic reciprocal relationships may have some of the same limitations suggested in the discussion of nonkin reciprocity.

It has been argued here that males and females should generally employ different strate-

gies and place different emphasis on the tactics within those strategies. Male strategies, in the species considered, cannot involve kin to the extent that female strategies do.³ Male social strategies should also rely heavily on reciprocity as a tactic. The benefits of kin altruism from social partners are denied a male outside his natal group and although one might expect a male to try to incorporate exploitative and cooperative tactics when possible, both of these, as discussed previously, have major restrictions limiting their usefulness in competitive situations. A male's main opportunity to compensate for the lack of kin altruism is to be found in reciprocity.

Given the contrast between the sexes, selection should have favored different social skills in males and in females. Relying, as they do, on kin-based strategies and very little on the tactic of reciprocity, we suggest that females need less sophisticated assessment and testing skills than do males. Because kin-based strategies have a large genetic component to them, one might say that a female's genes can do the evolutionary calculus for her. Although there is an underlying similarity between male and female strategies, because a male is in fact replicating kin-like relationships with unrelated individuals, his investment is social rather than genetic. Thus male nonkin strategies (with their particular emphasis on reciprocity) necessarily require for success greater assessment and testing of others, and more social investment and social manipulation. If there is a genetic basis for male strategies, it would have to be for the propensity to evaluate costs and benefits in a more sophisticated manner, before, during, and after social interactions.

THE EVOLUTION OF SOCIAL SKILLS

If social strategies have potential for elaboration, and if our argument is correct, we should expect an evolutionary elaboration, particularly of reciprocal altruism. Although reciprocity per se does not require organizational complexity (Axelrod and Hamilton, 1981), complex social strategies do depend upon memory, integrative

³ Even in those few cases where males are known to migrate to groups containing an older brother (rhesus macaques, see Lindburg (1969), Meikle and Vessey (1981)), the relative availability of kin to males still differs greatly from females.

capacity, and testing and assessment capabilities (Humphrey, 1976). If social manipulation can increase an individual's reproductive success (Packer, 1977; Strum, 1982a,b,c), and if the prerequisite skills are closely related to the level of encephalization, then selection would favor an increased brain size. Trivers (1971) comments in a similar vein in considering the selective pressures for reciprocal altruism in humans. He concludes that

Given the psychological and cognitive complexity the system rapidly acquires, one may wonder to what extent the importance of altruism in human evolution set up a selective pressure for psychological and cognitive power which partly contributed to the large increase in hominid brain size during the Pleistocene.

Humphrey (1976) alludes to a parallel evolutionary trend when he suggests that intellectual faculties in the higher primates have evolved as an adaptation to the complexities of social living.

Given that human reciprocal altruism is widely accepted and is extremely complex (Trivers, 1972), it seems unreasonable to believe that such behavior evolved recently and is confined to our own species. Varying levels should exist among other social mammals, especially the primates. Packer (1977) provides hints that this is so in baboons and Strum (1982a) argues that social skills may be a key feature in explaining male strategies when agonistic dominance alone proves inadequate.

Selection for skills other than those of social strategies may well have acted simultaneously on mental capacity. For example, foraging strategies vary with habitat and food resources in frugivorous and omnivorous small mammals (Eisenberg and Wilson, 1978), and frugivorous primates (Harvey et al., 1980) have relatively larger brains than folivorous primates, perhaps as a result of selection for the greater memory and integrative capacity associated with their lifestyle. Milton (1981) offers a similar argument to account for taxa-specific variations in primate encephalization and for human brain expansion. Since foraging skills depend on neural traits similar to those required for social strategies, selection leading to sophisticated foraging may well have contributed to the evolution of social skills. Another catalyst in the evolution of social strategies may have been the formation of large, multimale matrilineal groups in response to the

greater predation risks associated with a shift to ground living in primates (Crook and Gartlan, 1966; Clutton-Brock and Harvey, 1976), for these are the social conditions most favorable for the evolution of reciprocity among males.

Given the trend of increased brain size tied to more sophisticated foraging styles or social strategies, a variety of life history traits may have indirectly resulted that also fostered conditions favorable to reciprocity. For example, a larger brain size could have resulted in slower growth rates and increased lifespan as predicted by Sacher's (1978) theory of growth and aging. Changes in other parameters, such as longer gestation and lower reproductive rates that accompany encephalization (Western, 1979), would permit longer bonds between individuals in a social group. Such bonds would help to counteract "cheating," an important constraint on the evolution of reciprocity.

Since it need not be a long or complex step from selection for foraging skills to those of social skills that enhance reproduction, we might expect to find such skills among a number of primate species. Selection acting directly on social skills may have subsequently led to accelerated encephalization, especially in man.

It is in humans that social manipulation has attained its greatest sophistication, as evidenced by human political systems. The parallels here with nonhuman primates (Packer, 1977; Strum, 1982a,b,c) are obvious, although both the diversity and deference of benefits are more pronounced among humans. This is amplified on a geopolitical scale by a variety of technological innovations used by man to reduce the constraints of distance and communication.

If social strategies have reproductive benefit, then selection for them should have occurred in our primate ancestors. However, although such selection may have contributed to the rapid evolution of the brain, there is no need to expect differences in mental capacity between the sexes. The fitness of individuals of either sex would be enhanced by greater intelligence (Marler and Hamilton, 1966; Manning, 1967; Barnett, 1981). In fact, among humans, males and females do not differ in brain size (when this is controlled for differences in body size) (Passingham, 1979), or intelligence (Welsh and Baucom, 1977; Burnett et al., 1979).

There is, however, no reason why sex differences should not exist as a result of differ-

ential selection. Various sex differences have, in fact, been demonstrated in, for example, hemispheric specialization (Levy, 1978; Levy and Levy, 1978; Levy, 1981) and spatial, mathematical and verbal abilities (Maccoby and Jacklin, 1974; Royer, 1978; Burnett et al., 1979; Benbow and Stanley, 1981). As yet, the evidence is no more than suggestive, but we anticipate that the evolutionary origins of some sex-specific skills will be found partly in the different social strategies of males and females.

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