Behav Ecol Sociobiol (1998) 44: 43–55

Original article

David P. Watts

Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda

Received: 28 May 1997 / Accepted after revision: 16 May 1998

Abstract Cooperative mate guarding by males is unusual in mammals and birds, largely because fertilizations are non-shareable. Chimpanzees live in fission-fusion communities that have cores of philopatric males who cooperate in inter-group aggression and in defending access to the females in their community. Male contest mating competition is restrained within communities, but single high-ranking males sometimes try to mate guard estrous females. Data from an unusually large chimpanzee commmunity at Ngogo, Kibale National Park, Uganda, that contains more males than any previously studied community show new variation in chimpanzee mate-guarding behavior. Contrary to expectation given the large number of males, mate guarding was as common as, or more common than, at other sites, and males other than the alpha male guarded more often. More strikingly, pairs or trios of top-ranking males sometimes engaged in cooperative aggression to prevent estrous females from mating with other males, but tolerated each other's mating activities. Both single males and coalitions mostly guarded periovulatory females. Mate-guarding coalitions were previously unknown in chimpanzees. Coalitions occurred in large mating parties, seemingly because these often contained too many males for single males to maintain exclusive access to estrous females. Coalition members gained higher shares of copulations than they could have expected from solo mate guarding, and suffered lower per capita costs of guarding (as inferred from aggression rates). Two males who most often participated in coalitions formed two-male coalitions at about the point where the number of males present made it unlikely that either could get 50% or more of total copulations on his own, and formed trios when this value dropped below 33%. Kin selection could be a factor in cooperation among male chimpanzees, but coalition members were not necessarily close relatives and the apparent structure of payoffs fit that of mutualism. Furthermore, reliance of male chimpanzees on support from allies to maintain high rank could have led to trading of mating exclusivity for support against mating competitors.

Key words Chimpanzees · Coalitions · Cooperation · Mate guarding · Aggression

Introduction

Kin selection can lead to cooperation between relatives who share genes identical by descent (Hamilton 1964). The emergence of stable cooperation between non-relatives has attracted great theoretical and empirical interest (reviewed in Dugatkin 1997) because many factors oppose it. Reciprocal altruism (Trivers 1971) is one route to such cooperation, but few cases are well-documented (Dugatkin 1997). Most may instead involve mutualism (or "byproduct mutualism"; Dugatkin et al. 1992; Grinnell et al. 1995; Dugatkin 1997): because of a shared adverse environment, individuals gain higher payoffs by cooperating than by acting alone or by defecting, or defection brings untenable losses. Pied wagtails provide an example of immediate net gain: males that hold territories tolerate satellites when intruder pressure is high; satellites gain nutritionally, but also help with territory defense, which more than compensates territory holders for foraging losses (Davies and Houston 1981). Male lions provide a case in which defection would be too costly: members of male coalitions, who collectively defend access to female prides, cannot afford not to cooperate when faced with intruding males (Grinnell et al. 1995).

Male mammals and birds compete for mates in many ways. These include contesting access to individual

---

D.P. Watts
Department of Anthropology, Yale University,
PO Box 208277, New Haven, CT 06520, USA
e-mail: david.watts@yale.edu,
Tel.: +1-203-4323700, Fax: +1-203-4323669

females (sometimes within multi-male groups), contesting entry to female groups or trying to monopolize access to them, scrambling to locate fertile females, and producing large quantities of sperm and copulating at high frequencies in cases where females typically mate with multiple males (reviewed in Andersson 1994). Male-male cooperation in mating competition is unusual. One reason for this is that predominant male dispersal in mammals (Greenwood 1980; Waser and Jones 1983) means that opportunities for kin selection to lead to cooperation are generally uncommon. Cooperative breeders provide exceptions (e.g., dwarf mongooses: Creel and Waser 1994), but in primates, at least, cooperation occurs less often between males than between females (van Schaik 1996). Male philopatry is common in birds, but most do not form multi-male groups (Greenwood 1980). Also, although access to females is sometimes shareable, fertilizations are not (van Schaik 1996).

Nevertheless, males of some mammalian and avian species benefit (at least in some ecological circumstances) by cooperatively defending long-term access to females or to female groups (e.g., lions: Schaller 1972; cheetahs: Caro 1994; dunnocks: Davies 1992) and/or by cooperatively caring for young (e.g., saddle-back tamarins: Goldizen 1987; dwarf mongooses: Creel and Waser 1994; acorn woodpeckers: Koenig and Stacey 1990; splendid fairy wrens: Rowley and Russell 1990. Even so, males that cooperate against outside males often compete aggressively with each other to fertilize the females they defend (e.g. dunnocks: Davies 1992; alpine accentors: Nakamura 1998a). For example, territory-holding male dunnocks sometimes accept subordinate males that help defend their territories against rivals. Although polygynandrous or polyandrous mating benefits females, dominant members of male pairs try to prevent subordinates from mating (Davies 1992). Polygynandry in alpine accentors is similarly associated with reproductive benefits for females, but within-groups there is contest mating competition among males (Davies et al. 1995; Hartley et al. 1995; Nakamura 1998a, b). Male contests over mating opportunities are also common in cooperatively breeding species (e.g., golden lion tamarins: Baker et al. 1993; acorn woodpeckers: Mumme et al. 1983).

In other cases, male cooperation to gain access to females is associated with restraint on contest competition among the cooperators, although sperm competition may be high (e.g., lions: Bertram 1976; Packer and Pusey 1982; Packer et al. 1988; bottlenose dolphins: Conner et al. 1992; woolly spider monkey: Strier 1994; pukekos: Craig and Jamieson 1990). Cooperative caregiving is also associated with some restraint on mating competition between males (but not females) in dwarf mongooses (Keane et al. 1994) and African wild dogs (Creel et al. 1997); restraint in these cases may make subordinate males more likely to stay and provide help. Kinship can play a role in cooperation and competitive restraint in such cases, but not all cooperating males are related (e.g., lions: Packer and Pusey 1982; dwarf mongooses: Creel and Waser 1994). Males also sometimes cooperate to gain short-term access to fertile females at the expense of other males in the same social group or community (e.g., bottlenose dolphins: Conner et al. 1992; baboons: Noë 1990, 1992). Cooperation in these and some other situations involves joint acts: "coalitions" of two or more males; the term "alliance" applies to males that repeatedly and consistently form coalitions with each other (Harcourt 1989), although "coalition" and "alliance" have become synonyms in the literature on felids (Caro 1994). All members of a dolphin alliance consorting with a female typically copulate with her (Conner et al. 1992). After coalitionary consort takeovers by male baboons, however, only one coalition partner consorts with the female. Packer (1977) argued that these were cases of reciprocal altruism, but a male who accepts a solicitation to join a coalition may gain the consort, and is thus not an altruist, and the payoff distribution can be highly skewed (Noë 1990, 1992). Instead, these coalitions also may involve mutualism (Noë 1992).

Chimpanzees (*Pan troglodytes*) live in multi-male, multi-female communities in which individuals associate in temporary parties that vary in size and composition (Nishida 1979; Goodall 1986; Chapman et al. 1994; Boesch 1996). Males are philopatric and are more gregarious than females (Nishida 1979; Wrangham and Smuts 1980; Goodall 1986; Nishida and Hiraiwa-Hasegawa 1987). They often form coalitions within communities, and some male dyads become allies. Alliances can strongly affect agonistic relationships and mating behavior (de Waal 1982; Nishida 1983; Goodall 1986; Nishida and Hosaka 1996). Simultaneously, all males in a community are allies in aggressive competition with males of neighboring communities (Wrangham 1979; Nishida et al. 1985; Goodall 1986; Manson and Wrangham 1991). Relatedness among males is probably higher within than between communities (Morin et al. 1993; but see Gagneux et al., in press), but males sometimes form within-community alliances with non-relatives (de Waal 1982; Hemelrijk and Ek 1991; Goldberg and Wrangham 1997), and alliances between close maternal relatives, at least, may be uncommon (Goldberg and Wrangham 1997).

Most mating in chimpanzees involves "opportunistic" copulation by multiple males in parties (temporary groups) that include estrous females (Nishida 1979; Tutin 1979; Hasegawa and Hiraiwa-Hasegawa 1983, 1990; Goodall 1986; Morin 1993). Sperm competition is high (Short 1979), but little aggression between adult males occurs (although adults may prevent subadult males from mating).

However, a single male chimpanzee can mate exclusively with a female during some or all of her estrous period by inducing her to go on a consort, during which they avoid other males. Also, a single male sometimes temporarily mates exclusively with an estrous female in a multi-male party; this requires aggression, or threat of aggression, to those males and, often, to the female. Tutin (1979) called this "possessive" mating, but also used this term when males stayed close to females for at least an hour without trying to prevent copulations by other males (cf. Hasegawa and Hiraiwa-Hasegawa 1983, 1990). Aggressive maintenance of exclusivity can be distinguished as "mate guarding".

Mate guarding can increase a male's chances of fertilizing a female (e.g., Idaho ground squirrels: Sherman 1989), but is energetically expensive (e.g., yellow baboons: Alberts et al. 1996) and can impose costs on females (Smuts and Smuts 1993; Stockley 1997). A chimpanzee male's success at mate guarding should depend on his ability to win contests with other males; on the female's willingness to mate exclusively with him, or, conversely, her ability to elude him; on the number of competing males present; and on his level of vigilance and the vigor of his efforts to separate the female from those males. At Gombe (Tutin 1979; Goodall 1986) and Mahale (Nishida 1979, 1983; Hasegawa and Hiraiwa-Hasegawa 1983, 1990; Takasaki 1985), alpha males did all or most mate guarding and mate guarded more successfully than lower-ranking males. Mate guarding was more likely when females were periovulatory than earlier in their estrous periods. At Mahale, the alpha male in a small community with few males mate guarded more often than the alpha in a larger community with more males (Nishida 1979, 1983; Hasegawa and Hiraiwa-Hasegawa 1983, 1990). Conversely, males other than the alpha successfully mate guarded only in the larger community, in which two or more females were in estrous on the same day more often. Most (3/4) cases of guarding by non-alpha males occurred when the alpha was guarding a second female (Hasegawa and Hiraiwa-Hasegawa 1983). This restriction on mate guarding by non-alpha males is consistent with the "priority of access to estrous females" model of mating in cohesive, multi-male primate groups (Altmann 1962).

Two or three males in a large chimpanzee party who jointly prevented copulations between an estrous female and other males, then shared matings with each other, could benefit if solo mate guarding were too difficult and if cooperation gave each a better chance of fertilizing the female than if all males mated opportunistically. Allies may have the potential to form mate-guarding coalitions, especially because males who hold the balance of power in alliances can trade agonistic support for mating tolerance from higher-ranking partners (de Waal 1982; Nishida 1983). However, mate guarding by coalitions seems rare or absent despite the importance of male alliances, perhaps because the number of males in chimpanzee communities rarely exceeds a level at which a single, agonistically powerful male can successfully guard females. For example, Tutin (1979) noted one case of joint "possessiveness" by two males, but did not specify if they aggressively maintained mating exclusivity (but see Goldberg and Wrangham 1997).

Here, I present data from an unusually large chimpanzee community at Ngogo, Kibale National Park, Uganda, with a particularly large number of adult males. Mate guarding was common at Ngogo and involved many males other than the alpha male. Most strikingly, mate guarding coalitions occurred, and high-ranking males switched from single male to coalitionary mate guarding as the number of males in a mating party became too high for them to guard successfully on their own. Coalition members obtained relatively fewer copulations than when they mate guarded successfully on their own, but more than they could have expected in situations where females mated promiscuously.

Methods

Study site and subjects

Kibale National Park is located in western Uganda at 0°13′–0°41′N and 30°19′–30°32′E. The Makerere University Biological Field Station maintains two major Kibale research sites: Kanyawara, in the north, and Ngogo, 10–15 km south of Kanyawara. Mature forest, transitional between lowland and montane evergreen forest, covers most of the study area, in which the Ngogo chimpanzee community uses at least 25 km^2. The rest is a mix of regenerating forest, open-canopy forest with a dense herbaceous understory in valley bottoms, *Acanthus* scrub, and other, minor vegetation types (Struhsaker 1975, 1997; Ghiglieri 1984; Butynski 1990). Mean annual rainfall is about 1,600 mm and falls mostly in September–December and March–May (Butynski 1990; Struhsaker 1997).

Ghiglieri (1984) studied chimpanzees at Ngogo in the late 1970s. Work on chimpanzee socioecology resumed in the late 1980s, as part of a project focused on the habituated chimpanzee community at Kanyawara (Wrangham et al. 1991). Efforts to habituate chimpanzees at Ngogo were continuous from 1991 through late 1993 and then intermittent until mid-1995, and have been intensive since then. I did research on the Ngogo community in June to August 1993, June to December 1995, June to August 1996, and June to August 1997. Data presented here come from 1,500 h of observation in 1995, 1996, and 1997.

The exact size and composition of the Ngogo community is still unclear, but minimum counts of recognized individuals show it to be unusually large, with more adult males than previously identified in any chimpanzee community (Table 1). Why the Ngogo community is so large and so demographically unusual is unknown, although the study area may be ecologically relatively favorable to chimpanzees and at least one other Kibale community (at Kanyanchu) may also have about 20 adult males (R. Wrangham, personal communication). All adult and most adolescent males are individually known. They tolerate observers below them while they are in trees, and, in most cases, within 10 m on the ground. Most females are still poorly habituated and not all have been identified, but estrous females with male parties are relatively easy to follow.

Data collection and definitions

Data are from days when I found at least one fully swollen estrous female. Finding and following individual females for many consecutive days was difficult, so I often did not know exactly when they became fully swollen or when their swellings deflated. Ovulation in chimpanzees is most likely on the 2 days (D0, D-1) that precede the day of detumescence (Graham et al. 1972). I back-dated mate-guarding episodes from the day of detumescence when I knew that date exactly, and could back-date to within 1 day in a few cases when I saw detumescent females within 48 h of having seen them with full swellings.

"Adult male party size" was the number of adult males who associated with a given estrous female; "total male party size" was

Table 1 Chimpanzee community size and composition at Ngogo and other sites

Site	Adult males	Adult females	Adolescent males	Total	References
Kibale					
Kanyawara	8–12	≥14	5	44	Wrangham et al. (1996)
Ngogo	26	≥40	≥15	≥115	
Gombe	13–15	11–15	3–8	50	Goodall (1986)
	5–8	12–19	3–7	3–7	
Mahale, M	8–11	33–39	7–10	86–101	Nishida (1979, 1990); Hasegawa and Hiraiwa-Hasegawa (1983, 1990)
Tai	9	26		79	Boesch (1996)

the number of adults plus adolescents. Male age at fertility is unknown, but common adult male aggression towards adolescents suggests that they are reproductive competitors. I collected data on spatial association, affiliative and agonistic behavior, and sexual behavior for males and, especially, estrous females, using focal sampling. Samples on females were at least 0.75 h when mating was opportunistic and at least 2 h (range 2–8) when males were mate guarding. I also made *ad lib* observations of sexual behavior. I inferred male dominance relationships from the direction of "pant grunt" vocalizations (de Waal 1978).

Mating was "opportunistic" when females copulated with multiple males, without attempts by one or more adults to separate females from all other adult males (adult aggression at adolescents was common in situations where adults tolerated each other's mating). This corresponds to Tutin's (1979) definition (cf. Hasegawa and Hiraiwa-Hasegawa 1983, 1990).

"Mate guarding" refers to situations where one or more males interposed themselves between estrous females and other adult males, displayed at the females and/or at adult males, charged at other adult males who tried to copulate, or otherwise tried to prevent the females from mating with all other adult males.

"Coalitionary mate guarding" occurred when two or more males tolerated each other's mating attempts, but tried to prevent other adult males from copulating with an estrous female by displaying at or chasing them (or the female) or by directing "separating interventions" (de Waal 1982) at them. The guarding males sometimes acted singly, but also jointly directed aggression at the female and at other males. All coalition partners copulated in all cases of mate guarding. The simultaneous and individual charges, chases, and separating interventions that mate-guarding partners made was behavior typical of chimpanzee male coalitions (de Waal 1982; Goodall 1986; Nishida and Hosaka 1996).

Mate guarding was "successful" when only the guarding male(s) copulated; it was "unsuccessful" when other males copulated despite aggression by the guarding male(s). Sometimes mate guarding was unsuccessful because a female evaded a guarding male; sometimes the guarding male moved too far from the female to prevent another male from quickly approaching her (or vice versa) and copulating; sometimes a male could not prevent a higher-ranking male from mating; sometimes a guarding male seemed simply to give up. Ascription of success is somewhat arbitrary, because I sampled only parts of days and may have missed times when initially successful mate guarding later broke down. However, it should give a general index of mating exclusivity.

Statistical tests were two-tailed. I give descriptive statistics for adult male party size, total male party size, and aggression rates for all mate-guarding episodes. However, in statistical tests, I used data only on the two males who mate-guarded most often. These included ANOVAs that examined the relationships of party size to mate-guarding form (single male or coalitionary) and success, and of mate-guarding form and success to rates of male aggression. Each mate-guarding episode by a given male served as a replicate, and all probability levels were Bonferroni-adjusted. Data on the same two males served as the basis for analyses of copulatory success during single-male mate guarding in relation to party size and to aggression rates. Episodes of single-male mate guarding by these males were independent (none occurred in the same party). However, data points for their mate-guarding coalitions were not all independent, because they were each other's most frequent coalition partners (see below).

Results

Availability of estrous females

Estrous females were present on 34% of all observation days (96/282). I saw only one on most of these days, but days with two or more (not always in the same party) were common (Fig. 1), and the total number of "estrous days" was 133.

Male dominance relationships

The Ngogo community had a clear alpha male (MW), and the identities of the top five ranking males and of several bottom-ranking males were clear (Table 2), but many dyads could not be ranked relative to each other. In some, the apparent absence of dominance relationships may have been an artifact of the rarity with which the males were seen together. Male chimpanzees do not always have resolved dominance relationships, however (Bygott 1979; Nishida 1979; Goodall 1986), and this might have been common at Ngogo.

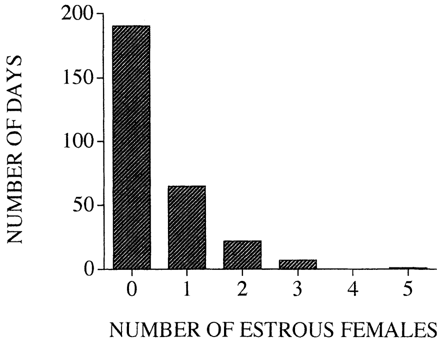


Fig. 1 Number of observation days on which 0–5 estrous females were encountered in chimpanzee parties at Ngogo

Table 2 Dominance relationships among adult males at Ngogo. Entries are the number of times that the row male pant-grunted to the column male. Data are from fieldwork in 1995–1996 only, and do not include one male identified only late in the 1996 field season and a second who was not fully adult until 1997

	MW	BA	CO	EL	RU	HA	LO	MI	PA	DO	HO	BF	PI	JR	AA	MZ	BL	MO	AR	OR	ST	BE	ML	DI
MW																								
BA	3																							
CO	3																							
EL	2	1	1																					
RU	2	1	1																					
HA	5	4	1	1																				
LO	2	2	1	1	1																			
MI	4	4	3	1																				
PA	4	6	2	1		1																		
DO	6	8	3	2	1	1	1																	
HO	7	9	1	1		1	1																	
BF	4	4	2	1	2	2	2																	
PI	3	2	2	5	1	1	1					1												
JR	4	5	1	3		2			1	1														
AA	5	7	1	1	1		1																	
MZ	2	1	1	1		1	1			1														
BL	1	5	2	2	1	1	1	1			1	1												
MO	3	3	2	1	1	2	2	1	1	1				1										
AR	2	1	1	1		1		1																
OR	2	1		1	1	1		1		2				1	1									
ST	2	3	1	2	2	1	1			1		1												
BE	2	2	1	1					1	1	1				1									
ML	3	2	1	1	2	1				1		1		1	1									
DI	5	2	2	2	1	2	2	1	1	1	1		1		1									

Frequency of mating types

Most mating situations were purely opportunistic (74% of estrous days). Mate guarding ($n = 33$ cases) occurred on 34% of days with mating, and on 25% of all estrous days. Two consorts accounted for the other estrous days.

Number and identity of males who mate guarded singly

Seven males (27% of all adult males) mate guarded females. Six did so individually, one (CO), only as a coalition member (Fig. 2). Two top-ranking males (MW and BA) accounted for 16/21 cases of mate guarding by single males. EL and RU, also high ranking, accounted for another 3; middle-ranking males HO and MI accounted for 1 case each (Fig. 2).

Number and identity of coalitions

Six different coalitions accounted for 12 episodes of coalitionary mate guarding (Fig. 2). Coalitions involved the five highest-ranking males, in two duos and three trios. Males MW (alpha) and BA each participated in four different coalitions (jointly, in three of these), and each was involved in 10 episodes (9 jointly; Fig. 2).

Mate guarding and female cycle state

Mate guarding was apparently focused on periovulatory females, and occurred during 23 individual female cycles. Most observed cases lasted only 1 day, but males guarded females for as long as 4 consecutive days. No information on cycle stage was available for 7 cycles (except that the females were fully swollen), because females were seen for 1 day only. The day of detumescence was unknown for another 6 cycles, although all of these females had been fully swollen for at least 4 days. The day of detumescence was known to within 1 day in 3 cases and exactly in the remaining 7. Males definitely mate guarded females on D0 in 3 of these cases; in 1 of

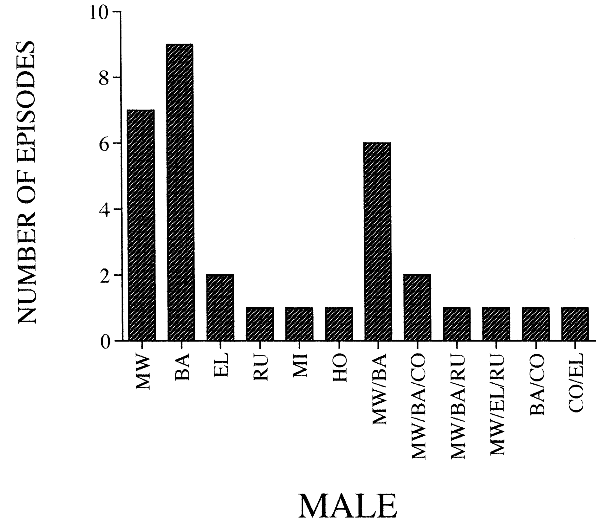


Fig. 2 Identity of males who mate guarded estrous females at Ngogo, and number of times each mate guarded. *Each two-letter acronym* refers to an individual, *multiple, adjacent acronyms* represent coalitions

these, the female had also been guarded on days D-1, D-2, and D-3, and a second of these females had also been guarded on D-1. They definitely guarded the other 7 females on D-1, and may also have guarded 4 of these females on D0. These 7 included 1 female guarded by coalitions on D-3, D-2, and D-1, but not D0.

Mate-guarding success

Mate guarding was successful in 67% of cases (22/33) by the criterion above. Overall success was not obviously different for coalitions (10/13) and for single males (12/20). Male MW's success on his own (5/7 cases) did not differ clearly from that in coalitions (7/10 cases; *G*-test, $G = 0.02$, $df = 1$, n.s.). Male BA was unsuccessful on his own more often than MW, but his success rate also did not differ significantly between mate-guarding forms (single male: 4/9 successful; coalitions: 8/10 successful; $G = 2.64$, $df = 1$, n.s.).

Four of five cases of mate guarding by single males other than MW and BA occurred when neither of those two males was present, and when the guarding male outranked all males present; mate guarding was successful in these cases. The fifth case, in a large party that included MW and BA, was unsuccessful.

One mate-guarding bout each by MW and BA ended when they joined many other males to hunt red colobus monkeys; whether they abandoned the females, or the females eluded them, was unclear, but the females subsequently copulated with several other males. A second of MW's bouts ended when he stopped following the female after several hours. Twice females eluded BA, once MW separated him from the female, and once, with 17 other adult males in the vicinity, he simply stopped trying. MW was present, but did not try to separate BA from the female, in one case when BA mate guarded successfully. In all seven cases of unsuccessful mate guarding by MW or BA, they still copulated more often than all other males.

Mate guarding and party size

Party size strongly influenced mate-guarding form and success. Parties in which mate guarding occurred were not larger than those in which mating was strictly opportunistic. However, most attempts by single males to guard females in large parties were unsuccessful, whereas coalitions formed in large parties and could successfully guard females even when 20 adult males were present.

Both mean adult male party size and mean total male party size were similar on estrous days with and without mate guarding (Fig. 3). MW experienced similar adult male party sizes when he mate guarded ($n = 17$, mean = 13.7, SD = 5.1) and when mating was opportunistic ($n = 47$, mean = 11.8, SD = 4.6; unpaired *t*-test, $t = -1.40$, n.s.). BA also associated with as many adult males when he mate guarded ($n = 19$; mean = 14.6, SD = 4.6) as when mating was opportunistic ($n = 46$, mean = 12.4, SD = 4.67, $t = -1.69$, n.s.). Data on total male party size gave similar results.

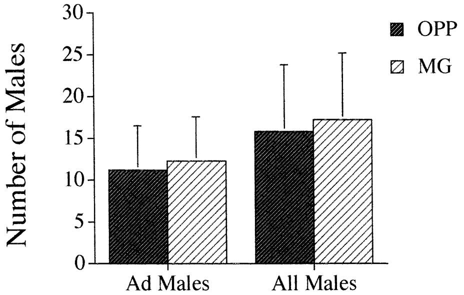


Fig. 3 Mean adult male party size (*Ad Males*) and mean total male party size (*All Males*) on days with opportunistic mating (*OPP*, $n = 64$) and days with mate guarding (*MG*, $n = 33$) (*bars* show 1 SD)

However, party size varied among the four mate-guarding categories (single male vs coalition, successful vs unsuccessful; Fig. 4). This variation was significant for both MW and BA (ANOVAs, $P < 0.001$ and $P < 0.005$, respectively; Table 3). Their success at solo mate guarding decreased as adult male party size increased; when they formed coalitions, these were in large parties where prospects for successful solo male mate guarding were poor. Bonferroni post hoc comparisons showed that parties in which MW mate guarded successfully on his own were smaller than those in which he did so unsuccessfully ($P = 0.01$) and in which he formed coalitions, either successfully or unsuccessfully (both $P < 0.05$; Table 3). Parties in which BA successfully mate guarded alone were also smaller than those in which he was unsuccessful alone ($P < 0.01$) and those in which he formed successful ($P < 0.01$) or unsuccessful ($P < 0.05$) coalitions (Table 3). For both males, mean party sizes were equal for unsuccessful single-male mate guarding, successful coalitions, and unsuccessful

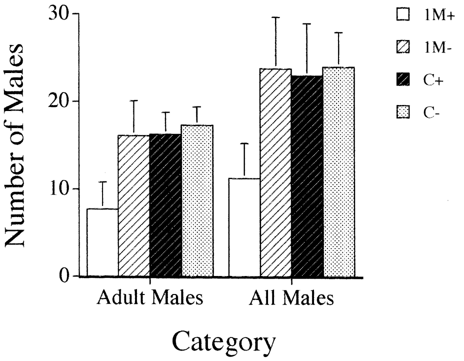


Fig. 4 Mean adult male party size and mean total male party size for days with different forms of mate guarding (*1M+* successful mate guarding by single males, *1M–* unsuccessful mate guarding by single males, *C+* successful coalitionary mate guarding, *C–* unsuccessful coalitionary mate guarding, *bars* show 1 SD)

Table 3 Adult male party sizes for different categories of mate guarding by males MW and BA. Entries are mean (SD) (*1M+* successful one-male mate guarding, *1M–* unsuccessful one-male mate guarding, *C+* successful coalitionary mate guarding, *C–* unsuccessful coalitionary mate guarding)

Male	Form				*F*	*df*	*P*
	1M+	1M–	C+	C–			
MW	7.40 (1.29) *n* = 5	16.50 (1.94) *n* = 2	16.43 (1.04) *n* = 7	16.67 (1.59) *n* = 3	12.92	3,13	< 0.001
BA	8.00 (1.60) *n* = 4	16.80 (1.43) *n* = 5	16.25 (1.13) *n* = 8	17.50 (2.26) *n* = 2	7.73	3,15	< 0.005

coalitions (although sample sizes for unsuccessful coalitions were very small; Table 3). ANOVAS of total male party size gave identical results for both MW and BA.

Mate-guarding success and aggression rates

A male trying to guard a female in a large party has a logistical problem. He must chase or herd the female, and charge or chase males to separate them from her, at high rates; this demands high vigilance and considerable energy expenditure. Meanwhile, the female needs only about 10 s to copulate with another male (Tutin 1979), and can easily do so when the male attempting to guard her is distracted or too far away (because he is chasing a male, for example). MW and BA solved this problem by forming coalitions and thereby decreasing their per capita need for aggression.

The absolute rate of aggression by mate-guarding males varied considerably across mate-guarding situations (Fig. 5). This variation was significant for MW and BA (ANOVAs, $P < 0.025$ in both cases; Table 4). Both were more aggressive when unsuccessfully engaging in solo mate guarding than when doing so successfully (Bonferroni post hoc comparisons: MW: $P < 0.01$; BA: $P < 0.05$; Table 4); unsuccessful mate guarding also happened in larger parties (see above). Conversely, per capita aggression rates in successful coalitions were the same as when MW or BA mate guarded successfully on his own (Table 4; Bonferroni post hoc comparisons, n.s.), despite the larger sizes of parties in which coalitions formed. Per capita rates in successful coalitions were significantly lower than rates for unsuccessful single-male mate guarding (MW: $P < 0.05$; BA: $P < 0.05$; Table 4). Aggression rates for unsuccessful coalitions did not differ from those for any other category (Table 4).

Data partitioned by age-sex class of targets showed that these differences occurred mostly because aggression at females varied significantly across categories (MW: $F = 4.77$, $df = 3,13$, $P < 0.05$; BA: $F = 4.64$, $df = 3,15$, $P < 0.05$). MW and BA were more aggressive to females during unsuccessful single-male mate guarding than while guarding successfully, either alone or in coalitions ($P < 0.05$ in all cases).

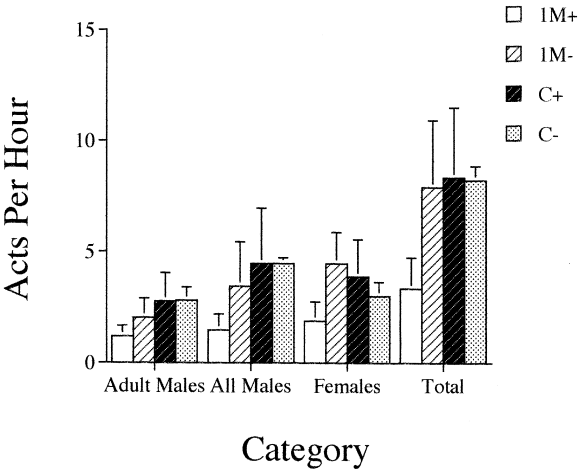


Fig. 5 Mean number of aggressive acts per hour that males directed at other adult males (*Adult Males*), at adult plus adolescent males (*All Males*), at estrous females (*Females*), and at males and estrous females combined (*Total*) while mate guarding (*1M+* successful single-male mate guarding, *1M–* unsuccessful single-male mate guarding, *C+* when in a successful coalition, *C–* when in an unsuccessful coalition, *bars* show 1 SD)

Table 4 Number of aggressive acts per hour that males MW and BA directed at others while mate guarding. Entries are the means (SD) (*1M+* successful one-male mate guarding, *1M–* unsuccessful one-male mate guarding, *C+* successful coalitionary mate guarding, *C–* unsuccessful coalitionary mate guarding)

Male	Form				*F*	*df*	*P*
	1M+	1M–	C+	C–			
MW	2.98 (0.76) *n* = 5	9.19 (1.20) *n* = 2	4.72 (0.64) *n* = 7	5.31 (0.98) *n* = 3	6.53	3,13	< 0.025
BA	3.86 (1.04) *n* = 4	8.79 (0.93) *n* = 5	4.57 (0.74) *n* = 8	5.80 (1.47) *n* = 2	5.52	3,15	< 0.025

Mating success within coalitions

Coalition partners shared copulations fairly equitably, although MW tended to copulate more than his partners in trios (Fig. 6). MW and BA each got a mean of 50% of copulations in their four, two-male coalitions and gained almost equal numbers of copulations overall (22 and 21, respectively). On average, MW copulated more (mean = 43%) than BA (mean = 31%) and CO (mean = 26%) in their three trios, and he copulated more than RU and EL in a fourth. Overall, though, differences were small, and BA copulated more than MW in one trio.

The data do not cover full days throughout periovulatory periods, and thus cannot address issues related to possible first- or last-male advantages in sperm competition. However, all coalition members copulated multiple times in all but one case (male RU got only one copulation in one trio).

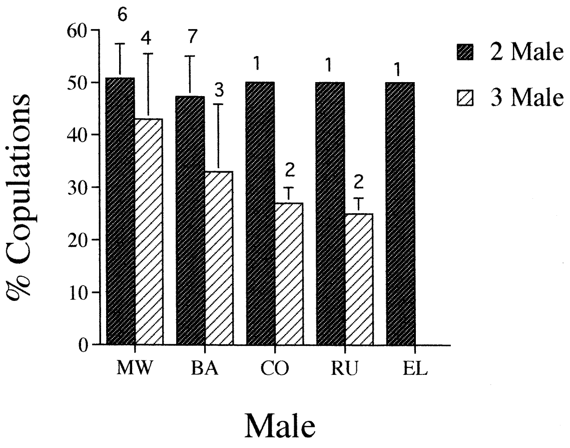


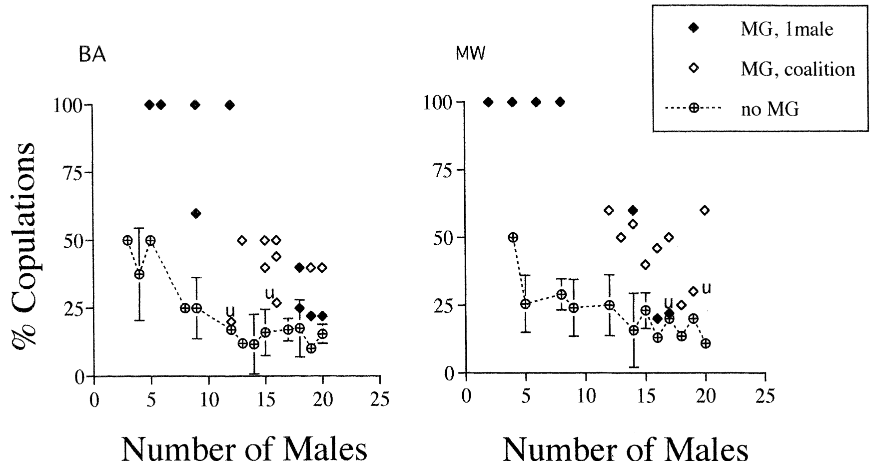
Fig. 6 Percentage of copulations that five males obtained as members of mate-guarding coalitions (*2 Male* two-male coalition, *3 Male* three-male coalition, *column height* mean; *bar height* 1 SD, *number above column* number of cases)

When should males form coalitions?

Decisions to accept and tolerate lower-ranking coalition partners, or to join a coalition, should depend on party size variation and on expected copulatory success from solo mate guarding and from opportunistic mating at any given party size. The importance of party size follows from the fact that, while the alpha male can aggressively prevent all others from mate guarding, even adolescents can prevent the alpha from mate guarding successfully in large parties by sneaking copulations while he is distracted or when he loses track of the female. Data on MW and BA show that their copulatory success in coalitions was higher than they could have expected from alternative tactics.

MW and BA always had mating advantages, assuming that sperm competition in chimpanzees is a lottery. They copulated disproportionately often when mating was opportunistic (Fig. 7). In parties with 15 adult males (and varying numbers of adolescents), for example, MW averaged 23% of all copulations and BA 16% (Fig. 7; MW and BA were not simultaneously present in all such parties). When unsuccessful at solo mate guarding, they still usually got a higher proportion of copulations for a given adult male party size than they could have expected from opportunistic mating (Fig. 7), although only slightly so in some large parties. However, forming mate guarding coalitions in parties too large for successful solo mate guarding usually gave them an even higher proportion of copulations (Fig. 7). The largest party in which MW mate guarded successfully on his own had 14 adult males. He formed one coalition in a party of 14 adult males; all others were in parties with more than 14. At all party sizes, his share of copulations was higher when he was in a coalition (even an unsuccessful one) than when mating was opportunistic. He obtained a greater share of copulations as a coalition member than by trying to mate guard alone in two of three comparisons (adult male party sizes of 16 and 17 in Fig. 7), but did slightly better on his own in the third case (n = 15 adult males; Fig. 7). Data on BA were

Fig. 7 Percentage of copulations by males BA and MW in parties with different numbers of adult males (*Number of Males*) (*no MG* parties in which mating was opportunistic; values are the mean ± 1 SD for party sizes that occurred more than once; *MG, 1male* single-male mate guarding; *MG, coalition* mate-guarding coalitions)



similar (Fig. 7). On his own, he mate guarded successfully with a maximum of 12 adult males present. All parties in which he formed coalitions had at least 13 adult males. For given adult male party sizes, he also usually gained a much higher share of copulations as a coalition member than when mating opportunistically, and more than when mate guarding unsuccessfully on his own (Fig. 7). Data on total male party sizes gave the same results.

Coalition size varied, however, and MW and BA only got about 25% of copulations when mate guarding individually in especially large parties (Fig. 7). This suggests a coalition formation rule: form a two-male coalition when the expected proportion of total copulations from attempted one-male mate guarding drops below 50%; form a three-male coalition when it drops below 33.3%.

Some estimate of expected success is required to see how well behavior matched this rule. It was apparently 100% for MW and BA up to a threshold of 12–14 adult males, then declined steeply with party size (Fig. 7; the value of 60% at $n = 9$ males for BA is the case in which MW interrupted him). Still, adult male party size explained a significant amount of the variation in copulatory success in a linear regression (pooled data on all single-male mate-guarding attempts: $n = 16$, $r^2 = 0.71$, $F = 37.29$, $P < 0.001$). The regression equation was: %copulations = $-5.57(n$ males$) + 133.82$, which gives an expected value of 50% of copulations at 15.04 adult males and of 33.3% at 18.05 adult males. (Analyses of data for MW or BA alone give nearly identical results.) A similar analysis for total male party size (Fig. 8) gives expected values of 50% at 20.97 males and of 33.3% at 25.26 males.

The observed distribution of party sizes fits these expectations reasonably well (Fig. 9). Six of eight two-male coalitions formed in parties with 15 or more adult males and with 21 or more males total. Three of four trios formed in parties with at least 18 adult males and at least 25 males total.

Copulatory success was also inversely related to aggression rates for single-male mate guarding ($n = 16$, $r^2 = 0.63$, $P < 0.01$). Steep increases in the energy cost of mate guarding and the risk of injury during arboreal chases may prompt coalition formation in some relatively small parties.

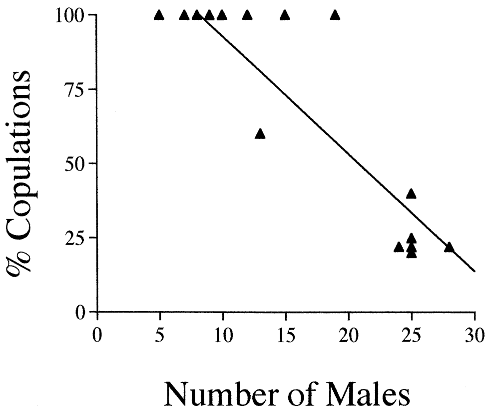


Fig. 8 Regression of the percentage of copulations that males MW and BA obtained on the number of adult and adolescent males per party for days on which MW or BA tried to mate guard on his own. The regression equation is: %copulations = 3.90 (number of males)– 131.80 ($n = 16$, $r^2 = 0.77$)

Discussion

Mate guarding at Ngogo

Mate guarding, focused on periovulatory females, was common at Ngogo. The alpha male and another high-ranking male mate guarded females most often. Other high-ranking or even mid-ranking males mate guarded successfully when they outranked all other males present. Single males could successfully guard females in parties with as many as 12–14 adult males and 20 sexually mature males. However, many mating parties at Ngogo had more males than this; when they did, even top-ranking males could not mate exclusively. The high rates of aggression by single males trying to mate guard in large parties, and the fact that females sometimes evaded them, indicate that failure was due to excessive

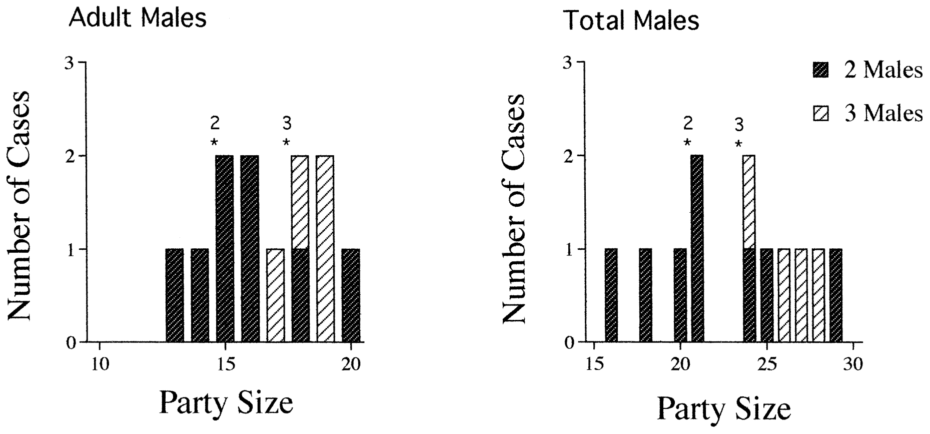


Fig. 9 Number of adult males (*Adult Males*) and of adult plus adolescent males (*Total Males*) in parties in which males MW and BA formed mate-guarding coalitions (*2 Males* two-male coalitions, *3 Males* three-male coalitions, *2** the party size at which the expected percentage of copulations for a male trying to mate guard by himself would drop below 50%, *3** the party size at which it would drop below 33%)

demands for vigilance and for chases and separating interventions. High-ranking males who formed coalitions in large parties could thereby maintain shared exclusive access to estrous females. Coalition formation reduced per capita costs of mate guarding: coalition partners gave aggression to others at rates that were lower than when they mate guarded unsuccessfully on their own in equally large parties, and that were similar to when they successfully mate guarded on their own in smaller parties.

The two males who most often tried to mate guard females on their own thereby gained disproportionate shares of copulations, independently of party size and even when they could not maintain mating exclusivity. Solo mate guarding always gave them a larger share than they received from opportunistic mating. However, coalition formation in large parties gave them a greater share of copulations than they could have expected from solo mate guarding in those parties (which would have been unsuccessful). Also, they tended to switch from solo mate guarding to two-male coalitions, and from two-male to three-male coalitions, when their expected share of copulations from attempts at solo mate guarding dropped below 50% and 33.3%, respectively. Copulation frequency is not always a good proxy for reproductive success in male chimpanzees (Gagneaux et al., in press). In so far as it is (particularly during periovulatory periods), however, and in so far as sperm competition is a lottery, both solo and coalitionary mate guarding of periovulatory females should increase the number of fertilizations that males can expect.

Contrasts with other chimpanzee communities

Goldberg and Wrangham (1997) state that males in another Kibale community sometimes cooperatively guard mates, but mate-guarding coalitions have not otherwise been described previously in chimpanzees. Besides showing new variation in male mating strategies, the Ngogo data are at odds with Hasegawa and Hiraiwa-Hasegawa's (1983, p. 83) argument that "the mating system of a given unit-group [community] will be more promiscuous when both the size of the group and the number of receptive females are large." Comparison of Ngogo data with those from other sites is complicated by the fact that previous reports (Tutin 1979; Hasegawa and Hiraiwa-Hasegawa 1983, 1990; Nishida 1983) give percentages of copulations during opportunistic and possessive mating situations, not percentages of estrous days on which those situations occurred. In the Mahale M group, with 12 adult males, 73% of copulations were opportunistic (Hasegawa and Hiraiwa-Hasegawa 1983). The corresponding figure for Ngogo was 60%, which suggests that mate guarding happened more often there despite the much larger number of males. Less mate guarding would probably have occurred had it been restricted to individual efforts, just as less occurred in the large M group than the small K group at Mahale (Hasegawa and Hiraiwa-Hasegawa 1983). Variation in community size and composition presumably helps to explain the absence of coalitional mate guarding in other communities. Single agonistically powerful males in smaller communities may generally be able to solve the logistical problems that defeat their Ngogo counterparts, who face many more competitors and are often in mating parties with more males than the total number present in other communities. To gain the maximum possible share of copulations in large parties, the alpha male at Ngogo and, to lesser extents, other top-ranking males may have had to share matings in exchange for agonistic support; alpha males in smaller communities may stand to gain less by sharing matings.

Relatedness, alliances, and cooperative mate guarding

This still begs the question as to why male chimpanzees cooperatively guard females when such behavior is otherwise rare in birds and mammals. Several factors are relevant here. First, given male philopatry, kin selection could promote cooperative mate guarding in chimpanzees, as may be the case for cooperative mate guarding by father-son pairs in acorn woodpeckers (Koenig and Stacey 1990). Relatedness among the males at Ngogo is not yet known. Some who formed mate-guarding coalitions may have been brothers, but maternal brothers, at least, are probably infrequent allies (Goldberg and Wrangham 1997), and almost certainly some coalition partners at Ngogo were not close relatives. Periods of instability and of partner switching are typical for chimpanzee male alliances, and power disparities can be more important than relatedness for potential allies (de Waal 1982; Goodall 1986; Hemelrijk and Ek 1991; Nishida and Hosaka 1996). Males who mate guarded cooperatively also formed coalitions in other contexts and showed reciprocity in agonistic support (D.P. Watts, unpublished data) in 1995 and thus could be considered allies. In 1996 and 1997, however, MW and CO no longer formed coalitions in any context, nor were coalitions between MW and EL seen in 1997 (although CO and EL remained allies and also had alliances with a third male who had risen in rank). Also, RU had dropped considerably in rank by 1997 and no longer formed coalitions with his former partners.

The important influence of such alliances on male agonistic relationships is a second factor. The dominance ranks of male chimpanzees can depend on the number and identity of their allies, rather than on their intrinsic power. In contrast, male alliances in savanna baboons do not influence dyadic dominance relationships, which helps to explain chimpanzee-baboon differences in which males form coalitions and in the mating behavior of successful coalition partners. Collaboration at Ngogo involved high-ranking males. Baboon coalitions typically involve middle- to low-ranking males, only one of whom consorts with the female if they separate her from the target male (Smuts 1985; Noë

1990, 1992; Noë and Sluijter 1995). Baboon allies directly challenge the consorting male and, to be successful, need a combined fighting ability that surpasses his (Noë 1992). In addition, they try to establish their own prolonged consorts; allies offer no benefits in terms of improved access to females in dyadic competition to offset the costs of sharing consorts with them. Chimpanzee males can sneak copulations without directly challenging a guarding male, and disruption of mate guarding typically leads to opportunistic mating, not replacement of one guarding male by another. The challenge to chimpanzee males is to prevent sneak copulations and to limit female choice (Smuts and Smuts 1993), and allies who help each other to do this in large parties can also improve each other's success in dyadic competition. Pervasive influence of alliances on male agonistic success is a point of similarity between chimpanzees and bottle-nosed dolphins, in which all mating is by male alliances that cooperatively guard females and in which allies tolerate each other's mating (Conner et al. 1992). However, such influence, especially in combination with male philopatry and cooperative defense of access to female groups, is rare. Similarly, critical reliance on male care for infants in cooperatively breeding species can induce dominant males to tolerate mating by subordinates (e.g., African wild dogs: Creel et al. 1997; dwarf mongooses: Creel and Waser 1994; saddle-back tamarins: Goldizen 1987).

The tactical complexity and flexibility, and the opportunism, of male chimpanzees (de Waal 1978, 1982; Nishida 1983; Goodall 1986; Hemelrijk and Ek 1991) epitomize the complexity that distinguishes many higher primates from most other animals with regard to alliance formation, maintenance, and use (Harcourt 1989). Bottle-nosed dolphin males at Shark Bay may be similar (Conner et al. 1992). Perhaps the cognitive abilities that underlie this complexity are absent in most other mammals, although invoking unspecified cognitive constraints is unsatisfying as a general explanation for the rarity of cooperative mate guarding.

Cooperative mate guarding as mutualism

The most likely alternative to kin selection as an explanation for chimpanzee mate guarding coalitions is mutualism. Coalitionary mate guarding between nonrelatives could be a stable, conditional tactic, like the tolerance that pied wagtails show for satellites in the presence of many competitors (Davies and Houston 1981). Relationships between male chimpanzees involve power asymmetries. At Ngogo, MW could interrupt mate guarding by subordinates and presumably could have "defected" from a coalition by refusing to pay the costs of aggressive guarding or by preventing a partner from mating after collaborating to keep a female away from rivals. BA could also have defected by appropriating the female from a subordinate partner. Conversely, subordinate members of chimpanzee coalitions presumably could not have defected by preventing their dominant partners from mating. Thus males deciding whether to participate in a coalition did not truly face a Prisoner's Dilemma, in which both partners have the option to defect unilaterally (Noë 1992). Also, the payoff matrix for chimpanzee mate-guarding coalitions probably did not satisfy conditions for a Prisoner's Dilemma, in which R (the reward for mutual cooperation) is less than T (the temptation to defect). As for male baboons (Noë 1992), single males at Ngogo had poor chances to reach the goal of pairs or trios, and relative payoffs probably met the conditions for mutualism ($R > T$; Dugatkin 1997; Mesterson-Gibbons and Dugatkin 1997). Partners shared an "adverse environment" (Mesterson-Gibbons and Dugatkin 1997) in which they had too many competitors, and logistical difficulties were too great, for any single male to maintain exclusive mating access to a female. Refusal to help guard a female would have been costly if guarding then broke down and mating became opportunistic. Similarly, interfering in a partner's copulation attempts could have prompted him to defect: he could no longer have expected to do better than by opportunistic mating, and should have switched to trying to sneak copulations or to separate the female from the guarding male (thus increasing pressure on him) instead of paying the costs of continued guarding. MW's disruption of one of BA's solo mate-guarding attempts was intriguing in this regard: BA subsequently made no effort to prevent other males from mating, and mating was opportunistic from the time of MW's disruption on. Given that cooperation led to higher percentages of all copulations than partners could have obtained from any other mating tactic in a multi-male party, they had no incentive to cheat (cf. Mesterson-Gibbons and Dugatkin 1997).

Acknowledgements I thank Gil Isibirye-Basuta and John Kasenene, Co-Directors of the Makerere University Biological Field Station, and the Makerere University Research Committee for their permission to work at Ngogo. I also thank Gil and John for their dedication to Kibale and MUBFS, and Gil for his fundamental contribution to long-term chimpanzee research in Kibale. The L.S.B. Leakey Foundation supported my research at Ngogo. Adolph Magoba, Godfrey Mbabazi, Lawrence Ndegezi, Gabriel Mutabazi, and Alfred Tumusiime provided field assistance and, with Lisa Hamburger and Martin Muller, greatly helped with habituation. Richard Wrangham provided a basis for long-term comparative research on chimpanzee behavioral ecology in Kibale, helped to establish and support the infrastructure for such research at Ngogo, and encouraged me to work there. I thank Colin and Lauren Chapman for similar reasons, and thank them, Richard Malenky, and Nancy Thompson-Handler for logistical help. Tom Struhsaker also inspired me to work at Ngogo and was an endless fount of information about the forest there. John Mitani taught me much about chimping and was a constant source of intellectual stimulation and a great field companion. I benefited from discussions with Beth Fox, John Mitani, Michael Pereira, and Richard Wrangham in developing ideas presented here. Peter Kappeler, Toshisada Nishida, Carel van Schaik, and one anonymous referee made helpful critical comments on earlier versions of the manuscript.

References

Alberts SC, Altmann J, Wilson ML (1996) Mate guarding constrains foraging activity of male baboons. Anim Behav 51:1269–1277

Altmann SA (1962) A field study of the sociobiology of the rhesus monkey, *Macaca mulatta*. Ann NY Acad Sci 102:338–435

Andersson M (1994) Sexual selection. Princeton University Press, Princeton, NJ

Baker AJ, Dietz JM, Kleiman DG (1993) Behavioural evidence for monopolization of paternity in multi-male groups of golden lion tamarins. Anim Behav 46:1091–1103

Bertram BCR (1976) Kin selection in lions and evolution. In: Bateson PPG, Hinde RA (eds) Growing points in ethology. Cambridge University Press, Cambridge, UK, pp 281–301

Boesch C (1996) Social grouping in Tai Forest chimpanzees. In: McGrew WC, Marchant LA, Nishida T (eds) Great ape societies. Cambridge University Press, Cambridge, UK, pp 101–113

Butynski TM (1990) Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high- and low-density subpopulations. Ecol Monogr 60:1–26

Bygott JD (1979) Agonistic behavior, dominance, and social structure in wild chimpanzees of the Gombe National Park. In: Hamburg DR, McKown ER (eds) The great apes. Benjamin-Cummings, Menlo Park, Calif, pp 73–121

Caro TM (1994) Cheetahs of the Serengeti plains. University of Chicago Press, Chicago

Chapman CA, White FJ, Wrangham RW (1994) Party size in chimpanzees and bonobos. In: Wrangham RW, McGrew WC, Waal FBM de, Heltne PG (eds) Chimpanzee cultures. Harvard University Press, Cambridge, Mass, pp 41–58

Conner RC, Smolker RA, Richards AF (1992) Dolphin alliances and coalitions. In: Harcourt AH, Waal FBM de (eds) Coalitions and alliances in humans and other animals. Oxford University Press, Oxford, pp 415–444

Craig JL, Jamieson IG (1990) Pukeko: different approaches and some different answers. In: Stacey PB, Koenig WD (eds) Cooperative breeding in birds. Cambridge University Press, Cambridge, UK, pp 385–412

Creel SR, Waser PM (1994) Inclusive fitness and reproductive strategies of dwarf mongooses. Behav Ecol 5:339–348

Creel SR, Creel NM, Mills MGL, Monfort SL (1997) Rank and reproduction in cooperatively breeding African wild dogs: behavioral and endocrine correlates. Behav Ecol 8:298–306

Davies NB (1992) Dunnock behavior and social evolution. Oxford University Press, Oxford

Davies NB, Houston AI (1981) Owners and satellites: the economics of territory defense in the pied wagtail *Moticilla alba*. J Anim Ecol 50:157–180

Davies NB, Hartley IR, Hatchwell BJ, Desrochers A, Skeer J, Nebel D (1995) The polygynadrous mating system of the alpine accentor, *Prunella collaris*. I. Ecological causes and reproductive conflicts. Anim Behav 49:769–788

Dugatkin LE (1997) Cooperation among animals. Oxford University Press, Oxford

Dugatkin LE, Mesterson-Gibbons M, Houston AI (1992) Beyond the prisoner's dilemma: towards models to discriminate among the mechanisms of cooperation in nature. Trends Ecol Evol 7:202–205

Gagneaux P, Boesch C, Woodruff DS (in press) Female reproductive strategies, paternity, and community structure in wild chimpanzees. Anim Behav

Ghiglieri M (1984) The chimpanzees of the Kibale Forest. Columbia University Press, New York

Goldberg TL, Wrangham RW (1997) Genetic correlates of social behavior in wild chimpanzees: evidence from mitochondrial DNA. Anim Behav 54:559–570

Goldizen AW (1987) Facultative polyandry and the role of infant carrying in wild saddle-back tamarins (*Saguinus fuscicollis*). Behav Ecol Sociobiol 20:99–109

Goodall J (1986) The chimpanzees of Gombe. Harvard University Press, Cambridge, Mass

Graham CE, Collins DC, Robinson M, Preedy JRK (1972) Urinary levels of estrogens and pregnanediol and plasma levels of progesterone during the menstrual cycle of the chimpanzee: relationship to the sexual swelling. Endocrinology 91:13–24

Greenwood PJ (1980) Mating systems, philopatry, and dispersal in birds and mammals. Anim Behav 28:1140–1162

Grinnell J, Packer C, Pusey AE (1995) Cooperation in male lions: kin selection, reciprocity, or mutualism? Anim Behav 49:95–105

Hamilton WD (1964) The genetical evolution of social behavior. J Theor Biol 7:1–52

Harcourt AH (1989) Social influences on competitive ability: alliances and their consequences. In: Standen V, Foley RA (eds) Comparative socioecology. Blackwell, London, pp 223–242

Hartley IR, Davies NB, Hatchwell BJ, Desrochers A, Nebel D, Burke T (1995) The polygynadrous mating system of the alpine accentor, *Prunella collaris*. II. Multiple paternity and paternal effort. Anim Behav 49:789–803

Hasegawa T, Hiraiwa-Hasegawa M (1983) Opportunistic and restrictive mating among wild chimpanzees in the Mahale Mountains, Tanzania. J Ethol 1:75–85

Hasegawa T, Hiraiwa-Hasegawa M (1990) Sperm competition and mating behavior. In: Nishida T (ed) The chimpanzees of the Mahale Mountains. University of Tokyo Press, Tokyo, pp 115–132

Hemelrijk CK, Ek A (1991) Reciprocity and interchange of grooming and "support" in captive chimpanzees. Anim Behav 41:923–935

Keane B, Waser PM, Creel SR, Creel NM, Elliot LF, Minchella DJ (1994) Subordinate reproduction in dwarf mongooses. Anim Behav 47:65–75

Koenig WD, Stacey PB (1990) Acorn woodpeckers: group living and food storage under contrasting ecological conditions. In: Stacey PB, Koenig WD (eds) Cooperative breeding in birds. Cambridge University Press, Cambridge, UK, pp 413–454

Manson JH, Wrangham RW (1991) Intergroup aggression in humans and chimpanzees. Curr Anthropol 32:369–390

Mesterton-Gibbons M, Dugatkin LA (1997) Cooperation and the prisoner's dilemma: towards testable models of mutualism versus reciprocity. Anim Behav 54:551–557

Morin P (1993) Reproductive strategies in chimpanzees. Yearbk Phys Anthropol 36:179–212

Morin PA, Moore JJ, Chakraborty, Jin L, Goodall J, Woodruff DS (1993) Kin selection, social structure, gene flow, and the evolution of chimpanzees. Science 265:1193–1201

Mumme RL, Koenig WD, Pitelka FA (1983) Mate guarding in the acorn woodpecker: within group reproductive competition in a cooperative breeder. Anim Behav 31:1094–1106

Nakamura M (1998a) Multiple mating and cooperative breeding in polygynandrous alpine accentors. I. Competition among females. Anim Behav 55:259–275

Nakamura M (1998b) Multiple mating and cooperative breeding in polygynandrous alpine accentors. II. Male mating tactics. Anim Behav 55:277–289

Nishida T (1979) The social structure of chimpanzees of the Mahale Mountains. In: Hamburg DR, McKown ER (eds) The great apes. Benjamin-Cummings, Menlo Park, Calif, pp 73–121

Nishida T (1983) Alpha status and agonistic alliance in wild chimpanzees (*Pan troglodytes schweinfurthii*). Primates 24:318–336

Nishida T, Hiraiwa-Hasegawa M (1987) Chimpanzees and bonobos: cooperative relationships among males. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 165–177

Nishida T, Hosaka K (1996) Coalition strategies among adult male chimpanzees of the Mahale Mountains, Tanzania. In: McGrew WC, Marchant LA, Nishida T (eds) Great ape societies. Cambridge University Press, Cambridge, UK, pp 114–134

Nishida T, Hiraiwa-Hasegawa M, Hasegawa T, Takahata Y (1985) Group extinction and female transfer in wild chimpanzees in the

Mahale Mountains National Park, Tanzania. Z Tierpsychol 67:284–301

Noë RA (1990) A veto game played by baboons: a challenge to the use of the prisoner's dilemma as a paradigm for reciprocity and cooperation. Anim Behav 39:78–90

Noë RA (1992) Alliance formation among male baboons: shopping for profitable partners. In: Harcourt AH, Waal FBM de (eds) Coalitions and alliances in humans and other animals. Oxford University Press, Oxford, pp 285–321

Noë RA, Sluijter AA (1995) Which baboon males form coalitions? Int J Primatol 16:77–106

Packer C (1977) Reciprocal altruism in olive baboons. Nature 265:441–443

Packer C, Pusey AE (1982) Cooperation and competition within coalitions of male lions: kin selection or game theory? Nature 296:740–742

Packer C, Herbst L, Pusey AE, Bygott JD, Hanby JP, Cairns SJ, Borgerhoff-Mulder M (1988) Reproductive success in lions. In: Clutton-Brock TH (ed) Reproductive success. University of Chicago Press, Chicago, pp 363–383

Rowley I, Russell E (1990) Splendid fairy-wrens: demonstrating the importance of longevity. In: Stacey PB, Koenig WD (eds) Cooperative breeding in birds. Cambridge University Press, Cambridge, UK, pp 3–30

Schaik CP van (1996) Social evolution in primates: the role of ecological factors and male behaviour. Proc Br Acad 88:9–31

Schaller G (1972) The Serengeti lion. University of Chicago Press, Chicago

Sherman PW (1989) Mate guarding as paternity insurance in Idaho ground squirrels. Nature 338:418–420

Short RV (1979) Sexual selection and its component parts, somatic and genital selection, as illustrated by man and the great apes. Adv Stud Behav 9:131–158

Smuts BB (1985) Sex and friendship in baboons. Aldine, Chicago

Smuts BB, Smuts RW (1993). Male aggression and sexual coercion in nonhuman primates and other mammals: evidence and theoretical implications. Adv Stud Behav 22:1–63

Stockley P (1997) Sexual conflict resulting from adaptations to sperm competition. Trends Ecol Evol 12:154–159

Strier KB (1994) Brotherhoods among atelins: kinship, affiliation, and competition. Behaviour 130:151–167

Struhsaker TT (1975) The red colobus monkey. University of Chicago Press, Chicago

Struhsaker TT (1997) Ecology of an African rain forest: logging in Kibale and the conflict between conservation and exploitation. University Press of Florida, Gainsville

Takasaki H (1985) Female life history and mating patterns among the M group chimpanzees of the Mahale National Park, Tanzania. Primates 26:121–129

Trivers RL (1971) The evolution of reciprocal altruism. Q Rev Biol 46:35–57

Tutin CEG (1979) Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). Behav Ecol Sociobiol 6:29–38

Waal FBM de (1978) Exploitative and familiarity dependent support strategies in a colony of semi-free living chimpanzees. Behaviour 66:268–312

Waal FBM de (1982) Chimpanzee politics. Johns Hopkins University Press, Baltimore

Waser P, Jones WT (1983) Natal philopatry among solitary mammals. Q Rev Biol 58:355–390

Wrangham RW (1979) On the evolution of ape social systems. Soc Sci Info 18:335–368

Wrangham RW, Smuts BB (1980) Sex differences in the behavioral ecology of chimpanzees. J Reprod Fertil Suppl 28:13–31

Wrangham RW, Conklin NL, Chapman CA, Hunt KD (1991) The significance of fibrous foods for Kibale Forest chimpanzees. Phil Trans R Soc Lond 334:171–178

Wrangham RW, Chapman CA, Clark-Arcadi AP, Isibirye-Basuta G (1996) Social ecology of Kanyawara chimpanzees: implications for understanding the costs of great ape groups. In: McGrew WC, Marchant LF, Nishida T (eds) Great ape societies. Cambridge University Press, Cambridge, UK, pp 45–57

Communicated by P.M. Kappeler