Does participation in intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees?

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Male chimpanzees, *Pan troglodytes*, engage in cooperative territorial defence and sometimes kill members of neighbouring communities. Observations of intergroup interactions suggest that escalation of aggression depends on numerical assessment, with lethal attacks occurring when numerical advantage reduces the costs of attacking. To gain a better understanding of the factors guiding participation in intergroup conflict, we conducted a series of playback experiments with the Kanyawara chimpanzee community of the Kibale National Park, Uganda. We tested whether the response to the playback of the 'pant-hoot' call of a single extragroup male depended on the number of adult males in the listening party, the location of the speaker relative to the territory edge, and each male's agonistic rank. These playbacks elicited cooperative responses, with the nature of the response depending on the number of adult males in the party. Parties with three or more males consistently joined in a chorus of loud vocalizations and approached the speaker together. Parties with fewer adult males usually stayed silent, approached the speaker less often, and travelled more slowly if they did approach. In contrast to many territorial species, the location of the simulated intruder did not affect the response. Although high-ranking males might be expected to benefit more from repelling outside males, both high- and low-ranking males showed a similar pattern of response. Each male responded as if he benefited from repelling intruders, but only if he had strength in numbers. This pattern of response is consistent with cooperation based on mutualism.

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Contests between social groups include striking examples of cooperation, in which individuals risk injury and death to acquire or defend shared resources. The mechanisms underlying cooperative intergroup aggression remain a central problem for behavioural biology. In general, animals should enter an intergroup contest when the benefits appear to outweigh the costs (Parker 1974), which may result from the perception of either high benefits or low costs. Benefits include the acquisition or defence of food, mates and territory. Individuals also may benefit from killing infant or adult members of other groups. For instance, infanticide may increase future mating opportunities for males (e.g. Hausfater & Hrdy 1984; Packer et al. 1988; Breden & Hausfater 1990; Palombit 1999), and killing adults may reduce the competitive strength of rival groups (Wrangham 1999). Failure to defend against intruders may result in loss of territory, resources and lives of group members, and eventually result in group extinction (e.g. Nishida et al.

1985; Goodall 1986; Packer et al. 1988; Soltis et al. 1995; Mech et al. 1998). The costs of entering an intergroup contest may depend critically on the number of opponents on each side. In territorial species, the expected benefits may vary with location relative to the opponents' territorial boundaries (e.g. Maynard Smith 1982). Furthermore, individuals may vary in the expected benefits from an intergroup contest, and may modify their participation accordingly. In many primate species, for instance, higher-ranking males participate more actively in intergroup contests than lower-ranking males (Nunn 2000).

In the present study, we conducted a series of experiments on chimpanzees, *Pan troglodytes*, designed to test how willingness to participate in an intergroup contest varies with the number of defenders, experiment location and individual agonistic rank. Chimpanzees live in fission–fusion communities of 20 to more than 120 individuals (Goodall 1986; Chapman et al. 1994; Watts 1998). Males breed in their natal communities and participate in a number of group-level activities, including hunting (Boesch 1994; Stanford et al. 1994), mate guarding (Watts 1998) and intergroup aggression (Nishida

1979; Goodall et al. 1979). Theoretical considerations suggest that chimpanzee home ranges are defendable (Mitani & Rodman 1979; Lowen & Dunbar 1994), at least in forest and woodland habitats, and in fact all long-term study sites with multiple social groups report territorial defence (reviewed in Wrangham 1999). Males form stable dominance hierarchies in which higher-ranking males appear to have greater mating success (e.g. Watts 1998). Females typically disperse before breeding. During inter-group conflict, females may participate by vocalizing or approaching, but females avoid direct physical attacks (Goodall 1986; Boesch & Boesch-Achermann 2000).

Contests between groups may have a profound effect on individual fitness and social organization. Over a 20-year period at Gombe, Tanzania, intergroup aggression accounted for 30% of adult male mortality (Goodall 1986). Although such high rates of mortality from inter-group aggression are unusual among mammals, similar rates have been reported for humans (e.g. Chagnon 1988; Soltis et al. 1995) and wolves, *Canis lupus* (Mech et al. 1998). Nevertheless, intergroup contests occur infrequently and are often difficult to observe. Playback experiments provide an opportunity to simulate inter-group interactions under controlled conditions, making it possible to test the relevant hypotheses.

EXPERIMENTAL DESIGN AND RATIONALE

We tested the response of chimpanzees to an intruder by playing back a recorded 'pant-hoot' call from a foreign male. Chimpanzees pant-hoot throughout the day, with a peak in frequency between 0700 and 1000 hours (Wrangham 1975). Pant-hoots can be heard over distances of 1–2 km (e.g. Reynolds & Reynolds 1965; Ghiglieri 1984), and are produced in a variety of circumstances, including arrival at fruiting trees and during reunions, hunts and intergroup encounters (Goodall 1986; Marler 1976; Clark 1993; Mitani & Nishida 1993). Pant-hoots appear to play important roles within and between groups, as do the long-distance calls of other species with fission–fusion societies (e.g. lions, *Panthera leo*: McComb et al. 1994; wolves: Harrington & Mech 1979; spotted hyenas, *Crocuta crocuta*: East & Hofer 1991). Pant-hoots enable allies and associates to maintain contact across long distances (Mitani & Nishida 1993), and by advertising the presence of large parties, pant-hoots may deter approach by extragroup chimpanzees (Nishida et al. 1985; Clark 1991).

We tested whether willingness to enter an intergroup contest depended on the following three factors: (1) numerical assessment, (2) experiment location and (3) individual agonistic rank. The following represents a brief synthesis of why we considered these three factors to be important for our experimental design.

Numerical Assessment

In many species, larger groups tend to defeat smaller groups (e.g. ants: Hölldobler 1981; Adams 1990; social carnivores: Kruuk & Macdonald 1985; primates: Cheney 1987; Isbell 1991; humans: Keeley 1996). Individuals seeking to minimize costs should therefore be more willing to enter contests in which their side has a numerical advantage. A recent series of experiments has demonstrated that such numerical assessment guides the decision of female lions to enter intergroup contests (McComb et al. 1994). Specifically, experiments simulating the intrusion of unfamiliar females found that resident females were more likely to approach a single intruder's roar if they outnumbered the intruder, and were more likely to approach a single roar than a chorus of three strangers' roars.

While numerical assessment should be widespread among species with intergroup contests, such assessment should be particularly important for species with fission–fusion social organization. Wrangham and colleagues (Manson & Wrangham 1991; Wrangham 1999) argue that in such species, intergroup encounters will sometimes involve extreme numerical imbalances, allowing members of one group to kill outnumbered opponents at relatively low cost. Members of such species should seek out opportunities to kill members of rival groups at low cost in order to reduce the coalitionary strength of rival groups, increasing likelihood of success in future territorial contests.

Observational data support the prediction that the outcome of intergroup contests in chimpanzees depends critically on numerical imbalances. Battles between parties of roughly equal size rarely lead to injury (Nishida 1979; Boesch & Boesch-Achermann 2000). In contrast, the five lethal attacks observed at Gombe involved parties with at least three adult males attacking alone (four cases) or outnumbered individuals (one case).

Experiment Location

The net benefits of entering an intergroup contest should depend not only on numerical assessment but also other factors, such as asymmetries in ownership (Davies 1978) and the value of the contested resource to each opponent (Austad 1983; Enquist & Leimar 1990). Lions, for instance, will approach intruders even if outnumbered, depending on such factors as the sex of the intruders and defenders (Grinnell et al. 1995), the presence of cubs (McComb et al. 1994) and population density (Heinsohn 1997).

It is possible that, under some circumstances, it would not pay for individuals to enter a contest even if they had a numerical advantage. For instance, arguments from evolutionary game theory predict that in territorial species, the benefits of range defence should be highest towards the centre of the territory (Maynard Smith 1982). In many territorial species, residents are more likely to win than intruders (e.g. Davies 1978; Cheney 1981), and response to the call of an extragroup individual decreases with increasing distance from the centre of the defenders' territory (many songbirds: Falls 1982; gibbons and siamangs *Hylobates* spp: Raemaekers & Raemaekers 1984; Mitani 1985; Chivers & MacKinnon 1977).

Nevertheless, response to intruders does not necessarily vary with location in all species. For instance, Waser (1977a) found that groups of grey-cheeked mangabeys, *Lophocebus albigena*, in Kibale Forest maintained spacing by mutual avoidance rather than territory defence, and location did not affect the response to a simulated intruder. Although chimpanzees, in contrast to mangabeys, actively defend territories, at least two lines of argument suggest that the response of male chimpanzees to intruders should not depend on location. First, van Schaik and others (van Schaik et al. 1992; Nunn 2000), have argued that males may be more concerned with defending females than with defending a particular geographic boundary, since male reproductive success depends more on access to females than on the resources within a particular boundary. By this argument, males should always seek to repel outsiders, regardless of location. Second, the observations and theoretical considerations discussed above suggest that the principal benefit of intergroup aggression in chimpanzees is the opportunity to reduce the coalition strength of neighbouring groups by killing rival adult males (Manson & Wrangham 1991; Wrangham 1999). The payoff for intergroup aggression in chimpanzees and species with similar social organization should therefore be independent of location.

Individual Agonistic Rank

Benefits may also vary among individuals within a group. In species with male dominance hierarchies, high-ranking males may gain greater benefits from excluding extragroup males, and may therefore be more willing to fight male intruders (Nunn 2000). For instance, in multimale groups of mangabeys, only one male in each group consistently approached the playback of a male intruder (Waser 1977a).

It is unclear from observational reports whether high-ranking male chimpanzees participate more actively in intergroup encounters. High-ranking males give pant-hoot calls at a higher rate than low-ranking males (Clark 1993), suggesting they are more willing to advertise their presence. Nevertheless, no obvious effect of dominance rank has been reported for participation in border patrols or battles (Goodall 1986; Boesch & Boesch-Achermann 2000).

METHODS

Study Site and Population

We studied the Kanyawara community of chimpanzees living in Kibale National Park, Uganda (0°34′N, 30°21′E). The study site is described in detail elsewhere (e.g. Struhsaker 1997). The rolling terrain varies in elevation from 1500 to 1700 m. The vegetation at Kanyawara includes a mosaic of moist evergreen forest, colonizing forest, swamp and exotic softwood plantations within the park as well as forest patches, tea plantations and subsistence farms outside the park. The Kanyawara
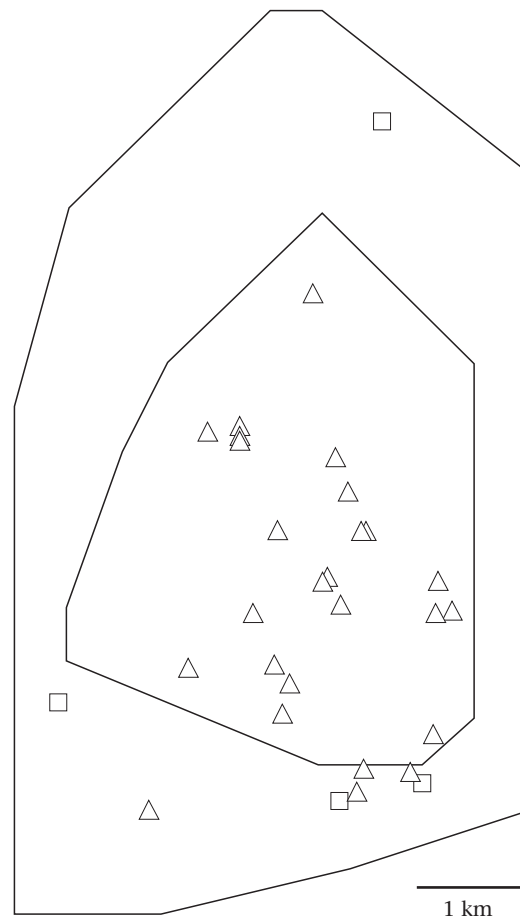
Figure 1. Kanyawara community range use, 1996–1998. The outside polygon encloses the centres of all 500 by 500 m grid cells used by the community. The inside polygon encloses the centres of grid cells containing 98% of nest sites used during the study. Triangles indicate the speaker location for each playback, and squares indicate locations for all intergroup interactions in which members of outside groups were directly observed during the study period.

community contained approximately 50 individuals during the study period (June 1996–December 1998), including 10–11 adult males, 1–2 subadult males, 15–16 adult females and 2–5 subadult females, all of which were individually recognized. Isabirye-Basuta initiated systematic study of this community in 1983 (Isabirye-Basuta 1989), and the community has been studied continuously since 1987 (e.g. Hauser 1990; Wrangham et al. 1992, 1996).

Playback Experiments

Overview

We played back a single foreign pant-hoot call to chimpanzees in parties of varying size and composition. The number of adult males in each party varied from zero to nine. The location of trials varied somewhat opportunistically, following seasonal changes in range use; we attempted, however, to balance the number of trials towards the edge and centre of the territory (Fig. 1).

Test stimuli

Test stimuli consisted of 12 different digitized recordings of pant-hoots collected by J. Mitani from five different individuals from the M-Group of chimpanzees in Mahale, Tanzania, with one to four exemplars per individual. No two consecutive trials used the same call. Calls were stored on digital audio tapes and played from a Sony TCD-D8 DAT recorder linked to a Peavey Impulse 652 speaker (frequency range 60 Hz–18 kHz; 100 W power). Calls lasted a median 6.9 s (range 5.7–14.6) and were played at a peak sound pressure level of $\bar{X} \pm SE = 92.4 \pm 2.5$ dB at 5 m.

Protocol

Two operators ran the playback equipment and maintained radio contact with observers. Up to six observers recorded the response. We selected situations in which the chimpanzees were likely to remain stationary for about 30 min (e.g. feeding, grooming or resting). Mornings offered the best such opportunities. The median playback time was 0932 hours (range 0727–1215 hours). Playbacks were conducted when subjects were calm and quiet.

Signal transmission varied considerably, depending on terrain and vegetation. We placed the speaker in a site suitable for transmission, a median of 300 m from the nearest chimpanzee (range 110–610 m). To confirm the audibility of the signal, and also to test whether subjects were responding to an odd noise rather than a species-specific call, the operators played a heterospecific control stimulus (the roar of a male black and white colobus, *Colobus guereza*, or the contact call of a juvenile crowned hawk-eagle, *Stephanoaetus coronatus*). Chimpanzees pay little attention to these calls when they occur naturally. We repeated the control stimulus until it was clearly audible to the observers, resulting in a median of two control stimulus playbacks per trial (range 1–7), a median of 16 min before the pant-hoot playback (range 1–120 min), with a median of 11 min passing between repeated control stimuli (range 1–84).

After playing the control stimulus, the operators played a pant-hoot. The operators removed the equipment immediately after playback so that chimpanzees never saw the equipment in operation. One operator remained concealed at the speaker site to observe the response of any approaching chimpanzees, which generally did not appear to see or react to the operator.

To prevent chimpanzees from habituating to the playbacks, we waited at least 5 days between trials in 1996, and in 1997 increased this minimum interval to 10 days. No more than three trials were conducted in any one month. A median of 12 days passed between trials (range 5–301 days). Because party composition varied across trials, each individual heard only a subset of the trials. The median interplayback interval experienced by each adult was 28 days for males (range 11–119) and 30 days for females (range 13–137).

We tested a total of 12 adult males and 15 adult females. Males heard a median of 11 trials (range 2–17) and females heard a median of four trials (range 1–13), including cases both directly observed and inferred (either because they approached the speaker within an hour of the playback, they were heard countercalling to the playback and later identified, or they were found within a few hundred metres of the speaker within an hour of the playback).

Documenting response to playback

Observers recorded the response using focal behavioural samples of selected adult males and females, all-occurrences sampling of pant-hoots and other loud calls, and ad libitum observations (Altmann 1974). Observers recorded the party composition at the beginning of the trial and when subsequent changes occurred. One observer recorded the vocal behaviour of the group on audio tape for 5 min before and after the playback, and seven trials were also recorded using a video camera. Observers conducted systematic observations for a minimum of 20 min before and after each playback, although in some cases observers lost rapidly moving subjects. Male chimpanzees generally responded in a coordinated fashion (see Results), so that observers generally documented the approach behaviour of all males in the party. When chimpanzees moved towards the speaker, observers recorded the order of individuals in the progression.

Every 2 min, each observer recorded the location of the focal subject with respect to the trail grid system or other landmarks, and, starting in 1997, the identity of all individuals within 1, 5 and 10 m of the focal subject. Within the central trail system, trails were spaced 25–50 m apart. In areas with lower trail density, this method provided little resolution of travel distance. Starting in 1997, we improved the resolution by marking the location of one male in each focal party with flagging tape every 2 min. We measured the position of flagged locations, trail intersections and the speaker site using a Garmin GPS 12 Global Positioning System (GPS) (position accuracy to 15 m RMS). In dense forest canopy, obtaining an accurate GPS reading can take 5–10 min, so all such readings were taken after the experiment. To verify the GPS readings, and also to obtain more accurate measurements of shorter distances such as closest approach to speaker, we used a 50-m measuring tape, Hip Chain measuring string and compass bearings, with reference to trail maps and a 1:50 000 scale map of the study area. With these measurements, we determined the rate of travel between known points, and used a map of the approach path to estimate latency to 100 m, the time taken to move 100 m closer to the speaker, to the nearest minute.

Sample size and independence of parties within trials

We conducted 26 playback trials during June 1996–July 1998, with a total of 28 focal parties observed. In four trials, the focal party included only females and their dependent offspring. The remaining 22 trials included from one to nine males in the focal party. Because of strong expectations that males and females should respond differently to the call of a foreign male, we

restricted analyses to parties with at least one male, discussing female-only parties separately, unless stated otherwise.

The definition of 'party' varies from study to study (see Chapman et al. 1994). Chimpanzee parties generally travel as discrete units but sometimes spread out over larger distances, and in dense forest it is seldom possible to determine the distance separating all individuals. Here we use 'party' to mean all individuals travelling, feeding, resting, or socializing within about 50 m of one another (e.g. Clark 1993; Wrangham et al. 1992). In two border-line cases, in which individuals were separated from the rest of the party by 50–60 m but had been together with other party members in the previous 15 min, we considered them all to be members of the same party. In practice, a minimum of 90 m separated the parties we considered to be distinct.

When chimpanzees assess their numbers relative to an intruder, they might include individuals present in nearby parties. In eight trials, evidence indicated that at least two parties heard the playback. For two of these trials, we conducted focal follows on members of both parties present. We examine whether parties within trials responded independently below (Results). To avoid possible pseudoreplication, we took the conservative approach of limiting analysis to one party per trial. In the two trials with multiple focal parties, the focal parties were of similar composition and responded in a similar manner, so in all but one case, neither the restriction of analysis to one party per trial nor the choice of which party to exclude affected the general pattern or statistical significance of the results. We discuss the one exception below (Results).

Within-community playbacks

We conducted two within-community playbacks, using pant-hoots recorded from Kanyawara males in 1997. We restricted playback of resident male calls to parties with fewer than three males, using the call of a male that had not recently been seen. We chose to use parties with few males for two reasons. First, the presence of few males would increase the probability that males for which we had playback stimuli would be absent. Second, we reasoned that parties with few males would be more likely to give a distinct response to resident males, based on the results of earlier trials. Specifically, males often call in response to the pant-hoots of resident males (Mitani & Nishida 1993), but males in small parties almost always remained silent when hearing the foreign male pant-hoot playback (see Results). Although this sample size is extremely limited, we report the results below, recognizing the need for more such trials in future experiments.

Determination of range boundaries

As in other populations, the Kanyawara community's range includes areas of extensive overlap with neighbouring communities, complicating any attempt to determine community boundaries. Different studies have used different criteria for determining the boundaries of animal territories (Maher & Lott 1995). For this study, we used the 'nesting range': the minimum convex polygon containing 98% of locations used for night nests during the study period. The nesting range is thus similar to the 'core' area of other studies (Goodall 1986; Williams 2000). Using the nesting range has the following advantages: nesting seems a good indicator of whether chimpanzees consider a given location to be safe, as chimpanzees are unlikely to nest deep inside neighbouring territory, and nesting provides independent data points for each party.

To determine the nesting range, we plotted a total of 494 nest locations during January 1996–December 1998 on a 500 by 500 m grid map of the area. Limiting the polygon to 98% of the nest sites eliminated overly influential outliers. We used ArcView GIS (Environmental Systems Research Institute 1997) software to measure the distance from the GPS measurements of the initial subject location and speaker location for each playback trial to the nearest edge of the nesting range polygon.

Dominance rank and approach rank

We determined the dominance rank of males from the direction of agonistic wins and losses, using a probabilistic model (Jameson et al. 1999) that permitted ranking of individuals with few observations. Because ranks changed from year to year, we calculated mean dominance rank, weighted by the number of trials in which each male was observed at a given rank. Approach rank was calculated following Heinsohn & Packer (1995). Each animal's order within the approaching party was standardized to a value between -1 (last) and 1 (first) to control for party size.

Statistical analysis

For statistical analyses, we used Stata 6.0 (Stata Corporation 1999), with two-tailed hypothesis testing and significance set at $P<0.05$. To facilitate comparison across studies, we followed methods described for similar studies with lions (e.g. McComb et al. 1994; Grinnell et al. 1995; Heinsohn & Packer 1995). We conducted analyses at two levels: parties and individuals. In party-level analyses, we used one value per trial, rather than the separate response of each chimpanzee, to avoid pseudo-replication (e.g. Grinnell et al. 1995). Analysis of individual behaviour, using repeated measures analysis of variance, enabled us to test both for differences among individuals and for the possibility that the observed patterns of response resulted from sampling bias. Although we describe the responses for parties with only females and dependents, due to the small sample size of such parties ($N=4$), we limit all statistical analyses to parties with at least one male.

We determined the readiness of the defenders to engage in a contest with the foreign male by whether they answered the playback with countercalls and whether they approached the speaker. Countercalling was scored as a binary response of 'yes' or 'no', describing whether any members of the focal party responded to the playback with loud calls (pant-hoots, waa-barks, screams: Goodall 1986) within 5 min of the playback. In practice, all responses scored as 'yes' occurred within seconds of

the playback, and all parties scored as 'no' stayed quiet for over 20 min, except for one case in which a male began pant-hooting 19 min after the playback. Approach was likewise scored 'yes' or 'no', describing whether any members of the focal party responded to the playback by moving forward at least 50 m within 20 min of the playback. In practice, all parties scored as approaching moved forward at least 120 m and all parties scored as not approaching moved forward 20 m or less. To understand which factors influenced the probability of countercalling and approaching, we ran backward stepwise logistic regressions with the following independent variables: number of adult males in the immediate party, number of adult males within acoustic range of the speaker, number of adult females in the immediate party, distance from speaker to the nearest edge of the nesting range, distance between speaker and subjects at the time of playback, and date; we used a *P*-level-to-retain of 0.10.

We examined two additional variables that should be related to willingness to enter an intergroup contest: distance travelled relative to the speaker in the 20 min following playback, and the speed of approach as measured by the latency to reach 100 m. We conducted stepwise regression with the following independent variables: number of males in the immediate party, number of males within acoustic range, number of females in the immediate party, distance from subjects to speaker at the time of playback, distance from speaker to nearest edge of the nesting range, and the date of the playback, with *P*-level-to-retain of 0.10.

We examined the grouping behaviour of males following playback, both to assess response to playback and also to verify that males tended to travel close enough together to justify our use of a single value for approaching parties. Sample size for this analysis was limited due to two factors: we did not begin systematic data collection on the number of individuals within 10 m until 1997, and in three subsequent cases we were unable to obtain sufficient data for paired comparisons because focal males were temporarily lost from view. Despite these limitations, we obtained grouping data both before and after playback for 18 focal males in 12 of the 18 parties that approached, giving one to three focal males per party. To avoid pseudoreplication, we calculated the median value for the focal males in each party, giving one measure per party.

The directness of approach to speaker clarifies whether movements following playback were in fact directed towards the simulated intruder, and also tests the minimum capabilities of chimpanzees to localize calls of conspecifics. To assess the directness of approach, we calculated the angular error of localization, following Waser (1977b). This method could only be used in cases where subjects moved past the speaker location, which restricted the sample size to 11 parties. The angle, θ, was calculated as follows: $\theta = \arctan(D_p/D_i)$, where D_p equals the distance from speaker to subject when the subject crossed the arc drawn through the speaker site and centred on the subject's initial location, and D_i equals initial distance between speaker and subject at the time of playback. Since approaching chimpanzees typically

travelled in single file, with each individual passing the speaker at roughly the same distance from the speaker, we report this result for approaching parties rather than for individuals.

Ethical Note

The possibility exists that playing back calls of foreign males may increase stress levels and even lead to inter-community violence. Nevertheless, playback experiments have been used extensively to explore territorial responses in birds and mammals, including species in which lethal intergroup aggression occurs, such as lions. In no case that we are aware of have these experiments resulted in increased levels of aggression between experimental subjects and their neighbours. Lions in particular experience high rates of injury and mortality from intergroup aggression (e.g. Packer et al. 1988), yet playback experiments conducted at a rate similar to those in this study have not resulted in any apparent increase of intergroup conflict (e.g. McComb et al. 1994; Grinnell et al. 1995). Although systematic comparisons are difficult due to the low rate of intergroup encounters in this population, the rate of intergroup encounters did not appear to change following the initiation of playback experiments. One lethal intergroup attack did occur after the completion of the foreign male playback series (Wrangham 1999), but such attacks also occurred before this study began. Moreover, the playback experiments did not appear to cause a long-term change in the community's home range area; only short-term changes in location occurred within a day or so following the playback.

RESULTS

During the study period, the Kanyawara community ranged over an area covering 37.8 km^2 and spent the night in nests built within a smaller area of 15.8 km^2. All intergroup encounters observed during the study period took place beyond the edge of the nesting range (Fig. 1). We located the speaker a median of 740 m inside the nearest edge of the nesting range (range −1050–1730, where negative values indicate distances beyond the nesting range).

In the 20 min prior to the pant-hoot playback, focal parties remained relatively quiet, producing a median of zero loud call bouts per party (range 0–3 bouts). Apart from individual movements of a few metres, such as changing position within the crown of a feeding tree or within a resting party, focal parties showed no tendency to move relative to the speaker. In fact, only in one party did individuals move a measurable distance; in this exception the two males in the party left the feeding tree and moved a net 40 m away from the speaker before stopping to rest and groom.

The heterospecific control stimuli consistently elicited responses from monkeys in the area. Mangabeys and red colobus, *Procolobus tephrosceles*, both responded to the crowned hawk-eagle call with alarm calls. Black and white

colobus responded to the colobus roar with roars of their own, whereas the same stimulus (possibly an alarm call) elicited alarm calls from redtail macaques, *Cercopithecus ascanius*, mangabeys and red colobus. The various monkey species thus responded to these stimuli in a manner consistent with previous studies at this site (e.g. Waser 1977a; Hauser & Wrangham 1990). The chimpanzee subjects, however, never gave any overt responses to the eagle or colobus playbacks.

In marked contrast, chimpanzees gave dramatic responses to the pant-hoot playbacks, and these responses were consistent with response to a foreign male's call. On hearing the pant-hoot playback, males and females alike oriented towards the speaker, and in some cases joined in a chorus of calls. Adult females unaccompanied by adult males often showed signs of fear, including fear grimaces. Males showed signs of aggressive arousal, including piloerection, similar to those observed during actual intergroup encounters (Goodall 1986). Whether or not chimpanzees counter-called or approached the speaker varied according to the number of adult males in the focal party, as described in detail below. Chimpanzees that approached the speaker site followed a direct route, with the adult males leading the way, travelling single file. Upon nearing the speaker site they sometimes searched the area, sniffed the ground, and then continued travelling in the direction of the stranger's call. The pant-hoot playbacks consistently elicited similar responses over the 2 years of testing, suggesting that our efforts to avoid habituation to playbacks succeeded.

Vocal Response

Of all the factors tested, countercalling depended only on the number of adult males in the party (Fig. 2a; stepwise logistic regression: $\chi^2=16.8$, $N=22$, pseudo $r^2=0.58$, $P<0.0001$; pseudo r^2 provides a description of the fit of logistic models but lacks the straight-forward explained-variance interpretation of true r^2 for ordinary least squares regression; Hamilton 1998). Parties with three or more adult males countercalled in 12 of 13 trials, with the one exception being a party with three males. Parties with one to two adult males countercalled in only one of nine trials; in the one exception, a male in a party with two males joined the calls of a male in a nonfocal party 90 m away. In none of the four trials without adult males present did individuals countercall.

Countercalling usually involved a chorus of most or all of the males present, with females sometimes joining as well. Although determining the individual vocal response for all males in the party was usually not possible, especially for large parties, in cases of countercalling we were able to determine the vocal response for a median of 55% of the males present (range 0–100%). In 12 cases 100% of the males whose vocal response was determined joined the countercalling chorus, in two cases a single male failed to join the chorus, and in one case the individuals present joined in a loud chorus but it was not possible to determine which of the males called. Overall, countercalling appeared to be an unambiguous response
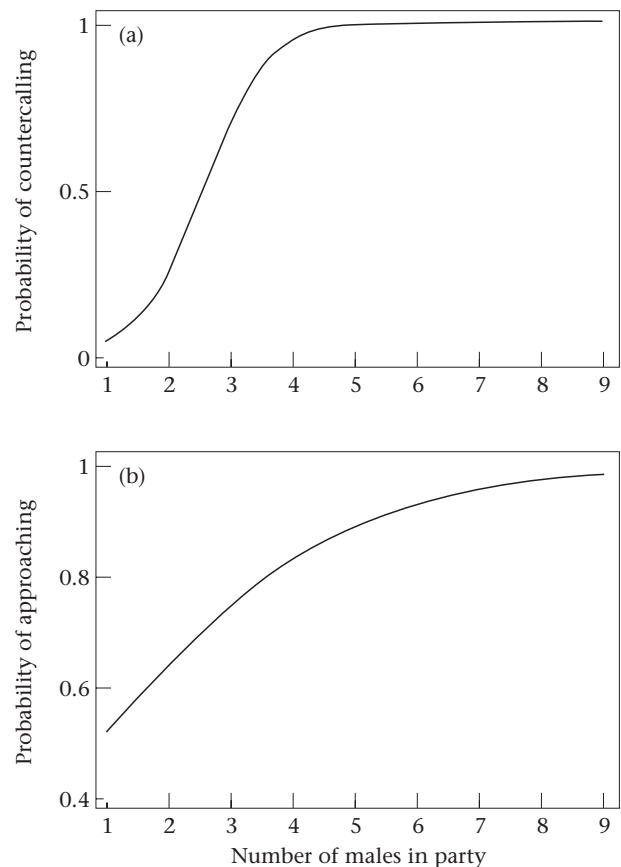

Figure 2. Logistic regressions fitted to the probability of (a) counter-calling and (b) approaching the speaker versus the number of adult males in the party.

to the playback, occurring immediately after the play-back, with individuals orienting towards the speaker and calling together.

The number of adult males present affected not only whether countercalling occurred, but also the number of loud call bouts produced. In the 5 min before playback, most parties remained silent, with no correlation between number of loud call bouts and number of adult males (multiple linear regression: $F_{1,20}=1.64$, NS). In the five min following playback, the number of loud call bouts produced increased with the number of males ($F_{1,20}=29.18$, $r^2=0.59$, $P<0.0001$).

Travel Response

Following the pant-hoot playback, individuals in many parties oriented towards the speaker, descended to the ground if in a tree, and began moving. Females, if unaccompanied by males, either stayed stationary or moved up to 160 m away from the speaker. Adult males either remained stationary or approached the speaker (Fig. 3). Parties with three or more adult males approached the speaker in 12 of 13 trials; in the one exception, the distance travelled (20 m) fell short of the 50 m required for an approach. Parties with one to two adult males approached in five of nine trials.
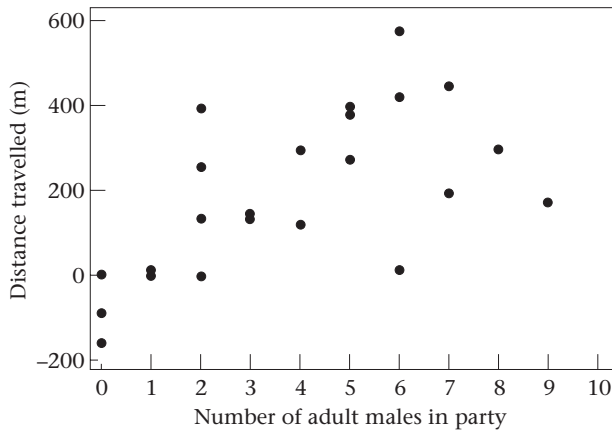
Figure 3. Distance travelled relative to the speaker in the 20 min after playback versus the number of adult males in the party. To show the full range of responses, values are shown for all focal parties whose response could be determined, including parties excluded from statistical analysis (namely, parties with only females and their dependents, $N=4$, and both parties for the two trials in which two focal parties were observed).

Approaching males generally grouped together and continued to stay close to one another as they approached the speaker. One minute before playback, a median of 25% (range 0–100) of each party's males were within 10 m of the focal males. By the time the approaching party had reached 100 m, a median of 4 min after the playback (range 1–13 min), the percentage of the party's males within 10 m of each focal had increased to 100% (range 0–100; Wilcoxon matched-pairs signed-ranks test: $U=17$, $N=12$, $P<0.01$). The distance separating males within each party was thus generally smaller than the resolution of our distance measures (± 15 m for GPS). We therefore give travel measurements for parties rather than for individuals. In cases where not all individuals approached or some lagged significantly behind, the party measurement given is the distance travelled by the leading subgroup.

Approaching parties travelled a median of 290 m towards the speaker in the 20 min following playback (range 120–580 m), and reached their closest approach to the speaker site, a median of 30 m (range 0–330 m), in a median of 12 min (range 3–49 min). Two parties were temporarily lost from view following playback, so their location at 20 min postplayback and distance travelled at that time could not be determined. In one case we lost a focal party with one male and three females 9 min after the playback. All members of this party initially moved away from the speaker, but after hearing pant-hoots from a distant party with four males, the male and a subadult female from the focal party began moving towards the speaker. We could not determine whether they satisfied the approach criteria of moving 50 m towards the speaker within 20 m, but we did find them 35 min after playback, by which time they had joined the other party and moved 240 m towards the speaker. In the other case, two males moved at least 300 m towards the speaker; although they remained within acoustic range of the

observers, they were temporarily lost from view several times.

Despite the uneven terrain and limited visibility in the forest, chimpanzees proved exceptionally accurate in finding the speaker location with a median angular error of 3° ($N=10$, range 0–23°). Although this represents group as opposed to individual approach data, the chimpanzees' capacity to localize the sound source from memory of a single pant-hoot lasting 6–15 s is at least as good, if not better, than mangabeys presented with a comparable problem at the same study site (Waser 1977b).

The probability of approaching, as determined by logistic models, proved to be the one case in which the significance of the result depended on limiting analysis to one party per trial and on the choice of which parties to exclude. When all parties with at least one male were included, the response depended significantly on the number of adult males in the party (Fig. 2b; stepwise logistic regression: $\chi^2=4.67$, $N=24$, pseudo $r^2=0.17$, $P=0.03$). When the analysis was limited to one party per trial, however, the only factor to approach statistical significance was either the number of males in the party ($\chi^2=3.43$, $N=22$, pseudo $r^2=0.15$, $P=0.06$), or the number of males in acoustic range ($\chi^2=3.26$, $N=22$, pseudo $r^2=0.14$, $P=0.07$), depending on which parties were excluded. In both cases the P value remained greater than 0.05.

Multiple linear regression found that only the number of adult males in the immediate party significantly affected the distance travelled in the 20 min following playback (multiple linear regression: $F_{1,18}=4.72$, $r^2=0.21$, $P<0.05$). This effect resulted from including parties that did not approach. Restricting analysis to approaching parties revealed that if males decided to approach, the distance travelled did not depend on the number of males in their party ($F_{1,13}=0.88$, NS).

Latency to 100 m depended on both the number of adult males within acoustic range and the number of adult females (Fig. 4; multiple linear regression: $F_{2,12}=8.45$, $r^2=0.58$, $P=0.005$). For the trials in which we could estimate latency to 100 m, however, the number of males in the party and the number of males in acoustic range were largely identical, differing only for two trials.

Independence of Parties Within Trials

To test whether the presence of nearby parties affected response, we compared the response of both parties in all eight trials with multiple parties. For this analysis, we used trials in which both parties were directly observed ($N=2$) and trials in which the response of the nonfocal party could be inferred ($N=6$), recognizing the limitations inherent in such data. Vocal response could be determined for both parties for all eight trials, because loud calls could be heard by distant observers. Travel response could be determined for both parties in six trials, excluding the two cases in which the nonfocal parties were not directly observed approaching the speaker. The distance between parties at the time of playback could be determined for four trials, in which a median of 125 m separated the parties (range 90–190 m). Estimates for four other trials, based on loudness of calls, time of arrival to
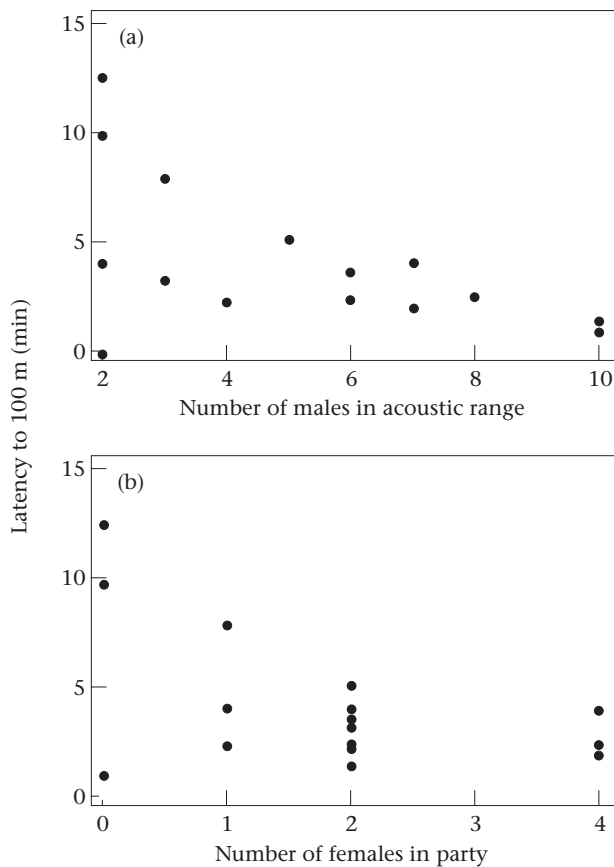
Figure 4. Latency to 100 m versus (a) number of males within acoustic range of speaker and (b) number of females in the party. Values are shown for both parties observed in one trial with 10 males within acoustic range. One of these parties was excluded from statistical analysis to prevent pseudoreplication, but the particular party excluded did not affect the results.

the speaker site, and location when first observed after the playback, ranged from 100 to 800 m.

The vocal response was independent of trial (Kruskal–Wallis test: $\chi^2_7=7.5$, $N=8$, NS) but depended significantly on party composition ($\chi^2_2=9.6$, $N=8$, $P<0.01$) with three levels of party composition (no males, one to two males, and three or more males). Similarly, travel response did not depend on trial ($\chi^2_5=4.0$, $N=6$, NS) but did depend on party composition ($\chi^2_2=8.8$, $N=6$, $P<0.05$). Nevertheless, other evidence suggests that individuals did modify their behaviour according to the presence of nearby parties. For example, in the one case of countercalling by an individual in a party with only two males, the caller in the focal party was joining the calls of a male 90 m away, which joined the focal party 9 min after the playback. In six of the eight trials the two parties eventually joined together after the playback, taking from 9 to 90 min to do so. The influence of neighbouring parties on response may depend on the distance between parties.

Experiment Location

In none of the above analyses did experiment location affect the response. Our inability to detect an effect of

location could in principle result from the limited statistical power of a small sample size as well as the small number of tests outside the nesting range. However, parties that did not approach were actually further (although not significantly further) towards the centre of the range than parties that did approach (median distance from speaker to nearest edge of nesting range: 840 versus 730 m; Kruskal–Wallis test: $\chi^2_1=0.018$, NS)
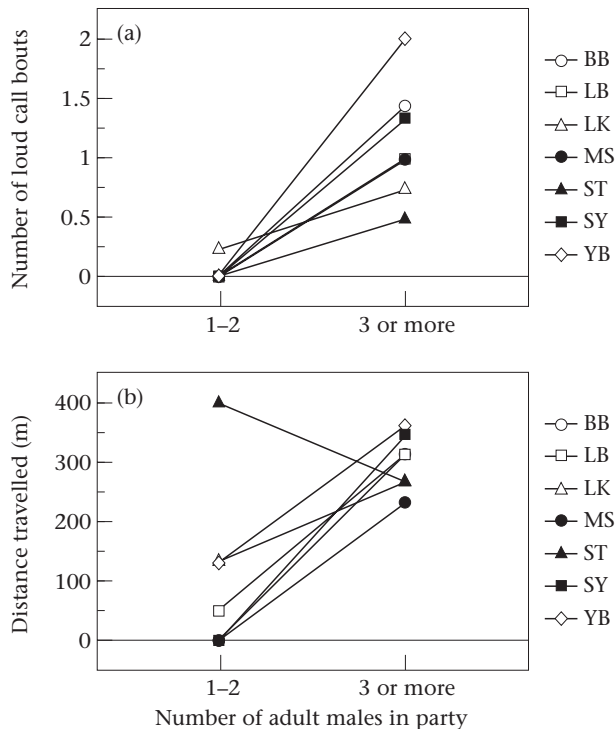
Within-community Playbacks

Because of time constraints and difficulty of finding parties with fewer than three males, we were only able to conduct two within-community playbacks before the end of the study. In both cases we played back the call of a male that had not been seen recently by observers (8 and 92 days, respectively). The party composition consisted of an adult female with her subadult male and infant male offspring for the first trial, and two adult males for the second trial. The subadult male in the first trial and both adult males in the second trial countercalled in response to the playback, and all members of both parties approached the speaker (latency to 100 m=4 and 5 min, respectively). While this small sample size prevents statistical comparison, this pattern of response contrasts strikingly with the response to foreign males, in which parties with fewer than three males almost always stayed silent and rarely approached. Furthermore, in neither case did subjects show any fear response to the playback, a further indication that the call was not perceived as a threat.

Differences Among Individuals in Vocal and Travel Response

The previously described results show that parties with three or more males were more likely to countercall and approach the speaker than parties with fewer males. To test whether this pattern of response was consistent across individuals, we compared the response of the seven males that were tested in two conditions of party composition: one to two males and three or more males. Trials with large parties were more likely to sample individuals repeatedly, with the result that each individual was tested less often in parties with up to two males (median number of times tested: 3; range 1–4) than in parties with three or more males (median: 8; range 4–9). We examined both vocal and travel response. Because of the difficulty of identifying all callers in a chorus lasting only a few seconds, the sample sizes for vocal response are somewhat smaller than for travel response.

For vocal response, we examined the number of loud-call bouts produced by each male in the 5 min following playback (Fig. 5a). All males called more frequently when in parties with three or more males. In fact, only one male (LK) ever called in the 5 min following playback when in a party with fewer than three males; he did so in the case described above in which he joined the calls of a male in a nearby party. When tested in parties with three or more males, four males always called in response to playback,
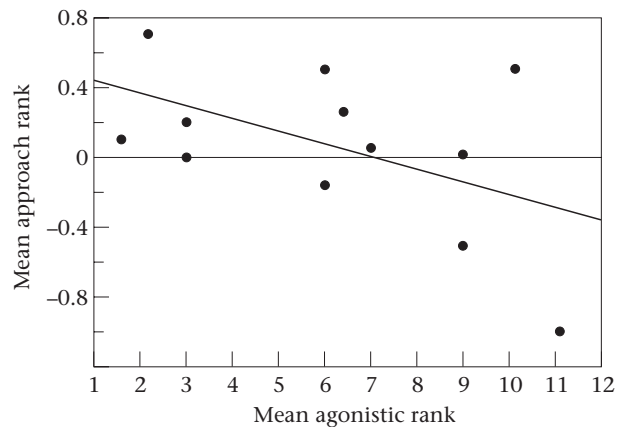
Figure 5. Individual variation in response, showing (a) mean number of loud call bouts produced by each individual in the 5 min following playback and (b) the mean distance travelled relative to the speaker in the 20 min after playback, for each of seven males tested in both conditions, one to two males and three or more males.

Figure 6. Mean approach rank versus mean agonistic rank for each of 12 males tested.

male, approximately 16 years old in 1998. All other adult males were at least 20 years old at the start of the study. All males that defected approached the speaker in earlier and later trials, suggesting that defection is a context-dependent behaviour, rather than a characteristic of particular individuals.

Approach Rank and Agonistic Rank

Analysis of variance found that individuals differed significantly from one another in the order in which they approached the speaker ($F_{11,39}=3.39$, $P<0.005$). Three males had negative mean approach ranks (i.e. they tended to stay at the rear of the approaching party: LM, an old male that died in 1996, mean rank$=-0.5$; LK, the youngest male, mean rank$=-1.0$; and AJ, a prime adult male, mean rank$=-0.16$). Five of the 12 males in this sample had serious injuries from snares or other causes (BB, LK, LM, SY, YB). Three of these had positive mean ranks, including the two individuals with the highest mean ranks (BB and SY), suggesting that approach rank was not primarily affected by injuries. Mean approach rank decreased with decreasing mean agonistic rank, but this relationship failed to reach statistical significance ($F_{1,10}=3.34$, $r^2=0.25$, $P=0.098$; Fig. 6).

DISCUSSION

An individual's decision to participate in cooperative intergroup conflict is likely to be influenced by a variety of social and ecological factors. Of the various factors measured in this study, including the number of defenders, the experiment location and individual agonistic rank, only the number of defenders significantly affected the response. Male chimpanzees countercalled and approached when the costs of aggression appeared to be low. Given the likely importance of avoiding unwinnable contests, as well as the demonstrated ability of lions to assess relative numbers (McComb et al. 1994), it is perhaps not surprising that chimpanzees should possess such an ability. Indeed, the capacity for numerical assessment may be widespread among animals (e.g. Hauser 2000).

and all seven males called in at least 50% of trials. Repeated measures analysis of variance, limited to the four males that were tested at least twice in both conditions of party size, found a significant effect of party composition (ANOVA: $F_{1,3}=56.16$, $P<0.01$), and no significant difference among individuals ($F_{3,3}=2.24$, NS).

Similarly, six of the seven males tested in both conditions travelled farther when in parties with three or males than in parties with one to two males (Fig. 5b). The one exception was a male in a party of one to two males whose travel response was determined for only one trial. As with vocal response, the distance travelled in the 20 min following playback did not differ among individuals (ANOVA: $F_{3,3}=0.36$, NS), but instead consistently depended on party composition ($F_{1,3}=10.54$, $P<0.05$).

Individuals did differ in that some but not all defected, defined as cases in which one or more individuals stayed behind while others approached the speaker. Defection occurred in three cases. In the first case, the second-highest-ranking male (MS) stayed behind with a female with a full sexual swelling (GO). Several other males made partial approaches before returning to the vicinity of MS and GO, while the highest-ranking male (BB) and several others approached the speaker. In the second case, MS showed interest in hunting red colobus monkeys shortly before the playback. After the playback, he actually moved away from the speaker while the other males approached. The third case involved LK, who stayed behind while YB approached. LK was the youngest adult

For male chimpanzees, countercalling depended more strongly on the number of defenders than did approaching. Parties with one to two males approached the speaker in five out of nine trials, whereas they only countercalled in one of nine trials. Males that failed to call in small parties did call in larger parties, showing that this pattern of response did not result from sampling bias. Countercalling probably serves at least three functions. First, calls present a challenge to the intruder, advertising willingness to defend their territory. Second, since chorused calls are overlapping and probably cannot be faked, they provide an honest signal of the number and hence fighting power of the defenders (e.g. McComb et al. 1994). Finally, calls may recruit allies (Mitani & Nishida 1993). That male chimpanzees failed to countercall except when in larger parties probably relates to the great potential costs of being caught outnumbered by one or more intruders. Although one or two males might risk little danger from a lone intruder, the call of a single intruder may represent an unknown number of silent intruders. Males in small parties appeared willing to silently investigate a single intruder's call, but they were unwilling to openly advertise their presence unless they appeared to outnumber the intruder.

Studies of lions present a useful context for interpreting the results of the present study. Lions have a complex social system with many interesting parallels to chimpanzees, including cooperative hunting, coalitionary aggression, fission–fusion ranging patterns and lethal intergroup aggression. Male chimpanzees resembled female lions in their unwillingness to approach an intruder without a numerical advantage. In contrast, male lions continue to approach, albeit more slowly, even when outnumbered 3:1 (Grinnell et al. 1995). This difference in response makes sense in light of the respective life history trajectories of the two species. Male lions stay with a pride for an average of 2 years before being deposed, and are unlikely to attain residence in another pride (Packer et al. 1988). Any failure to defend their territory against rival males could result in eviction, with complete loss of lifetime reproductive success. In contrast, male chimpanzees in Kanyawara face a situation similar to female lions in the Serengeti: intergroup encounters bring the risk of injury or death, especially to outnumbered individuals, and defeat may result in loss of territory. In contrast, an individual's lifetime reproductive success rarely depends on any single contest.

Experiments with lions have also demonstrated the importance of ecological factors in guiding response to intruders. Female lions living in the densely populated Ngorongoro Crater approach intruders even when outnumbered, but female lions that lack a territory fail to approach at all (Heinsohn 1997). Future experiments with chimpanzees in different populations may reveal similar sensitivity to population density and other ecological factors. The chimpanzee population density at Kanyawara, approximately one adult/km^2, is somewhat less than the maximum of roughly four/km^2 (reported for the Ngogo study site, 12 km southeast of Kanyawara; Watts 1998), and much higher than in savanna sites

(0.1/ km^2: Baldwin et al. 1982). Chimpanzees in extremely dense populations might enter contests at a lower ratio of defenders to intruders, and chimpanzees in extremely sparse populations might avoid such contests altogether.

Experiment Location

In contrast to many territorial species, chimpanzees did not modify their response to an intruder based on location. At least three explanations for this pattern are possible. First, the sample size is small, reducing statistical power. Although we attempted to balance the number of trials towards the centre and edge of the nesting range, few trials were conducted outside the nesting range. It is possible that tests far outside the nesting range would reveal some effect, such as an increase in caution. Nevertheless, the trials we did conduct outside the nesting range elicited approach and countercalling, and there was no tendency for decreased speed or distance of travel.

Second, if males in general attempt to defend females rather than a geographical boundary (van Schaik et al. 1992), males should always seek to repel outsiders. This model seems appropriate for many primate species, in which males and females travel together in cohesive groups. It is not clear whether this model applies to species such as chimpanzees, in which females generally travel alone or in small scattered parties and tend to avoid border areas (Chapman & Wrangham 1993). Given the spatial distribution of female chimpanzees, the best strategy for mate defence might indeed be to defend a territorial boundary, or at least increase intensity of defence towards the territory centre.

Third, the lethal raiding hypothesis predicts that the payoff for intergroup aggression should be independent of location. Although the small sample size warrants caution, the results presented here are consistent with this prediction.

Variation Among Individuals and Mechanisms of Cooperation

One surprising result of this study was the similarity of response across individuals. Theoretical considerations suggest that high-ranking males should be more willing to participate in intergroup conflict (Nunn 2000). This prediction finds some support in the (nonsignificant) tendency for low-ranking males to travel towards the rear of progressions. None the less, low-ranking males behaved remarkably like high-ranking males, in that they countercalled and approached whenever they had numerical superiority. The willingness of low-ranking males to participate in intergroup contests suggests that cooperation in chimpanzees does not depend on asymmetrical benefits or privileged groups.

The tendency for some males to travel towards the rear when approaching resembles the case for lions (Heinsohn & Packer 1995), in which some females consistently lagged behind by 50–200 m. Heinsohn & Packer (1995)

Table 1. Kinship and approach to speaker for parties with two males

Date	Males present	Maternal haplotype shared?	Maternal haplotype shared? (If LK's=AJ's)	Approach together?	Males that approached	Latency to 100 m (min)
13 May 97	BB LK	UNK	No	No	None	NA
18 Jun 98	MS LB	No	No	No	None	NA
07 May 97	SY LK	UNK	No	Yes	SY LK	10
16 Nov 97	YB LK	UNK	No	No	YB	4
06 Nov 97	MS YB	Yes	Yes	No	None	NA
23 Jul 97	MS YB	Yes	Yes	Yes	MS YB	4
14 May 98	LB LK	UNK	Yes	Yes	LB LK	13

In parties with two adult males, approaching the simulated speaker together did not depend on whether the males were matrilineal relatives (Fisher's exact test: NS; mtDNA sequence data from Goldberg & Wrangham 1997). LK's mtDNA has not been sequenced yet, but observations of AJ's association patterns when he was younger suggest LK and AJ are maternal brothers. UNK: Unknown; NA: not available.

argue that leading and lagging are fixed strategies for female lions. In contrast with lions, chimpanzees showed greater flexibility. As discussed above (Results), male chimpanzees sometimes defected by staying behind while others approached. Nevertheless, individuals that defected in some trials joined or even led approaches in other trials. Defection appeared to depend on immediate circumstances, such as the presence of an oestrous female. The greater flexibility apparent in chimpanzees may result from cognitive differences between the species, or may simply represent variability revealed by a greater number of trials conducted within a single social group.

At least four alternative explanations exist for the similarity of response among individuals. First, it is possible that high-ranking males benefit more from intergroup contests and are more willing to approach intruders, but low-ranking males join the approach for selfish reasons: the safest place to be during an intergroup encounter is with the largest available party. Nevertheless, low-ranking males approached the speaker even when no high-ranking males were present. In nine trials with parties of one to two males, four parties approached. Only one of the approaching parties contained a male with a higher rank than the median dominance rank, whereas four of the nonapproaching parties contained high-ranking males.

Second, cooperation in male chimpanzees is generally thought to depend on kinship resulting from male philopatry (e.g. Goodall 1986). In support of this, Morin et al. (1994) found that at Gombe, males were related to one another on the order of half-siblings. However, genetic study of one West African community did not replicate this finding (Gagneux et al. 1999). In addition, at Kanyawara, maternal relatedness failed to predict affiliation patterns (Goldberg & Wrangham 1997), and in the Ngogo study site, 12 km from Kanyawara, maternal relatedness failed to predict cooperative behaviours including alliances, meat sharing and border patrolling (Mitani et al. 2000). In light of these recent findings, it is perhaps not surprising that maternal relatedness did not

have a strong effect on whether males cooperated in response to playbacks. In playbacks to parties with two males, males that shared a maternal haplotype did not always approach, and males that probably did not share a maternal haplotype did approach together (Table 1). Although the genetic data for this population are still incomplete, sharing a maternal haplotype was a poor predictor of whether paired males approached the speaker. Kinship may facilitate cooperation among males, but specific instances of cooperation, such as alliances and response to intruders, appear to depend on additional factors.

Third, low- and high-ranking males might actually receive similar benefits from territory defence. Current mating success may be skewed towards high-ranking males, but rank varies over a male's life (Goodall 1986). Males may defend a territory to protect offspring they sired in the past. In support of this, the two former alpha males, BB and SY, had the highest mean approach ranks. Young but still low-ranking males may participate in defence to protect the territory for a future in which they expect to be high ranking. Furthermore, the varied mating strategies of chimpanzees, including consortships, may help moderate reproductive skew and give all males an incentive for territory defence. Such spreading of benefits, however, may actually result in a collective action problem, in which no single individual has enough to gain from territory defence to undertake such risks (Nunn 2000).

Fourth, if cooperation in male chimpanzees depends on mutualism, as Grinnell et al. (1995) argue for male lions, each male might indeed have a similar interest in territory defence. The conditions for cooperation through 'mutual dependencies' (Lima 1989) involve low probability of success when alone, and coalition partners that will participate in many interactions and that are difficult to replace. These conditions apply to male chimpanzees as well: they probably cannot defend territories when alone, they spend their entire lives with their coalition partners, and partners can only be replaced through birth and maturation of community males. Testing this

possibility clearly requires additional research, in which playback experiments would prove extremely helpful.

In conclusion, we found that male chimpanzees countercalled and approached strangers whenever they faced favourable odds. The decision to enter an intergroup contest depended on favourable numerical asymmetries, rather than range location or other factors known to affect response in other territorial species. In addition, males showed a striking similarity in their pattern of response, regardless of dominance rank. This pattern of response suggests that males may expect similar benefits from territorial defence, despite differences in rank and mating success, and is consistent with cooperation through mutualism.

Acknowledgments

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