INTRODUCTION
Although wild chimpanzees may spend hours resting and grooming peacefully in mixed social groups, and affiliative interactions among them may be more common than agonistic ones, intraspecific aggression is not the least a frequent occurrence in chimpanzee society. Both males and females exhibit an array of aggressive behaviors (from mild threats to lethal attacks) in a variety of contexts (from infant protection to sexual competition) against a range of competitors (from extracommunity males to newly immigrated females). Aggression, or merely the threat of aggression, can have a profound impact on individual patterns of ranging and association. For example, female immigrants at Gombe tend to settle in peripheral areas of the range and away from dominant females, where the risk of infanticide may be lower (Williams et al., Chapter 14).

The most dramatic examples of chimpanzee aggression come from observations of intercommunity encounters (e.g., Goodall et al. 1979). Male chimpanzees are philopatric, and they aggressively defend their community range against incursions from neighboring males (Nishida 1979; Goodall 1986; Watts & Mitani 2001). In the course of such defense, they sometimes cooperate to inflict lethal wounds on vulnerable strangers (reviewed in Wrangham 1999). Lethal coalitionary aggression is rare among mammals, having previously been documented as a major source of adult mortality only in wolves (Mech et al. 1998) and humans (van der Does 1995). In male chimpanzees, it may be part of a larger strategy to reduce the coalitionary strength of neighboring groups and to expand territorially at their expense (Wrangham 1999).

Within communities, male chimpanzees compete aggressively both for status within a linear dominance hierarchy and for access to estrous females. Coalitions can play an important role in both of these contexts, as males may cooperate either to challenge rivals (Nishida 1983; Nishida & House 1996) or to maintain exclusive access to an estrous female (Watts 1998). Intrasubcommunity aggression is normally less brutal than that between communities, perhaps in part because relatedness among males is higher within a community (Morin et al. 1994). However, dominance struggles are sometimes marked by intense dueling aggression and potentially lethal wounding (e.g., Goodall 1992; Nishida et al. 1995; Fairweather & Mahamutsa 2000).

Male chimpanzees appear to incur large costs as a result of competition for dominance. These include not only the risk of severe injury in escalated fighting, but the energetic demands of agonistic display. The presumption that such costs must be offset by considerable reproductive benefits has previously been supported by behavioral data indicating that high rank is associated with increased mating success (e.g., Nishida 1983). More recently, genetic tests of paternity have allowed for direct measures of reproductive success, and corroboration of the behavioral evidence (Canestra et al. 2001; for bonobos see Gerloff et al. 1999).

The potential influence of dominance rank on female reproductive success is not as well understood. Dominance relationships among female chimpanzees are less conspicuous than those of males, such that observers often find it difficult to rank them (Boycott 1974). On the one hand this is not surprising, as the limiting factor on female ape reproduction is normally considered to be food, and competition for food among female chimpanzees generally takes the form of scramble, rather than contest, competition (Wrangham 2000). On the other hand, the lack of overt competition among female chimpanzees is puzzling since recent evidence suggests that female dominance rank does influence factors such as infant survivorship and interbirth interval, probably through access to food (Pusey et al. 1997).

This chapter describes patterns of between- and within-group aggression among chimpanzees in Kibale National Park, Uganda. There are four main objectives. First, sex differences in rates, contexts, and targets of aggression are described, and accounted for in terms of reproductive strategies. Second, the relationship between aggression and dominance is explored, and the possible costs and benefits of high rank in this species are considered. Third, new inci-
dents of intercommunity aggression, including a lethal coalitional attack, are reported, and evaluated in light of the ‘imbalance-of-power’ hypothesis (Manson & Wrangham 1991). Finally, these data are compared with observations from other long-term study sites in Tanzania (Bygott 1974; Goodall 1986; Nishida 1989; Nishida & Hsoua 1996) and Ivory Coast (Boonsch & Boonsch-Achermann 2000) in an attempt to identify the broader patterns underlying behavioral variation.

METHODS

The Kanyawara community in Kihole National Park has been studied continuously by Richard Wrangham and colleagues since 1987. Struhsaker (1997) provides a detailed description of the research site. At the beginning of this study, the community consisted of 50 chimpanzees, including 11 adult males, 15 adult females, 1 subadult male, 2 moliparous females, 8 juveniles, and 15 infants. During the course of the study, three infants were born, and five individuals died.

The data in this study were collected by me from January through December, 1998 as part of a larger project investigating the hormonal correlates of dominance and aggression in chimpanzees. With the help of long-term field assistants, chimpanzees were followed, whenever possible, from the time that they woke in the morning, until the time that they constructed their night nests. If observers lost track of a chimpanzee party, a new one was located by either listening for long-distance vocalizations, or waiting near a fruiting tree. All-male and bi-sexual parties were followed preferentially, in order to facilitate data collection on male aggression.

Forty-minute group focal.s were used to generate rates of aggression for individual chimpanzees. This was equivalent to all occurrence sampling (Altman 1974), which was possible because the bistrocous nature of male chimpanzee agonism renders it highly conspicuous to observers. When observation conditions did not allow focal data to be collected, ad libitum observations of aggression and submission were made. Those were combined with focal data to rank the adult males in a linear dominance hierarchy (see below).

Behavioral categories followed those of Bygott (1979) and Goodall (1986); these are summarized in Nishida et al. (1999). Charging displays involved exaggerated locomotion, piloerection, sleaping, stamping, branch swaying and throwing; they were classified as either vocal or nonvocal, depending on the presence of the pant-hoot call.Chases were recorded when an individual pursued a fleeing conspecific, who was generally screaming. Attacks were recorded for all contact aggression. This included hits, kicks, or slips delivered in passing (Goodall’s level 1), more extended episodes of pounding, dragging, and biting (Goodall’s level 2), and incidents lasting more than 30 seconds or leading to serious injury (Goodall’s level 3). In behavioral analyses, charging displays were categorized as low-level aggression, while chases and attacks were classified as high-level aggression. Whenever both members of a dyad could be observed for 10 minutes following an aggressive interaction, affiliative contact (e.g. grooming, embracing, kissing) between the pair during that period was recorded as a reconciliation (de Waal 1993).

Behavioral contexts of aggression were recorded in the following categories: reason (incidents occurring within 5 minutes of a reunion), social excitement (incidents occurring upon hearing distant chimpanzee calls, or arrival at a fruiting tree), sexual competition, nest competition, plant food competition, protection (offspringing), and unknown context. For further description of these contexts see Bygott (1974) and Goodall (1986).

Dominance ranks are commonly assigned to male chimpanzees based on the distribution of pant-grunt vocalizations (e.g. Bygott 1979). Pant-grunt orientation is highly directional, and reliably correlates with several other measures of dominance (Bygott 1974). In the current study, however, observed pant-grunts were insufficient to distinguish male rank beyond the basic categories of alpha, high, medium, and low (cf. Bygott 1974).

In order to acquire enhanced resolution on relationships among the adult males, I assigned dominance ranks based on the outcome of directed agonistic bouts. To do this, I employed a probabilistic model (Jameson et al. 1999) that takes into account the number of opponents that an individual has successfully defeated, and the relative success of those opponents in their own agonistic encounters. This method has two major advantages over the standard techniques that provide ordinal dominance rankings. First, it can be used to predict dominance relationships for dyads that have not yet been observed encountering each other. Second, it provides information about how dominant individuals are over others. Specifically, scale values indicate the probabilities associated with pairs of ranks (males in the current study received scale values falling between 1 and 3). This probabilistic method is similar to those used for ranking chess players. Further discussion of the method,
Sex differences in aggression

Male chimpanzees at Kanyawara exhibited much more frequent and intense aggression than adult females. Figure 8.1 presents mean rates of aggression (charging, displays, chases, and attacks) for each sex. Though variability exists within each sex, adult males were aggressive approximately 14 times more often than adult females (males: mean = 0.28 acts per observation hour, n = 11; females: mean = 0.02 acts per observation hour, n = 10). This figure probably overestimates female aggression because it excludes observations made when focal individuals were traveling alone (or solely with dependent offspring), and female chimpanzees are more likely to be solitary than males (Nishida 1979; Goodall 1986; Wrangham 2000). Table 8.1 shows attack rates for males and females at both Kanyawara and Gombe. The same pattern of male-biased aggression is evident.

Aggression by female chimpanzees tended to take place in different contexts from aggression by males. Table 8.2 illustrates this sex difference with data from three long-term study sites; it only includes episodes in which a context could be clearly determined. Fifty-two percent of male aggression at Kanyawara and 46% at Gombe took place in indeterminate contexts. Most of these episodes appeared to be related to male dominance rivalry (Goodall 1986, personal observation). When contexts of male aggression could be determined, they were similar at Gombe and Kanyawara. A large proportion of male agonism took place either within 3 minutes of a reunion (34% at Kanyawara, 38% at Gombe) or during sexual competition (30% at Kanyawara, 17% at Gombe). Much aggression at Gombe also took place during competition for meat (17%); this figure was lower at Kanyawara (4%), where little hunting took place during 1988.

Contexts of female aggression were less ambiguous than those of male aggression; 53% of observations at Gombe, 41% at Kanyawara, and 28.6% at Mahale could not be assigned to a distinct context. The most frequent contexts of female aggression were competition for plant food (80% at Kanyawara, 38% at Gombe, 35% at Mahale) and protection of offspring (12% at Kanyawara, 35% at Gombe, 53% at Mahale). If interspecific interactions are considered at Kanyawara, an even higher percentage of female aggression took place there during feeding competition; female chimpanzees occasionally chased blue monkeys or mangabeys from preferred feeding sites in fruiting trees. These episodes were excluded from the present data set, but the aggression appeared identical to that directed toward conspecific feeding competitors.

Males and females tended to direct aggression at different targets. Table 8.3 shows the distribution of victims at two long-term study sites. At Kanyawara, most aggression by adult males (49.2%) was directed at other adult males; somewhat less (24.6%) was directed toward parasitic females. Few parasitic females were cycling during this study, but preliminary data from one popular female, Lisa, suggest that parasitic females receive more aggression when they exhibit sexual swellings than at other times. During 33 hours of
### Table 8.1. Frequency of attacks by males and females at ten long-term study sites

<table>
<thead>
<tr>
<th>Community</th>
<th>Year</th>
<th>Sex</th>
<th>Focal hours</th>
<th>Focal IDs</th>
<th>Total attacks</th>
<th>Observation hours per attack</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kanyawara</td>
<td>1998</td>
<td>Male</td>
<td>1428.3</td>
<td>11</td>
<td>45</td>
<td>51.7</td>
</tr>
<tr>
<td>Gombe</td>
<td>1978</td>
<td>Male</td>
<td>1570</td>
<td>7</td>
<td>23</td>
<td>68.3</td>
</tr>
<tr>
<td>Gombe</td>
<td>1976</td>
<td>Male</td>
<td>829</td>
<td>6</td>
<td>16</td>
<td>51.8</td>
</tr>
<tr>
<td>Gombe</td>
<td>1970</td>
<td>Male</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>33</td>
</tr>
<tr>
<td>Kanyawara</td>
<td>1998</td>
<td>Female</td>
<td>679.8</td>
<td>10</td>
<td>5</td>
<td>136</td>
</tr>
<tr>
<td>Gombe</td>
<td>1978</td>
<td>Female</td>
<td>1647</td>
<td>7</td>
<td>15</td>
<td>109.8</td>
</tr>
<tr>
<td>Gombe</td>
<td>1976</td>
<td>Female</td>
<td>877</td>
<td>6</td>
<td>9</td>
<td>99.7</td>
</tr>
</tbody>
</table>

**Note:** Kanyawara data include adults with more than 25 observation hours. Gombe data from 1978 and 1976 include only adults with more than 100 observation hours (Goodall 1986). Gombe data from 1970 are from Bygott (1974). Follows of lone targets (including females with dependent offspring) have been excluded.

### Table 8.2. Context of aggression in three long-term study sites

| Context          | Kanyawara 1998 | Gombe 1978 | Mahale | |
|------------------|----------------|-------------|--------|
|                  | Males | Females | Males | Females | Males | Females | |
| Reunion          | 34    | 0       | 18    | 5       | 5     |         | |
| Sexual competition | 36    | 8       | 17    | 2       | 7.5   |         | |
| Plant-food competition | 15    | 80      | 7     | 38      | 35    |         | |
| Meat competition  | 4     | 0       | 17    | 5       | 0     |         | |
| Social excitement | 8     | 0       | 13    | 1       | 2.5   |         | |
| Protection       | 1     | 12      | 5     | 38      | 35    |         | |
| Miscellaneous    | 2     | 0       | 3     | 11      | 15    |         | |
| Total observations | 212   | 25      | 274   | 149     | 40    |         | |

**Note:** Numbers refer to the percentage of aggressive acts that take place in each context.

Cases where the context was not clear to observers have been omitted (Gombe: 14% of male observations, 6.3% of female observations; Kanyawara: 52% of male observations, 11% of female observations; Mahale: 28.6% of female observations). Gombe data are from Goodall (1986). Only female data are available from Mahale; these were collected over three field seasons in the early 1980s by Nishida (1989).

Focal observation with no sexual swelling, Lia received aggression from adult males every 8.3 hours during 46 hours of observation with a partial or maximal swelling, Lia was the victim of male aggression every 3.8 hours. This increased rate of received aggression was partially due to the fact that more adult males were present when Lia was swollen. However, males also became more aggressive when traveling in parties with crouching females (see below). Adult females were not observed to exhibit any aggression towards other adult females; more than 70% of their aggression was directed at juvenile and subadult females.

At Gombe, adult males directed slightly more of their
aggression at adult females (48%) than adult males (34%) (Goodall 1986). Adult females at Gombe also appeared to be involved in aggressive interactions with other adult females more frequently than at Kanyawara; 33% of observed aggression by adult females at Gombe was directed at other adult females (Goodall 1986).

Dominance relationships
Most pant-grunts by adult males (64%) were directed toward the alpha male (n = 89). The two lowest-ranking males produced 39% of male pant-grunts. Consistent with data from Mahale (Nishida & Hosaka 1990), male dominance rank was positively and significantly correlated with the total number of pant-grunts received (n = 11, r = 0.66, p = 0.03), and the total number of agonistic initiations (n = 11, r = 0.60, p = 0.02) (both uncorrected for observation hours).

During the study period, the alpha-male, Inosou, was just beginning his tenure at the top. For 3 years, starting in mid-1994, Big Brown had been the alpha-male at Kanyawara, and his ally, Tofu, had held the beta position (Kibale Chimpanzee Project, long-term data). In mid-1997 Inosou, together with his ally Johnny, began to challenge these top-ranking males. By the end of that year they were clearly established as the new alpha and beta males. Tofu fell to third, and Big Brown to fourth place in the hierarchy.

Although the observed dominance hierarchy was of relatively recent origin, it appeared to be quite stable during the study period; no reversals were observed in male-male pant-grunt interactions. Only three reversals were recorded in 107 decided agonistic bouts.

It was not possible to rank the 15 adult females in a linear hierarchy because dominance interactions between them were extremely rare. In 680 hours of focal observation, not one aggressive interaction was recorded between parous females. Also, although parous females frequently pant-grunted to adult males, they were rarely observed pant-grunting to other parous females.

Patterns of male aggression
The most frequent form of male aggression was the charging display. Display rates differed among males, but the alpha male, Inosou, was clearly the most aggressive member of the community. His display rate (0.69 per observation hour) was 4.5 times the male average (0.13 per observation hour), and more than twice that of the next highest male (Tofu: third-ranking male, 0.29 per observation hour). Dominance rank and frequency of display were significantly correlated across the 11 adult males (r = 0.75, p = 0.008, Figure 8.2).

Consistent with reports from Gombe (Bryant 1974; Goodall 1986), vocal displays were rarely directed toward
specific individuals (only 6.8% of 148 vocal displays). Instead, they appeared to be directed either toward the group in general, or toward distant chimpanzees. Nonlocal displays, on the other hand, were frequently directed toward specific targets within a party (53.2% of 186 displays: Stiner and Kim procedure, p < 0.00001).

When only high-level agonistic acts (chases and attacks) are considered, the alpha male was still the most frequent aggressor in the community. Furthermore, rank and high-level aggression were positively and significantly correlated across the adult males (r = -0.11, p = 0.014). Table 8.1 shows mean attack rates for males at both Kanyawara and Gombe. Male attack rates from Kanyawara in 1998 are comparable to those reported from Gombe in 1970; they are higher than those reported from Gombe in 1974 and 1978.

The frequency of aggression in a given party at Kanyawara was positively and significantly correlated with the number of adult males in that party (r = 0.95, p = 0.0001, Figure 8.3). However, the rate of aggression per male did not increase with party size. Party composition, in contrast, had a substantial effect on rates of male aggression. When maximally swollen, parous females were present in a party, both the rate and intensity of male aggression increased.

The average daily rate of aggression in parties containing eight to nine adult males and no estrous females was 1.68 incidents per hour. These incidents tended to be mostly low-level aggression (30% charging displays only, 30% chases and attacks). The average daily rate of aggression in parties containing eight to nine adult males and a parous female in her periovulatory period was significantly higher, at 3.2 incidents per hour (Rust-Pigman rank-based test: Z = 6.01, p < 0.005) of mostly high-level aggression (59% chases and attacks).

Table 8.4 shows rates of reconciliation at Kanyawara together with those reported from captivity. Adult males at Kanyawara rarely reconciled with each other following a conflict (less than 9% of interactions). Across all age and sex classes, only 10% of conflicts were reconciled within 10 minutes. This is considerably lower than the rate of reconciliation reported from captivity (de Waal 1993). Similarly low rates of reconciliation reported from Tai (Wrangham 2000) suggest that chimpanzees in the wild are less motivated to reconcile conflicts, perhaps because in the short-term they can always avoid particular conspecifics by fissioning from a party.

**Intercommunity aggression**

Intercommunity relations among male chimpanzees are predictably hostile. Border patrols, aggressive territorial defense, and border avoidance by lone individuals have been reported from all the long-term study communities except Bossou, which has no neighbors (reviewed in Wrangham 1999). Cautionary intergroup attacks, sometimes lethal, appear to be a regular feature of chimpanzee society. Two such attacks occurred at Kanyawara during this study, one of which resulted in a fatality.
Table 8.4. Reconciled conflicts in wild and captive chimpanzees

<table>
<thead>
<tr>
<th>Study Population</th>
<th>Dyads observed</th>
<th>Number reconciled</th>
<th>Percentage reconciled</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kanyawara 1998</td>
<td>124</td>
<td>18</td>
<td>10.3</td>
</tr>
<tr>
<td>Male-male</td>
<td>91</td>
<td>8</td>
<td>8.8</td>
</tr>
<tr>
<td>Male-female</td>
<td>62</td>
<td>8</td>
<td>12.9</td>
</tr>
<tr>
<td>Female-female</td>
<td>8</td>
<td>1</td>
<td>12.5</td>
</tr>
<tr>
<td>Other</td>
<td>13</td>
<td>1</td>
<td>8.3</td>
</tr>
<tr>
<td>Captive chimpanzees</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arnhem 1975-76</td>
<td>130</td>
<td>52</td>
<td>24.7</td>
</tr>
<tr>
<td>Arnhem 1976 (outdoors)</td>
<td>200</td>
<td>59</td>
<td>29.5</td>
</tr>
<tr>
<td>Arnhem 1980 (outdoors)</td>
<td>395</td>
<td>105</td>
<td>26.6</td>
</tr>
</tbody>
</table>

Note:
Reconciliation is defined as any affiliative contact between individuals within ten minutes of their aggressive interaction. 'Other' includes interactions involving at least one juvenile. Interactions with juveniles have been excluded from the other categories. Captive data are from de Waal (1993).

On 12 August, 1998, five adult males from the Kanyawara community traveled to the southern boundary of their territory, where they encountered a nulliparous female and a subadult male from the neighboring community. The Kanyawara males attacked the pair, chasing them into a low tree. Both leaped approximately 7 m to the ground, and the subadult male fled to the south. Three Kanyawara males surrounded the female, striking her repeatedly. She was able to escape, however, and ran quickly to the southwest. Four adult males from the southern community arrived within 2 minutes of the female's departure, presumably attracted by the screaming. They displayed and exchanged aggressive vocalizations with the Kanyawara males, who subsequently retreated further than 1 km into their own territory.

In a second incident on 23 August, 1998, a group of ten adult males from the Kanyawara community patrolled the northern border of their territory. Observers lost the group at 17:05, but located them nearby the following morning with a dead male (aged 20-25 years) from the neighboring community. He had been killed the previous evening. The site and the body exhibited signs of a protracted and vicious assault. The dead male lay at the base of a steep slope in a 7-m\(\times\)12-m patch of trampled vegetation (Figure 8.4). His arms and legs were extended, suggesting that he had been immobilized by some individuals while others attacked (as occurs in both captive chimpanzees and bonobos). Amy Parish, personal communication). The pattern of injuries was consistent with this scenario, as more than 30 puncture wounds and lacerations, ranging from 0.5 cm to 12 cm in diameter, were distributed across his face and the ventral surface of his arms, legs, and abdomen. The dorsal surface was undamaged.

Compound fractures in four of the left ribs attested to severe blows delivered by fists or feet. The testicles had been ripped from the body, and were recovered nearby. Five fingerprints and one toenail had been torn from the digits with significant portions of both attached. The immediate cause of death appeared to be massive trauma to the throat, including a severed trachea (Figure 8.4).

The Kanyawara males were found with the dead stranger on the morning of 26th August. Several of the males were beating on the corpse when we arrived. As they had also been seen near the attack site on the evening of 25th August, when the male was killed, it seems likely that they were responsible. At approximately 10:45, at least three males from the neighboring community arrived near the attack site, and the two groups exchanged aggressive vocalizations. At 11:45 the Kanyawara males retreated to the south.

DISCUSSION AND CONCLUSIONS

Female-female competition
Consistent with reports from Gombe (Goodall 1986) and Mahale (Nishida 1989), female chimpanzees at Kanyawara were aggressive primarily in the context of feeding compe-
aggression primarily at newly immigrated females because such immigrants represent potential resource competitors. After dominance relationships are established between females, they remain stable because of the costs of escalated aggression, which include potential danger to offspring, outweigh the benefits of increased dominance standing. Since parasitic females are already settled in their core area, they have no pressing reason to strive for higher rank (Nishida 1989, p. 86).

Given that core areas may differ in both size and quality, however, and that core areas frequently overlap (e.g. Posey et al. 1997), the rarity of aggressive interactions between adult females remains puzzling. Data from Gombe suggest that high dominance rank accords female chimpanzees significant reproductive advantage. For example, high-ranking females there appear to maintain access to higher-quality core areas (Posey et al. 1997; Williams 1999). These females live longer than low-ranking females, and enjoy shorter inter-birth intervals and higher offspring survival. They also produce daughters who reach sexual maturity earlier than those of low-ranking mothers, presumably because of improved nutrition (Posey et al. 1997). With so much at stake, one might expect female chimpanzees to show more overt competition over dominance than they appear to.

One possible explanation for the low rates of aggressive competition observed among females at Kanyawara is that competition for space is not pronounced there as it is at Gombe; thus, the benefits of high rank to Kanyawara females are correspondingly less. This hypothesis has not yet been tested directly, but several observations suggest that female competition at Gombe is particularly intense. First, young females at Gombe exhibit a relatively low rate of transfer (Williams et al., Chapter 14). A female who stays in her natal community presumably bears increased costs associated with inbreeding, but may benefit from associating with a high-ranking mother, for example by settling in her core area. Second, both infanticide and attempted infanticide by high-ranking females against low-ranking mothers appear to be more common at Gombe than at Kanyawara (Table 8.3). In the present study, no aggressive interactions were observed between adult females at Kanyawara in more than 681 hours of focal observation. At Gombe in 1978, adult females targeted other adult females approximately 13% of the times that they were aggressive (n = 139 aggressive acts, Goodall)
1986). It is difficult to say whether this reflects a real differ-
ence, as Goodall does not provide overall rates of female ag-gression. Long-term data on female dominance rank and
reproductive success at Kanyawara will eventually help to
clarify this issue.

Male–male competition
Male–male competition in chimpanzees takes two general
forms, both of which were evident in this study. In the long-
term, male chimpanzees cooperate to defend a territory
against neighboring males. This cooperation includes
border patrols and retaliatory attacks on vulnerable rivals,
and is discussed below. In the short-term, males within a
community compete aggressively (e.g. Watts 1998) and
through sperm competition (Hasegawa & Hiraiwa-
Hasegawa 1990) for access to estrous females.

Male chimpanzees are sometimes able to avoid short-
term mating competition by escorting an estrous female to a
peripheral part of the range in an exclusive copulation
(Goodall 1986). Genetic data from Gombe indicate that this
is sometimes a successful reproductive strategy, particularly
for low-ranking males (Constable et al. 2001). Of fourteen
infants genotyped in that community, three were sired in the
copulation context, and two more were probably sired in the
copulation context, all by low- and middle-ranking males.

Behavioral data from three long-term study sites
(Gombe, Mahale, and Tai), however, indicate that most
chimpanzee conceptions occur in the context of multi-male
parties (75–94%: Hasegawa & Hiraiwa-Hasegawa 1990;
Wallis 1997; Boesch & Boesch-Achermann 2000). Although
copulations sometimes occur in such parties with little male
aggression or coercion (Tutin 1979), this is generally limited
to matings with pluriparous females, or parous females in the
mid-follicular phase. Once pluriparous females reach their peri-
avulatory period, they become much more attractive to
males, and coercion and aggression increase markedly
(reviewed in Muller & Wrangham 2001). In the current
study, males at Kanyawara showed both increased frequency
and intensity of aggression in the presence of pluriparous females.

Among male chimpanzees, success in short-term mating
competition is closely predicted by dominance rank.
Because low-ranking males may have access to pluriparous
females in the mid-follicular phase, and pluriparous females
throughout the cycle, overall copulation rates may or may
not correlate with dominance rank. However, alpha and
high-ranking males consistently exhibit the highest copula-
tion rates with parous females in the periovulatory period
(reviewed in Muller & Wrangham 2001).

Copulation frequency is not necessarily an accurate
proxy for reproductive success. However, preliminary
genetic data from Gombe support the idea that high rank is
reproductively advantageous. Of nine infants sired there in
the group-mating context, five were sired by the alpha male,
two by males who subsequently became alpha, one by a
high-ranking male, and one by a middle-ranking male
(Constable et al. 2001; for similar results from bonobos see
Gerloff et al. 1999).

The positive correlation between dominance rank and
aggression reported here is consistent with observations from
other long-term study sites. At Gombe in 1970, Bygott
(1974) found significant correlations between male domi-
nance rank and rates of both charging display and attack.
At Tai in 1993, the two highest-ranking males performed 80%
of all agonistic displays (Boesch & Boesch-Achermann
2000). At Mahale in 1992, dominance rank was strongly cor-
rrelated with total number of agonistic initiations (Nishida et
Hoaka 1996). Finally, long-term data from Kanyawara
indicate that two previous alpha males there also had the
highest rates of display during their tenures at the top
(Wrangham, unpublished data).

Among primates generally, however, high levels of
aggression are not consistently associated with high domi-
nance rank. Olive baboons (Papio anubis) are a well-studied
example. Sapolsky (1982) found that among male baboons in
Mau Maara, dominance rank in copulatory success was
related to success in a number of competitive behaviors.
During periods of dominance instability, however, frequency
of aggression was not associated with high rank. In fact, the
initiators of agonistic interactions lost those interactions
80% of the time when the hierarchy was stable. Only during
periods of dominance instability do dominant male baboons
consistently show the highest rates of aggression (reviewed
in Sapolsky 1993). Sapolsky characterizes a baboon hier-
archy as unstable when the overall rate of reversals in
approach–avoidance interactions exceeds 8%. Such periods
of instability are relatively rare in the wild, but may follow
shifts in troop membership (e.g. Alberts et al. 1992).

The chimpanzee data, however, suggest that high rates
of aggression are characteristic of high-ranking chimpanzees
males, even in stable hierarchies. The associations between
rank and aggression reviewed above all took place during
Agnostic relations among Kanyawara chimpanzees

periods of relative dominance stability. The rate of pant-grunt reversals among adult males at Gombe during 1970 was only 0.9% (2 of 222 interactions: Bygott 1974, Table 3.2). At Mahale in 1992 the rate was 1.1% (3 of 268 interactions: Nishida & Hoasca 1996, Table 9.3). At Tait in 1993, the rate was 0.9% (1 of 109 interactions, Boesch & Boesch-Achermann 2000, Table 6.3). In the present study, no reversals were recorded in 89 pant-grunt interactions between adult males.

The overall rate of reversals for decided agonistic bouts between adult males in this study was only 2.8%. A comparable figure is not available from Gombe during 1970, but the overall rate of reversals for attacks there was only 3.3% (calculated from Bygott 1974, Table 5.4). At Tait in 1993, the overall rate of reversals for agonistic interactions among adult males was, at 12.9%, slightly higher (calculated from Boesch & Boesch-Achermann 2000, Table 6.3).

Although the alpha male at Kanyawara had just started his tenure during the present study, at other sites high rates of aggression were exhibited by males who had been dominant for some time. During Bygott's (1974) Gombe study, the alpha male, Mike, was in the 6th year of his tenure. At Tait in 1993, Fritz was in the 3rd year of a 4-year tenure (Boesch & Boesch-Achermann 2000). At Mahale, Nishida reacquired his alpha status approximately 3 months prior to Nishida's 1992 observations; he had been the alpha male in 1991, but was briefly ousted from the position by a coalition of two other males (Nishida & Hoasca 1996).

Thus, male chimpanzees living in what are normally considered to be stable hierarchies tend to exhibit patterns of aggression similar to those of male baboons living in extremely unstable hierarchies. What accounts for this element of perpetual instability in dominance relationships among chimpanzee males? One possibility is that the fusion-fission nature of chimpanzee social organization makes it relatively more difficult for high-ranking individuals to keep track of social relationships among other males in the group. Male baboons range in relatively stable groups, so their knowledge of the dominance hierarchy and their place in it should be fairly accurate. Chimpanzee males, in contrast, frequently leave groups and meet their harem mates, or even work later. Since a high-ranking male can never be certain what political maneuvering has occurred in his absence, it is necessary for him continually to reestablish his dominance when parties come together. This could help to explain the large proportion of aggression that takes place in the context of reunions.

Coalitions are important to chimpanzee males in both maintaining and improving their dominance standing (Nishida 1983; Goodall 1986; Nishida & Hoasca 1996). These coalitions can be very fluid, with males showing high degrees of "allegiance flexibility" (i.e. a male may frequently turn against his former alliance partner if it is in his interest to do so) (Nishida 1983). The fluid nature of both male chimpanzee coalitions and party composition, then, is likely to explain some, but not all of the apparent instability in male chimpanzee hierarchies. For, despite their frequent use of coalitions, males can generally be ranked in a linear hierarchy (Boesch & Boesch-Achermann 2000), and although baring a coalition partner may raise a male's confidence to the point that he challenges a higher-ranking individual, actual reversals in rank generally result from dyadic fights (Goodall 1986; Boesch & Boesch-Achermann 2000).

The possibility that dominance hierarchies among male chimpanzees are inherently unstable has important implications for the presumed costs and benefits of social dominance in this species. When baboon hierarchies are unstable, high rank is often associated with elevated glucocorticoid secretion, probably reflecting severe psychological stress (Sapolsky 1992). Chronic exposure to high levels of circulating glucocorticoids is associated with a suite of adverse physiological effects, including depressed immune function (e.g. Sapolsky 1993). Furthermore, among baboons the most aggressive males also tend to exhibit the highest levels of circulating testosterone (Sapolsky 1993). Additional costs associated with chronically high levels of circulating testosterone include increased metabolic rate and immunosuppression (reviewed in Wingfield et al. 1997). If the most aggressive, highest-ranking chimpanzee males are maintaining chronically elevated levels of cortisol and testosterone, then these would represent previously unknown costs to social dominance. Preliminary hormonal data from Kanyawara indicate that this is indeed the case; during the study period both testosterone and cortisol were positively and significantly correlated with rank across the adult males (Moller 2002).

Intercommunity aggression

Coalitional killing has previously been reported from two long-term chimpanzee study sites in Tanzania. In Gombe, males from the Kanukul community made systematic incursions into the neighboring Chabusa group's territory over a period of 3 years, eliminating their rivals one by one in a
series of vicious gang attacks (Goodall et al. 1979; Goodall 1986). Subsequently, the Kasekela males appropriated much of the Kahama group’s range. A similar group extinction was later documented in Mahale National Park (Nishida et al. 1985). Because chimpanzees at both of these sites were provisioned, it has been argued that lethal intergroup attacks are an adverse effect of artificial feeding, not a natural aspect of chimpanzee behavior (Powell 1991).

The coalititary attacks described above add to a growing body of evidence that lethal, intergroup aggression is a common strategy employed by male chimpanzees to reduce the coalititary strength of their neighbors and expand their territories (Wrangham 1999). The evolution- ary benefits of such expansions are clear. First, larger terri- tories may include the ranges of more females. Second, females living in larger territories may have shorter inter- birth intervals and improved offspring survival (Williams 1999). After the group extinctions at Gombe and Mahale, the aggressors appropriated both territory and females from their defeated neighbors (Goodall et al. 1979; Nishida et al. 1985; Goodall 1986). Animals generally avoid escalated dyadic aggression because of the inherent risk of severe injury from other, similarly armed adults (e.g. Maynard Smith & Price 1973). Coalititory aggression, however, may allow chimpanzees to mitigate these costs. At both Gombe and Kibale, cooper- ating males inflicted lethal injuries without sustaining appreciable wounds. Selection may therefore have favored a strategy by which male chimpanzees utilize lethal aggres- sion against foreign males whenever there is an extreme imbalance of power (Manson & Wrangham 1991; Wrangham 1999). This idea is supported by the observa- tions from Kanyawary, in which cooperating males attacked a subadult male and a nulliparous female, and appear to have attacked and killed a less male, but in both cases retreated upon the arrival of additional strangers. This may also explain why killings have not yet been witnessed at Tai, where food availability is high, party size is consistently large, and individuals are rarely forced to forage alone (Boesch & Boesch-Achermann 2000).

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