# RESEARCH ARTICLE

## Alpha Male Chimpanzee Grooming Patterns: Implications for Dominance "Style"

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In social primates, individuals use various tactics to compete for dominance rank. Grooming, displays and contact aggression are common components of a male chimpanzee's dominance repertoire. The optimal combination of these behaviors is likely to differ among males with individuals exhibiting a dominance "style" that reflects their tendency to use cooperative and/or agonistic dominance tactics. Here, we examine the grooming behavior of three alpha male chimpanzees at Gombe National Park, Tanzania. We found that (1) these males differed significantly in their tendency to groom with other males; (2) each male's grooming patterns remained consistent before, during and after his tenure as alpha, and (3) the three males tended to groom with high- middle- and low-ranking partners equally. We suggest that body mass may be one possible determinant of differences in grooming behavior. The largest male exhibited the lowest overall grooming rates, whereas the smallest male spent the most time grooming others. This is probably because large males are more effective at physically intimidating subordinates. To achieve alpha status, a small male may need to compensate for reduced size by investing more time and energy in grooming, thereby ensuring coalitionary support from others. Rates of contact aggression and charging displays conformed to this prediction, suggesting that each male exhibited a different dominance "style." Am. J. Primatol. 71:136–144, 2009.    © 2008 Wiley-Liss, Inc.

Key words:  chimpanzee; alpha male; grooming; dominance style; body mass

## INTRODUCTION

In social primates, individuals use various tactics to increase and maintain their dominance rank [de Waal, 1982; Nishida & Hosaka, 1996; Schino, 2001]. For example, male chimpanzees (*Pan troglodytes*) use charging displays [Bygott, 1979; Simpson, 1973], agonism [de Waal, 1982; Watts, 2000a,b], coalitionary networks and grooming [Hemelrijk & Ek, 1991; Nishida & Hosaka, 1996] to establish and maintain their position in the hierarchy. The benefits of high rank include increased access to food [de Waal, 1982] and sexual partners [Nishida & Hiraiwa-Hasegawa, 1987]. These advantages ultimately lead to greater reproductive success for high-ranking males [Constable et al., 2001].

There is strong evidence that grooming is a critical component of a male chimpanzee's competitive strategy. At Gombe National Park, Tanzania, high-ranking males exhibited higher grooming frequencies and typically received more from their lower-ranking partners than they gave [Simpson, 1973]. Studies in the Arnhem Zoo, the Netherlands

[de Waal, 1982], Mahale Mountains National Park, Tanzania [Nishida & Hosaka, 1996] and Kibale National Park, Uganda [Watts, 2000a,b] suggest that high-ranking males are attractive grooming partners that other males compete to groom. In return, high-ranking males may be more likely to provide coalitionary support to males that groom them. However, later studies in Mahale [reviewed in Watts, 2000b] and Budongo Forest, Uganda [Arnold & Whiten, 2003] found that partner rank had little effect on overall grooming and coalition choices.

Despite considerable interest in the causes and consequences of high rank [Boesch & Boesch-Achermann, 2000; Bygott, 1979; Goodall, 1986; Hemelrijk & Ek, 1991; Mitani et al., 2002; Newton-Fisher, 2002; Nishida, 1968, 1979; Nishida & Hiraiwa-Hasegawa, 1987; Pusey et al., 2005; Simpson, 1973; Watts, 2002], the extent of within- and between-individual variation in dominance strategies, and grooming in particular, is unclear. Grooming is the most common affiliative behavior among all primates [reviewed in Goosen, 1981] and correlates highly with other tactics males may use to placate rivals or reward coalition partners, such as tolerance of copulation and meat-sharing [Mitani & Watts, 2001; Muller & Mitani, 2005]. Previous studies that examined dominance strategies looked exclusively at agonistic behaviors, specifically dominance displays and contact aggression [Boesch & Boesch-Achermann, 2000; Bygott, 1979; de Waal, 1982; Goodall, 1986; Muller, 2002; Nishida & Hosaka, 1996; Wrangham & Peterson, 1996]. Here, "first investigate the grooming rates of males who were alpha during a 10 year study period, and then relate these findings to their average rates of agonistic behaviors" and then relate these findings to the alpha males' average rates of agonistic behaviors. This approach leads to a fuller understanding of the relationship between grooming and dominance. We focus upon alpha males because they presumably utilize the most ''successful'' dominance strategies.

Two factors are likely to influence male chimpanzee dominance strategies: males differ considerably in size [Pusey et al., 2005] and temperament [Goodall, 1986]. Evidence from Gombe suggests that large, aggressive males may rely on brute strength to achieve and maintain alpha status [Bygott, 1979; Goodall, 1986]. As these males can physically dominate their rivals, they may not need to maintain high rank through grooming rivals or form coalitions. In contrast, smaller males may use grooming and other tactics to placate rivals and/or foster cooperative alliances. De Waal [1989] and de Waal & Luttrell [1989] use the term ''dominance style'' to describe variation in levels of ''tolerance'' and agonism among individuals. It has been suggested that chimpanzee alpha male dominance style can be classified on a continuum from ''cooperative'' to ''despotic,'' and that a given male's relative size and strength may be among several factors that determine his optimal strategy [de Waal, 1982; Goodall, 1986].

If all males compete to groom with the highest-ranking partners, [Seyfarth, 1977] high-ranking males themselves may tend to be involved in grooming more frequently than males of other ranks, regardless of their physical size [Nishida & Hosaka, 1996; Simpson, 1973; Watts, 2000a,b]. It is therefore likely that the alpha male participates in grooming more than any other male. Moreover, his partners are likely to be high-ranking because they will outcompete their subordinates to groom him. This predicts that a male should exhibit higher overall grooming rates when he is alpha than during pre- or post-alpha periods and should groom predominantly with higher-ranking males.

Here, we use long-term data from Gombe National Park to compare the grooming behavior of three males that became alpha during a 10-year study period. We explore the hypothesis that these males exhibit grooming patterns that vary within and among individuals according to their dominance strategy. We test the following predictions: (1) overall grooming rates will be negatively associated with body mass—the larger the male is, the lower his rates of total grooming will be; (2) rates of directional grooming will also be associated with body mass, with larger males less likely to groom others; (3) the grooming rates of each male will be higher during his tenure as alpha than during pre- or post-alpha periods; (4) alpha males will groom most often with the highest-ranking partners.

## METHODS

### Study Site and Data Collection

All research was approved by the Tanzanian Wildlife Research Institute (TAWIRI), Tanzania National Parks (TANAPA), the Tanzania Commission for Science and Technology (COSTECH) and complied with the regulations of the Institutional Animal Care and Use Committee of the University of Minnesota. Gombe is a small ($35 \, km^2$) park situated between Lake Tanganyika in the west and a rift escarpment in the east. It consists of several steep valleys of evergreen forest that are separated by woodland and grassland ridges [Clutton-Brock & Gillett, 1979]. We used long-term data on the Kasekela community, which has been studied continuously since 1960 [Goodall, 1986]. We used data from 1992 to 2001, during which the community contained between 40 and 49 chimpanzees (11–17 adult males). Goodall [1986] observed that Gombe males reached physical and social maturity at age 16. However, we included males that were at least 10-years old in our analyses because at this age they begin to frequently travel independently of their mothers with adult males, enter the male hierarchy [Goodall, 1986; Pusey, 1983], father offspring [Boesch et al., 2006] and groom adult males [Pusey, 1990].

Since 1975, the fieldwork has been conducted by a team of Tanzanian field assistants under the direction of Dr. Jane Goodall, Dr. Janette Wallis (1990–1994), Dr. D.A. Collins (1994–1997) and Dr. Shadrack Kamenya (1997–2003). Two observers follow a focal chimpanzee, typically from dawn to dusk, systematically recording the individual's behavior. Each month the observers usually follow each adult male at least once, and the alpha male several times (Table I). One observer records the identity of

**TABLE I. The Number of Focal Follows of Each Male Per Year**

| | AL | AO | BE | EV | FD | FO | FR | GB | GD | GL | KS | PF | PX | SL | TB | WL | Annual means |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1992 | 12 | 2 | 8 | 30 | 26 | | 19 | 33 | | 3 | | 36 | 3 | | 6 | 43 | 18.4 |
| 1995 | 10 | 6 | 11 | | 79 | | 23 | 18 | | 13 | 4 | 23 | 5 | 5 | 9 | 19 | 17.3 |
| 1996 | 10 | 8 | 10 | | 50 | | 26 | 21 | | 14 | 6 | 15 | 8 | 5 | 10 | 18 | 15.5 |
| 1999 | | 12 | 7 | | 19 | | 24 | 17 | 0 | 7 | 10 | | 7 | 6 | 9 | 17 | 11.3 |
| 2000 | | 14 | 12 | | 21 | 0 | 16 | 12 | | 18 | 11 | | 9 | 6 | 14 | 13 | 12.2 |
| 2001 | | 17 | 16 | | 19 | 0 | 26 | 19 | | 14 | 11 | | 12 | 16 | 13 | 12 | 14.6 |
| Total mean | | | | | | | | | | | | | | | | | 14.9 |

Shaded boxes indicate if a male was either a juvenile or deceased.

**TABLE II. The Ranks of All Males by Year**

| | AL | AO | BE | EV | FD | FO | FR | GB | GD | GL | KS | PF | PX | SL | TB | WL |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1992 | Low | Low | Middle | Middle | High | | Middle | High | | Low | Very Low | Middle | Very low | | Low | Alpha |
| 1995 | Low | Low | High | | Alpha | | High | High | | Middle | Low | Middle | Very low | Very low | Middle | Low |
| 1996 | Low | Low | Middle | | Alpha | | High | High | | Middle | Low | Middle | Very low | Low | High | Low |
| 1999 | | High | Low | | Middle | | Alpha | High | Very low | Low | Middle | | Very low | Low | Middle | High |
| 2000 | | High | Low | | High | Very low | Alpha | High | | Low | Low | | Very low | Middle | Middle | Middle |
| 2001 | | High | Low | | High | Very low | Alpha | Middle | | Low | High | | Very low | Middle | Middle | Low |

Adult males are ≤10-years old. Shaded boxes indicate if a male was either a juvenile or deceased.

all chimpanzees within visible range of the focal chimpanzee (party composition) every 15 min and the other records social interactions in longhand narrative notes. The narrative notes thus contain data on grooming by the focal individual, including partner, direction (give, receive, mutual) and duration. These data are digitized and stored in a relational database at the Jane Goodall Institute's Center for Primate Studies at the University of Minnesota.

## Study Subjects

We studied three adult males, Wilkie (WL), Freud (FD) and Frodo (FR), each of which was alpha at some point during the study period (Table II). These males differed considerably in body mass [Pusey et al., 2005]. WL weighed an average of 37.0 (±1.6 SD) kg during the study period. This was small compared with the median weight of males aged 15–30 of 39 (±1.22 SD) kg [Pusey et al., 2005]. He was born in 1972 and was alpha from October 1989 to February 1993. FD became alpha after WL and weighed an average of 44.8 (±2.62 SD) kg during the study period. He was considerably larger than most of the mature males in Gombe [Pusey et al., 2005]. Born in 1971, he was alpha male from February 1993 to September 1997. FR became alpha after FD and was the second largest male ever measured at Gombe [Pusey et al., 2005]. He weighed an average of 51.2

**TABLE III. The Classification of Social Status Positions for Each Male and Years for Study**

| | WL | FD | FR |
|---|---|---|---|
| 1992 | Alpha | Pre-alpha | Pre-alpha |
| 1995–1996 | Post-alpha | Alpha | Pre-alpha |
| 1999–2001 | Post-alpha | Post-alpha | Alpha |

(±2.4 SD) kg during the study period. He was born in 1976 and was alpha from October 1997 to January 2003.

## Analysis

We used data from 694 male focal follows that were conducted during three periods, each corresponding to one of the subject males' tenure as alpha (Table III). The mean number of follows per month for all focal individuals included in this analysis was 1.73, with a range of 1–6.6 (Table I).

### Grooming

We defined a grooming bout as a grooming engagement in one direction that lasted at least 1 min. To avoid biased sampling, we analyzed only those bouts that involved the focal male. For each bout, we recorded (1) the date, (2) the ID of the focal chimpanzee, (3) the ID of the focal's grooming

partner, (4) grooming direction: give (the focal groomed), receive (the focal was groomed), mutual (the participants simultaneously groomed one another) and (5) bout duration. We excluded 167 bouts in which the direction and/or duration were not recorded in the narrative notes.

We calculated the following annual grooming indices for each adult male dyad that spent at least 30 hr together (in the same party) over the course of a year.

*Overall grooming rate*:

$$\frac{\text{Total grooming (give + receive + mutual) duration}}{\text{Total time together}}$$

(1)

*Directional grooming rate*:

$$\frac{\text{Give + mutual duration}}{\text{Total grooming duration}}$$

(2a)

$$\frac{\text{Receive + mutual duration}}{\text{Total grooming duration}}$$

(2b)

*Mutual grooming rate*:

$$\frac{\text{Mutual grooming duration}}{\text{Total grooming duration}}$$

(3)

Our Directional Grooming Index (Equation (2)) is comparable to indices used in other studies that include mutual grooming in calculations of given and received grooming rates [Goodall, 1986; Hemelrijk & Ek, 1991; Simpson, 1973; Watts, 2000a,b]. However, we also consider mutual grooming separately (Equation (3)), as in other studies [e.g. Arnold & Whiten, 2003; Boesch & Boesch-Achermann, 2000; Nishida & Hosaka, 1996]. The first approach assumes that the value of grooming within a mutual bout is equivalent to that of a unidirectional bout. The latter allows us to relax the assumption that the payoff for mutual grooming is not simply a sum of its parts. Instead we assume that mutual grooming is more costly than receiving, yet more beneficial than giving. We chose to use grooming duration rather than number of bouts, as a more thorough measure of the energy investments involved with grooming [Parr et al., 1997; Watts, 2000b].

*Dominance rank*

We used submissive pant–grunt vocalizations [Bygott, 1979; Noë et al., 1980] and, for some years, direction of dyadic aggression recorded in the narrative notes to determine annual, linear dominance hierarchies among all males [MATMAN© (Noldus Information Technologies 1998, version 1.1. Wagengien, The Netherlands). [E.Wroblewski, unpublished data] and then assigned each male to one of five categorical ranks (Table II): alpha, high (ranks 2–4), middle (ranks 5–7) and low (ranks 8–11). Young males aged 10–12 years were categorized as very low ranking. Adult male, PX, whose castration during an attack at an early age permanently retarded his physical growth and social development, almost never received pant–grunts from males and was also categorized as very low ranking (Table II). For each time period, we classified the three subject males (FD, FR, WL) as ''pre-alpha,'' ''alpha'' and ''post-alpha'' (Table III).

*Agonistic behaviors*

We extracted contact aggression and displays from focal follow narrative notes within the subject males' alpha periods. Contact aggression included instances when the focal male kicked, slapped, hit or bit another adult male. Dominance displays included events noted as displays, charges or a series of other agonistic events that are commonly observed in displays, such as piloerection, branch swaying, stamping, slapping and throwing objects [Bygott, 1979; Goodall, 1986; Nishida et al., 1999]. We excluded 280 agonistic events for which details were unclear due to limited visibility and 51 displays that occurred ≤ 2 min after another display. We calculated the rates of contact aggression and displays per 100 focal follow hours.

*Statistics*

We used R version 2.1.1 [The Insightful Corporation, 2004, Seattle, WA] for all statistical tests. We used two-sample Wilcoxon-signed rank tests for all analyses. When applicable, we used a sequential Bonferroni adjustment of $\alpha = 0.05/N$, where $N$ represents the number of simultaneous tests being performed.

## RESULTS

WL, FD and FR had a mean of 9.61 grooming partners per year (Table IV). The mean number ($\Sigma/6$ years) of grooming bouts for each individual per year was 90.8, 151 and 34.5 for WL, FD and FR, respectively.

### Between-Individual Variation in Grooming Rates

FD, FR and WL exhibited different grooming rates over the whole study period. First, FR, the largest male, spent a significantly smaller proportion of his time grooming with other chimpanzees (regardless of direction, Equation (1)) than both WL, the smallest male, ($W = 3,056, P < 0.005$) and FD ($W = 3,334.5, P < 0.005$) (Fig. 1). FD and WL did not differ significantly in total time spent grooming ($W = 2,471.5, P = 0.699$).

**TABLE IV. Number of Grooming Partners for Each Subject Male (FD, FR, WL) by Year**

| Year | Males | AL | AO | BE | EV | FD | FO | FR | GB | GD | GL | KS | PF | PX | SL | TB | WL | Yearly Total | Yearly Mean |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1992 | FD | | | | | NA | ■ | | | ■ | | ■ | | | ■ | | | 10 | |
| | FR | | | | | | | NA | | ■ | | ■ | | | ■ | | | 10 | |
| | WL | | | | | | | | | ■ | | ■ | | | ■ | | NA | 10 | 10 |
| 1995 | FD | | | | ■ | NA | ■ | | | ■ | | | | | | | | 12 | |
| | FR | | | | ■ | | | NA | | ■ | | | | | | | | 7 | |
| | WL | | | | ■ | | | | | ■ | | | | | | | NA | 8 | 9 |
| 1996 | FD | | | | ■ | NA | | | | ■ | | | | | | | | 10 | |
| | FR | | | | ■ | | | NA | | ■ | | | | | | | | 9 | |
| | WL | | | | ■ | | | | | ■ | | | | | | | NA | 9 | 9.33 |
| 1999 | FD | ■ | | | ■ | NA | | | | | | | ■ | | | | | 9 | |
| | FR | ■ | | | ■ | | | NA | | | | | ■ | | | | | 9 | |
| | WL | ■ | | | | | ■ | | | | | | ■ | | | | NA | 10 | 9.33 |
| 2000 | FD | ■ | | | | NA | | | | ■ | | | | | | | | 11 | |
| | FR | ■ | | | | | | NA | | ■ | | | | | | | | 10 | |
| | WL | ■ | | | | | | | | ■ | | | | | | | NA | 9 | 10 |
| 2001 | FD | ■ | | | | NA | | | | ■ | | | ■ | | | | | 11 | |
| | FR | ■ | | | | | | NA | | ■ | | | ■ | | | | | 10 | |
| | WL | ■ | | ■ | | | | | | ■ | | | ■ | | | | NA | 9 | 10 |
| Total | | | | | | | | | | | | | | | | | | | 9.61 |

Gray cells indicate that the dyad was observed to groom at least once that year. White cells indicate that the dyad was not observed to groom that year. Black cells indicate that the individual was a juvenile or deceased.
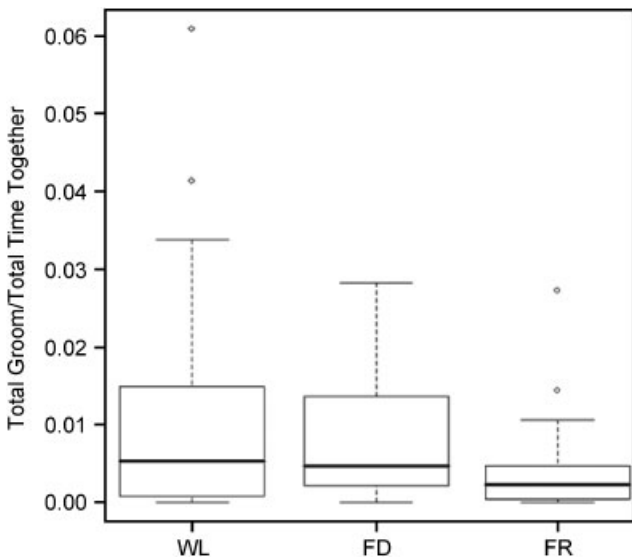


Fig. 1. *Total grooming rates for the three males*, regardless of direction. Annual dyadic grooming rates were calculated using Equation (1). Boxplots of the grooming rates are included for each male. Outliers are denoted by open circles.

Second, when we considered grooming direction, WL spent a greater proportion of his grooming time grooming others (Equation (2a)) than both FD ($W = 3,269$, $P < 0.005$) and FR ($W = 3,857$, $P < 0.0001$), and FD groomed others more than FR did ($W = 3,578$, $P < 0.0001$). WL spent a significantly smaller proportion of his grooming time being groomed (Equation (2b)) by others than FR ($W = 1,786$, $P < 0.0001$) and FD ($W = 5,177.5$, $P < 0.0001$), whereas FD and FR received grooming at similar rates ($W = 2,619.5$, $P = 0.904$) (Fig. 2).

Finally, the three males exhibited different rates of mutual grooming (Equation (3)). FR groomed mutually at a significantly lower rate than both WL ($W = 2,434$, $P < 0.0001$) and FD ($W = 2,662$, $P < 0.005$) (Fig. 3). WL and FD had statistically similar mutual grooming rates ($W = 1,790.5$, $P = 0.7247$).

### Status Effects on Individual Grooming Rates

Each male's overall grooming rate (regardless of direction, Equation (1)) did not change with his social status (Fig. 4). None of the males exhibited different overall grooming rates across time periods (WL: [Post-$\alpha$ vs. $\alpha$] $W = 375$, $P = 0.6$; FD: [Pre-$\alpha$ vs. $\alpha$] $W = 165$, $P = 0.49$; [$\alpha$ vs. Post-$\alpha$] $W = 468$, $P = 0.25$; [Pre-$\alpha$ vs. Post-$\alpha$] $W = 211$, $P = 0.75$; FR: [$\alpha$ vs. Pre-$\alpha$] $W = 625$, $P = 0.71$).

Similarly, grooming directionality (Equation (2)) did not change with a male's social status. For each male, there was no difference in the ratio of grooming given to grooming received across time periods (WL (($\alpha$ vs. Post-$\alpha$) Given: $W = 416.5$, $P = 0.816$, Received: $W = 398.5$, $P = 0.61$) or FR: (($\alpha$ vs. Post-$\alpha$) Given: $W = 128.5$, $P = 0.558$, Received: $W = 135.5$, $P = 0.764$)). The tendency for FD to receive more grooming as a post-alpha than he did as alpha approached statistical significance ($W = 288$, $P = 0.0167$, Bonferroni adjusted $N = 3$, $\alpha = 0.05/3 = 0.0167$).

Finally, males groomed mutually at similar rates regardless of social status (Equation (3)). (WL: ($\alpha$ & Post-$\alpha$) $W = 177.5$, $P = 0.164$; FD: (Pre-$\alpha$ & $\alpha$) $W = 110$, $P \approx 1.0$; ($\alpha$ & Post-$\alpha$) $W = 281$,
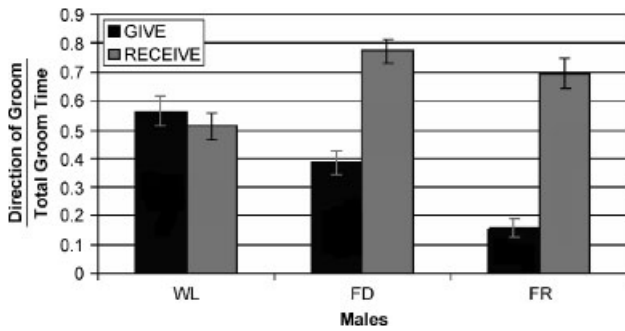
Fig. 2. *Given and received grooming rates of the three males,* regardless of social status. Annual combined directional grooming rates were calculated using Equation (2). We report the mean annual dyadic grooming rate with error bars of 1 standard deviation.
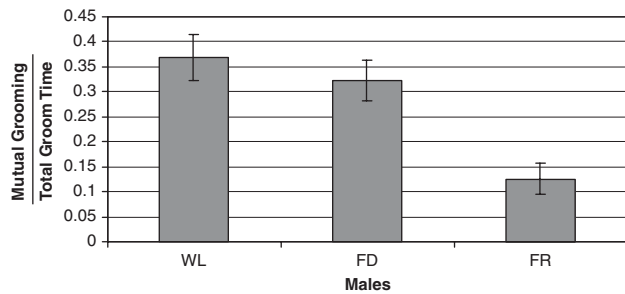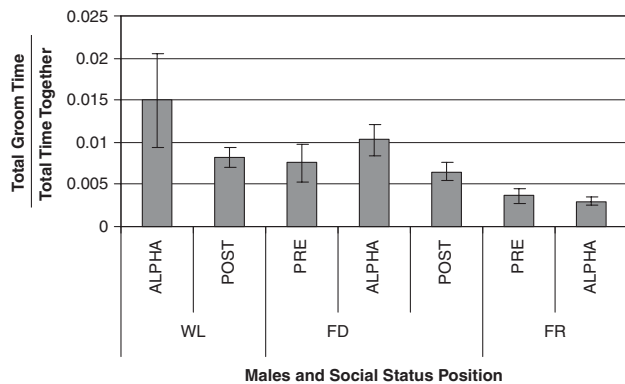


Fig. 3. *Mutual grooming rates of the three males,* regardless of social status. Annual dyadic mutual grooming rates were calculated using Equation (3). We report the mean annual dyadic grooming rate with error bars of 1 standard deviation.



Fig. 4. *Total grooming for the three males in each social status position,* regardless of direction. Annual dyadic grooming rates were calculated using Equation (1). We report the mean dyadic grooming rate with error bars of 1 standard deviation for each status.

$P = 0.277$; (Pre-$\alpha$ & Post-$\alpha$) $W = 127.5$, $P = 0.406$; FR: ($\alpha$ & Post-$\alpha$) $W = 384$, $P = 0.3383$).

## Partner Rank

Alpha males participated in grooming equally with high-, middle- and low-ranking partners (Equation (1)) ($n = 3$ males, high vs. middle:
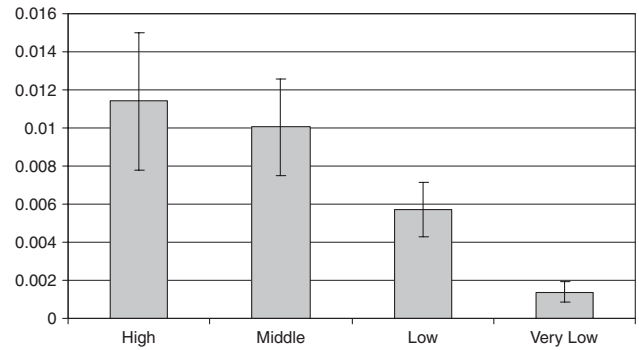


Fig. 5. *Partner rank and total grooming for the three alpha males,* regardless of direction. Total grooming rates were calculated using Equation (1) during each alpha's tenure. We report the mean annual dyadic grooming rates with error bars of 1 standard deviation for each rank.

$W = 168$, $P = 0.8636$; middle vs. low: $W = 235$, $P = 0.3210$; high vs. low: $W = 243$, $P = 0.2263$). However, very low-ranking males participated in grooming significantly less than all other ranking males (high vs. very low: $W = 172$, $P = 0.00054$; middle vs. very low: $W = 160$, $P = 0.0034$; low vs. very low: $W = 183$, $P = 0.0091$) (Fig. 5).

## Agonistic Behaviors

WL, FD and FR exhibited different rates of agonistic behaviors while they were alpha. FR showed the highest rates of contact aggression with an average 0.0217 contacts per focal follow hour when compared with FD (0.0178) and WL (0) (Fig. 6). Conversely, WL exhibited the highest rates of charging displays with an average of 0.343 displays per focal follow hour when compared with FR (0.297) and FD (0.231) (Fig. 7).

## DISCUSSION

We found significant differences in the grooming behavior of male chimpanzees that were alpha during a 10-year study period in Gombe National Park. First, we found that the three males differed significantly in grooming frequency and direction. FR's overall grooming rates were lower compared with WL and FD, and he received more grooming than he gave. In contrast, WL had a relatively high overall grooming rate, gave and received grooming at equal rates, and participated in mutual grooming more often than the other two males. FD was similar to WL in that he was a frequent grooming participant and often groomed mutually. However, he was also similar to FR in that he tended to receive more grooming than he gave. Nevertheless, he groomed his partners more than FR did.

There was no evidence that a male's grooming habits changed as a function of his dominance rank. None of the three males exhibited differences in overall or directional grooming rates across pre-alpha, alpha and post-alpha periods. This suggests
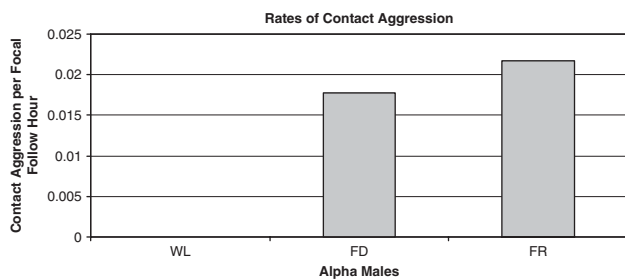
Fig. 6. *Rates of contact aggression for the three alpha males.* The total number of contact aggression events is divided by the total focal follow hours for each alpha's tenure.
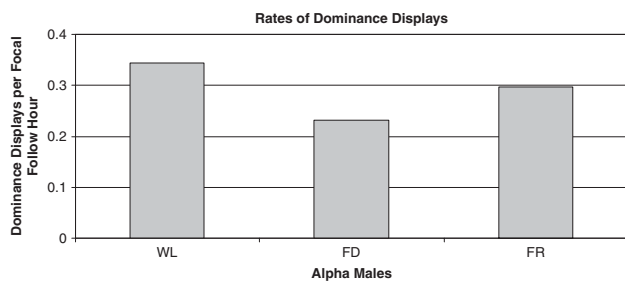


Fig. 7. *Rates of dominance displays for the three alpha males.* The total number of dominance displays is divided by the total number of focal follow hours for each alpha's tenure.

that a male's grooming tendencies may be rather inflexible. This is inconsistent with other studies showing that high-ranking males tend to receive more than they give and only groom with each other [Nishida & Hosaka, 1996; Simpson, 1973; Watts, 2000a,b], which predict that a male's grooming habits should change with rank. This inconsistency is likely due to the fact that previous studies tend to represent a ''snapshot'' in time rather than tracking the behavior of individual males. Additionally, this article addresses individual differences among three males, and does not report overall correlations between grooming behaviors among all possible dyads.

We suggest that body size may partially explain this persistence in male grooming habits. Coalition formation may be one of several behaviors a small male uses to attain and maintain dominance, as he might have difficulty intimidating other males with agonistic or aggressive tactics. If males trade grooming and coalitionary support [Watts, 2002], we would therefore expect a small alpha male to exhibit high grooming rates. Indeed, as predicted, the smallest male in our study, WL, had the highest (predominantly mutual) grooming rates, whereas both FD and FR tended to receive grooming. This suggests that grooming others was particularly important for WL because of his low rates of contact aggression. We

suggest that because most other males had the physical potential to dominate him, WL avoided contact aggression and instead, used grooming to form alliances and placate rivals. His high rates of dominance displays (and associated pilo-erection that exaggerates size) would serve to intimidate others without physical aggression. In contrast, coalitions should be less important for a large male who can easily intimidate others through directed charging displays and attacks. Indeed, the largest male in the study, FR, had the lowest grooming rates, received more grooming than he gave, displayed less than WL and had the highest rates of contact aggression.

FD's grooming patterns suggest a dominance strategy intermediate to WL and FR. Like WL, he exhibited relatively high overall grooming rates, but like FR, received grooming more than he gave. As FD's rate of contact aggression was much greater than WL's, this suggests that his large size allowed him to physically intimidate his rivals without the need for frequent displays. However, as a male 5–7 kg lighter than FR he additionally relied on grooming to placate the other adult males and directed aggression at other males less than FR. As this study examined only three males, we cannot conclude that there is a direct correlation between rates of grooming and the size of dominant males. However, these findings should stimulate future studies that more broadly examine the influence of body size on aggressive, agonistic and other affiliative behaviors among larger social groups over longer periods.

Our results indicate that the dominance styles of the three males were consistent over time. Another possible explanation for stable grooming preferences is that in small social groups, competition for grooming partners is less intense than in larger social groups [Arnold & Whiten, 2003; Sambrook et al., 1995; Watts, 2000a,b]. In Gombe's relatively small group of 11–17 males, the three study subjects could potentially achieve their grooming preferences regardless of their own status. Similarly, rank did not influence grooming patterns in other small populations (M Group, Mahale National Park, nine males [reviewed in Watts, 2000b]; Budongo, 9–11 males [Arnold & Whiten, 2003]). By comparison, male chimpanzees in the larger Ngogo community (~25 adult males) predominantly groomed within their own ranks [Watts, 2000b].

## Partner Rank

As alpha males, WL, FD and FR groomed with high-, middle- and low-ranking partners equally. This differs from our prediction that alphas would engage in grooming mostly with high-ranking males [Nishida & Hosaka, 1996; Simpson, 1973; Watts, 2000b]. Once again, this may be because our study

community contained relatively few males, allowing for middle-ranking males to participate in grooming with alphas as much (or more) than high-ranking males [Arnold & Whiten, 2003; Sambrook et al., 1995; Watts, 2000a,b]. Finally, the three alphas participated in grooming with high-, middle- and low-ranking partners significantly more than with very low-ranking partners. This outcome is expected because very low-ranking males are new to the male hierarchy [Goodall, 1986; Pusey, 1990] or anomalous (PX) and have little access to the highest-ranking individual. Owing to limited sample size, we were unable to examine grooming direction or individual rates with partners of different ranks. In future research we will examine the relationship between the number of available partners and group-wide grooming patterns.

### Conclusion

Our study demonstrated differential grooming patterns among three male chimpanzees that were alpha during the study period, providing preliminary support for the notion that males may adopt distinct dominance ''styles'' that correlate with rates of agonistic behaviors. This may explain why male dominance rank was not correlated with body mass at Gombe [Pusey et al., 2005]. Males seem to compensate for smaller body size by investing more time and energy in grooming in order to ensure coalitionary support or to placate their rivals. FR's success as an alpha may be attributed to his greater mass, whereas WL and FD adopted a more ''political'' strategy.

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