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Food Competition and Linear Dominance Hierarchy among Female Chimpanzees of the Taï National Park

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Dominance rank in female chimpanzees correlates positively with reproductive success. Although a high rank obviously has an advantage for females, clear (linear) hierarchies in female chimpanzees have not been detected. Following the predictions of the socio-ecological model, the type of food competition should affect the dominance relationships among females. We investigated food competition and relationships among 11 adult female chimpanzees in the Taï National Park, Côte d'Ivoire (West Africa). We detected a formal linear dominance hierarchy among the females based on greeting behaviour directed from the subordinate to the dominant female. Females faced contest competition over food, and it increased when either the food was monopolizable or the number of competitors increased. Winning contests over food, but not age, was related to the dominance rank. Affiliative relationships among the females did not help to explain the absence of greetings in some dyads. However comparison post hoc among chimpanzee study sites made differences in the dominance relationships apparent. We discuss them based on social relationships among females, contest competition and predation. The cross-site comparison indicates that the differences in female dominance hierarchies among the chimpanzee study sites are affected by food competition, predation risk and observation time.

KEY WORDS: linear dominance hierarchy; female relationships; contest competition; *Pan troglodytes verus*; Taï National Park.

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INTRODUCTION

Dominance relationships in many primates fit to a linear hierarchy, though in some species rank orders are unclear or ambiguous (Walters and Seyfarth, 1987). Both seem to be true for chimpanzees. While male chimpanzees rank either in linear hierarchies (Mahale K-group: Nishida, 1979; Mahale M-group: Nishida and Hosaka, 1996; Kibale Ngogo: Watts, 1998; Taï North-group: Boesch and Boesch-Achermann, 2000) or at least in narrow rank categories (Budongo Sonso: Newton-Fisher, 2002; Gombe Kasakela: Bygott, 1979; Goodall, 1986), linear hierarchies in female chimpanzees have not been detected. Dominance relationships among females were either ordered in broad rank categories (Gombe Kasakela: Pusey *et al.*, 1997; Kibale Kanyawara: Wrangham *et al.*, 1992), or at least two-thirds of the dyadic dominance relationships were unknown to researchers (Mahale M-group: Nishida, 1989; Budongo Sonso: Fawcett, 2000). Nevertheless high-ranking females in Gombe had significantly higher infant survival, faster maturing daughters, and more rapid production of offspring (Pusey *et al.*, 1997). Thus female chimpanzees increase reproductive success in a similar way to male chimpanzees, wherein the alpha male or high-ranking males are more successful in siring offspring (Gombe: Constable *et al.*, 2001; Taï: Boesch *et al.*, in preparation). Although the outcome might be similar in both sexes, the reason for the variance in reproductive success seems to be different. While males can monopolize mating partners and secure exclusive mating, high-ranking females may obtain access to the best foods. A better fed female can invest more energy in reproduction and thereby produce more offspring, or she can supply more food to her offspring.

Ecological factors have far reaching consequences on the relationships formed among primate females (Wrangham, 1987). The socio-ecological model predicts that food distribution and predation risk shape the competitive regime and therefore the relationships formed among females of diurnal primate species (Koenig, 2002; Sterck *et al.*, 1997; van Schaik, 1989). Species facing scramble competition or no competition should have egalitarian dominance relationships, in which hierarchies are unclear and non-linear, if distinguishable at all. In contrast, species facing contest competition should have despotic dominance relationships, in which dominance relationships are clearly established and form usually linear hierarchies. Such despotic females have often formalized dominance relationships, which are expressed in ritualized signals where in the direction is independent of the context (de Waal, 1986, 1989).

Contest-type competition occurs when food distribution allows some individuals to exclude others from accessing the resource. Therefore, contest competition should increase with the monopolizablity of the resource and with the number of competitors. A linear hierarchy should be adaptive when contest is so strong that the number of aggressive interactions needs to be reduced by clear dominance relationships among the competitors. Indeed, intra specific and inter specific comparisons have proved that females that face more contest competition have a more linear and formalized hierarchy, e.g. *Saimiri oerstedi* versus *Saimiri sciureus* (Mitchell *et al.*, 1991), sympatric *Presbytis thomasi* and *Macaca fascicularis* (Sterck and Steenbeek, 1997), and 3 neighboring groups of *Semnopithecus entellus* (Koenig, 2000).

Dominance relationships develop from repeated contests within dyads (Bernstein, 1981; Drews, 1993). Many group-living animals use ritualized signals to avoid aggression (de Waal, 1986). Such formalized submissions are one of the last behaviors to indicate rank changes and therefore serve as an indicator for acceptance of the relationship (*Macaca fascicularis*: de Waal, 1977; *Macaca mulatta*: de Waal and Luttrell, 1985; *Papio cynocephalus*: Walters, 1980; *Pan troglodytes*: de Waal, 1982; Wittig, 1997). De Waal and Luttrell (1985) concluded that social integration is a condition for a formal hierarchy as it clarifies the social status of an individual in the group. Clear relationships among all individuals should lead to an interaction pattern, where in all individuals can be accepted as partners for affiliative interactions, though interaction frequencies and intensities among dyads differ due to the quality of the relationship.

Chimpanzees of all study sites live in multimale-multifemale, fission-fusion societies, where the composition of parties can change frequently (Boesch, 1991; Goodall, 1986; Nishida, 1990; Sugiyama, 1984; Wrangham *et al.*, 1992). When meeting each other, subordinates greet dominants by emitting pant-grunt vocalizations, which in chimpanzees serve the function of formalized submission, as they provide a unidirectional and context-free assessment of dominance relationships (Bygott, 1979; de Waal, 1978; Noë *et al.*, 1980). However, as an exchange of greetings is only possible when associated, the greeting frequency should increase with association.

Most chimpanzee communities are probably male-bonded (Mitani *et al.*, 2002), as males are philopatric, while females emigrate from their natal community (Watts and Pusey, 1993). Furthermore, males create long-term alliances (de Waal, 1982; Nishida and Hosaka, 1996; Riss and Goodall, 1977), and female chimpanzees are usually characterized as egalitarian (Sterck *et al.*, 1997). However, genetic data have shown that both Taï and Gombe males are not more related than females within the same community (Vigilant *et al.*, 2001), though they are still the philopatric sex. Furthermore, it has been argued that Taï chimpanzees are bisexually-bonded because females build co-operative long-term relationships, occasionally with stronger association than males (Boesch and Boesch-Achermann, 2000). As Taï females are nut-crackers (Boesch and Boesch, 1983, 1984a,b) and have frequent access to meat (Boesch, 1994a,b; Boesch and Boesch, 1989), contest competition might be more important among them than in other communities. Therefore Taï females may benefit from forming a linear dominance hierarchy.

We investigated the existence of formal dominance relationships among females of a community of wild chimpanzees in the Taï National Park, Côte d'Ivoire. We fit the formal dominance relationships of the females to a hierarchy and test for linearity. We next quantify contest competition over food resources in females and hypothesize that females increase aggressive interactions when more competitors are present or with monopolizable food. Additionally, dominant partners are expected to possess the food after the conflict. We also investigated the relationship among dominance hierarchy, age and contest aggression. As females in other study sites did not establish linear hierarchies, though they had different ages, dominance rank should only correlate with contest aggression. Finally we assess the association and grooming relationships among the females and discuss possible explanations for different findings in hierarchies in other chimpanzee populations. Taï females should associate more frequently and have more grooming dyads, indicating a stronger integration of females in the social network. The same principles should work within the community, and female dyads with unknown relationships should be less associated and have weaker grooming relationships.

METHODS

We collected data between October 1996 and April 1999 on the North-community, which has been observed continuously since 1979 (Boesch and Boesch-Achermann, 2000) in the Taï National Park, Côte d'Ivoire (West Africa, 5°52 N, 7°22 W). In October 1996, the community comprised 4 males (3 adults; 1 adolescent), 14 females (11 adults; 3 adolescents) and 13 juveniles and infants. During the observation period 5 chimpanzees disappeared or died (1 adult male; 2 adolescent females; 2 juveniles) and 6 infants were born.

Wittig collected the following 3 types of data during all-day follows on the 4 males and 10 habituated adult females (adult female Ricci was not habituated to full-day follows) via: (a) focal animal sampling (Altmann, 1974) on one target chimpanzee per day from nest to nest, recording activities (feed, rest, travel), social interactions (aggressive and affiliative) and vocalizations; (b) 10-min scan sampling (Altmann, 1974), recording the target's party composition and (c) recording specific information at each feeding site about the foods eaten by the focal individual, food monopolizability and number of competitors. He entered data into a Psion Organiser® hand-held computer via The Observer® (Noldus, 1989).

The data set consists of 123 full-day observations of focal females. Wittig observed each female between 10 and 15 days during the observation period, which provided a total of 1028 h of female focal observation time. The death of Brutus in March 1997 changed the association pattern in the community, so we analyzed the 2 periods separately for the questions related to association.

Operational Definitions

We assess the dominance relationships of dyads by greetings, which are specific vocalizations emitted by the subordinate to the dominant, usually accompanied by an approach and submissive behavior, such as crouching or bobbing, of the subordinate. Three vocalizations serve the function of greetings in Taï: (a) pant-grunt (PG), a repeated grunt exhaled with an open mouth; (b) greeting-hooh (GH), a repeated and intense hooh; and (c) greeting-pant (GP), a repeated pant accompanied by submissive behavior.

Food is monopolizable when it was accessible only in one spot or by one tool in the feeding site, e.g., one stone hammer. One food spot is only one fruit, water hole, insect-nest or whole colobus. All these situations gave one individual the possibility to feed on the food exclusively. The number of competitors are all the adult and independent subadult chimpanzees present in the feeding site (=feeding party), which excludes all members of the party that stay outside of the feeding site, e.g., resting under the food tree, but visibile. We calculated the observation time for feeding parties and the time a type of food was present from the focal female observations. An aggressive interaction over food is a food conflict and was won by the individual that possessed the food after the conflict. We excluded food conflicts with infants and juveniles from the analysis.

Association is presence in the same party (being in visibility). We used the dyadic association index (DAI) to measure how frequently 2 individuals were associated: $\mathrm{DAI}_{\mathrm{AB}} = \frac{\sum(A+B)}{\sum A+\sum B-\sum(A+B)}$, wherein A is the time individual A was seen, B is the time individual B was seen and A + B is the time A and B were seen together (Nishida, 1968). The greeting rate is the number of greetings within dyad AB divided by the observation time of females A and B. The conflict rate is the number of aggressive interactions among females in a feeding party of size X divided by the total observation time of feeding parties of size X. The grooming rate is the duration of grooming of dyad AB divided by the observation time of female A and B. Generally, rates are the number of events per total observation time; however, corrected rates are divided by the DAI because as females in fission-fusion societies can only interact with a partner when associated in the same party. For comparisons with other study sites we had to calculate the rates as number of events among all females divided by the total observation time of all females, due to lack of data for relationships among female chimpanzees.

Statistics

We tested for linearity of hierarchies via MATMAN© (Noldus, 1998), which provides several measures to describe the linearity. We implemented two tests:

The linearity test, including Landaus linearity index (h) and Kendall's coefficient of linearity (K), provide a measure of the degree to which a dominance hierarchy is linear, and both range from 0 to 1, with 1 describing complete linearity. While h basically compares the number of dyads in which A dominates B to the total number of dyads (Chase, 1974; Landau, 1951), K basically compares the number of circular triads with the total number of dyads (Appleby, 1983). Linearity is evidenced when the proportion of circular triads is less than expected by chance based on a χ^2 distribution (Appleby, 1983). Both measurements give similar results but they are problematic when the matrix of the dominance relationships contains unknown relationships.

We conducted an improved linearity test when >10% of the relationships were unknown or tied. Unknown relationships are dyads with no greeting exchanged. Tied relationships are dyads with an equal number of greetings in both directions. For the improved linearity test we used the corrected linearity index (h'), which is the average of all h values calculated for the complete set of each possible dominance matrix. The complete set of dominance matrices is produced by systematically switching the direction of dominance for unknown relationships, while the tied relationships are always assigned half dominant and half subordinate status (de Vries, 1995). We obtained the significance of the linearity by a randomisation test, that compares the h value of 10000 randomly chosen matrices with h'. Linearity is documented when >95% of the randomly chosen matrices have a smaller h than the corrected linearity index (h').

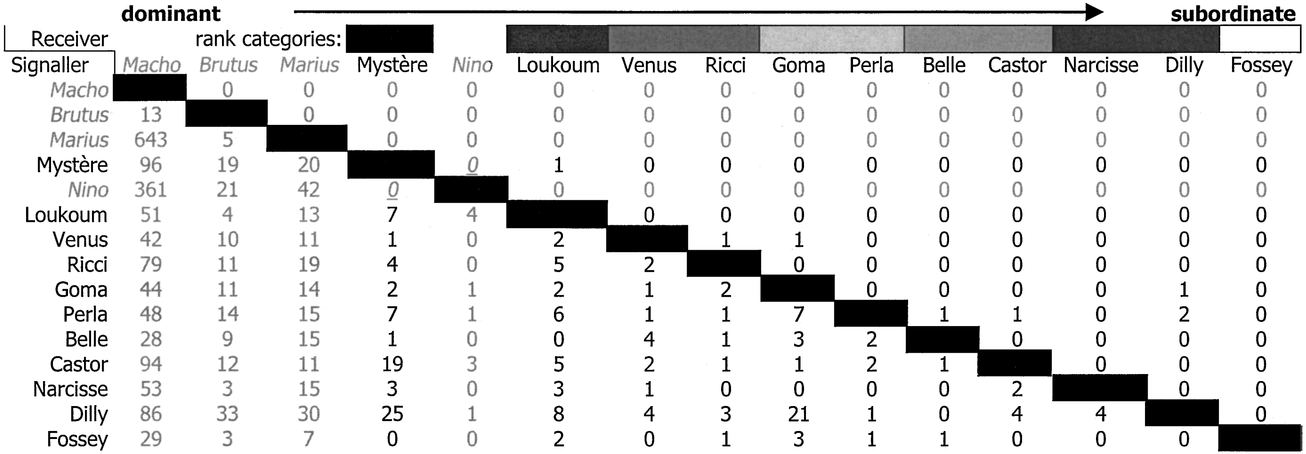
To compare differences of interactions in dyads, we applied a permutation test that takes the dependency of the data in account. The test is an extension of the network subgroup analysis test by Dow and de Waal (1989). We created a matrix of the social interactions of all individuals and calculated the mean difference between subgroups to compare. Afterwards we sampled the data set with replacement and calculated from this bootstrap sample the mean differences between the subgroups again. We repeated the procedure 1000 times and checked if the difference between the original means was outside of the 95% confidence interval of the approximate distribution of distances between means. The test is two-tailed with a significance level of $P < 0.05$ and is Bonferroni corrected for comparisons of >2 subgroups. We conducted further non-parametric statistics in STATXACT© 4 (CytelSoftware, 1998) as a two-tailed exact test, because of small sample size (Mundry and Fischer, 1998). We calculated the correlations via STATISTICA© 99 edition (StatSoft, 1999), apart from Kendall partial rank-order correlation coefficient, in which we used the procedure described by Siegel and Castellan (1988).

RESULTS

Female hierarchy

We observed 187 female greeting interactions that included PG (62%), GP (30.5%) or GH (7.5%). Of the 55 female dyads, two-thirds showed unidirectional greeting (67.3%), 12.7% of them had bi-directional greetings and 20% of the dominance relationships remained unknown as no greeting was exchanged. This lack of greetings might be due to the rather low greeting rate (GR) in female dyads ($G\hat{R}_{\mathrm{FF}} = 0.011$ greetings/hour). Greetings among females occurred 16 times less frequently than greetings among males ($G\hat{R}_{\mathrm{MM}} = 0.178$ g/h; Permutation test: $P < 0.05$) and 4 times less frequently than in bisexual pairs ($G\hat{R}_{\mathrm{MF}} = 0.047$ g/h; Permutation test: $P < 0.05$).

When analyzing the direction of greeting events, we detected a linearity in the hierarchy among females (Figure 1; Improved linearity test: $h' = 0.67$, $P < 0.01$). Forming narrow rank categories (Figure 1; 2 rank-neighboring females per category, and the three adolescent females in the lowest rank category), females showed a clear rank order (Linearity test: $h = 0.97$; $K = 0.97$; $\chi^2_{30} = 51$, $P < 0.01$), which has an equivalent strength to the linear hierarchy of the males (Figure 1; Linearity test: $h = 1$; $K = 1$). The hierarchy of the complete community (females and males) is linear with females subordinate to males (Improved linearity test: $h' = 0.80$, $P < 0.001$) except the unknown



Signaller \ Receiver	*Macho*	*Brutus*	*Marius*	Mystère	*Nino*	Loukoum	Venus	Ricci	Goma	Perla	Belle	Castor	Narcisse	Dilly	Fossey
Macho		0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brutus	13		0	0	0	0	0	0	0	0	0	0	0	0	0
Marius	643	5		0	0	0	0	0	0	0	0	0	0	0	0
Mystère	96	19	20		0	1	0	0	0	0	0	0	0	0	0
Nino	361	21	42	0		0	0	0	0	0	0	0	0	0	0
Loukoum	51	4	13	7	4		0	0	0	0	0	0	0	0	0
Venus	42	10	11	1	0	2		1	1	0	0	0	0	0	0
Ricci	79	11	19	4	0	5	2		0	0	0	0	0	0	0
Goma	44	11	14	2	1	2	1	2		0	0	0	0	1	0
Perla	48	14	15	7	1	6	1	1	7		1	1	0	2	0
Belle	28	9	15	1	0	0	4	1	3	2		0	0	0	0
Castor	94	12	11	19	3	5	2	1	1	2	1		0	0	0
Narcisse	53	3	15	3	0	3	1	0	0	0	0	2		0	0
Dilly	86	33	30	25	1	8	4	3	21	1	0	4	4		0
Fossey	29	3	7	0	0	2	0	1	3	1	1	0	0	0	

Fig. 1. Dominance relationships, based on greetings, among the adult chimpanzees in the North community in Taï. The signaller (vertical) is greeting the receiver (horizontal). Individual rank is in increasing order from left to right. The six narrow rank categories of females are indicated by different bars above the females' names. Note that the last category (white) includes the greetings of the subadult females. For dyads including males (grey *italic* letters) pant-grunts are shown only (grey numbers), whereas among females, greeting-pants and greeting-hoohs are inserted as well.

dominance relationship between α-female Mystère and subadult male Nino. Thus the dominance relationships of Taï female chimpanzees fitted a linear hierarchy.

Food Competition

We observed 103 conflicts over food among females, giving a rate of about 0.1 food conflicts per hour of observation and about 0.22 food conflicts per hour in a feeding party. Although only 8% of the community's feeding time was on monopolizable food, it was the reason for 50% of the food conflicts among females (Table I). Comparing the indices of difference (observed minus expected frequency) for each female showed that females initiate conflicts over monopolizable food more frequently than over non-monopolizable food (Wilcoxon exact: $T = 66$, $N = 11$, $P < 0.01$). Females fought over many different types of monopolizable food, such as meat, stone hammers to crack nuts, water holes in trees, eggs of ants, honeycombs, fruits of *Treculia africana* and tree-mushrooms. Although only 42% of the feeding time on monopolizable food was attributed to meat, almost 70% (34 of 49 cases) of the conflicts on monopolizable food were over it. Meat was the main reason for contests over monopolizable food among Taï female chimpanzees (Goodness of fit exact: $\chi_1^2 = 15.04$, $P < 0.001$).

Table I. Food conflicts among female chimpanzees in the North community in Taï

conflict initiator	N	Conflicts over monopolizable food[a] (%)	Possessor of food after conflict		
			Dominant (N)	Subordinate (N)	3rd Individual (N)
MYSTERE	9	22	9	0	0
LOUKOUM	35	63	27	5	3
VENUS	5	60	5	0	0
RICCI	3	33	2	1	0
GOMA	6	33	4	0	2
PERLA	11	36	8	1	2
BELLE	2	100	1	1	0
CASTOR	11	9	6	2	3
NARCISSE	1	100	0	1	0
DILLY	17	59	7	5	5
FOSSEY	3	33	3	0	0
Mean		50%	66%	23%	11%
Expected		8%			

Note. The number of conflicts is presented per initiating female in declining dominance rank order. While the left column shows the proportion of conflicts over monopolizable food, the right columns show the possessor of the food depending on the dominance relationships of the conflict partners. Average proportions and expected proportion for conflicts over monopolizable food in the last rows.

[a] Conflicts over non-monopolizable food complete proportions to 100%.

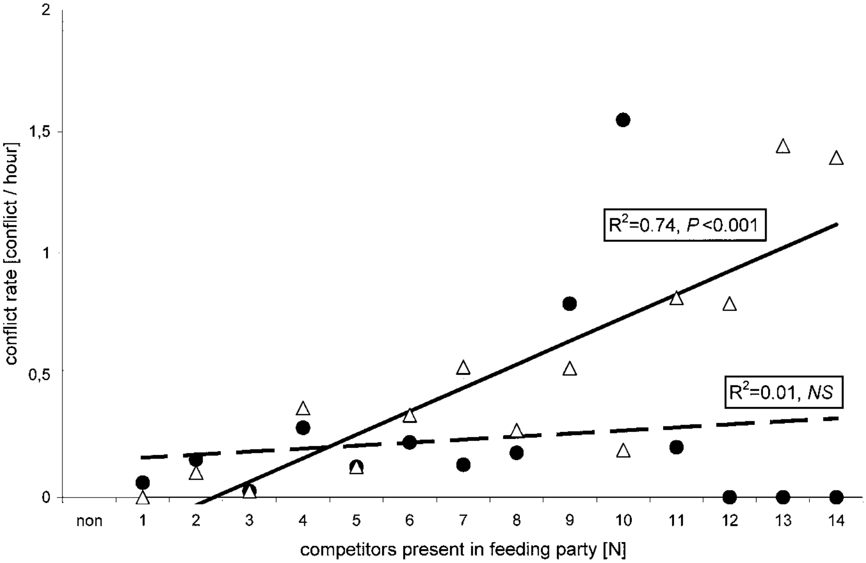


Fig. 2. Conflict rate among females over food with different numbers of competitors present in the feeding party in Taï chimpanzees. Feeding parties attending non-monopolizable food (△) are considered separately from those attending monopolizable food (•). Regression lines are calculated for non-monopolizable (solid line) and monopolizable food (dashed line).

The conflict rate, when feeding on non-monopolizable food, strongly increased with the number of competitors present in the feeding party (Figure 2; Pearson: $R = 0.86$, $N = 14$, $P < 0.001$). However, there is no correlation for monopolizable food (Pearson: $R = 0.12$, $N = 14$, NS), indicating no difference in strength of competition over food between one and more competitors, when the food can be monopolized by one individual (Figure 2). Although females faced competition with between 1 and 17 chimpanzees in their feeding parties, we only included feeding parties ≤ 14 competitors, as cumulative feeding time reaches a plateau with 14 competitors and feeding time with more competitors was rare: <1 hour.

On average, the dominant female of the conflict dyad ultimately possessed the food in 66% of cases (Table I). Being dominant over a competitor provided an advantage in female contests, as dominant conflict partners possessed the food significantly more frequently after conflicts than did subordinates independent from the initiator (Table I; Wilcoxon exact: $T = 53.5$, $N = 11$, $P < 0.01$). However in 15 cases no female was successful (Table I), as both lost the food to a third party (in 5 cases to a male, 4 to a dominant female, 5 to a group of females and once to a subordinate female). In sum, Taï female chimpanzees faced contest competition over food, as females fought

Table II. Correlates of dominance rank in Taï females

Name	Dominance rank	Contest rank	Age (years)[a]
MYSTERE	1	2	24
LOUKOUM	2	1	27
VENUS	3	7	21
RICCI	4	3	36
GOMA	5	5	26
PERLA	6	4	23
BELLE	7	8	23
CASTOR	8	6	23
NARCISSE	9	10	16
DILLY	10	9	21
FOSSEY	11	11	20

Note. The females are ordered in declining dominance rank order and show the assigned dominance rank, contest rank, and age.

[a] Approximate age in 1999, as dates of birth are estimated except for Belle (Boesch and Boesch-Achermann, 2000).

more for monopolizable food or with increasing numbers of competitors, and dominant females possessed the food after a conflict.

Correlates of the Linear Hierarchy

We tested 2 correlates of the linear ranking in Taï females. First, dominance rank order of females was related to age, with older females dominating younger ones (Table II; Spearman rank: $R = -0.70$, $N = 11$, $P < 0.05$). Second, we created a linear hierarchy based on contest aggression interactions over food (contest rank), with winners being assigned higher ranking (Table II; Improved linearity test: $\mathrm{h}' = 0.43$, $P = 0.06$), and found that contest rank correlates with dominance rank (Spearman rank: $R = 0.86$, $N = 11$, $P < 0.001$). However, when eliminating the influence of either contest rank or age, the correlation between dominance rank and age disappeared (Kendall partial correlation: $T = 0.05$, $N = 11$, NS), while the correlation between dominance rank and contest rank remained significant (Kendall partial correlation: $T = 0.54$, $N = 11$, $P < 0.05$). Thus, the linear hierarchy is related to the outcome of the contest, while it is independent from age.

Social Relationships

Taï females have a median $D\hat{AI}_{\mathrm{FF}}$ of 0.27 (Appendix A). Although their association is very high compared to other populations (Table III),

Table III. Comparison of dominance relationships among female chimpanzees in 5 study sites in the wild

Study site (community)	Mean female observation time (h)[a]	Adult females (N)	Rank categories	Proportion of non-unidirectional greeting dominance relationships	DAI[b]	Grooming pattern[c]	Greeting rate[d] (*corrected rate*)[f]	Food conflict rate[e] (*corrected rate*)[f]
Budongo[g] (Sonso)	54	12	α and not-α	74%	0.09	—	0.002 (*0.24*)	—
Gombe[h,i] (Kasakela)	436[i]	11–17[h]	High, middle, low[h]	—	0.05[i]	35/26/39[i]	—	0.003[i] (*0.06*)
Kibale[j] (Kanyawara)	7	13	High and low	—	0.08	0/0/100	—	—
Mahale[k,l,m,n] (M-group)	63[k]	13[k]	1–13[k] (linear)	69%[k]	(0.39)[l] ≈0.05[m]	45/55[n]	0.046[k] (*0.92*)	0.016[k] (*0.32*)
Taï[o] (North-group)	103	11	1–11 (linear)	33%	0.27	55/32.5/12.5	0.113 (*0.42*)	0.1 (*0.37*)

Note: Parameters Presented in the table describe the hierarchy social relationships, and contest competition of females.

[a] Mean observation time of target females in hours.

[b] Average dyadic association index of females.

[c] Grooming pattern shows proportion of bidirectional/unidirectional/nongrooming female dyads (Mahale: grooming/nongrooming).

[d] Greeting rate is all greetings exchanged by females per total female observation time.

[e] Food conflict rate is all food conflicts among females per total female observation time.

[f] Corrected rate (*in italic numbers*) are rates divided by the DAI.

[g] Fawcett, 2000.

[h] Pusey *et al.*, 1997.

[i] Goodall, 1986, observation time: 8 focal females for the 2-year period of 1978–79 from appendix c, DAI: from 1978–81 (appendix d), grooming pattern: calculated from in camp grooming sessions of 3 adult females within 31 dyads (Fig. 14.2), conflict rate: from Fig. 12.4 and multiplied with 0.66 as only two-thirds of female conflicts are with other females (chapter: aggression).

[j] Wrangham *et al.*, 1992.

[k] Nishida, 1989, conflict rate: from Table 8.

[l] Nishida, 1968, K-group.

[m] Nishida and Hosaka, 1996, DAI: with a correction factor for DAI in not artificial feeding areas (correction method described in: Boesch and Boesch-Achermann, 2000, Table 5.9).

[n] Huffmann, 1990, from focal data of females in 1985: Fig. 12.2, of 29 F–F dyads representing grooming dyads vs. nongrooming dyads.

[o] This study.

—No data available.

inter female association in Taï was about one third less than inter male association ($\hat{DAI}_{\mathrm{MM}} = 0.42$; Permutation test: $P < 0.05$), but more frequent than bisexual association ($\hat{DAI}_{\mathrm{MF}} = 0.23$; Permutation test: $P < 0.05$). Before the death of Brutus, the association among the females was *ca.* 25% lower than after (Appendix A; with Brutus: $\hat{DAI}_{\mathrm{FF}} = 0.21$; Permutation test: $P < 0.05$). If the lack of clear dominance relationships in other study sites is due to low greeting rates because of a lower association (Table III), we would expect a lower corrected greeting rate (CGR) during the period of lower association. However, there is no difference in the CGR between the periods of lower and higher association (Permutation test: *NS*). We even found a higher CGR during the period of lower association, when analyzing the 15 female dyads that showed greetings in both periods (with Brutus: $C\hat{G}R_{\mathrm{FF}} = 0.171$ greetings/associated hour (25%: 0.147, 75%: 0.311); without Brutus: $C\hat{G}R_{\mathrm{FF}} = 0.074$ g/ah (25%: 0.032, 75%: 0.128); Permutation test: $P < 0.05$).

Finally we tested whether the 11 female dyads of unknown dominance relationships were rare associates and non-groomers. The median $\hat{DAI}_{\mathrm{unknown}}$ of the 11 dyads is 0.27 (combine Figure 1 and Appendix A), hence the females of unknown dominance relationships associated the same amount as females with unidirectional or bidirectional relationships ($\hat{DAI}_{\mathrm{unidirectional}} = 0.29$; Permutation test: *NS*; $\hat{DAI}_{\mathrm{bidirectional}} = 0.31$; Permutation test: NS). Female pairs have a median grooming rate of 2.71 sec/h (25%: 0.32 s/h, 75%: 4.90 s/h), spread over 30 bi-directional grooming, 18 unidirectional grooming and 7 non-grooming relationships. The 11 unknown dominance relationships are represented by 5 bi-directional, 5 unidirectional and 1 non-grooming dyads. Thus there is no difference in the grooming pattern between dyads of unknown and unidirectional dominance relationships (Goodness of fit exact: $\chi^2_2 = 0.83$, NS). Accordingly, within the community, an increase in association does not imply more greetings, and neither association nor grooming patterns among Taï females could explain the lack of dominance relationships in some dyads.

DISCUSSION

The dominance relationships of Taï female chimpanzees fit to a linear hierarchy. While the linear hierarchy is independent of age, winning a contest over food is related to the dominance rank order. Taï females face food competition with higher competition over monopolizable food or with more competitors in the feeding site. They maintain affiliative relationships with almost all other females in the community and show higher association patterns than those of females in other chimpanzee sites. Neither association nor grooming patterns explain the occurrence of unknown dominance relationships within the community.

Despite the fact that there is a linear hierarchy among Taï females, some dyads emitted greetings in both directions. This is similar to other chimpanzee populations wherein females sometimes used mutual pant-grunts during greetings (Gombe: Goodall, 1986; Mahale: Nishida, 1979). Even among males, among which unidirectionality of pant-grunts has been generally reported, dominance reversed pant-grunts also occur (Gombe: Goodall, 1986; Mahale: Nishida and Hosaka, 1996; Taï: Boesch and Boesch-Achermann, 2000), indicating that they are not exclusively unidirectional. Even though we studied a combination of different greeting vocalizations among Taï females, they still showed strong directionality. Therefore, the greetings provide a good indicator for female dominance relationships, showing that they form a stable and linear hierarchy.

Taï female chimpanzees appeared to show clearer linearity in their hierarchy than have females in 5 other chimpanzee populations (Table III). Only 2 dyads (Perla-Dilly and Dilly-Fossey) remained unclear when taking triadic relationships into account. In contrast more than two-thirds of the dominance relationships were unknown in Mahale, *ca.* three-quarters of the dominance relationships were unknown in Budongo (Table III) and in Gombe 12% of the females did not fit to a rank, even though broad categories were implemented (Pusey *et al.*, 1997).

Taï female chimpanzees used aggression to keep resources or to gain them from other females. Unequal access, especially to monopolizable food such as meat, might be an explanation for the development of the linear hierarchy in Taï females. For example, dominant females may access 500 g of meat per successful hunt, a substantial benefit compared to 80 g obtained by average females (Boesch and Boesch-Achermann, 2000). There was even unequal access to non-monopolizable food due to contests in large feeding parties (Figure 2). It seems that Taï females contest over feeding space in food patches, e.g., crowns of fruit trees, as observed in Thomas langurs (*Presbytis thomasi*: Sterck and Steenbeek, 1997). Being dominant seems to give females priority of access to a higher quality and quantity of food. However, the question remains whether the frequency of contest is regular enough to actually cause the linear hierarchy. Comparing the individual aggression rates of Taï females attending a feeding site reveals that they are in the upper range of primate species of which several fit to linear hierarchies (individual female food contest rate [conflict/h feeding]: *Cercocebus torquatus*: 0.04 c/h, Range and Noë, 2002; *Chlorocebus aethiopis*: 0.07 c/h and *Erythrocebus patas*: 0.04 c/h, Pruetz and Isbell, 2000; *Saimiri sciureus*: 0.28 c/h, Mitchell *et al.*, 1991; *Pan troglodytes*: 0.22 c/h, this study).

Thus, contest competition seems to be high and beneficial for the dominant females.

It seems that being older enhances the chance to win the contest. Taï females, like females in other populations, may increase their individual rank as they age (Gombe: Pusey *et al.*, 1997; Mahale: Nishida, 1989). However, the dominance rank order in Taï females is related to contest rank but not to age. Thus, competition over food is the main determinant for the development of the linear hierarchy in Taï females.

In spite of contest competition, Taï females have affiliative interactions with almost all other female community members. Although neither association nor dyadic grooming relationships could explain the variability in Taï dominance relationships, the comparison with other populations reveals remarkable differences (Table III). In addition to an almost five fold higher association rate among Taï females, they have the most dyads with bidirectional grooming and the fewest females that never groomed together versus other populations. Taï females build long-lasting friendships, including food-sharing and support (Boesch and Boesch-Achermann, 2000), and they seem to take such factors into account when initiating aggression (Wittig and Boesch, in press). Therefore, Taï female society might be shaped through advantages of female bonding when access to food is affected by contest competition.

Why did we find such differences in the female relationships among different communities of the same species? One argument might be that linear hierarchies have not been detected yet in the other study sites. On one hand, linearity is easier to find in small groups (Drews, 1993), but the number of females examined was similar across sites (Table III). On the other hand, longer observations increase the chance to observe greetings between females. Observation time is surely not the problem for Gombe, while it is perhaps a problem in the Kibale study (Table III). However, observation times in Taï, Mahale and Budongo are similar; consequently, differences among the female hierarchies should be independent of observation time. Less than 50% of greetings among females occurred in Mahale and Budongo compared to Taï (greeting rate) which could explain the large number of non-unidirectional relationships (Table III). However in Mahale, but not in Budongo, females actually greeted more frequently when they met each other than Taï females did (Table III; corrected greeting rate). This is a similar observation to our findings of a higher corrected greeting rate during the lower association period. It may be, that female chimpanzees have to confirm their submissive position more often the less frequently they meet when a dominance relationship exists. Thus in Mahale a linear hierarchy might exist, but may require more data for detection, whereas the dominance relationships are ambiguous among the females in Budongo.

Another possibility might be that female dominance relationships do not fit to linear hierarchies in other populations. As food distribution and predation risk are suggested to influence female gregariousness, which shapes the competitive regime of females, contest competition should depend on the association of females (Sterck *et al.*, 1997). Although food conflicts occur 6–30 times less frequently in other populations than at Taï (Table III; food conflict rate), the actual rate of food conflicts among 2 females when associated is the same at Taï and Mahale (Table III; corrected food conflict rate). Thus Mahale females face similar levels of contest competition as Taï females, whereas in Gombe, contest competition among females is lower. However, females in Mahale and Taï cope differently with the contest competition. While Mahale females seem to disperse to reduce contest competition, Taï females build a formal linear hierarchy to endure the contest competition. This may reflect a higher advantage in staying together for Taï females, perhaps to reduce predation risk (Boesch, 1991; Caraco *et al.*, 1980; van Schaik *et al.*, 1983). Although mortality rates for Taï and Mahale chimpanzees are similar and the highest among chimpanzee communities (Hill *et al.*, 2001), predation by leopards is only known to exist in Taï (Boesch, 1991; Boesch and Boesch-Achermann, 2000; Hiraiwa-Hasegawa *et al.*, 1986). Hence Taï females may have evolved a clearer linear dominance hierarchy than females of other chimpanzee populations, as an adaptation to stronger contest competition (versus Gombe) and a higher predation risk (versus Mahale).

The comparison among chimpanzee populations (Table III) revealed strong differences, not only in female dominance relationships but also in their competitive regimes, their levels of association and affiliation, and the predation risk females and their offspring face. Although there are some limitations with the cross-study comparison, as data have been collected using different methods or during different periods and adjusted post hoc for comparison, our comparison supports the predictions of the socio-ecological model (Sterck *et al.*, 1997; van Schaik, 1989). We did not consider data on general food distribution and abundance because it was not available (Fawcett, 2000; Anderson *et al.*, 2002).

Our findings of a linear dominance ranking in females and a stronger female integration in the social network, support the bisexual model of Taï chimpanzee social organization (Boesch, 1991), as do other findings from Taï (Lehmann and Boesch, in preparation). Accordingly, social structure in chimpanzees is more flexible than previously thought and adapts to ecological circumstances.

Appendix A. Dyadic association index (DAI) of males and adult females in the North community of Taï chimpanzees. DAIs for the period before the death of Brutus (10.1996–2.1997) are shown above the diagonal in *italic numbers*, while DAIs without Brutus are shown under the diagonal. Individuals are separated by sex (males in *italic letters*) and in alphabetical order.

DAI	*Brutus*	*Macho*	*Marius*	*Nino*	Belle	Castor	Dilly	Fossey	Goma	Loukoum	Mystère	Narcisse	Perla	Ricci	Venus
Brutus		*0.35*	*0.42*	*0.25*	*0.14*	*0.13*	*0.17*	*0.11*	*0.14*	*0.17*	*0.19*	*0.15*	*0.19*	*0.25*	*0.18*
Macho			*0.48*	*0.35*	*0.13*	*0.15*	*0.13*	*0.11*	*0.14*	*0.32*	*0.19*	*0.15*	*0.15*	*0.24*	*0.17*
Marius		0.68		*0.31*	*0.11*	*0.13*	*0.15*	*0.12*	*0.13*	*0.16*	*0.19*	*0.14*	*0.16*	*0.27*	*0.25*
Nino		0.45	0.41		*0.15*	*0.18*	*0.15*	*0.15*	*0.18*	*0.25*	*0.19*	*0.16*	*0.17*	*0.38*	*0.29*
Bele		0.34	0.29	0.33		*0.23*	*0.21*	*0.22*	*0.19*	*0.11*	*0.26*	*0.19*	*0.24*	*0.22*	*0.15*
Castor		0.24	0.20	0.25	0.24		*0.30*	*0.52*	*0.34*	*0.16*	*0.41*	*0.17*	*0.29*	*0.18*	*0.16*
Dilly		0.18	0.18	0.21	0.23	0.31		*0.31*	*0.47*	*0.11*	*0.30*	*0.16*	*0.29*	*0.18*	*0.22*
Fossey		0.19	0.18	0.23	0.21	0.46	0.27		*0.35*	*0.11*	*0.36*	*0.15*	*0.25*	*0.19*	*0.17*
Goma		0.18	0.17	0.22	0.22	0.32	0.48	0.35		*0.15*	*0.36*	*0.21*	*0.29*	*0.17*	*0.28*
Loukoum		0.32	0.27	0.30	0.25	0.25	0.25	0.23	0.25		*0.16*	*0.13*	*0.14*	*0.15*	*0.23*
Mystère		0.24	0.23	0.28	0.26	0.39	0.35	0.30	0.37	0.26		*0.19*	*0.31*	*0.23*	*0.17*
Narcisse		0.20	0.18	0.24	0.25	0.29	0.27	0.25	0.31	0.24	0.31		*0.21*	*0.21*	*0.15*
Perla		0.24	0.22	0.24	0.26	0.31	0.38	0.27	0.36	0.29	0.36	0.30		*0.21*	*0.16*
Ricci		0.27	0.28	0.41	0.29	0.24	0.21	0.25	0.21	0.25	0.26	0.28	0.23		*0.19*
Venus		0.24	0.26	0.28	0.23	0.28	0.30	0.27	0.31	0.38	0.30	0.29	0.35	0.25	

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