

RESEARCH ARTICLE

How Feeding Competition Determines Female Chimpanzee Gregariousness and Ranging in the Taï National Park, Côte d'Ivoire

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Socioecological theory suggests that feeding competition shapes female social relationships. Chimpanzees (*Pan troglodytes*) live in fission–fusion societies that allow them to react flexibly to increased feeding competition by forming smaller foraging parties when food is scarce. In chimpanzees at Gombe and Kibale, female dominance rank can crucially influence feeding competition and reproductive success as high-ranking females monopolize core areas of relatively high quality, are more gregarious, and have higher body mass and reproductive success than low-ranking females. Chimpanzee females in Taï National Park do not monopolize core areas; they use the entire territory as do the males of their community and are highly gregarious. Although female chimpanzees in Taï generally exhibit a linear dominance hierarchy benefits of high rank are currently not well understood. We used a multivariate analysis of long-term data from two Taï chimpanzee communities to test whether high-ranking females (1) increase gregariousness and (2) minimize their travel costs. We found that high-ranking females were more gregarious than low-rankers only when food was scarce. During periods of food scarcity, high rank allowed females to enjoy benefits of gregariousness, while low-ranking females strongly decreased their gregariousness. High-ranking females traveled more than low-ranking females, suggesting that low-rankers might follow a strategy to minimize energy expenditure. Our results suggest that, in contrast to other chimpanzee populations and depending on the prevailing ecological conditions, female chimpanzees at Taï respond differently to varying levels of feeding competition. Care needs to be taken before generalizing results found in any one chimpanzee population to the species level. *Am. J. Primatol.* 71:1–9, 2010. © 2010 Wiley-Liss, Inc.

Key words: *Pan troglodytes*; gregariousness; ranging; dominance rank; chimpanzee density

INTRODUCTION

Group living provides a number of advantages including better protection from predators [Dunbar, 1988; Schaik van, 1989], better access to resources [Krebs & Davies, 1993], and increased cooperation [Emlen, 1991]. One important disadvantage of group living is increased competition for food [Dunbar, 1988]. As suggested by Schaik van [1989] and Sterck et al. [1997], intra- and intergroup feeding competition may shape female social relationships, dispersal, and the structure of social groups in non-human primates. In particular, clumped resources may lead to contest competition over food, which may promote the emergence of strong dominance hierarchies in female primates [Isbell & van Vuren, 1996]; high-ranking females have priority of access to food and higher energy intake rates. The resulting skew in energetic and nutritional benefits according to rank can lead to fitness benefits for high-ranking females, which have frequently been observed to have higher mating and lifetime reproductive success than low-ranking females [Koenig, 2002; Sterck et al., 1997].

In contrast to most primates, chimpanzees (*Pan troglodytes*) live in fission–fusion societies whereby individuals form smaller foraging parties when food abundance is low [Boesch, 2009; Boesch & Boesch-Achermann, 2000; Goodall, 1986; Mitani et al., 2002]. This flexible system may help to reduce within-group contest competition over food, and reduces the linearity of female dominance hierarchies in some chimpanzee communities [Fawcett, 2000; Nishida, 1989] whose females can be assigned only to larger rank categories [Pusey et al., 1997; Wrangham et al., 1992]. Regardless of whether dominance ranks are linear or categorically assigned, studies of chimpanzees

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in Gombe and Kibale have shown that female rank can strongly influence feeding competition and reproductive success. At Gombe, high-ranking females are more gregarious with other females than are low-ranking females [Williams et al., 2002b]. High-ranking females have higher body mass, monopolize core areas with higher food plant productivity, and spend less time foraging [Murray et al., 2006, 2007; Pusey et al., 2005]. They also live longer and have higher infant survival and reproductive success than low-rankers [Pusey et al., 1997]. Similar results have been found in Kibale, where high-ranking females occupy higher quality core areas [Kahlenberg et al., 2008] and females with access to these areas have higher reproductive success [Emery Thompson et al., 2007]. In addition, higher rank is associated with lower stress hormone levels and this effect of rank is particularly pertinent for lactating females [Emery Thompson et al., 2010].

Chimpanzee females in the Taï National Park, Côte d'Ivoire have in general a linear dominance hierarchy, suggesting strong contest competition over food [Wittig & Boesch, 2003] that may derive from greater gregariousness: male–male, female–male, and female–female association rates are all higher than in Gombe and Kibale chimpanzees [Boesch, 2009; Boesch & Boesch-Achermann, 2000; Lehmann & Boesch, 2008; Wittig & Boesch, 2003]. In contrast to Gombe and Kibale [Goodall, 1986; Williams et al., 2002a], females at Taï do not monopolize core areas but travel throughout the entire community home range [Lehmann & Boesch, 2005]. These ranging and association patterns in Taï chimpanzees have been described by the bisexually bonded ranging model of Lehmann and Boesch [2005], and may result from a high risk of predation by leopards [Boesch, 1991, 2009] as well as differences in food distribution [Boesch, 2009; Doran, 1997; Wrangham, 2000].

Although previous studies have emphasized differences in the behavior of chimpanzees in Taï compared with other study sites [Boesch & Boesch-Achermann, 2000; Lehmann & Boesch, 2005], relatively little is known about how dominance rank affects female gregariousness and ranging. The only known effect of rank on ranging behavior in Taï is that high-ranking females use larger home ranges that include more peripheral areas, presumably because high-ranking females are more likely to participate in border patrols [Lehmann & Boesch, 2005]. The potential effects of rank on female ranging (travel distance) or gregariousness (weighted party size (WPS)) have not yet been explored and it remains unclear whether high-ranking females are more gregarious than low-ranking females as observed in Gombe and whether higher ranked females show more optimized ranging behavior. To address these gaps, we analyzed long-term data from two Taï chimpanzee communities (north and south community).

High-ranking females in Taï might increase gregariousness like the females in Gombe because

they would win fights over food with other females [Wittig & Boesch, 2003] while simultaneously maximizing the benefits of group living such as offspring protection and socialization [Williams et al., 2002b], protection from predators, increased cooperation [Boesch, 2009; Boesch & Boesch-Achermann, 2000], and greater opportunity to build and maintain strong social bonds [Lehmann & Boesch, 2008]. On the basis of these arguments, we predicted that high-ranking females would be more gregarious than low-ranking females, so that female rank is positively correlated with WPS.

In Gombe, high-ranking females spent less time foraging and foraged more efficiently because they occupied higher quality habitats [Murray et al., 2006]. Although females in Taï do not monopolize different core areas, we hypothesized that high-ranking females might use their rank to optimize their ranging behavior by minimizing travel costs. Therefore, we predicted a negative correlation between female dominance rank and daily travel distance.

On the basis of the previous studies investigating gregariousness and ranging in Taï chimpanzees [Anderson et al., 2002; Boesch & Boesch-Achermann, 2000; Doran, 1997; Lehmann & Boesch, 2003, 2004, 2005, 2008], we chose the following predictor variables, and interactions among them, in our multivariate analysis: female dominance rank, chimpanzee density, fruit abundance index (FAI), number of females in estrus, whether the female had a dependent offspring, and community identity.

We included whether the female had a dependent offspring because other studies have shown that chimpanzee mothers were less social [Goodall, 1986; Murray et al., 2007; Otali & Gilchrist, 2006; Sakura, 1994; Takahata, 1990; Williams et al., 2002b; Wrangham, 2000] and traveled more slowly and less far than other females [Williams et al., 2002b; Wrangham, 2000].

The interaction of estrous females and fruit abundance was included because Anderson et al. [2002] found that the number of females in estrus was positively related to fruit abundance and that if fruit abundance increased, party size increased as well, though this effect was limited to situations when no estrous females were present.

The interaction between rank and fruit abundance was included because during seasons with low fruit abundance, chimpanzees in Taï were less gregarious and had party sizes similar to those of Gombe and Kibale chimpanzees [Doran, 1997]. It is possible that there is a strong within-group contest competition and a high level of energetic stress during periods of low fruit abundance [Emery Thompson et al., 2010], such that rank effects on contest competition over food might become more pronounced. During periods of high fruit abundance, all Taï females benefit from gregariousness because of the protection from predators. Predation due to

leopards was and is still very high at Taï, whereas predation is absent or very low in most other chimpanzee study sites [Boesch, 1991, 2009].

METHODS

Study Site, Subjects, and Data Collection

We analyzed data on adult female gregariousness and ranging from the north and south habituated chimpanzee communities in the Taï National Park (TNP), Côte d'Ivoire. TNP comprises evergreen lowland rainforest covering an area of approximately 5,400 km² [for a detailed description of the study site see Boesch & Boesch-Achermann, 2000]. Habituation of the north and south communities started in 1979 and 1989. Both communities have since been continuously observed by researchers and local field assistants. Since 1992 in the north community and 1999 in the south community, assistants carried out daily focal animal follows [Altmann, 1974]. Each day, a focal (target) chimpanzee in each community was followed from nest to nest (full-day follow), or for as long as possible (mean daily observation time for both communities = 9.8 ± SD 2.4 hr). Assistants selected targets with the aim of following each adult chimpanzee at least once per month. They plotted the target's daily travel route on a map and used check sheets to make continuous records of the target's social interactions, feeding and ranging behavior, as well as the number and identity of estrous (maximally swollen) females encountered throughout the observation day. In addition, party size and composition were continuously monitored by noting all independently traveling individuals (older than 5 years) in the target's party, i.e. within view of the observer, and presumably the target as well. A party is a particular combination of chimpanzees that stay within sight of each other for at least 1 min. Each new combination of individuals was identified as a new party; all membership changes were noted and timed, allowing the calculation of party duration.

The data presented here include target follows from adult females ≥ 14 years old that lasted at least 7 hr: our sample included 998 follows of ten females in the north community (average per female = 100 ± SD 51 follows) and 1,109 follows of 19 females in the south community (average per female = 58 ± SD 30 follows). The data encompass a 10-year period for the north community (February 1997–October 2006) and an 8-year period for the south community (October 1999–September 2006). During this time, the north community decreased from 32 to 21 individuals (10–5 adult females, 2–0 adult males) and the south community from 54 to 32 chimpanzees (19–11 adult females, 2–4 adult males). The south community was always larger than the north community, with more adult females and more adult males.

Five field assistants conducted target follows. We measured inter-observer reliability when two assistants followed the same target throughout the day and recorded party sizes. In these cases, there was no significant difference in daily WPSs between assistants (Wilcoxon Matched Pairs Signed Ranks Exact Test, $T^+ = 20$, $N = 9$ (3 Ties) days, $P = 0.84$), and WPSs of the two assistants were highly correlated ($r_s = 0.99$, $N = 11$ days, $P < 0.001$). Deschner et al. [2004] reported similar results for inter-observer reliability among Taï assistants.

Assistants trained in botanical monitoring censused fruit tree phenology every month using established routes [sensu Malenky et al., 1993] in both chimpanzee territories. They observed at least seven fruit trees from each of 38 species ($N = 818$ trees in total per month for the north community, $N = 654$ trees in total per month for the south community) whose fruits were chimpanzee foods, noting the presence of ripe fruits [Anderson et al., 2002, 2005 provide further details].

All field protocols, data collection procedures, and data analyses were conducted in accordance with wildlife research protocols and ethical standards of the Max Planck Society in Germany, the Centre Suisse de Recherches Scientifiques in Côte d'Ivoire, the Ministère de la Recherche Scientifique, and the Ministère de l'Environnement et des Eaux et Forêts in Côte d'Ivoire.

Data Analysis

Behavioral data were analyzed at a daily time scale. Details of the response variables are as follows:

Weighted party size: For each target follow, we calculated the daily WPS as

$$\text{WPS}_d = \sum_{p=1}^{n_d} \frac{\text{party duration}_p}{\text{total observation time}} * \text{partysize}_p$$

where n_d is the daily total number of different parties of which the target was a member and p indexes the different parties. We excluded parties where not all members were identified (these accounted for only 0.5% of all parties).

Travel distance: To measure daily travel distance, we entered daily travel maps using a digitizing tablet into the Digitizing and Geo referencing program Didger 3.06 (Golden, CO). We derived travel distance of the target by using the perimeter length variable returned by Didger and divided this value by the target's total daily observation time to obtain an approximate distance traveled per hour. To estimate total distance traveled per observation day, we multiplied these values by 12 hr. Lehmann and Boesch [2004] showed that the digitized maps underestimated travel distances by about 11% in comparison with distances from 30-min GPS location readings, but that these underestimates are consistent regardless

of the daily travel distance value and hence are unlikely to influence our results.

We considered the following predictor variables:

Dominance rank: We assigned annual dominance rank categories to females according to the direction of greeting behavior, including pant-grunts (PG), greeting-hoos, and greeting-pants [Wittig & Boesch, 2003]. PG are submissive vocalizations that function as formal indicators of subordination [Bygott, 1979]. We were able to detect annual linear female hierarchies in both communities but not for all years (7 of 8 years for the south community and 7 of 10 years for the north community). Because matrices with a high proportion of empty cells or small numbers of females prevented the detection of linear hierarchies as implemented by Wittig and Boesch [2003], we decided to use rank categories (low, middle, and high) following Pusey et al. [1997]. We determined rank categories as follows. High-ranking females either gave no PG to any females or gave occasional PG to other high-ranking females and received PG from middle- and low-ranking females. Middle-ranking females gave PG to high- and some middle-ranking females and received them from low- and some middle-ranking females. Low-ranking females rarely, if ever, received PG from any adult females but often gave them to middle- and high-ranking females. Female rank categories remained stable across years, with 24 of 29 individuals maintaining a single rank category over the study period. Four females moved to the adjacent category, and one female occupied all three categories; she was initially high-ranking but dropped in rank during the 2 years before her death, becoming first middle- and then low-ranking as her physical condition deteriorated.

Density: We calculated chimpanzee density for each of the two communities separately based on yearly community size divided by yearly home-range size (chimpanzee/km²). We determined community size by averaging the monthly maximum number of community members over 12 months and dividing that by the annual home range. We estimated annual home-range size using the minimum convex polygon method, based on all adult chimpanzee travel routes recorded on maps. We considered all areas used by adults as part of the annual home range.

Fruit abundance index: We incorporated records of monthly fruit phenology with data on density (stems/ha) and basal area (cm²) of fruit trees with a diameter at breast height ≥ 10 cm, as reported by Anderson et al. [2005] for the north community and by Goné Bi [2007] for the south community. The FAI for month m was calculated following Anderson et al. [2002, 2005]:

$$FAI_m = \sum_{p=1}^n D_k * B_k * P_{k,m}$$

where D_k is the density of species k across the study area, B_k is the mean basal area of species k across the

study area, and $P_{k,m}$ is the percentage of observed trees of species k presenting ripe fruits in month m .

Estrous females: Field assistants coded sexual skin swellings following Furuichi [1987], recognizing three stages of tumescence: (1) no swelling: minimal size and maximal degree of wrinkling; (2) partial swelling: relative increase/decrease in size and loss/appearance of wrinkles compared with stage 1 or 3; and (3) maximum swelling: maximum size with no wrinkles and tight appearance. We calculated the number of estrous females as those with maximal swellings on each observation day.

Dependent offspring: We recorded whether the female had a dependent offspring (≤ 5 years old) [Boesch & Boesch-Achermann, 2000] on the day of her follow.

Community: This was either north or south community.

Statistical Analyses

To assess the importance of the above predictor variables in describing gregariousness (WPS) and ranging (travel distance), we estimated their effect using generalized linear mixed models (GLMMs). Predictor variables included as fixed effects were dominance rank, community, dependent offspring, density, FAI and estrous females, and interactions between estrous females and FAI, and between rank and FAI. For the ranging model, we included the additional predictor variable WPS as a fixed effect.

We used the R package lme4 [version 0.999375-20; R version 2.7.1; Bates et al., 2008; R Development Core Team, 2008] to fit our GLMMs. We log_e-transformed WPS, FAI, and estrous females and standardized all predictor variables to have mean = 0 and standard deviation = 1 before analysis. We checked for multi-collinearity by running multiple linear regressions with all predictor variables in SPSS version 15.0 [SPSS Inc., 1999]. In the GLMMs, we used values per individual and focal day as the unit of analysis. By including individual as a random effect, we controlled for multiple observations from the same female. To control for potential temporal autocorrelation (due to observations taking place sequentially in time), we included an autocorrelation term as a covariate in the model. This term was calculated from the residuals of the model without the autocorrelation term, and separately for each female. In detail, for each data point, the autocorrelation term was the weighted mean of all other residuals derived from the same female, with the weight equaling the inverse number of days between respective data point and the residual.

Models were assumed to have a Gaussian error distribution predicting the frequency of the response variables. We visually checked residuals plotted against predicted values for homogeneity of error variance. WPS was log_e-transformed to achieve homogeneous error variances. We tested whether

each full model had a reasonable fit to the data by fitting the model to 1,000 bootstrapped data sets with the response variable permuted within individuals. We derived P values for the model fit by dividing the number of models for the permuted data that had a log-likelihood at least as large as the model fit to the original data by 1,000 (the number of permutations; original data were included as one permutation). We tested the significance of fixed effects by applying non-parametric bootstrapping within individuals. We established variables of which the confidence interval of the coefficient estimated from 1,000 bootstraps did not include 0 as significant (Table 1).

In cases when interactions in the full model were not significant, we produced a reduced model including only the significant interactions to calculate the estimates and confidence intervals for predictor variables and interactions. In this way, we were able to determine whether predictor variables like dominance rank had an influence alone.

We calculated the effect sizes of the full GLMMs using the t values from the models to approximate r statistics and the formula proposed by Nakagawa and Cuthill [2007] for non-independent data:

$$r = \frac{t[1+(n_i/n_o)R]\sqrt{1-R}}{\sqrt{t^2[1+(n_i/n_o)R]^2(1-R)+n_o-k}}$$

where t is the t -value from the mixed-effects model, n_o is the number of observations, n_i is the number of individuals, k is the number of parameters including the intercept, and R is the repeatability or intraclass correlation [e.g. Zar, 1999], which consists of two variance components: the between-individual and the within-individual variance or residual variance, which are obtained from the random-effect part of the mixed-effects model.

RESULTS

Model fits for the permuted data of the response variables were both highly significant (both full models: $P = 0.001$). We calculated the effect sizes (r) of the full GLMMs and included the r values in Table 1.

We found no support for our prediction that high-ranking females are in general more gregarious than low-ranking females. Instead, we found that decreasing FAI led to substantially lower WPS in low-ranking females (average WPS for high FAI > 42,042 = 10.0 ± SD 4.7 individuals and for low FAI < 5,338 = 5.2 ± SD 4.2 individuals) and only slightly lower WPS in high-ranking females (average WPS for high FAI > 42,042 = 9.4 ± SD 5.0 individuals and for low FAI < 5,338 = 7.6 ± SD 4.9 individuals) as indicated by the significant interaction between

TABLE 1. Analysis of Ecological and Demographic Factors Influencing the Gregariousness and Ranging of Tai Chimpanzee Females

Response variable	Predictor variable	Estimate	CI	Effect size
Weighted party size	Intercept	1.84	1.76 to 1.91	0.70
	Dominance rank	0.02	-0.02 to 0.05	0.03
	Community (south)	0.08	0.01 to 0.13	0.05
	Dependent offspring (yes)	0.06	-0.03 to 0.13	0.04
	Density	0.07	0.05 to 0.10	0.13
	Estrous females	0.19	0.18 to 0.23	0.31
	FAI	0.09	0.06 to 0.11	0.16
	Estrous females × FAI	-0.05	-0.07 to -0.03	0.10
	Dominance rank × FAI	-0.03	-0.05 to -0.01	0.06
	Autocorrelation term	0.89	0.59 to 0.82	0.42
	Travel distance	Intercept	2.91	2.71 to 3.10
Dominance rank		0.13	0.05 to 0.19	0.08
Community (south)		0.78	0.61 to 0.90	0.22
Dependent offspring (yes)		0.09	-0.08 to 0.31	0.02
Density		0.01	-0.06 to 0.09	0.01
Weighted party size		0.26	0.19 to 0.33	0.14
Estrous females		0.25	0.17 to 0.33	0.14
FAI		0.34	0.28 to 0.40	0.20
Estrous females × FAI		-0.01	-0.06 to 0.04	0.01
Dominance rank × FAI		0.01	-0.04 to 0.08	0.01
Autocorrelation term		0.54	0.21 to 0.50	0.21

Summary statistics of generalized linear mixed models and their effect sizes (r): $r = 0.1$ is considered a small effect, $r = 0.3$ a medium and $r = 0.5$ a large effect. Predictor variables and interactions were assumed to have a significant effect when the estimated 95% confidence intervals (CI) from 1,000 non-parametric bootstrapped data did not include zero. The corresponding estimates are marked bold. The estimates and confidence intervals of predictor variables, the intercept and the autocorrelation term of the GLMM for travel distance come from a reduced model, whereas the estimate for the two non-significant interactions are from the full model. The main results are marked in grey, except the intercept and the autocorrelation term. The response variable WPS was \log_e -transformed to achieve homogeneous error variances. FAI, estrous females and WPS were \log_e -transformed and all continuous predictor variables were standardized to mean = 0 and standard deviation = 1. WPS, weighted party size; FAI, fruit abundance index; GLMM, generalized linear mixed model; CI, confidence interval.

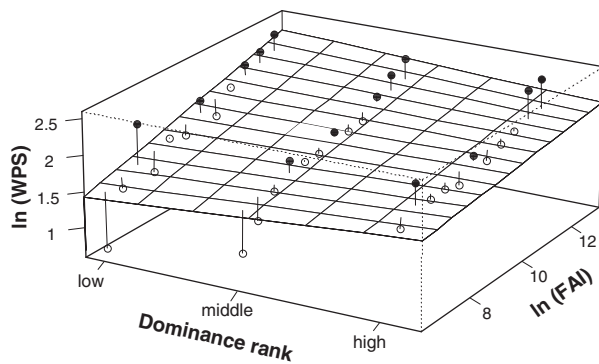


Fig. 1. Effect of female dominance rank and FAI on WPS in Tai chimpanzee females. Grids show predicted values of the GLMM and dots show means of grouped data (dashes indicate corresponding residuals). FAI and WPS were \log_e -transformed. A decreasing FAI led to lower gregariousness in low-ranking females but not in high-ranking females (Table 1). FAI, fruit abundance index; WPS, weighted party size; GLMM, generalized linear mixed model.

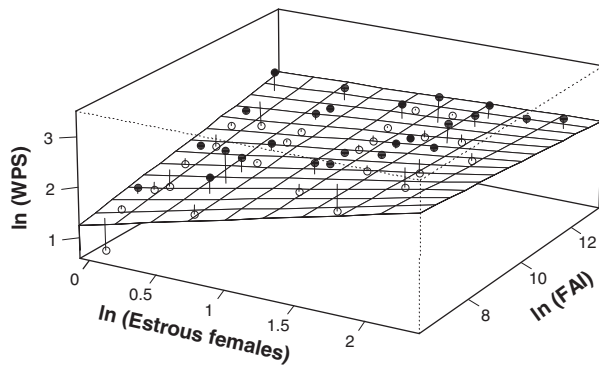


Fig. 2. Effect of the number of females in estrus and FAI on WPS in Tai chimpanzee females. FAI, estrous females, and WPS were \log_e -transformed. A decreasing FAI led to decreasing WPS when few females were in estrus, but not when many females were in estrus (Table 1). FAI, fruit abundance index; WPS, weighted party size.

dominance rank and FAI (Table 1, Fig. 1). WPS increased significantly when chimpanzee density increased. Females with dependent offspring were as gregarious as the females without dependent offspring. The significant interaction between estrous females and FAI (Table 1, Fig. 2) indicated that decreasing FAI led to decreasing WPS only when few females were in estrus, but not when many females were in estrus. Females in the south community were significantly more gregarious than females in the north community.

We found no support for our prediction that high-ranking females travel less than low-ranking females. Instead, we found that daily travel distance was significantly higher in high-ranking females (Table 1), which traveled on average 335 m (10%) more per day than low-ranking females. In addition, females traveled more when parties were large, fruit was abundant, and many females were estrous (Table 1). Density and dependent offspring had no

influence on female travel distance. Females of the south community traveled on average 1.2 km (35%) more per day than females of the north community.

DISCUSSION

As we found no support for our hypothesis that high-ranking females in Tai are in general more gregarious and travel less than low-ranking females, our results suggest different effects of female rank on gregariousness and ranging compared with chimpanzees at Gombe. At Tai, a high rank appears to allow females to be more gregarious in times of low fruit abundance, whereas during seasons of high fruit abundance, all females were highly gregarious, regardless of their rank. When fruits were scarce, low-ranking females decreased their gregariousness, whereas high-ranking females' social behavior changed little. A high rank appeared to allow females to maintain relatively stable gregariousness over potentially stressful periods, while low-ranking females were more affected by seasonal change in competitive regime and foraged solitarily or in very small parties. High-ranking females benefited from their position by remaining highly social during seasons of low fruit abundance, allowing them to forage in relatively large parties. They can deal with higher contest competition because they win fights over food with low-ranking females [Wittig & Boesch, 2003], it is possible that the associated gains in physical condition allowed these females to continuously associate with others despite the competitive costs of gregariousness. When rank effects on feeding competition become stronger, low-ranking females reduce their gregariousness, presumably to avoid competition over scarce resources, which they are ill-equipped to win [Wittig & Boesch, 2003].

Female dominance rank was not the sole influence on female gregariousness. When investigating the interaction of fruit abundance and number of estrous females, we confirmed the findings of Anderson et al. [2002] that party size of Tai chimpanzees increased when many females were estrous, independent of higher feeding competition associated with periods of low fruit abundance. We also found that the party size increased with increasing density and that females with a dependent offspring were as gregarious as those without a dependent offspring. This finding contrasts with observations from other study sites, where mothers are less gregarious than non-mothers [Goodall, 1986; Murray et al. 2007; Otali & Gilchrist, 2006; Sakura, 1994; Takahata, 1990; Williams et al., 2002b; Wrangham, 2000]. Gregarious mothers who are well-integrated within the social system may be better able to protect their infants from leopard predation which is relatively high at Tai compared with other study sites [Boesch 1991, 2009; Boesch & Boesch-Achermann, 2000].

Our results show that females at Taï, like those in other chimpanzee study sites, adapt their gregariousness to high levels of competition [Mitani et al., 2002; Wittig & Boesch, 2003; Wrangham, 2000]. Taï females are more gregarious compared with those from the East African study sites where females are relatively asocial [Goodall, 1986; Williams et al., 2002b; Wrangham & Smuts, 1980; Wrangham et al., 1992]. We propose that this difference may result from a combination of higher fruit abundance [Boesch, 2009] and higher predation pressure at Taï [Boesch, 1991, 2009]. Future studies of female chimpanzee gregariousness might benefit from cross-site comparisons of fruit abundance and gregariousness. In addition, it might be interesting to expand the party size variable to include party composition. Females may choose to join or leave a party depending on who is present and these choices might differ depending on the dominance rank of the female.

Our results suggest that low-ranking females adjust their ranging patterns to reduce travel costs. To respond to an increase in feeding competition, primates can either follow a strategy of maximizing food intake by increasing the day range to find food or, conversely, follow a strategy of minimizing energy expenditure by decreasing the amount of travel [Dunbar, 1988]. We found that high-ranking females traveled more than low-rankers, which contradicts our hypothesis that high-ranking females follow a ranging strategy that minimizes their travel costs. By contrast, low-ranking females seemed to follow a strategy that minimizes energy expenditure. It may be that they cannot incur the increased costs of traveling long distances in search of resources because of the risk that a high-ranking individual is already monopolizing the resource. This risk could explain why low-ranking females prefer a strategy of minimizing energy expenditure. Our results are consistent with the idea that low-ranking females suffer higher levels of contest competition over food, which leads to an energy-saving strategy of decreased travel and gregariousness when fruits are scarce.

An alternative explanation could be that high-ranking females travel more because they are simply more gregarious and larger parties show an increase in travel [Williams et al., 2002b]. In addition, high-ranking females at Taï use larger home ranges that include more peripheral areas, presumably because they are more likely to participate in border patrols [Lehmann & Boesch, 2005], resulting in their relatively high daily travel distances. Although chimpanzees generally respond to low fruit abundance with reducing party size, they nevertheless sometimes tolerate increased travel costs incurred by the presence of companions and the benefits of gregariousness [Wrangham, 2000]. High-ranking females might be able to tolerate increased travel costs better than low-rankers because they incur lower energetic stress [Emery Thompson et al., 2010].

As predicted and shown by other studies [Williams et al., 2002b; Wrangham, 2000], we found that females in Taï traveled more when party size was large, fruit abundance was high, and many females were in estrus. These results also agree with the findings of Lehmann and Boesch [2004], in which density was not correlated with female travel distance. Interestingly, dependent offspring had no influence on female travel distance. Other studies have shown that chimpanzee mothers travel more slowly and less than other females [Williams et al., 2002b; Wrangham, 2000] because of delays caused by the infant traveling independently or because infants are heavy. Mothers with a dependent offspring tend to travel at the rear of a party, typically arriving at the next fruit tree several minutes after the males and therefore losing feeding opportunities to the faster individuals [Wrangham, 2000]. Females with a dependent offspring in Taï were as gregarious and traveled as much as females without offspring. High predation risk at Taï might increase the benefit of gregariousness to mothers due to the better protection of infants inherent in a group setting. This benefit might be enough to offset the increase in travel costs and energetic stress levels associated with traveling with a dependent offspring.

When compared with the findings from the other chimpanzee study sites, our results suggest that female chimpanzees respond differently to varying levels of feeding competition and that low- and high-ranking females differ in their gregariousness and ranging strategies. In particular, the low-ranking females are more influenced by feeding competition. We propose that ecological conditions, such as predation pressure and food distribution, affect gregariousness and ranging in fission–fusion societies in a more complex way than previously anticipated and that results from a single chimpanzee population are not necessarily characteristic of the entire species [Boesch & Boesch-Achermann, 2000].

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complies with the American Society of Primatologists principles for the ethical treatment of animals and was conducted in accordance with the animal care regulations and national laws of Côte d'Ivoire and Germany.

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