



Dominance rank influences female space use in wild chimpanzees, *Pan troglodytes*: towards an ideal despotic distribution

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Studies from many different taxa have demonstrated that dominance rank greatly influences individual space use. While the importance of dominance among female chimpanzees, *Pan troglodytes*, was debated in the past, mounting evidence now shows that rank is very important. In particular, rank has been shown to influence body mass, foraging strategies, association patterns, and ultimately, reproductive success. In this study, we investigated how rank influenced female space use among chimpanzees, *P.t. schweinfurthii*, at Gombe National Park, Tanzania. Analysing 10 years of data, we found that new immigrants used areas away from dominant females, and that subordinates had lower site fidelity. We also found that high-ranking females had smaller core areas and that this size difference was pronounced during periods of food scarcity when food competition is highest. These patterns suggest that dominant females outcompete subordinates, forcing them to settle elsewhere, range more widely, and shift their space use across time.

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Social factors, including dominance rank, can greatly influence individual space use. The ideal despotic distribution (Fretwell 1972; Sutherland & Parker 1985) models the effects of dominance on space use in a simple way. In this model, high-ranking individuals occupy preferred habitats and subordinates may be forced to settle elsewhere. Although this model is difficult to test in the field, particularly in environments where resources vary (Ruxton et al. 1999), studies with both experimental and wild populations support the model (e.g. oystercatchers: Ens et al. 1995; side-blotched lizards: Calsbeek & Sinervo 2002; spotted owls: Zimmerman et al. 2003).

Although many studies have focused on how dominance rank influences space use in territorial species, rank effects have also been reported in group-living and fission–fusion species. In spatially cohesive groups, subordinate individuals often occupy edge positions, even though individuals occupying edges experience increased

predation risk (e.g. geese: Black et al. 1992; capuchin monkeys: Hall & Fedigan 1997). High-ranking individuals may also force subordinates to use areas of lower resource value (e.g. Japanese macaques, *Macaca fuscata*: Saito 1996). Compared to spatially cohesive groups, subgroups in fission–fusion systems are temporary. Although relatively rare, fission–fusion species provide an excellent context in which to consider the factors that influence grouping patterns. While the fluidity of fission–fusion systems may buffer the effects of dominance on space use, a recent study of hyenas reported rank effects none the less. High-ranking females had smaller, centrally located home ranges (Boydston et al. 2003). Females with smaller ranges may conserve energy by travelling less, and a central position may afford added protection against interclan aggression. In this study, we tested how dominance rank influences space use in wild female chimpanzees, *P. troglodytes*, another fission–fusion species.

Chimpanzees live in a multimale, multifemale society in which subgroups (called ‘parties’) exist within a permanent community (Goodall 1986). In contrast to most other primates, dispersal in chimpanzees is female biased (Pusey & Packer 1987). Although female–female aggression rates are generally low, resident females often fiercely attack new immigrants (Pusey 1980; Nishida 1989; Jane

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Goodall Institute's Center for Primate Studies, unpublished data). While males are gregarious and range widely, female social and ranging patterns vary by subspecies. West African females, *P. t. versus*, have patterns similar to males (Bossou, Guinea: Sugiyama 1988; Sakura 1994; Taï National Park, Cote d'Ivoire: Boesch 1996; Lehmann & Boesch 2005; but see Doran 1997). East African females, *P. t. schweinfurthii*, by comparison, are less social and concentrate their space use in small, overlapping core areas to which they have high site fidelity (Gombe: Wrangham & Smuts 1980; Williams et al. 2002a; Budongo Forest, Uganda: Fawcett 2000; Kanyawara, Kibale National Park, Uganda: Wrangham et al. 1992; Mahale Mountains National Park, Tanzania: Hasegawa 1990). It seems likely that females maximize their foraging efficiency by feeding in these familiar core areas (Wrangham & Smuts 1980; Williams et al. 2002a). At two long-term study sites (Gombe: Williams et al. 2002a; Kanyawara: Emery Thompson et al. 2007), females appear to cluster their core areas into neighbourhoods centred on abundant food resources. These studies also reported neighbourhood differences in reproductive success.

It is thought that females space themselves out in core areas to dissipate competition for food resources (Wrangham 1979; Wrangham & Smuts 1980). The mode and importance of resource competition among female chimpanzees, however, has been debated in the past. The infrequency of aggression among females (reviewed in Murray *in press*) led some researchers to question the importance of dominance (de Waal 1982). Although difficult to discern, stable differences in female chimpanzee dominance relationships have now been described at most study sites (Mahale: Nishida 1989; Kanyawara: Wrangham et al. 1992; Kahlenberg 2006; Gombe: Pusey et al. 1997; Murray et al. 2006; Taï National Park: Wittig & Boesch 2003). Of these, only one study site thus far has detected a linear hierarchy among females (Taï National Park: Wittig & Boesch 2003; Lehmann & Boesch 2005). Wittig & Boesch (2003) suggest that this may reflect more intense competition at Taï than at other sites coupled with increased predation risk. Compared to some female cercopithecine monkeys in which females are philopatric and ranks are matrilineal (macaques: Chapais 1992; savanna baboons: Hausfater et al. 1982; Silk et al. 1999; vervet monkeys: Bramblett et al. 1982), mothers and daughter chimpanzees do not occupy adjacent ranks. Rather, dominance rank in female chimpanzees increases with age (Nishida 1989; Pusey et al. 1997; Greengrass 2005; Kahlenberg 2006; Murray et al. 2006) and new immigrants generally occupy the lowest ranks (Mahale: Nishida 1989; Budongo: Reynolds 2005).

Several studies have demonstrated correlations between categorical dominance rank and aspects of fitness. At Gombe, high-ranking females have higher reproductive success (Pusey et al. 1997), high-ranking females have higher and more constant body mass (Pusey et al. 2005), and low-ranking females forage less efficiently: they eat a lower quality diet, have a greater diet breadth, and spend more time foraging (Murray et al. 2006). These results suggest that high-ranking females have access to better quality resources, which is further supported by a study from Taï National Park, which found a strong correlation between dominance rank and winning contests over food

(Wittig & Boesch 2003). In addition, high-ranking females at Kanyawara fed higher in trees where fruit quality is better (Kahlenberg 2006).

Given the link between reproductive success and space use, it seems likely that female chimpanzees compete for long-term access to higher-quality habitats. Previous work (Nishida 1989) showing that low-ranking females at Mahale occupied peripheral areas where they were at higher risk from intergroup aggression supports this suggestion. Furthermore, immigrant females at Gombe tended to settle away from the highest-ranking female (Williams et al. 2002a). Here, we analysed 10 years of data on females at Gombe National Park, Tanzania, to investigate the influence of dominance rank on settlement patterns, site fidelity, and core area size. Dominant females may use their higher resource holding potential (Maynard Smith & Parker 1976) to buffer themselves against resource heterogeneity while subordinates frequently suffer negative consequences of resource variation. To compensate, lower-ranking females may adjust their space use to meet their nutritional requirements. We, therefore, hypothesized that subordinate females would have lower site fidelity and larger core areas than dominant females. While we expected that low-ranking females would have larger core areas in general, we predicted that periods of food scarcity would exacerbate the effects of competition on core area size. To test this hypothesis, we examined the effects of rank and food availability on core area size.

METHODS

Study Site

This study focuses on space use among female chimpanzees of the Kasekela community in Gombe National Park, Tanzania. Since 1973, researchers and field assistants have conducted full-day follows on Kasekela community members. Each day, one member of the community (the 'focal') is followed from nest to nest, and researchers generally follow each adult at least once per month. However, some females (particularly low-ranking and immigrant females) are rarely followed because they are not well habituated. During full-day follows, group composition, female reproductive state, and location data are recorded every 15 min. Using these data, we investigated how dominance rank influenced female space use from 1995–2004. During this time, the community contained 41–53 chimpanzees with 10–12 adult males and 12–21 adult females (adult age ≤ 12). We divided our study period into 2-year intervals, beginning in 1995–1996, 1997–1998, etc. These 2-year intervals confined analyses to periods with similar inter-community dynamics that may confound space use as females adjust their space use to stay within community boundaries (Williams et al. 2004).

Female Dominance Rank

We ranked females within each 2-year period on the basis of the direction of pant grunts (submissive vocalizations that function as formal indicators of subordination: Bygott

1979) and the outcome of aggressive interactions. The average number of female–female interactions per 2-year time period during our study was 102.2, which is comparable to the sample sizes used in other studies that assigned female rank (e.g. 81 interactions over 3 years: Lehmann & Boesch 2005; 131 interactions over 7 years: Kahlenberg 2006; 67 interactions over 2 years: Murray et al. 2006). Scaled rank estimates were available for 2001–2002 and 2003–2004 when there were two studies focusing specifically on female–female competition (Greengrass 2005; Murray in press). Both these studies ranked females using a method developed for matrices with empty cells where competitors are ranked on the basis of their wins and losses and the rank of individuals met in contests (Jameson et al. 1999). For all periods, however, we ranked females as high, middle or low ranking and defined our categories following Pusey et al. (1997) (Table 1). This follows the precedence of other studies, which have also ranked females categorically (e.g. Gombe: Pusey et al. 1997; Kanywara: Wrangham et al. 1992; Kahlenberg 2006) and found reproductive and foraging consequences by rank class (Pusey et al. 1997; Kahlenberg 2006).

Effect of Dominance Rank on Sociality

Time spent alone by dominance rank

Grouping may influence day range because of increased competition (Janson & Goldsmith 1995; Wrangham 2000; Williams et al. 2002b). To ensure that core area size and site fidelity results were not simply by-products of differences in sociality, we first tested time spent alone by dominance rank within a given period. In this analysis, we included females with at least 10 follow days during the

period under consideration to eliminate biases due to observation time. We plotted time alone curves for several females and found that estimates for time spent alone stabilized after 5–10 follows. We, therefore, chose a conservative criterion of 10 days. This criterion was met by 13 high-, 21 middle-, and five low-ranking females. To estimate the amount of time spent alone, we determined the group size for each 15-min point sample in which a female was the focal individual. We then calculated time spent alone as the proportion of the point samples in which no other adults were present. Since mothers and daughters have high levels of association, mother/daughter pairs with nonadult offspring were still considered 'alone' (following Wrangham & Smuts 1980; Goodall 1986; Williams et al. 2002a). This definition of 'alone' applies to our other metrics as well.

Quantifying Female Space Use

Generating female alone core areas

To quantify space use for as large a set of females as possible, we used encounter data rather than focal follow data. During full-day follows, researchers noted when individuals were encountered by the focal. Individuals could be encountered alone or with others. We followed Williams et al. (2002a) in calculating a female's core area from locations at which she was encountered alone when not in oestrus since oestrous females alter their ranging patterns (e.g. Wrangham & Smuts 1980; Goodall 1986). By our definition, females were encountered 'alone' when no other adults arrived within 5 min, excluding mother/daughter pairs as described above. With these criteria, the average number of alone encounters within a time period was 25.6 (range 18–32) per adult female. Using encounter data was advantageous because it allowed us to quantify space use for all females, including those not targeted in full-day follows. Relying only on focal data would have confined our analyses to regularly followed females, which tend to be high-ranking, central individuals.

We delineated core areas from 50% usage kernels of alone encounter locations. While this may seem a restrictive measure of space use compared to other studies, it accounts for ambiguity when party members are frequently unobserved upon arrival. Prior to analyses, however, we first validated our method by comparing core areas derived from alone encounters to core areas derived from full-day data when the focal female was alone. To ensure we had very good estimates for follow-based ranging patterns, we included females that were followed at least 30 times during a given time period. We then compared the areas obtained via the two methods with a simple linear regression and found that the core area sizes were significantly correlated ($N = 15$, $F = 18.3$, $P < 0.001$, $R^2 = 0.584$). By visualizing kernels generated via the two methods, we also found that the core areas overlapped substantially. Figure 1 shows kernels that we provided for two representative females. These results validated our use of 50% alone encounter data as a means by which to estimate alone space use.

Since seasonal analyses spanned smaller intervals and included fewer alone encounters for each female, we

Table 1. Female categorical ranks

Female	Years				
	1995, 1996	1997, 1998	1999, 2000	2001, 2002	2003, 2004
BAH	—	—	—	—, 3	3
CD	2	2	2	2	2
FF	1	1	1	1	1, —
FN	3	3	2	2	2
GM	2	2	2	2	1
HO	2	2	2	2	2
JF	3	3	3	2	2
KP	—	3	3	3	3
NAS	—	—	—	—, 3	3
MAK	—	—	—	—	3
NUR	—	—	—	—	3
PI	1	1	1	1	1
SA	2	2	2	2	2
SIF	—	—	—	3	3
SS	3	2	2	2	2, —
SW	2	2	2	1	1
TTA	—	—, 3	3	3	3
TG	—	—	3	3	3
TZ	3	2	2	2	2

Categories 1: high; 2: middle; 3: low.

Blank cells correspond to females that were not present in the community or were not yet adult (TG).

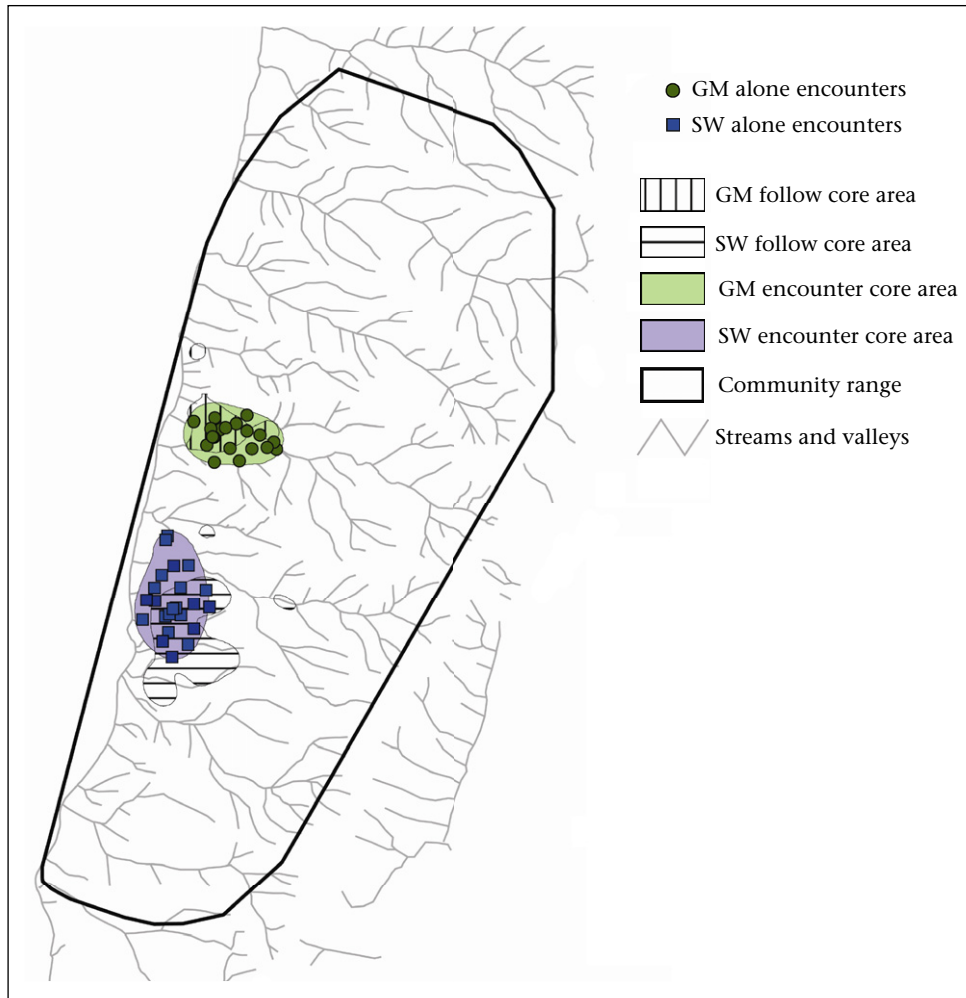


Figure 1. Representative female alone core areas (2003–2004). Here, we provide alone core areas for two females. We defined core areas from 50% kernels of the locations at which a female was encountered alone. To quantify spatial similarity, we used alone encounters located inside of a female's core area and the L-function, a point pattern analysis technique. This method allowed us to quantify space use for all community females and matched well with core areas derived from focal follow data on regularly followed females.

supplemented encounter data with focal follow data. Focal females were alone when no other adults were present at a 15-min point sample. To reduce temporal autocorrelation, we only included locations separated by the time required to traverse the community range as determined from range size and the mean female travel rate (following Newton-Fisher 2002; Murray 2006). The mean travel rate varied between 0.63 and 0.65 km/h and the time required to traverse the community range varied between 4.1 and 6.4 h, depending largely on community range size. We used the combined data sets to generate seasonal core areas for regularly followed females as described above. All kernels were created with the ArcView 3.0 Animal Movement extension (ESRI; Hooge & Eichenlaub 2000).

Point Pattern Analysis

In our analyses, we examined alone core area size and overlap (for two females in the same period or the same

female in two different periods). We calculated core area size from kernel areas. To quantify overlap, we used the distribution of alone encounters located inside of a female's core area (Fig. 1). We then applied the L-function, a point pattern analysis technique that measures the ratio between the observed and expected pairs of points (here, encounter locations) within distance d of each other, over a spatial area (Besag 1977). Expected values assume complete spatial randomness and depend on the intensity of each distribution. An L-function value of zero corresponds to complete spatial randomness (spatial independence), a positive value indicates clustering (dependence) and a negative value indicates repulsion. We calculated L-function values using the SPLANCS package (Rowlingson & Diggle 1993) and R Software (R Development Team 2005).

The L-function depends on the distance (d) chosen and either increases with d or remains the same with increasing d . For subsequent analyses, we chose a distance that would be biologically meaningful within the constraints of our data set, chimpanzee communication, and topographical considerations specific to Gombe. On these

bases, we used a distance of 400 m, which exceeded the limitations of our data set (mean location error = 133 m; Gilby et al. 2006). Given the topology of Gombe, a 400-m radius around a point also represents the maximum distance at which chimpanzees can readily detect conspecifics (i.e. influence each other's space use). Chimpanzees primarily communicate over longer distances via pant-hoot vocalizations, the loudest of which is generally audible within single major valley (C. M. Murray, personal observation).

Effect of Dominance Rank on Space Use

Area observation curves conducted on five randomly chosen females indicated that we needed 15–20 alone encounters to estimate lone female space use. To ensure we had confidence in ranging patterns, we confined our analyses to females with 20 or more core area locations within a given period, or period and season.

Effect of Dominance Rank

Female settlement

To test our hypothesis that immigrants settle away from high-ranking females, we compared the mean dominance rank of the neighbours of immigrant females to the mean dominance rank of non-neighbours. We used dyadic L-function values as a dissimilarity measure. Since positive L-function values indicate spatial dependence, we classified female dyads with positive values as 'neighbours'. For each immigrant ($N = 9$ females), we then compared the mean rank for neighbours to that for non-neighbours with a two-sample t test. During our study period, we observed two immigrations in 1997–1998, one in 1999–2000, three in 2001–2002, and three in 2003–2004 (Table 1).

Site fidelity

To test our hypothesis that high-ranking females have higher site fidelity, we first calculated dyadic L-function values for two distributions for the same female in sequential time periods. We then performed 999 Monte Carlo simulations between the two distributions under an assumption of complete spatial randomness. We ranked the observed value within the simulated distribution such that high ranks correspond to high site fidelity with a maximum value of 1000. We refer to this as site fidelity score. To investigate how well dominance predicted site fidelity, we tested dominance against fidelity score in sequential time periods. For two time periods, we assigned dominance rank from the earlier period since this should influence space use in the subsequent time period. For example, all females analysed in the period 1 to period 2 transition were assigned their rank in period 1, and so forth. It should be noted that any female that had adequate encounter data to calculate core areas in two sequential time periods was included in our analyses ($N = 11$ females).

Core area size

To test our hypothesis that high-ranking females have smaller core areas, we calculated core area size from a female's 50% kernel within a given time period. We included any female with rank and sufficient encounter data in a given period ($N = 12$ females). In this analysis, we classified females in terms of the presence/absence of dependent offspring (≤ 5 years). Mothers with dependent offspring may have smaller day ranges, presumably because of increased travel costs associated with carrying infants (Boesch & Boesch-Achermann 2000; Wrangham 2000; Williams et al. 2002b; but see Lehmann & Boesch 2005). The presence/absence of dependent offspring was determined from the midpoint of the time period.

Effect of Rank and Food Availability on Core Area Size

To relate core area size differences to food availability, we tested how size varied as a function of dominance and food availability. We relied on seasons that were previously classified in terms of food availability (Murray 2006). In accordance with that study, we divided each year into a period of food abundance (Nov–Feb), a period of food scarcity (March–July), and a period of intermediate food availability (Aug–Oct).

Statistical Methods

All statistical tests were performed with SAS version 9.1 (SAS Institute, Cary, NC, U.S.A.). To test for differences in time spent alone by rank, we used a mixed linear model while controlling for the time period and for repeated measures on the same female. We also included a term for the presence/absence of dependent offspring since females with dependent offspring may 'fall out' of groups because of the increased travel costs described above or spend more time alone to reduce risk to infants from male aggressors (Otalí & Gilchrist 2006). We used linear mixed models to test each of our space use metrics (site fidelity, core area size, and core area size by season) against categorical rank and the time period, controlling for repeated observations on each female. We also included a term for the presence/absence of dependent offspring. For our analysis of core area size by season, we fitted a similar model but included an interaction term for season and categorical rank.

RESULTS

Effect of Dominance Rank on Sociality

Time spent alone by dominance rank

The average amount of time spent alone by period ranged between 39.1 and 48.4% (Table 2). Time spent alone was not predicted by either dominance rank or the time period ($N = 9$ females, dominance rank: $F_{2,22} = 1.70$, $P = 0.21$; time period: $F_{4,22} = 0.34$, $P = 0.85$). The presence of dependent offspring, however, significantly influenced

Table 2. Average time spent alone by time period

Years	Average proportion of follow time alone	Number of females
1995–1996	0.405 (0.150–0.610)	5
1997–1998	0.451 (0.143–0.671)	7
1999–2000	0.391 (0.116–0.572)	8
2001–2002	0.406 (0.247–0.665)	9
2003–2004	0.484 (0.360–0.615)	7

Average time spent alone (when no other adults were present, excluding mother/daughter pairs) by period. Individual ranges for time spent alone are provided in parentheses.

time alone, as females with dependent offspring spent more time alone than did females without dependents ($N = 9$ females, $F_{1,22} = 5.25$, $P = 0.03$). Since dominance rank did not predict the amount of time alone during our study period, we felt confident that the influence of dominance on core area size and site fidelity was not an artefact of general sociality differences.

Effect of Dominance Rank on Space Use

Female settlement

We found that immigrating females concentrated their alone space use near lower-ranking females (two-tailed t test: $t = 2.87$, $N = 9$ immigrants, $P = 0.005$). The mean dominance rank \pm SE for immigrant neighbours was 2.15 ± 0.086 while for non-neighbours it was 1.76 ± 0.094 .

Site fidelity

We found that dominance rank significantly predicted the observed variation in site fidelity between successive time periods. Higher-ranking females were more faithful ($N = 11$ females, $F_{2,16} = 5.72$, $P = 0.01$; Fig. 2). Post hoc group comparisons revealed that high- and low-ranking females differed significantly as did middle- and low-ranking

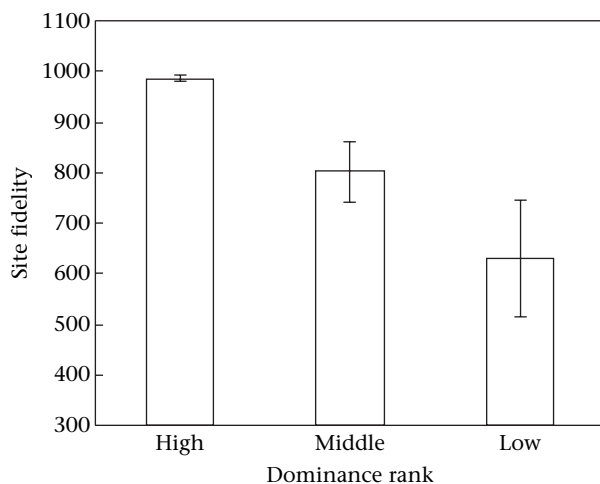


Figure 2. Effect of rank on female site fidelity. The Y axis is the mean site fidelity rank as calculated from dyadic L-function values. High site fidelity ranks indicate higher site fidelity, and the maximum value is 1000. Error bars give ± 1 SE.

females (Tukey–Kramer adjusted, $P < 0.05$). The mean \pm SE fidelity score between successive time periods was 980 ± 6.5 for high-ranking females and 812 ± 58 for middle-ranking females. Low-ranking females had much lower site fidelity, with a mean fidelity score of 629 ± 116 . Neither the time period ($N = 4$ sequential time periods, $F_{3,16} = 1.24$, $P = 0.33$) nor the presence of dependent offspring ($F_{1,16} = 0.02$, $P = 0.89$) influenced site fidelity.

Core area size

Dominance rank influenced alone core area size in general, as high-ranking females used smaller core areas ($N = 12$ females, $F_{2,16} = 4.78$, $P = 0.02$; Fig. 3). The mean \pm SE core area size for high-ranking females was 0.52 ± 0.09 km² while middle-ranking core areas averaged 0.68 ± 0.10 km² and low-ranking core areas averaged 0.96 ± 0.13 km². Post hoc group comparisons revealed that the difference between high versus middle, and high versus low groups were significant (Tukey–Kramer adjusted, $P < 0.05$). Core area size also varied with time periods ($N = 5$ time periods, $F_{4,16} = 4.51$, $P = 0.01$), but the presence/absence of dependent offspring did not significantly influence size ($N = 12$ females, $F_{1,16} = 0.14$, $P = 0.94$).

Effect of Rank and Food Availability on Core Area Size

We found that both season and the rank*season interaction influenced core area size ($N = 12$ females, rank: $F_{2,41} = 1.10$, $P = 0.34$; season: $F_{2,41} = 3.15$, $P = 0.05$; rank*season: $F_{6,41} = 4.52$, $P < 0.01$). The mean \pm SE female core area during periods of food abundance was 0.15 ± 0.04 km². Core areas were larger during periods of intermediate food availability (mean core area size = 0.23 ± 0.07 km²) and periods of food scarcity (mean core area size = 0.51 ± 0.08 km²). Post hoc group comparisons revealed that the difference between core area sizes during high and low food availability were significant (Tukey–Kramer adjusted, $P < 0.05$). The rank*season interaction is best illustrated in Fig. 4. When food was

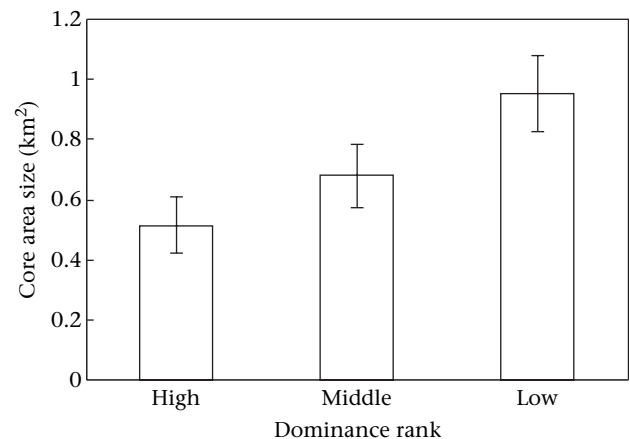


Figure 3. Effect of rank on core area size. The Y axis is the mean alone core area size (km²). Error bars give ± 1 SE.

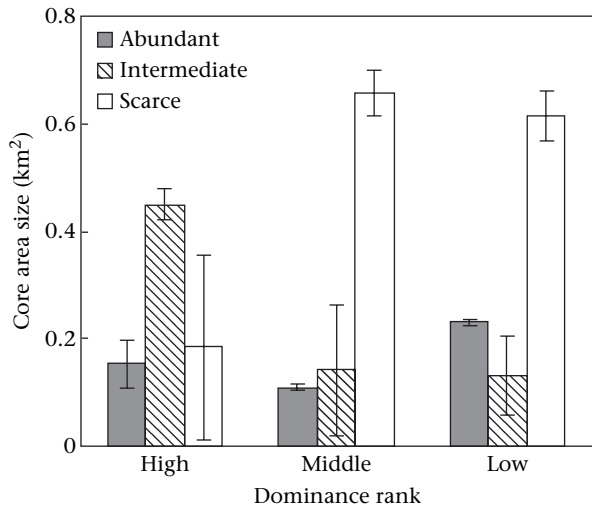


Figure 4. Effect of rank and food availability on core area size. The Y axis is the mean alone core area size (km²). We divided each period based on food availability, and calculated core area sizes accordingly. Error bars give ± 1 SE.

scarce, high-ranking females had significantly smaller core areas than either middle- or low-ranking females (Tukey–Kramer adjusted, $P < 0.05$). During periods of intermediate food availability, the opposite pattern was observed whereby high-ranking females had significantly larger core areas than subordinates (Tukey–Kramer adjusted, $P < 0.05$).

DISCUSSION

Assessing the importance of female competition in chimpanzees is difficult given their fission–fusion social system, the infrequency of aggression, and the fact that females can avoid interacting directly. Dominance interactions in this species may, therefore, be more subtle than direct contests that can be observed in spatially cohesive groups. None the less, our results suggest that dominance plays a key role in how female chimpanzees use space. In particular, we found that lone immigrants concentrated their space use away from dominant females. In addition, we found that dominant females had higher site fidelity and smaller core areas than subordinates. These patterns suggest that dominant females outcompete subordinates, forcing them to settle elsewhere, they range more widely, and shift their space use across time. We suggest that these differences may account, in part, for rank differences in reproductive success (Pusey et al. 1997).

We found that lone immigrants concentrated their space use away from dominant females. This suggests that competition for space is particularly pronounced when new females immigrate into the community and is consistent with previous observations of intense aggression towards new immigrants (Pusey 1980; Goodall 1986; Nishida 1989). It seems likely that resident females direct aggression towards immigrants as a means to avoid long-term competition in shared areas. Given that reproductive success has been linked to space use at two study sites

(Gombe: Williams et al. 2002a; Kanyawara: Emery Thompson et al. 2007), it is somewhat surprising that resident females do not have more frequent aggression over space. However, the potentially high costs of fights may preclude elevated levels of aggression once females are established (Nishida 1989). Even though most immigrants settled away from dominant females, some subordinates overlapped with dominant individuals (Murray 2006). Sharing space may not be costly when resources are abundant and competition relaxed. We propose that when resources are limited, however, subordinates avoid costly dominance interactions by moving away from dominant females or ranging further.

Individual site fidelity has been documented in a wide variety of taxa (e.g. birds: Newton 1993; reptiles: Webb & Shine 1997; insects: Switzer 1997), and several studies have reported that fidelity varies with age, habitat quality, or prior reproductive success. Older individuals or those occupying prime habitats have higher fidelity (e.g. sparrow hawks, *Accipiter nisus*: Newton 1993; red squirrels, *Sciurus vulgaris*: Wauters et al. 1995). Furthermore, the influence of past reproductive success has been well documented in birds as successful breeders are more faithful to particular sites (Newton 1993). While low fidelity might provide individuals with access to different resource patches or lower competitor density, it may also carry substantial costs in terms of foraging efficiency since fidelity affords individuals with access to known resources (Hinde 1956; Greenwood 1980). Familiarity with resources is probably a key reason that female chimpanzees maintain core areas (Pusey et al. 1997; Williams et al. 2002a). In our study, we found that most females exhibited high site fidelity. This finding is consistent with earlier reports from our study site and from other chimpanzee populations (Gombe: Wrangham & Smuts 1980; Williams et al. 2002a; Budongo Forest, Uganda: Fawcett 2000; Kanyawara, Kibale National Park, Uganda: Wrangham et al. 1992; Emery Thompson et al. 2007; Mahale Mountains National Park, Tanzania: Hasegawa 1990; Taï National Park: Lehmann & Boesch 2005). We found that fidelity varied both within- and between-females. Our results demonstrate that dominance predicted this variability. High-ranking females had higher site fidelity than subordinates. Given the correlation between age and rank in our data set (Pusey et al. 1997; Murray et al. 2006), we were concerned that age could confound our results. To assess this possibility, we ran identical analyses but substituted age for rank, and found that rank was a stronger predictor of differences in site fidelity during our study period. The consequence of low fidelity needs additional study, although females probably suffer from reduced foraging efficiency in less familiar areas.

Numerous studies have demonstrated an inverse relationship between home range size and food availability (e.g. roe deer: Tufto et al. 1996; red squirrels: Lurz et al. 2000). Accordingly, we found that the mean core area size was largest when food was scarce. While high-ranking females had smaller core areas in general, seasonal analyses revealed a more complex relationship. We found that rank-related differences depended upon food availability. During periods of food scarcity (when competition for

food is most pronounced), high-ranking females had smaller core areas. Presumably, dominant females have priority of access to limited resources while subordinates may be forced to range more widely to meet their nutritional requirements. It was initially surprising to find that dominant females had larger core areas during periods of intermediate food availability. However, this difference probably reflects the distribution of foods rather than competition for food resources. Two upper elevation fruit species, *Parinari curatellifolia* and *Uapaca nitida*, make up a large proportion of the diet during that time of year. Since most dominant females concentrate their space use in lower parts of valleys that contain evergreen forests (Pintea 2006), they may range in higher elevations when these species fruit. The biological significance of larger core areas for subordinates warrants further investigation. However, subordinates probably incur increased energetic costs associated with ranging in larger areas and traversing steep valleys. In contrast to our findings, we should note that a recent study of West African females reported that dominants had larger home ranges (Lehmann & Boesch 2005). Lehmann & Boesch (2005) proposed that dominant females may have ranged more widely to participate in territorial defence. During the study period, the Tai community had an unusually low number of adult males. However, such participation by females in territorial defence is rare in our study community.

While explicitly testing an ideal despotic distribution in wild populations is difficult, many empirical studies have demonstrated the effects of dominance on space use (e.g. white-footed mice, *Peromyscus leucopus*: Halama & Dueser 1994; red squirrels: Wauters et al. 2001; side-blotched lizards: Calsbeek & Sinervo 2002). The ideal despotic distribution predicts that immigrants settle according to the distribution of resources, and the density and rank of resident individuals. Settlement according to these factors has not been previously reported in any group-living primate, but has been found in a variety of nonprimates (e.g. birds: Ens et al. 1995; reptiles: Calsbeek & Sinervo 2002). Assessing the applicability of this model to female chimpanzees is complicated by their fission–fusion social structure, the diversity of their diet, pronounced resource heterogeneity, and extensive overlap of individual ranges. The results presented here, however, clearly demonstrate rank effects on female space use. Given these results, we hypothesize that Gombe females conform to a nonterritorial ideal despotic distribution (Cassini & Föger 1995), particularly during periods of reduced food availability. More detailed data on resource distribution is needed to test this hypothesis explicitly.

Although studies often focus on individual space use patterns in territorial species, fission–fusion systems provide an interesting context in which to consider how individuals share space. Interestingly, patterns similar to those reported here have been observed in another fission–fusion system, spotted hyaenas, *Crocuta crocuta* (Boydston et al. 2003). Low-ranking females at Masai Mara National Reserve, Kenya, had larger home ranges, especially when prey was scarce. We expect that analogous patterns may be observed in other species with female dominance and overlapping individual ranges.

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