

Adult Male Chimpanzees Inherit Maternal Ranging Patterns

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Summary

Space use often correlates with reproductive success [1, 2]. Individual site fidelity is ubiquitous across a variety of taxa, including birds, mammals, insects, and reptiles [3–9]. Individuals can benefit from using the same area because doing so affords access to known resources, including food and/or breeding sites. The majority of studies on site fidelity have focused upon strictly territorial species in which individuals range in well-defined, exclusive areas (e.g., [4, 9]). By comparison, the transient groups that define fission-fusion species allow for considerable flexibility in individual space use. Although there is evidence that individual space use can influence reproductive success [2], relatively little is known about individual ranging patterns in fission-fusion species. Here, we investigate three potential correlates of male site fidelity (age, habitat quality, and maternal space use) in wild chimpanzees (*Pan troglodytes*). We found that when alone, each male preferentially concentrated his space use near the area where his mother ranged when he was dependent. We suggest that solitary ranging allows males to avoid direct competition with conspecifics and that foraging in familiar areas maximizes foraging efficiency. These results highlight the importance of male foraging strategies in a species in which male ranging is typically explained in terms of mating access to females.

Results

To investigate potential correlates of male chimpanzee site fidelity, we analyzed four years of spatial and group composition data (2001–2004) from Gombe National Park, Tanzania (see [Experimental Procedures](#)). During

the study period, the study community contained 41–53 chimpanzees with 10–12 adult males (Table 1) (adult age ≥ 12). The average yearly percentage of time spent alone by males was 14.2% compared to 44.0% for females [10], although this is probably an underestimate because groups are easier to locate and follow than solitary individuals.

Comparison to Female Site Fidelity

In the East African subspecies (*P.t. schweinfurthii*) considered here, males are more social than females and range more widely [11]. Aggregation into parties allows males to hunt red colobus monkeys (*Procolobus spp.*) communally and to maintain cooperative alliances for group territorial defense or competition for social dominance [12, 13]. However, the formation of large parties is a suboptimal foraging strategy because larger parties suffer from increased feeding competition [13, 14]. Individual chimpanzees are likely to minimize feeding competition by traveling solitary or by adjusting their space-use patterns to distribute individual ranges optimally across food resources [15]. Empirical evidence suggests that females employ both strategies, by spending much of their time alone and by occupying distinct but overlapping core areas to which they have high site fidelity [5, 10, 16]. Familiarity with food resources is probably one reason why females maintain core areas [5, 17]. Despite the benefits of sociality, the costs of grouping might sometimes force males to travel solitary in order to forage more efficiently. We hypothesized that when traveling alone, males will behave like females (who are predominantly driven by food acquisition) and concentrate their space use in specific areas of the range.

To test this hypothesis, we compared male and female site fidelity during our study period. Site fidelity was determined by point-pattern analyses of the distributions of solitary locations for the same individual in the two time periods (2001–2002 and 2003–2004) (see [Experimental Procedures](#)). An individual's site-fidelity score reflects the degree of overlap between the individual's ranges during different time periods. Site-fidelity scores range from 0–1000, with 1000 representing maximum fidelity. This method is identical to that previously used to measure female site fidelity during the same study period [10]. The mean site-fidelity score was 791 (standard error [SE] = 238) for males and 739 (SE = 147) for females, a difference that was not statistically significant ($F_{1,17} = 0.10$, $p = 0.75$, $n = 11$ males and 8 females). Figure 1 shows the similarity between the core areas of one male (GB) during two different time periods, demonstrating high site fidelity.

Correlates of Male Site Fidelity

Various studies have demonstrated that older individuals or those occupying prime habitats have higher site fidelity [4, 9]. Older individuals might have less to gain by shifting because their remaining reproductive

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Table 1. Adult Males and Mothers

Male	Mother	Mother's Death	Dependent Years
AO	AT	1987	1979–1988
FD	FF	2004	1971–1980
FO	FF	2004	1989–1998
FR	FF	2004	1976–1985
GB	ML	1986	1974–1975 ^a
GL	ML	1986	1977–1986
KS	KD	1992	1982–1991
PX	PS	1982	1977–1986
SL	SW	ALIVE	1983–1992
TB	LB	1987	1977–1986
WL	WK	1988	1972–1981

^a Because uniform data collection began in 1974, we did not have ranging data for ML throughout GB's dependency. We therefore used two years of data from which to estimate her core area when he was between 8–10 yr old.

life is relatively short [7]. We therefore hypothesized that older males or males in higher-quality areas would have higher site fidelity. To test this hypothesis, we examined the relationship between male site fidelity, age, and habitat quality in our dataset. Site-fidelity scores were tested against age at the end of the earlier time period and against core-area fruit productivity. We used stem density of preferred foods to quantify core-area quality (see [Experimental Procedures](#)). We did not find a significant correlation between male site fidelity and either age ($F_{1,10} = 1.17$, $p = 0.31$, $n = 11$ males) or habitat quality ($F_{1,10} = 0.50$, $p = 0.49$, $n = 11$ males).

Core-Area Heritability

Territorial inheritance, whereby an individual assumes parental ranging patterns, occurs in some species [18, 19]. Remaining in the natal area is likely to be advantageous in both territorial and nonterritorial species because individuals are familiar with the resources in their parents' range. An individual that ranges in its natal area will not have to learn the spatio-temporal distribution of food and can therefore quickly maximize its feeding efficiency. This will be particularly important for ripe-fruit specialists living in heterogeneous habitats. Given that male chimpanzees are philopatric and remain in their natal community, we hypothesized that males should concentrate their solitary space use in the area where they were raised, thereby foraging in known areas.

To test this prediction, we compared the spatial similarity of a male's core area to his mother's historical range and to the core areas of unrelated females during the study period. Because males presumably learn an area when they are dependent (traveling almost exclusively with their mother), we determined the maternal core areas when the male was 0–10 yr old (Table 1). The data on unrelated females were from 2001–2002 and 2003–2004, and we added the mother's historical range as if she were alive in each time period. The degree of spatial overlap (mean dyadic L function value) for mother-son pairs ($n = 11$) was 420.0 (± 84.3 SE) versus 140.9 (± 21.4 SE) for unrelated male-female dyads, a difference that was statistically significant ($F_{1,420} = 10.23$, $p = 0.002$) (Figure 2). Thus, a male preferentially concentrated his solitary space use in the area where his mother ranged when he was a dependent. Males remained faithful, regardless of the time since

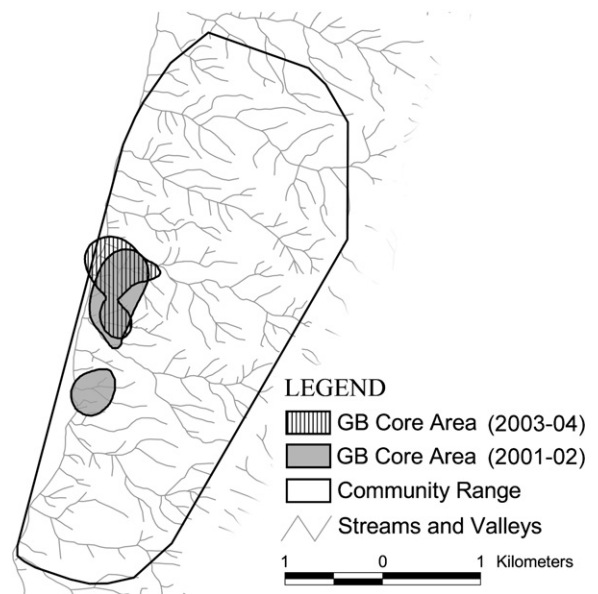


Figure 1. Representation of Male Site Fidelity

We defined solitary core area from the 50% kernels of locations at which a male was alone. Here, we present core areas for one male (GB) in the two different time periods to illustrate how males remained faithful to particular areas of the range across time.

a mother's death (regression of fidelity on years since mother's death: $F_{1,8} = 0.60$, $p = 0.46$, $n = 7$ mothers, excluding SW who was still alive during the study period). In Figure 3, we provide a representative comparison between an adult male's range (AO) and his mother's range when he was a dependent (AT).

Discussion

Among mammals, male space use is generally geared toward maximizing mating opportunities, whereas female space use is dictated by the distribution of food resources. Accordingly, many studies have demonstrated that male ranging patterns change with the distribution of receptive females (e.g., vole, *Microtus agrestis* [20]) and that male ranges are larger and encompass those of several females (e.g., raccoon, *Procyon lotor* [21]; spider monkey, *Ateles belzebuth* [22]). Likewise, male East African chimpanzees range more widely than females [16, 23, 24] and defend a group territory containing multiple females [25]. Although travel in parties allows males to hunt communally and facilitates the formation of cooperative alliances (reviewed in [12, 13]), the formation of large parties is nevertheless a suboptimal foraging strategy. As food competition increases in larger groups [13, 14], males must balance the conflicting demands of obtaining mates and obtaining adequate food resources. Males probably maximize their foraging efficiency by periodically traveling alone. The only other study that investigated solitary space use by males reported that solitary males consistently arrived at a provisioning area from a particular direction distinct from that of other males [16]. Wrangham and Smuts [16] concluded from these data that solitary males concentrated their space use in particular areas. Another study using direction of arrival data (but not distinguishing solitary

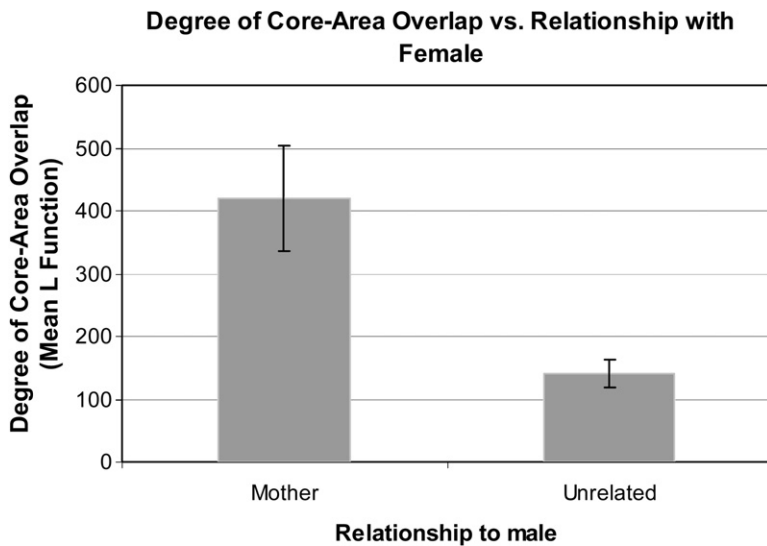


Figure 2. Spatial Overlap by Relationship
The x axis indicates the relationship between the male and female. The y axis gives the degree of core-area overlap, as calculated from dyadic L function values for the distribution of locations where an individual male or female was alone. For mother-son dyads, n = 11. Error bars represent 1 standard error.

arrivals) found that some males tended to arrive from the same general direction for several years, and that some arrived from the same direction as their mother [26]. Our results, based on actual ranging data, demonstrate that when Gombe males were alone, they had levels of site fidelity that were as high as those for females. Furthermore, males preferentially concentrated their space use in their mother's historical range. These results suggest that solitary travel allows males to avoid direct competition with conspecifics while foraging in known areas.

Male site fidelity is particularly striking given the pronounced resource heterogeneity at Gombe, where

all lone males could theoretically concentrate their space use in the richest area of the range or alternatively, an alpha male could occupy the best site during his tenure. Previous work demonstrated that higher-ranking females occupied higher-quality core areas and had higher site fidelity [10]. Testing of the influence of rank on male site fidelity was problematic given that the male-dominance hierarchy was in flux through most of 2003–2004. However, case studies of the deposed alpha male (FR) and his immediate successor (SL) indicate high site fidelity despite changes in dominance status (FR site fidelity score = 991, SL site fidelity score = 998 out of a maximum 1000). Interestingly, SL had one of the least productive core areas (mean diameter at breast height [DBH] in SL's core area = 181.7 versus mean DBH for all males = 353.3) but did not shift when he became alpha. The long-term stability of female rank as compared to the instability of the male hierarchy might account for the influence of rank on site fidelity among females but not among males. Given that high rank can be ephemeral, foraging in an unknown area might be disadvantageous to dominant males. Although additional data are needed to rigorously test the effects of dominance rank on male ranging, our results suggest that social status, habitat quality, and age are not strong determinants of male site fidelity. Rather, maternal space use during dependency drives adult-male spatial patterns.

The influence of parental space use on offspring ranging has been observed in both territorial and nonterritorial species. Offspring sometimes inherit parental territories in cooperatively breeding species such as tropical wrens [18] and clownfish [19]. In nonterritorial systems, similar spatial patterns between parent and philopatric offspring can result in spatial clustering of families [27]. For example, female sea lions range in areas shared with their mother, despite having very little social interaction [6]. Our results demonstrated that lone male chimpanzees preferentially used the area where they spent their dependency. This is especially compelling given that 7 of the 8 mothers died as much as 20 yr before the study period. The observed patterns, therefore, did not occur through current association of the male with his mother. As has been proposed for females in

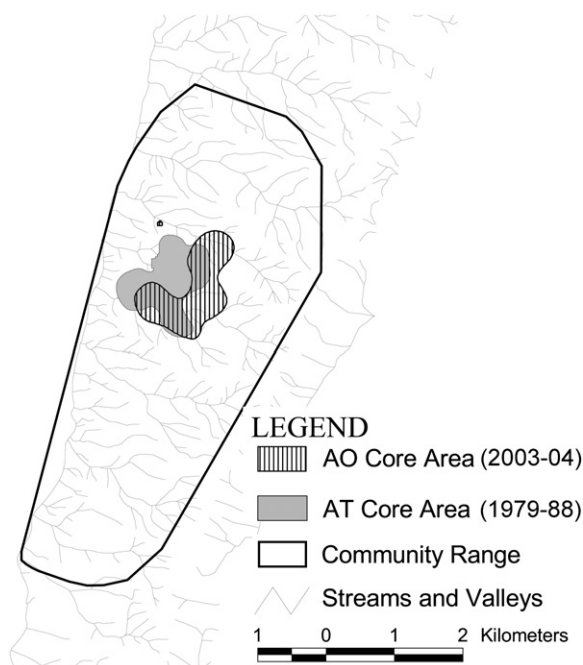


Figure 3. Representation of Male Inheritance
Core areas are delineated by the 50% kernels for solitary locations. Here, we illustrate how one male (AO) ranges where his mother (AT) ranged when he was a dependent. AT died in 1987.

[5, 17], we suggest that site fidelity allows males to forage in areas with which they have an intimate resource knowledge. This might allow males to increase their foraging efficiency by reducing search time and/or by exploiting smaller food patches. More detailed foraging data are needed to test the hypothesis that males forage more efficiently in their core areas.

The results of this study complement a strong body of literature on individual space use and site fidelity in territorial species. Much less is known about individual space-use patterns in fission-fusion species. Nonetheless, individual space use can be a critical determinant of survival and, ultimately, reproductive success in these systems.

Experimental Procedures

Data Collection

Researchers and field assistants have conducted full-day follows on members of the Kasekela chimpanzee community at Gombe since 1973. Each day, a research team follows one individual from night nest to night nest. The team continuously records the party composition of the focal chimpanzee and records its location on a map at 15 min intervals [11].

Quantifying Space Use

Generating Male Core Areas

To facilitate comparison of male and female core areas, we followed previous studies from Gombe that investigated lone female space use [5, 10]. We identified individual adult-male core areas by using 50% kernels of locations when a male was solitary. To maximize our dataset for each male, we combined data from the locations (1) when a male was the focal individual and there were no other adults present and (2) when that male was encountered alone by another focal chimpanzee. During full-day follows, researchers recorded the times when individual males were encountered by the focal individual. Solitary encounters occurred when the focal male met the individual male by himself and no other adults were encountered within 5 min. In each 2 yr period, the average number of follows per male was 36.8 and the average number of solitary locations for each male was 45.1. All kernels were created with the ArcView 3.0 Animal Movement extension [28].

Point-Pattern Analysis

To quantify spatial similarity, we used the solitary locations inside the 50% core-area kernels for point-pattern analysis with the L function [29]. The L function measures the difference between the number of observed and expected pairs of points (locations inside of solitary core areas) within distance d of each other. Expected values assume complete spatial randomness over the community range and depend upon the intensity of each distribution. An L function value of zero corresponds to complete spatial randomness (independence), a positive value indicates clustering, and a negative value indicates repulsion (refer to [29] for more details). For all analyses, we used a distance (d) that was biologically meaningful within the constraints of our dataset, chimpanzee communication, and topographical considerations specific to Gombe. On these bases, we used a distance of 400 m, which exceeded the limitations of our dataset (mean location error = 133 m) [30]. 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).

To quantify site fidelity, we calculated dyadic L function values for two distributions for the same male in time periods 1 and 2. We then performed 999 Monte Carlo simulations between the two distributions under an assumption of complete spatial randomness. We ranked the observed L function value within the simulated distribution such that high ranks corresponded to high site fidelity with a maximum value of 1000.

Core-Area Quality

To quantify fruit productivity, we collected vegetation data in 150 400 m² plots from January–June 2004. Given the diversity of

plant species consumed by Gombe chimpanzees ($n = 141$ species), we collected abundance data on a subset of ten preferred tree species that accounted for an average of 48.7% of the yearly vegetation diet. Given the well-supported relationship between diameter at breast height (DBH) and biomass production [31], we measured the DBH for each tree. We then summed DBH inside a plot as a proxy for plot productivity. We estimated habitat quality for males from the average plot productivity inside his solitary core area.

Statistical Methods

We performed all statistical tests with SAS version 9.1 (SAS Institute, Cary, North Carolina). To compare male and female site fidelity, we used an analysis of variance. To test for male inheritance, we used a linear mixed model that controlled for the time period and repeated observations of the same individual. This test compared dyadic L function values for each male with those of adult females alive during the two time periods and with those of his mother's range when he was dependent (≤ 10 yr old). We categorized each male-female dyad as "mother-son" or "unrelated."

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