



## Competing for space: female chimpanzees are more aggressive inside than outside their core areas



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Female space use can have important fitness consequences, which are likely due to differential access to food resources. Many studies have explored spatial competition in solitary species, but little is known about how individuals in social species compete over shared space. In this study, we investigate spatial patterns of aggression among female East African chimpanzees, *Pan troglodytes schweinfurthii*. This species provides an excellent opportunity to study spatial competition since (1) female chimpanzees occupy overlapping core areas (small areas of the community range in which individuals concentrate their space use) and (2) female core area quality is correlated with reproductive success, suggesting that females compete over long-term access to core areas. Here, we examine how female aggression towards other females varies inside and outside individual female core areas during a 14-year period at Gombe National Park, Tanzania. Overall, females showed higher rates of aggression inside than outside their own core areas. This pattern was driven by spatial variation in aggression in nonfeeding contexts. While food-related aggression did not vary spatially, females were more aggressive in nonfeeding contexts inside their core areas than they were outside their core areas. These results suggest that female chimpanzees follow a mixed strategy in which they compete for long-term access to resources in their core areas as well as for immediate access to food throughout the community range.

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Spatial competition is generally studied in the context of territory defence, in which an individual or group of individuals excludes competitors from a particular range (Maher & Lott, 1995). Excluding competitors can increase reproductive fitness (Stamps, 1994), and the adaptive value of territoriality has been documented in a wide variety of vertebrate taxa (reviewed in Maher & Lott, 2000). Territoriality can occur at an individual level (Eurasian red squirrel, *Sciurus vulgaris*: Wauters, Lens, & Dhont, 1995; green anoles, *Anolis carolinensis*: Leuck, 1995; bank voles, *Clethrionomys glareolus*: Koskela, Mappes, & Ylönen, 1997; Rich Mountain salamanders, *Plethodon ouachitae*: Anthony, Wicknick, & Jaeger, 1997; brown trout, *Salmo trutta*: Johnsson, Carlsson, & Sundström, 2000), or at the group level (e.g. cichlids, *Neolamprologus pulcher*: Taborsky, 1984; gibbons, *Hylobates lar*: Brockelman & Srikosamatara, 1984; golden lion tamarins, *Leontopithecus rosalia*: Peres, 1989; fiddler crabs, *Uca annulipes*: Milner, Booksmythe, Jennions, & Backwell, 2010).

Relatively little is known about spatial competition within social groups that lack individual territories. Nevertheless, home range quality has previously been linked to reproductive outcomes in group-living species that have overlapping individual home ranges (meadow voles, *Microtus pennsylvanicus*: Ostfeld, Pugh, Seamon, & Tamarin, 1988; red deer, *Cervus elaphus*: Stophor et al., 2012; chimpanzees, *Pan troglodytes*: Emery Thompson, Kahlenberg, Gilby, & Wrangham, 2007). Despite a reproductive advantage associated with maintaining a high-quality home range, the mechanisms through which individuals maintain differential access to shared areas within groups are largely unknown.

East African female chimpanzees, *Pan troglodytes schweinfurthii*, present an excellent opportunity to explore competition for space in a social mammal since they concentrate their space use in small areas of a larger community range. Chimpanzees live in multimale, multifemale communities ranging in size from as few as 12 individuals (Bossou, Guinea: Hockings, Anderson, & Matsuzawa, 2012) to as many as 187 individuals (Ngogo, Kibale National Park, Uganda: Carlson, Rothman, & Mitani, 2013). Males are philopatric and jointly defend the community territory, whereas most females transfer and settle in new communities before breeding (Mitani,

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Watts, & Muller, 2002). Members of a community form temporary subgroups that vary in size and composition throughout the day. East African chimpanzee females are less gregarious than males and often forage alone or with maternal kin (Wrangham & Smuts, 1980). Females concentrate their space use in small, overlapping core areas of the community range to which they have high fidelity (Gombe, Tanzania: Murray, Mane, & Pusey, 2007; Williams, Pusey, Carlis, Farm, & Goodall, 2002; Wrangham & Smuts, 1980; Budongo Forest, Uganda: Fawcett, 2000; Kanyawara, Kibale National Park, Uganda: Kahlenberg, Emery Thompson, & Wrangham, 2008; Wrangham, Clark, & Isabirye-Basutu, 1992; Mahale National Park, Tanzania: Hasegawa, 1990). This behaviour is thought to minimize feeding competition (Wrangham, 1979) and maximize feeding efficiency through intimate familiarity with the distribution of food resources (Pusey, Williams, & Goodall, 1997; Williams et al., 2002). There is evidence that female chimpanzee core areas vary in the quality of food resources within them (Emery Thompson et al., 2007; Kahlenberg, Emery Thompson, & Wrangham, 2008; Murray, Eberly, & Pusey, 2006) and that these differences in core area quality are correlated with reproductive success (Emery Thompson et al., 2007). The advantages of foraging in a known area have also been demonstrated in other species (red-winged blackbirds, *Agelaius phoeniceus*: Beletsky & Orians, 1991; western barbastelle bats, *Barbastella barbastellus*: Hillen, Kiefer, & Veith, 2009).

How does a female chimpanzee maintain access to her core area? Several lines of evidence support the hypothesis that female chimpanzees engage in aggressive competition for long-term access to space. First, resident females have been observed killing the newborn infants of within-community females at Gombe (Goodall, 1986; Pusey et al., 2008), Budongo (Townsend, Slocombe, Emery Thompson, & Zuberbühler, 2007), and have been suspected to do so at Tai National Park (Boesch & Boesch-Achermann, 2000). Such infanticide accounted for 7.2% to an estimated maximum of 31.3% of the mortality of infants in their first 2 months at Gombe over a 19-year period (Pusey et al., 2008) and has been suggested to be an extreme manifestation of resource competition (Muller, 2007; Pusey et al., 2008). Second, resident females are often aggressive to newly immigrated females (Goodall, 1986; Kahlenberg, Emery Thompson, Muller, & Wrangham, 2008; Kahlenberg, Emery Thompson, & Wrangham, 2008; Nishida, 1989; Pusey, 1980) and can even prevent immigrant females from settling in a new community (Pusey et al., 2008).

Finally, evidence suggests that females actively compete over long-term access to core areas within the community range. Social dominance rank is correlated with core area quality at Gombe and Kanyawara (Kahlenberg, Emery Thompson, & Wrangham, 2008; Murray et al., 2006). At Gombe, higher-ranking females occupy smaller ranges to which they have higher fidelity (Murray et al., 2007). Also, newly immigrated females tend to settle away from high-ranking females (Murray et al., 2007; Williams et al., 2002). Nevertheless, the extent to which females aggressively defend and maintain access to their core areas is not known. In general, aggressive interactions among females are infrequent but occur most commonly over food resources as would be expected based on nutritional constraints on female reproduction (Goodall, 1986; Wittig & Boesch, 2003; reviewed in Murray et al., 2007). It is unknown whether females are more likely to fight for food in their core areas, but it seems probable since those areas contain known resources that may be contestable.

In this study, we use 14 years of long-term data from Gombe National Park to test the hypothesis that female chimpanzees defend access to their core areas by showing higher rates and severity of aggression towards females within their core areas than they do outside their core areas. Because females may be more

protective of food resources in their own core areas, we examined interactions in feeding and nonfeeding contexts separately.

## METHODS

### Study Population

We investigated how aggression among female chimpanzees varied in relation to location in the Kasekela community in Gombe National Park, Tanzania. Gombe is a small park (ca. 35 km<sup>2</sup>) with a diverse habitat ranging from evergreen forest in the valleys to grasslands on the ridges (Clutton-Brock & Gillett, 1979). Researchers have studied the Kasekela community since 1960, with data on space use standardized in 1973. Since then, pairs of Tanzanian researchers have conducted almost daily dawn-to-dusk ‘follows’ of focal individuals, during which they record subgroup composition, feeding behaviour and location on a map at 15 min point samples (Gilby, Eberly, Pintea, & Pusey, 2006; Goodall, 1986). They also record detailed narrative notes on conspicuous social interactions, including aggression, among all group members. The researchers rotate through adult community members each month to ensure adequate sampling of all individuals.

We examined patterns of female aggression during a 14-year period (1995–2008), for which social interaction notes had been completely translated from Swahili into English. During this period, the community ranged in size from 41 to 62 members and contained 10–13 adult males and 13–26 adult females.

### Female Core Areas

We defined core areas as areas in which females spent their time when alone or with adult female kin. ‘Alone’ locations were determined as the locations at which a female was encountered alone, with dependent offspring, or with an adult daughter (and dependent offspring) by the target individual for the follow (as described above); this allowed us to include females that were not regularly followed by field staff but were nevertheless frequently observed. While previous studies at Gombe employed kernels to delineate core areas (Murray et al., 2007; Murray, Gilby, Mane, & Pusey, 2008; Williams et al., 2002), we defined core areas as the 50% minimum convex polygon of alone locations of nonoestrous females to create a contiguous area that could be easily delineated. We excluded oestrous alone locations, as ranging patterns during this time are more likely to reflect sexual and social needs rather than personal space use. The resulting polygon indicated where a female concentrated her space use during a given period. Areas in which a female ranges alone are highly consistent, and presumably extremely important to foraging; competitors in this area may represent a particular risk to foraging efficiency. While female chimpanzees exhibit high site fidelity and often use the same general area for their entire lives, their core areas sometimes shift slightly over time (Murray et al., 2007; Williams et al., 2002). For that reason, we divided our study into three periods (1995–1999, 2000–2004, 2005–2008) and determined core areas for each period. These 5-year segments allowed us to capture site fidelity while accounting for slight shifts over time in response to events such as immigration or death of an individual in the community. We classified every aggressive event directed at another female for each adult female according to its location (inside versus outside) relative to her core area during the period in which it occurred. Delineation of core areas and all spatial analyses were conducted using Biotas™ 2.0 Alpha (Ecological Software Solutions LLC, Hegy-magas, Hungary).

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