Fission–fusion dynamics in wild giraffes may be driven by kinship, spatial overlap and individual social preferences

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Many species exhibit fission–fusion dynamics, yet the factors that influence the frequent changes in group size and membership in these species have not been widely studied. Social ties may be influenced by kinship but animals may also form preferred associations because of social attraction or may only associate because they have similar habitat preferences. We investigated the association patterns of 535 wild giraffes, *Giraffa camelopardalis*, in Etosha National Park, Namibia using behavioural and genetic data from individually identified giraffes. We collected 726 records of group composition over a 14-month period and calculated pairwise association indices, which were tested against a null model. We found that female–female pairs, but not male–male pairs, showed both preferred and avoided relationships. We tested whether females' relationships could be explained by the degree of relatedness between pairs and whether pairs overlapped spatially. Correlations between matrices of pairwise associations, spatial overlap and relatedness showed that female–female associations were strongly correlated with amounts of spatial overlap and pairs that exhibited preferred relationships were more closely related than would be expected by chance. However, only about one-quarter of the variation in observed associations could be explained by spatial overlap and relatedness and therefore much of this variation may have been related to individual social preferences.

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The social organization of animals reflects the relationships formed between pairs of individuals, with the patterning of these relationships across a population defining its social structure (Hinde 1983). Despite the social organization of a species being a vital component of its life history, social relationships are still poorly understood for many species. The patterns of social relationships are of particular interest in populations with fission–fusion dynamics, in which individuals temporarily associate so that group membership and group size change frequently (e.g. Brager 1999; Cross et al. 2005; Bashaw et al. 2007; Smith et al. 2007; reviewed by Aureli et al. 2008).

Fission–fusion dynamics within a population may be influenced by the relationships between kin or by repeated encounters between pairs of animals with overlapping home ranges. Although not all fission–fusion species show preferential associations among relatives (e.g. big brown bats, *Eptesicus fuscus*: Metheny et al. 2008), many do. For instance, in species such as spotted hyaenas, *Crocuta crocuta*; African elephants, *Loxodonta africana*, and dolphins, *Tursiops* spp., relatedness has been documented to influence the strength and nature of social bonds (Wahaj et al. 2004; Archie et al. 2006; Frère et al. 2010b; Möller 2012). However, when two animals show a preference to associate with each other, it can be difficult to ascertain whether this preference is related to kinship, social attraction or other factors such as shared preference for similar habitats.

Lusseau et al. (2006) and Wey et al. (2008) warned that observed association patterns between individuals may not reflect true relationships because individuals with similar habitat preferences are more likely to be seen associating and therefore their associations may only result from their shared use of space. In addition, individuals can have preferences or avoidances for other individuals that are masked by the amount of spatial overlap between pairs of animals (Carter et al. 2009). For example, two individuals that show a high degree of spatial overlap may tend to avoid each other, or those with small amounts of spatial overlap may prefer to associate but not have many opportunities to do so.

Despite this, few studies of animal social systems have incorporated the amount of spatial overlap between pairs of animals as a predictor variable (but see Chaverri et al. 2007; Carter et al. 2009; Frère et al. 2010b).

In many animal societies, the spatial distributions and behaviours of males and females are determined by different factors; females are mostly driven by the distribution of resources (Wittemyer et al. 2005), whereas males are motivated more by the distribution and social organization of females (Wittemyer et al. 2005; Wolf et al. 2007). The importance of resources to female mammals, driven by the costs of reproduction, might suggest that females in species with fission–fusion dynamics would not go out of their way to associate with particular other individuals. However, females have been shown to form both long-term and preferred/avoided associations with conspecifics in fission–fusion social systems (Whitehead 1997; Silk 2007b; Carter et al. 2009; Frère et al. 2010b). Stronger bonds may be promoted under a high predation risk (Kelley et al. 2011); however, other potential advantages gained by females from associating strongly with particular female conspecifics include increased reproductive output, increased survival and psychological wellbeing (Frère et al. 2010a; Massen et al. 2010). For example, female chacma baboons, *Papio hamadryas ursinus*, with strong female relationships live longer than those with weak female relationships (Silk et al. 2010) and female savannah baboons, *Papio cynocephalus*, that have more social contact show higher offspring survival (Silk et al. 2003, 2009). Therefore, preferred relationships may be influential factors in females' decisions on whether to stay with, or leave, a temporary group.

Owing to their variable grouping patterns, giraffes, *Giraffa camelopardalis*, have been described by some authors as having little social structure, weak social bonds between individuals and no apparent pattern to their relationships (Foster & Dagg 1972; Moss 1976; Leuthold 1979; Le Pendu et al. 2000). However, recent studies of giraffes have shown that they exhibit fission–fusion dynamics with some structure to their pairwise relationships (Shorrocks & Croft 2009; Bercovitch & Berry 2012). Such variability in grouping patterns suggests that giraffes are a higher fission–fusion species ('higher-FF'), which is a species characterized by high levels of variation in group size and composition with temporal variation in spatial cohesion (Aureli et al. 2008). Other species exhibiting such high levels of variability include chimpanzees, *Pan troglodytes*, spider monkeys, *Ateles* spp., and spotted hyaenas (Aureli et al. 2008). These 'higher-FF' taxa are ideal model species for testing the importance of kinship and patterns of spatial overlap on females' social relationships because the frequent changes in group compositions allow large data sets on association patterns and their possible determinants to be accumulated quickly. The giraffe is a large, diurnal species that is easy to observe and can be individually identified by coat patterns. Female giraffes are nonseasonal breeders and do not have a dominance hierarchy (Moss 1976; Bashaw et al. 2007), which avoids an added complexity to association patterns that may otherwise mask the effects of kinship and spatial overlap on fission–fusion dynamics. Because giraffes do not display the complex cooperative behaviours typical of primates and cetaceans that show fission–fusion sociality, they provide an interesting test of whether the evolution of structured association patterns may have preceded the evolution of more complex cooperative behaviours (Aureli et al. 2008; Shultz et al. 2011).

In this study we combined behavioural and genetic data to investigate the social structure of a population of 535 wild giraffes in Etosha National Park, Namibia, with a particular focus on females. Our first aim was to test for sex differences in patterns of preferred or avoided relationships with others. Our second aim was to test whether spatial overlap or genetic relatedness between pairs of female giraffes could explain any observed nonrandom association patterns.

METHODS

Study Area and Population

Group composition and GPS location data were recorded for 726 giraffe groups observed between May 2009 and June 2010 in Etosha National Park, Namibia (19°10′S, 15°54′E). The park covers an area of 22 270 km^2, with almost one-quarter (4590 km^2) of the park covered by a salt pan that is seasonally inundated during the annual rainy season from January to April (Osborne & Versfeld 2007). The giraffe subspecies *G. c. angolensis* inhabits Etosha National Park, with an estimated population of 3550 individuals across the entire park and an estimated density in 2004 of 0.20/km^2 (Brand 2007). In our ca. 1000 km^2 study area situated around the main settlement of Okaukuejo in the central section of the park, we identified 535 giraffes. The study area contained a mix of grassland, woodland, acacia thicket and broadleaved mopane, *Colophospermum mopane*, habitats. Both a previous study of giraffes in the Okaukuejo area by Brand (2007) and our study observed stability of spatial use for many females, which did not show large-scale seasonal migrations. The number of sightings of individual male giraffes in our study was not sufficient to make conclusions about the stability of spatial use among males.

Individual giraffes were identified by their unique coat patterns using both sides of the entire body, with photos of all giraffes sighted entered into a database (females $N = 266$, males $N = 269$). Photos were taken of every giraffe, at every sighting, to enable accurate identification. A photographic mark–recapture analysis software package was used to facilitate individual identifications (Wild ID, http://www.dartmouth.edu/~envs/faculty/bolger.html), with all Wild ID matches confirmed by eye. If Wild ID did not match an individual with any giraffes in the database, the matching process with the entire catalogue of photos of individual giraffes was repeated by eye.

Data Collection

The study area was divided into four road transects, each of which could be fully explored by vehicle in half a day, enabling the study area to be completely sampled over a 2-day period. Each transect included approximately 65 km of tourist roads plus a number of staff-only access roads. Transects were not sampled more than once every 2 days to ensure independence of samples, as giraffe were expected to have adequate opportunity to move throughout the study area and change associates over a 2-day period because group composition has been reported to change in a matter of hours (Leuthold 1979) or daily (Moss 1976). To reduce sampling biases, both the starting times and the directions of travel along transects were varied. Owing to National Park requirements, all observations were recorded from a vehicle and all driving was confined to roads. Data were collected under research/collecting permit numbers 1365/2009 and 1468/2010 from the Ministry of Environment and Tourism, Namibia.

Data collection occurred during two sampling periods each day. The morning period commenced between dawn and 0800 hours and continued until 1200 hours or until the transect was completed, whichever came first. The afternoon sampling period commenced between 1300 and 1500 hours and continued until the transect was completed or until dusk, whichever came first. Data were not collected during the hot midday hours as giraffes were often resting in the shade and therefore behavioural observations and detection of giraffe groups were difficult. During transects, the identity, sex