Associations are more strongly correlated with space use than kinship in female eastern grey kangaroos

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Understanding the relationship between kinship and female social preferences in mammalian societies is frequently complicated by philopatric behaviour and variation in pairwise home range overlap. While the influence of space use on association patterns is increasingly being considered in studies using network analysis, methods are needed for generating null models that control for pairwise home range overlap. We investigated female associations in a wild population of eastern grey kangaroos, *Macropus giganteus*, a species with higher fission–fusion dynamics, to test the influences of home range overlap and kinship on pairwise association strengths. Genetic analysis revealed that females were highly philopatric and we found that association strengths were significantly correlated with home range overlap. To test for social preferences, we compared observed associations with random associations based on individuals' space use, simulated using Digiroo2. HWIG, a version of the half-weight association index that controls for among-individual variation in gregariousness was used for all analyses. Preferred associates had significantly higher pairwise relatedness than expected. Although some females had strong social relationships with some of their close kin, in general, space use had a much stronger correlation with association strengths than both pairwise relatedness and maternal lineage. This suggests that familiarity may play a key role in driving association patterns in female kangaroos. We recommend controlling for individuals' space use when undertaking studies on social preferences and social structure in general.
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Social relationships in animal societies are often nonrandom (Barocas, Ilany, Koren, Kam, & Geffen, 2011; Croft, James, & Krause, 2008; Patriquin, Leonard, Broders, & Garroway, 2010; Wolf, Mawdsley, Trillmich, & James, 2007). Individuals differ in their numbers of associations (Croft et al., 2005; McDonald, 2007; Smith, Memensis, & Holekamp, 2007) and their choices of preferred associates (Gero, Bejder, Whitehead, Mann, & Connor, 2005; Mourier, Vercelloni, & Planes, 2012). The formation of social relationships can provide fitness advantages, such as greater offspring survival and higher birth rates independent of factors such as dominance, habitat quality and age (Cameron, Setsaas, & Linklater, 2009; Frère, Krützen, Mann, Connor, et al., 2010; Silk, Alberts, & Altmann, 2003; Silk et al., 2010). Increasingly, network analysis tools are being used to quantify and interpret the extent to which individuals choose with whom they interact and the factors influencing these choices. These methods are particularly helpful for societies with higher fission–fusion dynamics, in which individuals frequently join and leave groups of varying size and composition (Aureli et al., 2008).

Social networks represent snapshots of dynamic societies and can be influenced by both temporal and spatial factors (Cantor et al., 2012). Temporal structure is often controlled for in the study of social networks by choosing appropriate time intervals for analysing association patterns. However, it is much harder to control for spatial structuring within societies as individuals rarely have identical space use. Traditionally, network analyses assumed that with regard to space use, all individuals had an equal opportunity to associate with one another. More recently, studies have begun to consider spatial factors in their analyses (Carter, Macdonald, Thomson, & Goldizen, 2009; Chaverri, Gamba-Rios, & Kunz, 2007; Gilby & Wrangham, 2008; Pinter-Wollman et al., 2013; Schauber, Storm, & Nielsen, 2007; Wakefield, 2013). It is reasonable to assume that social interactions reflect spatial proximity (Clutton-Brock, 1989; Smolker, Richards, Connor, & Pepper, 1992), especially in sedentary or territorial species (Sih, Hanser, & McHugh, 2009). For example, two individuals that share large portions of their home ranges are expected to be much more likely to associate with one another than are two individuals whose home ranges barely touch. Indeed, association patterns have been found to correlate with home range overlap in a number of species, including blacktip reef sharks, *Carcharhinus melanopterus* (Mourier et al., 2012), chimpanzees, *Pan troglodytes* (Wakefield, 2013), tent-making bats,

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Artibeus watsoni (Chaverri et al., 2007), giraffes, *Giraffa camelopardalis* (Carter, Seddon, Frère, Carter, & Goldizen, 2013), and bottlenose dolphins, *Tursiops aduncus* (Frère, Krützen, Mann, Watson-Capps, et al., 2010). Questions relating to association strengths should therefore include a spatial dimension and be phrased along the lines of 'do individuals A and B show preferred or avoided associations given their degree of home range overlap?' However, methods for generating the random models of association that control for pairwise home range overlap, needed for answering such questions, are not readily available.

Kinship is another factor that can influence association patterns. Female mammals often exhibit social preferences towards associating with maternal kin (Bergman, 2010; Silk, Altmann, & Alberts, 2006; Wittemyer et al., 2009). Social preferences towards kin can be driven by benefits such as allomaternal care, reduced aggression and infanticide risk, and shared social and ecological knowledge (McComb, Moss, Durant, Baker, & Sayialel, 2001; Pusey & Packer, 1994; Silk, 2002). However, in some species with higher fission–fusion dynamics, the overall relationship between the association strength of pairs of females and their genetic relatedness is weak (e.g. chimpanzees, Langergraber, Mitani, & Vigilant, 2009; bottlenose dolphins, Frère, Krützen, Mann, Watson-Capps, et al., 2010; Wiszniewski, Lusseau, & Möller, 2010; giraffes, Carter et al., 2013). Among nonterritorial species, it is often unclear whether strong associations among related individuals occur through choice, or simply reflect high levels of home range overlap caused by philopatry. Studies on sociality that consider the simultaneous effects of home range overlap and kinship on association patterns are necessary to begin to understand the role of social preference in the evolution of social systems and sociality (Carter et al., 2013; Frère, Krützen, Mann, Watson-Capps, et al., 2010; Maher, 2009).

Eastern grey kangaroos, *Macropus giganteus*, are among the most social of the macropod species (Kaufmann, 1975), and exhibit higher fission–fusion dynamics (Best, Seddon, Dwyer, & Goldizen, 2013). Females' home ranges overlap with those of many others, and are relatively evenly distributed in response to food availability; there is no evidence of dominance hierarchies or territorial defence among them (Kaufmann, 1975). In addition female kangaroos do not exhibit foraging specializations or cooperative behaviour but studies on their sociality have shown that associations are not simply predicted by overlapping space use (Carter et al., 2009; Jarman, 1994). Female kangaroos form social communities of up to around 50 individuals that at least in some places partially overlap in their space use (Best et al., 2013; Jaremovic & Croft, 1991; Jarman, 1994; Kaufmann, 1975). These communities represent clusters of individuals that are more densely socially connected among themselves than they are to the rest of the population. In a population at Sundown National Park in Queensland, individuals assorted socially by community membership in areas utilized extensively and concurrently by two communities (Best et al., 2013). This suggests that female kangaroos actively choose with whom to associate. However, it is unclear to what extent pairwise social preferences may be explained by the intensity of use of the areas of spatial overlap between individuals' home ranges. In relation to the influence of kinship on female kangaroos' association patterns, microsatellite markers showed that there was high pairwise relatedness within communities at Sundown National Park but mitochondrial DNA analyses revealed that these communities did not reflect matrilines (Best et al., 2013). It is thus unclear to what extent female kangaroos preferentially associate with kin after accounting for probable spatial proximity caused by philopatry. Kin have been reported to show lower levels of agonistic interactions towards each other during foraging (Jarman, 1991), but as agonistic interactions among female kangaroos are generally infrequent and mild, they may not act as a significant selection pressure on association preferences.

In this study, we investigated simultaneously the influences of space use and kinship on pairwise associations among females within a wild population of eastern grey kangaroos. Our first aim was to determine the degree to which female kangaroos were philopatric. Our second aim was to examine the extent to which space use influenced the strength of pairwise associations. Third, we aimed to examine the influence of kinship on association strengths and social preferences. Finally, we aimed to investigate the combined influences of space use and kinship on pairwise association strengths in female kangaroos.

METHODS

Between January 2010 and December 2011, 240 adult and subadult female eastern grey kangaroos were observed foraging within our 37.4 ha study site, a mosaic of pasture and woodland, in Sundown National Park, Queensland, Australia (28°55′03″S, 151°34′46″E). The kangaroos were observed while they fed in groups on pasture during early morning (sunrise + 2 h) and late afternoon (sunset − 2 h). Following Jarman et al. (1989), natural markings including scars, spots, pale and dark facial markings and ear shape were used to identify individual kangaroos. The accuracy of identification in our study (based on reidentifying randomly selected photos from a digital catalogue containing multiple images of each female) was 99% (Best et al., 2013). This research was approved by the University of Queensland's Animal Experimentation Ethics Committee, and conducted under a Scientific Purposes Permit from Queensland's Environmental Protection Agency.

To quantify female social structure, we completed 10–14 daily surveys of the group memberships of foraging adult and subadult females each month (274 surveys in total). Males were excluded from our analysis; the study site had considerably fewer adult males than adult females (approximately 80 males and 240 females; Best et al., 2013). Young-at-foot were recorded but not included in group memberships as it was assumed that their grouping was dependent on that of their mothers since they were still suckling. Undertaking surveys once a day, alternating between morning and afternoon field sessions, provided ample time for groups to fission and fuse to ensure independence between consecutive surveys. During each 2 h survey the study site was walked by the observer in a haphazard manner, ensuring that all the areas were visited equally but in different orders on different days. Kangaroos were approached to a minimum distance of 5 m (distance determined by each female's level of alertness in response to observation) and observed briefly to identify females. Photographs were taken of any females not immediately recognized and compared after each survey with a digital photo catalogue containing the profiles of all individuals within the population. In all cases this led to a correct identification being made, or very occasionally, the addition of a new female to the study. The 15 m chain rule was used to assign group membership, whereby any individual within 15 m of at least one group member was included within the group (Best et al., 2013; Carter et al., 2009; Dannock, Blomberg, & Goldizen, 2013; Edwards, Best, Blomberg, & Goldizen, 2013; Favreau, Goldizen, & Pays, 2010; Jarman, 1987). This definition appeared to fit the distribution of kangaroos at our study site very well and individuals within such groups at this site synchronized their vigilance behaviour, showing that they exhibited coordinated behaviour (Favreau et al., 2010). In the vast majority of groups all females were identified, with the rare exceptions being occasions when something scared the kangaroos and they fled before being identified. During the study period female kangaroos were found in groups of 1–30 individuals and the group size experienced by an average individual, known