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Few sex effects in the ontogeny of mother-offspring relationships in eastern grey kangaroos

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Social relationships established early in life can have effects on social structure and influence individual fitness. Eastern grey kangaroos, *Macropus giganteus*, nurse their young for at least 18 months, allowing for a strong bond to develop between mothers and young. Because most female kangaroos are philopatric, the mother-offspring relationship established during lactation could persist into adulthood, resulting in clusters of female kin. Strong social bonds, however, are based on affiliative behaviours and frequent interactions. In particular, one might not expect strong bonds among related individuals unless there are advantages to interacting with relatives compared to associating with unrelated conspecifics. We examined development of the mother-offspring relationship in eastern grey kangaroos from permanent emergence from the pouch to the time of weaning. We studied a high-density population at Wilsons Promontory National Park, Victoria, Australia. There were few differences in the behaviour of sons and daughters towards mothers. However, daughters foraged slightly closer than sons to their mothers and daughters were weaned approximately 2 months later than sons if the mother did not have a surviving large pouch young. Mothers associated more closely with their daughters than their sons when offspring were aged 10–29 months but neither sex associated closely with their mothers beyond 33 months of age. Mothers never intervened to defend their young from aggressive individuals and it was the offspring that maintained spatial proximity to their mothers. Kangaroo mothers had few interactions with their juvenile offspring other than nursing. Females may be philopatric and settle near close kin as adults but kangaroos appear to have few of those early affiliative interactions necessary for social bonds to develop.

In philopatric species, kin of one or both sexes are likely to settle near each other and associate as adults (Clutton-Brock & Lukas, 2012; Michener, 1983). Kin may thus form clusters within a population and behave cooperatively (Hamilton, 1964), which can lead to kin selection (Maynard Smith, 1964). Social relationships established early in life among kin can have extensive effects on social structure and influence individual fitness (Viblanc, Arnaud, Dobson, & Murie, 2010). Many species of mammals have social systems based on female kinship, for example African elephants, *Loxodonta africana* (Archie, Moss, & Alberts, 2006), spotted hyaenas, *Crocuta crocuta* (Holekamp, Smith, Strelioff, Van Horn, & Watts 2012), yellow baboons, *Papio cynocephalus* (Silk, Altmann, & Alberts, 2006) and bottlenose dolphins, *Tursiops aduncus* (Frère et al. 2010). Frequent interactions, such as allogrooming, appear necessary to maintain bonds among kin in many species of primates (Silk, 2002). These bonds often occur between mother and offspring and close associations may develop when offspring are young and still dependent on their mothers (Silk, 2002). If females tend to be philopatric and have preferential associations with kin as adults, daughters may be expected to develop stronger bonds than sons with their mothers (Greenwood, 1980).

There are various accounts of the development of mother-offspring relationships in eutherian mammals that have not taken offspring sex into account, for example rhesus monkeys, *Macaca mulatta* (Suomi, 2005), vervet monkeys, *Chlorocebus aethiops* (Hauser & Fairbanks, 1988), South African giraffes, *Giraffa camelopardalis giraffa* (Langman, 1977), bottlenose dolphins (Mann & Smuts, 1999; Mann & Watson-Capps, 2005) and humpback whales, *Megaptera novaeangliae* (Szabo & Duffus, 2008). Sex-specific social patterns developed early in life, however, predict long-term bonds in vervet monkeys (Fairbanks & McGuire, 1985),

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baboons (Pereira, 1988) and dolphins (Stanton, Gibson, & Mann, 2011). Juvenile mammals thus preferentially approach and spend time with conspecifics of the sex that are likely to be potential future allies (Fairbanks, 1993; Pereira, 1988).

Few studies of mother-offspring relationships have focused on marsupial mammals. In marsupials, gestation is short and lactation is prolonged compared to eutherians (Tyndale-Biscoe & Renfree, 1987). One of the largest marsupial species, the eastern grey kangaroo, *Macropus giganteus*, nurses its young for at least 18 months after birth, with weaning occurring about 8 months after the offspring has permanently left the pouch (Poole, 1975). Adult kangaroos are highly sexually dimorphic (Jarman, 1989) and there is probably greater variation in reproductive success among males than females (Jarman, 1983). The mother-offspring relationship involving young-at-foot (young permanently out of the pouch but not yet weaned) is characterized by the offspring closely following the mother and interactions comprise greeting, allogrooming and play, with little evidence of agonistic behaviour of mothers towards young at the time of weaning (Russell, 1989). Because female kangaroos are weakly philopatric (King, Garant, & Festa-Bianchet, 2015), the mother-offspring bond that occurs during lactation may persist into adulthood, resulting in clusters of female kin that form temporary feeding groups. Indeed, there is evidence that some adult females associate with close kin, although this pattern is not strong (Best, Dwyer, Seddon, & Goldizen, 2014; Jarman, 1994). In mammals that show kin-preferential behaviour, availability of close kin could affect a female's ability to access resources, avoid predation and care for her offspring (Clutton-Brock, 2002). In kangaroos, however, females do not appear to exhibit cooperative behaviour as adults (Best, Seddon, Dwyer, & Goldizen, 2013) and thus such benefits are unlikely. Because eastern grey kangaroos are one of the most social marsupials with a social system of loose associations within a fission–fusion society (Jarman & Southwell, 1986), they are ideal for investigating the importance of mother-offspring relationships in a species in which cooperative behaviours do not occur (Aureli et al. 2008).

Here we examined development of the mother-offspring relationship from permanent emergence from the pouch to the time of weaning in a high-density population of eastern grey kangaroos. We predicted that females would have closer and more affiliative relationships with their daughters than with their sons because, as suggested by Best et al. (2014), adult females may associate with relatives, and if so, females could become familiar with relatives at a young age and then extend these relationships into adulthood (Viblanc et al. 2010). We specifically examined how mother-offspring relationships developed over time. We also evaluated whether females had closer and more amicable relationships with their daughters than their sons as quantified by spatial measures, amounts of different behavioural interactions, frequency of distress calls and time spent together. Finally, we compared vigilance rates of females with daughters compared to sons.

METHODS

Study Site, Population and Captures

The 110 ha study site at Wilsons Promontory National Park (38°57′S, 146°17′E) was centred on a grassy landing strip and surrounding meadows. There were no wild dogs but predators on juveniles included red foxes, *Vulpes vulpes*, and wedge-tailed eagles, *Aquila audax*. Between about 500 and 800 kangaroos inhabited the study area, depending on the year, and there were 80–125 marked adult females each year. This population had been studied since 2008, so the kangaroos were habituated to human presence. Adult females were marked for visual identification with plastic collars and plastic ear tags (King, Wilson, Allen, Festa-Bianchet, & Coulson, 2011). Offspring were marked with small plastic ear tags, usually while still in the pouch. Most captures to mark pouch young took place in late winter/early spring. Birthdates were derived from body measurements (mean date based on length of the head, hindleg and hind foot) taken when the young were marked in the pouch and calculated for males and females separately (Poole, Carpenter, & Wood, 1982). Most offspring were marked at the age of 8 or 9 months. Body condition of mothers and young was estimated when the mothers were captured and the pouch young were marked, as the standardized residual of the linear relationships between hindleg length and log body mass (Schulte-Hostedde, Zinner, Millar, & Hickling, 2005). Females do not reach reproductive maturity until about 36 months of age in this population (King et al. 2015).

Focal Sampling

We made focal animal observations (Altmann, 1974) on 25 mother-offspring pairs (13 daughters and 12 sons) between September 2010 and December 2011 and on 30 mother-offspring pairs (13 daughters and 17 sons) between September 2011 and June 2012. Observations on the first cohort (born 2009/2010) were extended because some individuals were observed to be suckling beyond 18 months. Observations on the second cohort (born 2010/2011) ceased on a set date, when 80% of offspring were at least 17 months old. There were 174 focal observations on sons (mean ± SE = 6.0 ± 0.4) and 191 on daughters (mean ± SE = 7.3 ± 0.5). Each pair was observed three to 12 times and five individual mothers were watched in both years. Offspring ages were estimated to 0.1 month, using birthdates calculated from sex-specific growth curves in Poole et al. (1982). Observations usually began when the offspring was 10 or 11 months of age and had permanently emerged from the pouch, and were repeated monthly until offspring were no longer found with their mothers or until 21 months of age, whichever came first, except for the second cohort. The mean ± SE age of young across all focal observations was 14.6 ± 0.1 months.

Focal sampling took place in the early morning or late afternoon, when most animals were actively foraging. Each pair was followed for 5 min from a median distance of 24 m (range 7–121 m) using 8 × 32 binoculars (Leitz, Germany) and always began when the mother was foraging. Observations were split between the two times of day (190 in the morning and 175 in the afternoon). Wind speed was measured using a Kestrel 2000 anemometer (Nielsen-Kellerman, Boothwyn, PA, U.S.A.) and the mean and maximum speed over 5 min were recorded (mean ± SE = 5.2 ± 0.2 and 11.0 ± 0.5 km/h, respectively). The observer (W.J.K.) noted all behaviours of both individuals continuously and the distance between the pair (in m) at the start and at 1 min intervals. Behaviours were categorized as feeding (biting and chewing in crouched position with head below horizontal, including pentapedal movement while feeding), vigilant (head raised above horizontal in crouched or upright position and scanning; according to the criteria of Pays and Jarman (2008)), grooming (scratching and/or licking body), moving (bipedal hopping or pentapedal stepping), resting (lying, sitting crouched or standing upright with no head movement) and interacting. A bout consisted of a continuous behaviour and ended when the behaviour changed. When one member of the focal pair hopped off and left a group, the observer noted whether the other member followed within a few seconds and the observation continued if both members of the pair remained within sight. Most observations (84%) were of mother-offspring pairs that remained together in the same group for the entire focal sample. Sometimes the offspring attempted to suckle but the mother moved away