





Wild kangaroos become more social when caring for young and may maintain long-term affiliations with popular individuals

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ARTICLE INFO

Article history:

Received 30 November 2022

Initial acceptance 20 January 2023

Final acceptance 30 June 2023

Available online 16 September 2023

MS. number: A22-00563R2

Keywords:

eigenvector centrality

long-term study

macropod behaviour

male harassment

predation risk

reproductive success

social network

Kangaroos are an iconic group of Australian fauna. Despite considerable research on kangaroo behaviour, key gaps remain in our understanding of their social organization in the wild. In particular, it remains largely unknown whether kangaroos form long-term social bonds and what factors might prompt individuals to associate or dissociate from one another. Over 6 years, we monitored the social affiliations of individually identified eastern grey kangaroos, *Macropus giganteus*, in a large wild population. We investigated the short-term and long-term relationships of kangaroos and the extent those relationships varied with age, sex and reproductive state. We found evidence that long-term relationships among eastern grey kangaroos are possible, especially between adult females. Those individuals that were more sociable within years were also more likely to establish affiliations across years. Contrary to previous studies, we observed females actively associating with other mothers in the years in which they had young. These data suggest that the fission–fusion dynamics of eastern grey kangaroo social behaviour allow females to modulate their social position with conspecifics according to their current reproductive state. We highlight the adaptive implications of the formation of long-term bonds and the changes in social behaviour observed in females.

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A gregarious lifestyle has evolved in a variety of animal groups, with familiar examples including shoaling in fish, flocking in birds and herding in herbivorous mammals. In each case, the evolution of gregarious sociality is expected to balance the benefits over the costs of associating with a group, such as the dilution of predation risk at the expense of increased disease transmission or competition for food and other resources (e.g. [Port et al., 2017](#); [Vander Wal et al., 2012](#)). While gregarious behaviour can be quantified in a variety of ways (e.g. measures of group or flock size, physical distance to conspecifics), a particularly powerful approach uses a graphical representation of individual associations to create social networks ([Wey et al., 2008](#)). These networks can be constructed based on the spatial proximity of individuals to one another or affiliative behaviours such as allogrooming or play among individuals. The utility of networks lies in allowing the social organization of animals to be quantified with explicit consideration of both the strength and number of social connections an individual might have within a particular group ([Krause et al., 2009](#)). This

connectedness has in turn been linked to an animal's survival and fitness (reviewed by [Ostner & Schülke, 2018](#); [Snyder-Mackler et al., 2020](#)). For example, being socially connected can improve an individual's mating success ([Feh, 1999](#)), predator detection ([Favreau et al., 2015](#)) and foraging efficiency ([Whiteside et al., 2016](#)). That is, gregariousness is not simply a species characteristic, but a behaviour that varies among individuals within species. This can be quantified through an individual's position within a social network and used to examine the potential adaptive pressures that might prompt an individual to associate (or not) with others. The extent to which different individuals are more or less gregarious can provide a clearer picture of the factors that might influence the demography of a population and the evolution of social behaviour more generally ([Clutton-Brock & Sheldon, 2010](#)).

The evolution of fission–fusion sociality offers one means by which animals might tailor their behaviour to manage the trade-offs of group association more effectively ([Sueur et al., 2011](#)). Fission–fusion societies are characterized by the formation of groups that change fluidly in size and composition over time (e.g. over the course of the day, from one day to the next, or week to week). Classic examples of species exhibiting fission–fusion dynamics include bats ([Kerth et al., 2011](#)), elephants ([Archie et al.,](#)

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2006), giraffes (Wolf et al., 2018) and dolphins (Bruck, 2013). Fission–fusion dynamics are assumed to evolve when the balance of the benefits and costs of forming associations varies over space or time (Sueur et al., 2011). For example, guppies, *Poecilia reticulata*, fission (split) or fusion (form) their social groups depending on the perceived risk of predation (Kelley et al., 2011). Despite the fluidity of social relationships within fission–fusion systems, repeated associations can still occur among particular individuals as they return to associate with one another at various time points (e.g. bats: Kerth et al., 2011; birds: Aplin et al., 2021; ungulates: Brambilla et al., 2022; dolphins: Bruck, 2013). These preferred associations can form the basis of long-term social bonds (Couzin, 2006).

Animals choose their long-term associates based on a variety of factors; similar sex and size to themselves being common in many species (e.g. sharks: Mourier et al., 2012; cichlids: Schürch et al., 2010; prairie dogs: Kusch & Lane, 2021). Associations can also form among juveniles and remain into adulthood (e.g. hyaenas: Ilany et al., 2021; dolphins: Gerber et al., 2019; deer: Taillon & Côté, 2006). There are likely adaptive reasons for forming long-term associations as well, such as facilitating cooperation (Gerber et al., 2019; Papastamatiou et al., 2022; St-Pierre et al., 2009), increasing reproductive success (Cameron et al., 2009; Clutton-Brock & Sheldon, 2010; Feh, 1999; Feldblum et al., 2021; Pope, 2000), improving infant survival (Silk et al., 2003, 2009) and enhancing adult longevity (Silk et al., 2010).

Eastern grey kangaroos, *Macropus giganteus*, are known to exhibit fission–fusion sociality, with the size and composition of mobs changing throughout the day (Best et al., 2013; Kaufmann, 1975). Yet, despite being an iconic symbol of Australia's identity (the kangaroo is featured on the national coat of arms and is culturally important to many First Nation Australian communities) and despite grey kangaroos, in particular, being a classic focus of research (e.g. Caughley, 1964; Jarman, 1987; Jarman et al., 1989; Kaufmann, 1975; Southwell, 1984; Taylor, 1982), there are still important gaps in what we know about kangaroo sociality and how similar or different it might be from other fission–fusion animals. For example, it remains largely unknown whether kangaroos form long-term social bonds in the wild, or what factors might prompt individuals to associate or dissociate from one another to manifest in fission–fusion sociality. Given that long-term associations have been observed in other large fission–fusion herbivores such as elephants (de Silva et al., 2011), giraffes (Carter et al., 2013) and alpine ibex, *Capra ibex* (Brambilla et al., 2022), it might be assumed that kangaroos have the capacity to form long-term associations as well. Yet kangaroos are known to exhibit social patterns that are unique among large social herbivores, such as not forming strict dominance hierarchies or sexual harems (Caughley, 1964), making inferences from other taxonomic groups difficult. The existing data on kangaroo sociality are similarly hard to interpret in this context because most focus on group associations more generally, rather than whether individuals preferentially associate with certain individuals over others within (or outside) a group setting.

Eastern grey kangaroos seem to exhibit preferred associations at least over the short-term, and possibly based on genetic relationships to a limited extent (Best et al., 2014). However, spacing patterns are also dependent on factors affecting food availability (Hill, 1982; Letnic & Crowther, 2013) or predation risk (Banks, 2001; Best et al., 2015), rather than a preference for maintaining close social bonds with other individuals more specifically. For example, 'shy' or risk-averse females tend to aggregate in larger groups but maintain fewer preferred associations within those groups compared to 'bold' females (Best et al., 2015). Staying within a large network reduces the need to be vigilant of potential predation threats, with the added benefit of allowing more time to graze (Carter et al., 2009; Favreau et al., 2015). Conversely, females with young are

reported to temporarily disassociate from groups (Banks, 2001; King et al., 2017; Menz et al., 2017) because young have lower survival when mothers spend more time with conspecifics (King et al., 2017). The reproductive success of females, in general, is negatively correlated with a female's sociability as well (Menz et al., 2020). Although close associations between female kangaroos do exist, there are probably many factors that contribute to their formation, including the pros and cons of group membership in general. Currently, more evidence is needed to determine whether or not long-term associations exist among females and, if so, why they form.

In this study, we monitored the social affiliations of eastern grey kangaroos in the wild over 6 years to document the presence or absence of short-term and long-term relationships among individuals and the extent to which relationships varied with age, sex and reproductive state. First, we mapped the social networks of the population to quantify the network position of all individuals within the population at yearly intervals. These networks were based on the spatial proximity of individuals to one another. We quantified the network position of individuals by eigenvector centrality, which measures the number of associations or connections an individual has with neighbours, weighed by the connectedness of those neighbours. Eigenvector centrality is a good metric for quantifying highly social animals, including those existing in fission–fusion groups, because sociability often reflects an individual's ability to maintain connections across multiple groups and with multiple individuals. High centrality scores indicate that an individual has many connections with other individuals or connections with individuals that themselves have many connections, or both, showing that a particular individual belongs to a cohesive social network. Eigenvector centrality is a commonly used metric of an individual's sociability or 'popularity' (e.g. Aplin et al., 2012; Boogert et al., 2014; Fuong & Blumstein, 2019; Gomes et al., 2022; Ramos et al., 2019; Wooddell et al., 2020). The benefits of this sociability can include access to a higher level of information exchange (e.g. the presence of potential predation threats) and increased mating opportunities, as well as more influence over factors such as group dynamics and other collective behaviours (Couzin, 2006; Kelley et al., 2011; Pays et al., 2009; van Schaik, 1999). Second, we used networks to track the affiliations of individuals from one year to the next to identify any instances of repeated association among particular individuals.

Our overall objective was to evaluate how reproduction might be related to the fission–fusion dynamics of group affiliations and the extent to which eastern grey kangaroos might have the potential to form lasting social bonds in the wild. To this end, we tested (1) whether the centrality of males, females and juveniles within networks differed from one another, (2) the extent to which the centrality of females was linked to their odds of reproduction, (3) whether females changed network position when they had young, (4) the extent to which juvenile centrality predicted adult centrality and (5) whether short-term centrality predicted the formation of long-term bonds among adult kangaroos.

METHODS

Data Collection

Study population and survey methodology

The study was based on identifying individual eastern grey kangaroos from high-resolution digital photographs. These were taken during a systematic annual survey of a wild population on private property near the locality of Wollar in the New South Wales Central Tablelands. This population ranged in size from 34 to 71 individuals. The photographic survey was conducted annually over

6 years (2015–2020) by the second author and at approximately the same time each year (see below for the exception). The survey was done in the austral spring, except for 2016, when it took place in winter. Photographs were taken using a 200 mm lens on a Canon EOS 7D digital SLR from portable hides placed at least 12 h prior to the first day of observation. The survey was conducted over 2–3 h at dawn and again at dusk for 3–4 consecutive days.

This population of eastern grey kangaroos was particularly suited for this study because individuals rested during the day within a eucalypt woodland surrounding an open grassy valley. At dusk, kangaroos progressively moved out into the grassland of the valley from the woodland to graze and ultimately dispersed out into the surrounding areas around the valley after dark. At dawn, kangaroos would return to the valley to graze until midmorning and then return to shelter in the eucalypt woodland. This meant that hides could be strategically placed around the valley to survey virtually all individuals moving in or out of the valley. Hides would be entered at least 1 h before dawn and prior to kangaroos returning to the valley, and again at midafternoon before kangaroos had left diurnal rest spots inside the eucalypt woodland.

Multiple photographs of individuals and their associates were taken to ensure kangaroos could be adequately identified in most instances. Each annual survey typically resulted in a photographic library of 500–700 images and was considered to be an exhaustive survey of all individuals residing in the valley. In general, a photographic survey is an optimal choice for kangaroos because of its minimal invasiveness (e.g. Austin & Ramp, 2019). Similar survey designs have also been used to take representative ‘snapshots’ of individual associations and social behaviour of eastern grey kangaroos (Toni et al., 2021) and other animals (Piefke et al., 2021).

Individual identification

A source library of identified individuals was made with the help of I³S Contour (den Hartog & Reijns, 2015), which uses pattern recognition to aid researchers in identifying individual animals based on some measurable and individually unique feature. The software was originally designed to evaluate the fluke shape of whale tails, although it has since been used in a variety of other contexts (e.g. Russo & Loy, 2020). We applied the method to the unique ear shape of individual eastern grey kangaroos. In a controlled indoor test, I³S Contour was shown to have a 100% success rate in identifying photographs of the western polecat, *Mustela putorius* (Russo & Loy, 2020). The photographs in our survey were taken outside under various lighting conditions and so required manual inspection to confirm identifications.

The 3546 photographs acquired over the 6 years of study were examined individually by the first author, N.E.C., with a subset (~38%) selected to make formal identity checks of the individuals depicted. These subsets were based on a selection of good-quality images in which both ears of the focal individual were front facing (pointed towards the camera) and unobstructed by other individuals, grass and other vegetation. The outline of the ear was manually traced using I³S Contour, which then used a pattern recognition algorithm to recover a list of potential candidate individuals from a subset of individuals who had been previously identified. The images of candidate individuals were then compared to the target photograph by N.E.C. and used to manually confirm the identity of the individual. All identifications were made by N.E.C. and verified in many cases by T.J.O. when further confirmation was needed. The sex of individuals was usually obvious from visible sexual characteristics, such as a pouch or scrotum. The stability of ear shape as an indicator of individual identification across years and age classes is illustrated in the Appendix, Fig. A1.

We then cross-referenced the subset of photographs of identified individuals back to the remaining images in the survey library

to determine affiliations based on the presence of any individual within approximately two to three adult body lengths (roughly 3 m) from the focal. To assign this proximity classification, other individuals seen in frame needed to be within the same focus range as the focal, indicating they were at a position that was equivalent in distance from the camera (i.e. not in front of or behind the focal, but in line with the focal relative to the camera). The body length of the focal was then mentally inverted by the observer to determine whether any of those animals in line with the focal were in turn within two to three body lengths of that focal. We consider this proximity measure to be conservative because there were likely animals in front or behind the focal that were otherwise within 3 m of the focal but were not countered. The consequence of this would be a general underestimate of proximity associations in the population. In addition to sex, we determined the age of the focal from its gross size and categorized as it as either ‘juvenile’ or ‘adult’. Females with young were easily identified by a clear bulge to the pouch, the protrusion of a head or legs from the pouch or suckling young-at-foot.

Ethical Note

The work described in this paper was approved by the Animal Care and Ethics Committees of the University of New South Wales under projects 16/8B and 19/143A.

Analyses

All analyses were performed using R version 3.0.1 (R Core Team, R Foundation for Statistical Computing).

Social networks

Network graphs were created using the package ‘igraph’ version 1.2.7 (Csardi & Nepusz, 2006). Two sets were constructed.

The first set included networks of the population for each annual survey (six networks across 6 years) and was used to compute eigenvector centrality for every individual observed in a given year. Eigenvector centrality is the number of connections that a node has in a network and is weighted so that a connection to a node with a higher centrality score contributes more to its score than a connection to a node with lower centrality (Bonacich, 2007). When choosing eigenvector centrality, we used the decision tree outlined in Sosa et al. (2020) to narrow down the relevant network indices to ones suited for our research questions. Eigenvector centrality was chosen as it considers both the node’s degree and strength as well as those of its connections, making it a valuable tool for identifying key individuals with a high level of influence in a social network (Webber et al., 2020). If influence within a network is a beneficial social trait, then it is likely to affect other aspects of kangaroo sociality, including the potential for forming long-term relationships or increased mating opportunities simply because an individual interacts with more individuals (e.g. individuals of the opposite sex). Furthermore, dingoes, *Canis dingo*, invasive red foxes, *Vulpes vulpes*, and feral dogs, *Canis familiaris*, are predators of kangaroos, and eastern grey kangaroos, in particular, have been shown to adjust their vigilance with that of their group (Favreau et al., 2015). Such threat-monitoring predator defence has therefore been implicated as a key reason for kangaroos to maintain strong associations with other socially connected individuals (Pays et al., 2009). Conversely, eastern grey kangaroos decrease group size and sociability in areas where predators have been removed (Banks, 2001), which by extension, highlights the potential role of social connections in areas with predators (including our study site).

The second network included affiliations across the entire study period (one network, 2015–2020 inclusive) and was used to identify affiliations among individuals that occurred across multiple years.

For each network set, we created separate node and edge spreadsheets. The node spreadsheet contained the identity of every kangaroo observed, its age, sex, the presence or absence of young (in the case of adult females) as well as the number of unidentified associations an individual might have had (i.e. the total number of kangaroos seen with the focal kangaroo that could not be reliably identified). For the network inclusive of all years, the node spreadsheet did not note whether a female kangaroo had young as this factor varied from one year to the next. The edge spreadsheet included each identified kangaroo and all individuals that they had been observed associating with. Kangaroos seen together multiple times during a given observation period (e.g. during the same dawn observation on a given day) were counted as having a single association to negate the bias of multiple photographs being taken of the same group of kangaroos. 'Multiple associations' were only counted if they occurred during separate observation periods. For the network inclusive of all years, the edge spreadsheet treated repeat associations between individuals across days in the same year as a single association.

Statistical analysis

Confirmation of appropriate specification of models applied was determined using the package 'performance' version 0.9.0 (Lüdtke et al., 2021) and the 'check_model' function. This function provides a comprehensive visualization of a suite of diagnostic checks, including tests of linearity, homogeneity of variance, influential outliers, collinearity among predictors and normality of residuals and random effects.

We first used a random regression (mixed-effects model) to test whether the eigenvector centrality of males, females and juveniles within networks in any given year differed from one another using the package 'lme4' version 1.1–7 (Bates et al., 2015). The model included additional factors of mean-centred sex ratio and mean-centred population size, and a random intercept for individual identity (ID). An interaction term between sex ratio and each reproductive category (females with young, females without young, juveniles, males) was initially considered to test for potential changes in centrality as a function of fluctuating numbers of females and males. The effect of this interaction term was not found to be statistically distinguishable from zero for most reproductive categories, with only individuals of unknown sex exhibiting a decrease in centrality with increasing sex ratio. Given that this category was included in models as a methodological control and subsequently was not biologically interpretable (this category reflects an inability to confidently assign sex, rather than a biological reproductive state), we removed the interaction from the final model. Full model details with interaction terms with sex ratio are provided in the Appendix. Population size was based on the number of identified individuals (nodes) observed in a given year. It was included as a covariate in the model because the opportunity for individuals to exist in a network, and the size of that network, could potentially vary as a function of population size and subsequently affect centrality estimates. We used the package 'jtools' version 2.1.4 (Long, 2020) to compute a Satterthwaite approximation of the 95% confidence intervals and *P* values for predictor variables.

To explore the potential impact of zero-inflated data, given instances where individuals not found to associate with others in any given year were computed to have a centrality of 0, we

repeated the analysis above as a compound Poisson random-effects model using the 'cplm' package 0.7–9 (Zhang, 2013) and the 'cpglmm' function. This function evaluates the distribution of the data to specify the most appropriate error distribution from a family of Tweedie probability distributions. In essence, the model weighed an individual's centrality in the years in which it was observed in proximity to other individuals (i.e. centrality > 0) by the proportion of years it was not observed to be in proximity to other individuals (centrality = 0). The model outcome was qualitatively unchanged from the random-effects model applied using the 'lmer' function, and we subsequently focused on this latter model for simplicity. Full details on the compound Poisson random-effects models are provided in the Appendix.

To compute individual coefficients of changes in female centrality as a function of the presence or absence of young, we applied an additional random regression on adult females only, with the single predictor variable of the presence or absence of young in a given year coded as 1 or 0, respectively. This model included a random intercept and slope for female ID to better resolve individual differences in centrality as a function of reproductive status and was used to graphically represent shifts in centrality within females. An initial model that included sex ratio and population size as covariates was considered, but neither variable had a credible statistical effect on the model outcome and was excluded. This full model is reported in the Appendix.

Second, we used a random logistic regression to provide a clearer evaluation of the association between the odds of reproduction and eigenvector centrality for adult females. In this model, the presence or absence of young was scored as 1 or 0, respectively, and used as the dependent variable in a mixed-effects model applied using 'lme4' with a binomial distribution and a random intercept for female ID. The model included two predictors: (1) the mean adult centrality computed across all years that a female was observed in the population (X_{mean}) and (2) the observed difference in centrality from that mean within a given year for that female ($X_{\text{mean}} - X_{\text{year}}$). This model was used to help establish whether females that were more central in networks, on average, were more likely to reproduce (X_{mean}) and whether they in turn changed their position within networks when caring for young ($X_{\text{mean}} - X_{\text{year}}$). Mean-centred population size was included as a covariate under the assumption that the opportunity for females to reproduce varies with population size. Confidence intervals and *P* values were computed using Satterthwaite approximation in 'jtools'.

Third, we tested whether network position as a juvenile predicted the position as an adult using a regression of adult eigenvector centrality as a function of juvenile eigenvector centrality. This analysis was focused on females because only a single male was tracked from juvenile to adulthood in the study. Two models were applied. The first model used a random regression with a random intercept for female ID implemented in 'lme4' and considered the centrality of females as adults regardless of the presence of young. The second model focused on a single estimate of adult centrality when a female did not have young and was examined using a linear regression implemented using the base function in R.

Finally, we examined whether individuals revealed to have affiliations across years were also those individuals that tended to be more central in networks within years. Two random regressions were applied. In both, an individual's eigenvector centrality was the dependent variable, and we included whether or not the individual exhibited multiyear affiliations as a dichotomous predictor variable (coded 1 or 0, respectively). These models included a random intercept for individual ID. The number of years an individual was observed was initially

included as a covariate, given that the chances of observing an individual in proximity to another might increase depending on how often that individual was generally observed. In no case was this covariate found to contribute a statistical effect in models and it was subsequently excluded from the model to provide better computation of parameter estimates. Full models that include a covariate for the number of years observed in the population are provided in the Appendix. The first model considered all individuals in the population regardless of sex and age, while the second considered only adult females. This second analysis was applied because several males were observed to affiliate with the same female across years. This was likely because these females happened to be oestrus at the time the annual survey was conducted. Several females and juvenile associations were also observed in consecutive years, which were most likely mother and young. The second analysis on adult females removed these potential confounds. Confidence intervals and *P* values were computed using Satterthwaite approximation in 'jtools'. The difficulty with both analyses was the co-dependency of multiyear associates among individuals found to exhibit them, which could result in nonindependence of centrality. We therefore repeated the analyses with one of the pair in the multiyear association removed (the choice of individual was randomly selected). This necessarily reduced the number of individuals observed to exhibit multiyear affiliations by half but removed the issue of nonindependence.

RESULTS

Population size fluctuated to some extent across years but dropped dramatically in 2020, probably due to severe drought and the putative mortality of many individuals. Overall, 130 individual kangaroos were identified across the 6-year study: 70 females, 30 males, 19 of unknown sex and 11 juveniles. Of these 130 individuals, 38 were never seen in a network in any year (29%; 15 females, 9 males, 9 of unknown sex, 5 juveniles). Many of these were individuals observed only in a single year (19; 50%).

The network graphs showed some shifts in the social structure of the population across years, namely a larger clustering in social networks in 2018 and 2019, and smaller, more modular clustering in 2015 and 2020 (Fig. 1). Most individuals (71%) were members of at least one network (Fig. 1). The larger networks were centred around a few key individuals, most often adult females with young. This observation is consistent with the analyses of eigenvector centrality, which confirmed that females with young, on average, had the highest centrality within networks in any given year (Table 1, Appendix, Tables A1–A2). The centrality of juveniles was not statistically distinguishable from females with young (Table 1), although the number of juveniles included in the analysis was relatively small (11 individuals). Nevertheless, this would be consistent with juveniles remaining in close proximity to their mothers and subsequently associating with the same individuals as their mothers in those networks. In contrast, males and adult

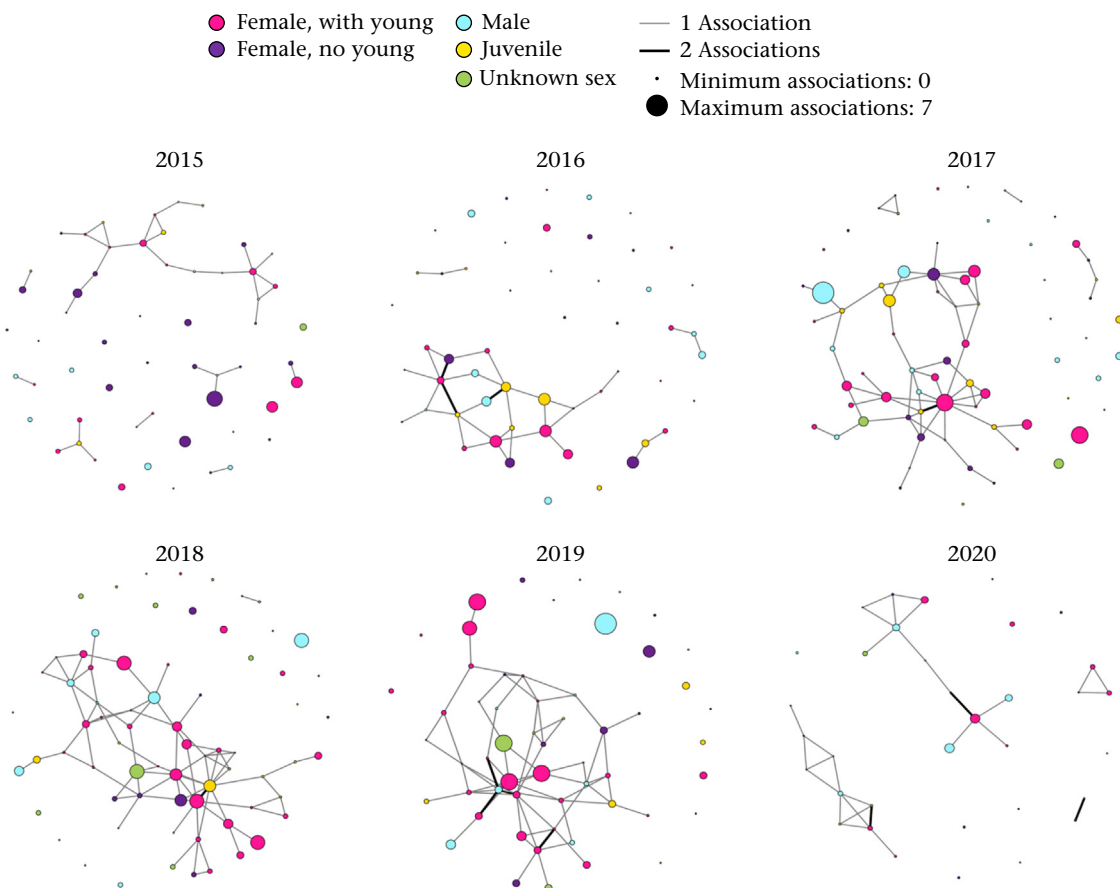


Figure 1. Proximity social networks (animals within roughly 3 m of one another) illustrating affiliations of all individually identified kangaroos in each year of the study. Each dot or 'node' represents an individual kangaroo, with its colour corresponding to its sex, age and reproductive status. The size of the node provides additional information on the total number of unidentified kangaroos an individual was also seen with (i.e. individuals that could not be reliably identified because of obstructions or postures facing away from the camera). Each line or 'edge' is weighed according to the number of instances (effectively the total number of dawn and dusk sessions) those individuals were observed together. Those individuals observed alone or only observed with an unidentifiable individual remain unconnected.

Table 1

Differences in the centrality of kangaroos as a function of reproductive category, controlling for annual mean-centred adult sex ratio (females: males) and annual mean-centred population size (network nodes)

Variable	Estimate (95% CI)	<i>t</i>	<i>P</i>
Intercept (females with young)	0.16 (0.12, 0.20)	7.79	<0.001
Females without young	−0.11 (−0.17, −0.04)	−3.27	0.001
Juveniles	0.01 (−0.06, 0.09)	0.32	0.753
Males	−0.07 (−0.14, −0.002)	−2.01	0.046
Unidentified Sex	−0.04 (−0.13, 0.05)	−0.92	0.359
Sex ratio (mean-centred)	0.02 (−0.02, 0.05)	0.92	0.357
population size (mean-centred)	−0.002 (−0.004, 0.000)	−1.61	0.108
<i>N</i> _{individuals, observations} =130, 343			

CI: confidence interval. The model applied includes a random intercept for individual identity. An interaction term between reproductive category and sex ratio was originally considered but not found to have a statistically distinguishable effect from zero for biological reproductive categories and was subsequently removed from the final model (see Appendix, Table A1 for full model details and Appendix, Table A2 for the outcome of an alternative compound Poisson random-effects model).

females without young were, on average, the least centralized within networks (Table 1). Visual inspection of network graphs (Fig. 1) shows that males and adult females without young were usually connected to a network, but often on its periphery. While individuals of unknown sex also tended to be less central in networks, they were nevertheless statistically indistinguishable from females with young (Table 1). Sex ratio was not found to be a statistically significant covariate of centrality (Table 1). This was also the case for population size, but the 95% confidence intervals of population size only marginally overlapped zero (Table 1), implying that as population size increased, there was a general tendency for the centrality of all individuals to decrease in networks.

In general, there was an even odds of adult females reproducing in any given year (i.e. being observed with young), and these odds were unrelated to a female's average adult centrality within networks across years (X_{mean} : $z = 1.19$, $P = 0.24$; Table 2). That is, more popular or connected females were not more likely to reproduce. Instead, females changed position in networks to become more central in those years they were observed with young ($X_{\text{mean}} - X_{\text{year}}$: $z = 2.86$, $P < 0.01$; Table 2, Fig. 2, Appendix, Tables A3–A4).

An adult's centrality in a network was not predicted by its centrality as a juvenile (Table 3). Twenty-three juvenile females and one juvenile male in the population were tracked to adulthood over the 6-year study. Focusing on these females, there was no statistical relationship between the position of juvenile females within networks and their later centrality as adults, irrespective of how the data were analysed (Table 3). This is consistent with the finding that juvenile centrality probably reflected the mother's position within networks, and this position was, on average, higher because mothers were caring for those young (Table 1). Once juvenile females reached maturity, however, their centrality within networks depended on their reproductive state (Appendix, Tables A3–A4), not their past centrality as a juvenile (Table 3).

Finally, 21 kangaroos affiliated with the same individuals across years (Fig. 3, Appendix, Fig. A2). There was no evidence for preferred associations among males. Excluding instances of male–female and female–juvenile affiliations across years, which

likely reflect mating and caring for young, respectively, the vast majority of observations of repeat associations among adult females or individuals of unknown sex (likely other adult females) occurred across consecutive years (Fig. 3). Only two females were observed together in nonconsecutive years. Overall, 12 females and two individuals of unknown sex were seen repeatedly associating with one another across years. This represents approximately 13% of the total number of individuals recorded in these categories across the 6 years of study (12 of 70 females and 2 of 19 individuals of unknown sex). Those individuals observed to have preferred social affiliations across years were also individuals that were, on average, more central in networks within years, regardless of how the data were handled or whether or not the number of years an individual was observed was included as a covariate (Table 4, Appendix, Tables A5–A6). For example, adult females observed to affiliate with one another across years were generally females with eigenvector centrality scores roughly double those of females not observed in affiliations with other females across years (Fig. 4).

DISCUSSION

We found that some eastern grey kangaroos were more gregarious than others, and this in turn varied depending on reproductive status. Some individuals, predominantly adult females, were observed preferentially associating with one another in consecutive years (Fig. 3). These individuals were, on average, more centrally connected within networks (Fig. 4). Adult females who tended to be more gregarious within years were, in particular, more likely to associate with other popular females across years. Why this was the case is unclear, but long-term bonds among individuals have been found in a number of other large, gregarious herbivores with fission–fusion social structures, including elephants (de Silva et al., 2011), giraffes (Carter et al., 2013) and alpine ibex (Brambilla et al., 2022). These bonds can reflect genetic relationships among preferred associates (e.g. sisters or maternal lines). Macropods do seem to be capable of discriminating close relatives, including nonparental kin (Blumstein et al., 2002).

Table 2

The odds of an adult female kangaroo having young as a function of her mean adult centrality across years (X_{mean}) and her observed difference in centrality from that mean within a given year ($X_{\text{mean}} - X_{\text{year}}$), controlling for annual mean centred population size (network nodes)

Variable	Estimate (95% CI)	<i>z</i>	<i>P</i>
Odds			
Intercept (having young in any given year)	1.62 (0.90, 2.94)	1.60	0.109
Odds ratio			
Among female centrality (X_{mean})	8.80 (0.24, 320.29)	1.19	0.236
Within female centrality ($X_{\text{mean}} - X_{\text{year}}$)	56.05 (3.54, 886.61)	2.86	0.004
Population size (mean-centred)	1.03 (0.99, 1.06)	1.60	0.109
<i>N</i> _{females, observations} =70, 195			

CI: confidence interval. A female's mean centrality was based exclusively on her adult centrality because juvenile centrality did not predict adult centrality (Table 3) and was instead likely reflective of their mother's centrality (Table 1).

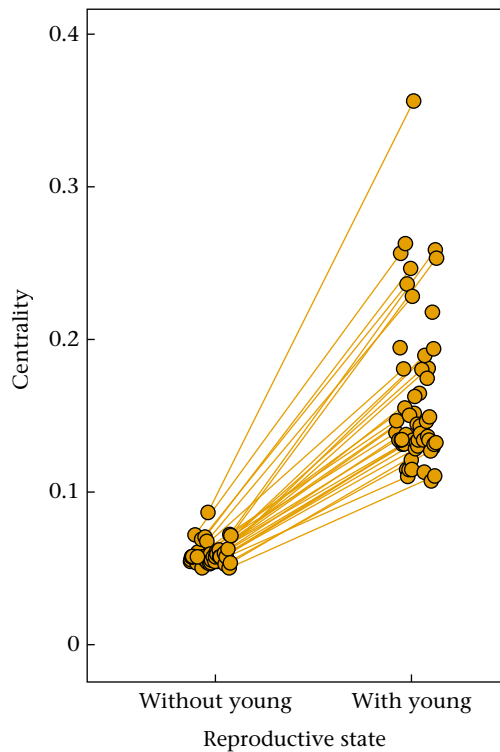


Figure 2. The centrality of females in networks when caring for young versus those years in which a female was not observed with young. Values are eigenvector centrality computed from networks shown in Fig. 1 and derived from coefficients obtained from the random-effects model reported in the Appendix, Table A3 (see also Table A4). These values are weighted averages across years for each female, relative to all other females observed in the same year. High centrality scores indicate a female has many connections with other individuals, or connections with individuals that themselves have many connections, or both.

Eastern grey kangaroos also exhibit preferred associations with close kin, although this tendency is generally weak and associations appear to be better predicted by general space use (Best et al., 2014). For example, juvenile kangaroos are sexually mature at 20–36 months (Poole, 1983), at which point they tend not to maintain familial relationships with their mothers (Best et al., 2013). Female kangaroos generally remain in the same population for many years, in contrast to males, which move more frequently among populations (Coulson et al., 2014). Females would therefore be more likely to establish familiar relationships. The greater centrality of females and their tendency to associate with other connected females across years would be consistent with associations forming among familiar females (Best et al., 2014).

Otherwise, the proximity of conspecifics might simply reflect resource clumping, such as grazing sites near areas of shelter or

refuge. This would predict little differentiation in network positions based on sex or maturity, which is not consistent with our data (Table 1). Our proximity ‘rule’ for generating networks was also comparatively strict. Other studies have classified associating kangaroos as those occurring within 10–15 m of one another (King et al., 2017; Menz et al., 2017). We categorized affiliating individuals as those observed within roughly 3 m, with repeat associations assigned only if individuals were observed close together across separate dawn or dusk observations within years, and in repeated proximity to one another across years. The area available for grazing (and grazing close to shelter) is extensive for this population, making it less likely that individuals clumped together because some areas were more favourable than others for grazing or were closer to adjacent diurnal rest sites. Finally, population size was included as a covariate in our analyses but had only a marginal effect on the centrality of connected individuals. If anything, centrality across the population tended to decrease with increasing population size, consistent with individuals tending to space themselves more evenly across the landscape, rather than to clump. Taken together, affiliations among adult females, at least, appear to reflect familiarity among those females and are not simply the product of nonsocial patterns of space use.

Each annual survey was a brief snapshot of the social dynamics of the population over a matter of days. Our proximity rule was also dependent on observing individuals alongside one another because of the difficulty of confidently judging distance of other individuals in front of or behind the focal in two-dimensional photographs. Our sampling methodology was therefore almost certainly biased against detecting long-term affiliations among individuals unless they were especially common. It required individuals to be observed within 3 m of each other on separate occasions during the 3–4-day survey period, and then repeatedly in separate years. Given the area occupied by the population, and the number of individuals in the population, the chances of recording these long-term affiliations would have been low. Yet, we observed a large number of individuals apparently associating with one another across years. We suspect the true extent of long-term associations forming in this population is likely much higher than what we recorded. At an individual level, this propensity increased with the sociability of a given female, with more popular females (those of high centrality) tending to be more likely to associate with other popular females across years. Overall, our data set implies that long-term associations in kangaroos (particularly between females) may be common, but further studies are needed to confirm the extent to which these multiyear associations are maintained among individuals.

In addition, a female's position within a network varied from one year to the next depending on whether or not she was caring for young (Fig. 2). Several studies of eastern grey kangaroos have reported mothers isolating themselves when caring for young (Banks, 2001; Jaremovic & Croft, 1991; King et al., 2017; Menz et al.,

Table 3

Relation of juvenile centrality to future adult centrality in females for all adult years regardless of the presence of young and only for adult years when observed not to have young

Variable	Estimate (95% CI)	<i>t</i>	<i>P</i>
Irrespective of presence of young			
Intercept (adult centrality)	0.12 (0.04, 0.20)	2.89	0.008
Juvenile centrality	0.07 (−0.05, 0.19)	1.21	0.233
<i>N</i> _{females, observations} = 23, 65			
In the absence of young			
Intercept (adult centrality without young)	0.03 (−0.03, 0.08)	1.16	0.288
Juvenile centrality	−0.02 (−0.22, 0.19)	−0.18	0.866
<i>N</i> _{females} = 8			

CI: confidence interval.

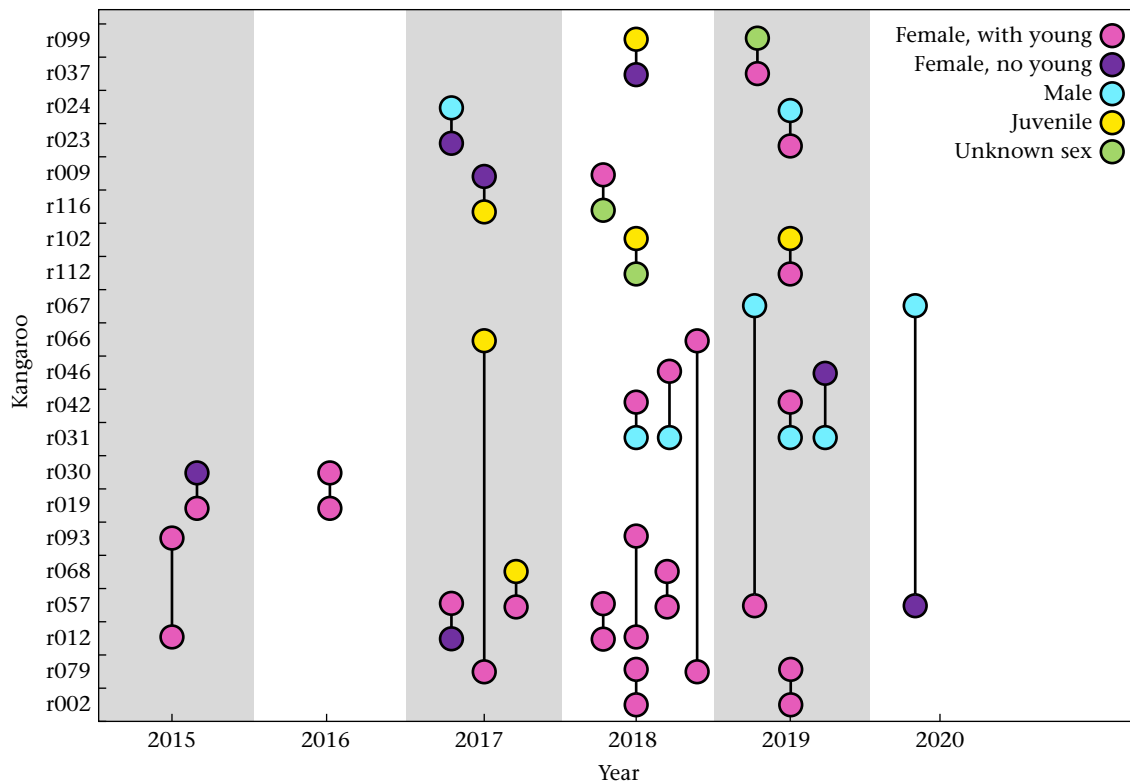


Figure 3. Individual kangaroos observed to associate with one another across years.

2017). This seems to be a classic observation for most large macropods as well (reviewed by Jarman & Coulson, 1989). Yet female eastern grey kangaroos in our population actively shifted to more central positions in networks in the years they were caring for young and, consequently, were in closer proximity to other individuals (i.e. within 3 m), compared to years when they were not observed to have young. This discrepancy might be a quirk of how associations were measured. In our study, we used eigenvector centrality as it could take into account both the number of neighbours within 3 m over an observation period of 2–3 h and the number of neighbours those associates themselves had with others during that period (Bonacich, 2007). This means that mothers might have still tended to congregate in smaller mobs, but these smaller mobs frequently shifted in composition such that these females ultimately had a higher number of preferred associates with other mothers, compared to years when they were not caring for young. For example, a previous study showed that bold (less wary) female kangaroos preferred to associate in smaller mobs but

had more preferred associates than shy (warier) females (Best et al., 2015). This type of fluidity is inherent in social species with fission–fusion dynamics. Nevertheless, visual inspection of the networks in Fig. 1 does suggest that females with young tended to form large networks with other mothers each year. At the very least, mothers were certainly not isolating themselves from conspecifics in our population.

Previous explanations (Croft, 1981) of why females might isolate when caring for young largely rest on mothers attempting to reduce conspecific aggression towards young or reduce the chances of young becoming separated when the mob flushes suddenly to some perceived danger (e.g. predator presence). Neither explanation has been directly tested in eastern grey kangaroos or any other large macropod. Banks (2001) observed that eastern grey kangaroo females with young tended to occur in smaller groups or in isolation in areas of low, but not high, predation. Menz et al. (2017) found that females progressively increased their isolation from other eastern grey kangaroos as their joeys got older, not vice versa.

Table 4
Differences in the network centrality of kangaroos as a function of whether those kangaroos were also observed to affiliate with certain individuals across years regardless of the sex and maturity of associated individuals and among adult females only

Variable	Estimate (95% CI)	<i>t</i>	<i>P</i>
All individuals			
Intercept (no affiliations across years)	0.09 (0.06, 0.12)	6.59	<0.001
Individuals exhibiting multiyear affiliations	0.14 (0.08, 0.19)	4.94	<0.001
<i>N</i> _{individuals} , observations=130, 343			
Adult females only			
Intercept (no affiliations across years)	0.11 (0.07, 0.14)	6.21	<0.001
Females exhibiting multiyear affiliations	0.11 (0.03, 0.20)	2.53	0.014
<i>N</i> _{females} , observations=70, 195			

CI: confidence interval. See Appendix, where Table A5 provides model output considering the number of years observed in the population as a covariate, and Table A6 focuses only on unique multiyear affiliations.

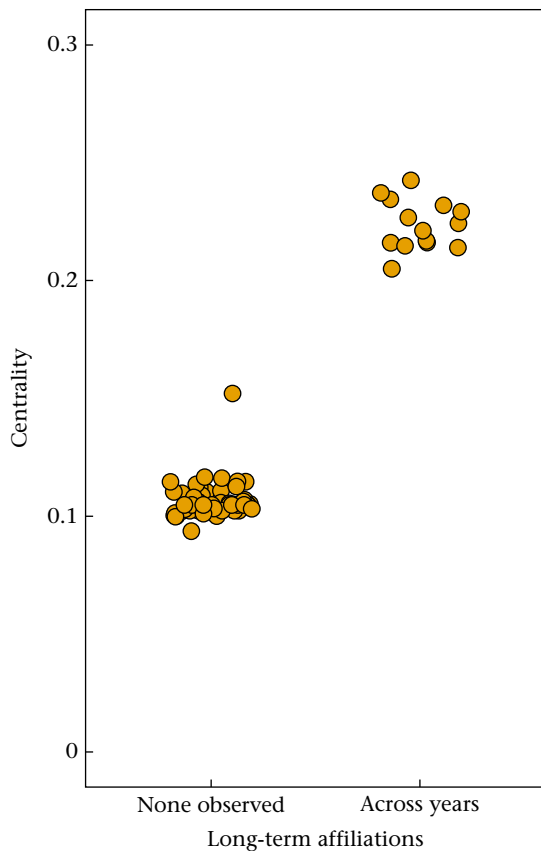


Figure 4. The centrality of females in networks that were observed to form preferred associations with the same females across years (long-term affiliations) compared to females that were not observed to associate with the same females. Values are eigenvector centrality computed from networks shown in Fig. 1 and derived from coefficients obtained from the random-effects model reported in Table 4. These centrality values are weighted averages across years for a given female, relative to other females observed in the same years. See figure legend of Fig. 2 for other details.

Vigilance time in eastern grey kangaroos and other macropods decreases with increasing group size (Blumstein & Daniel, 2003; Blumstein et al., 1999, 2001; Favreau et al., 2018; King & Goldizen, 2016), because being in a large group increases the detection of a predation threat (the ‘many eyes’ effect) and dilutes the individual risk of attack (‘safety in numbers’). Given that the youngest joeys are presumably the most vulnerable to predation, and most likely to become confused and separated from their mothers when startled, the increased isolation of mothers with older joeys is not consistent with a strategy for reducing predation risk. Rather, mothers view older offspring as less vulnerable and reduce their associations with conspecifics to balance other factors (Menz et al., 2017). For example, aggression directed at young can increase as those young become more independent (King & Goldizen, 2016), prompting females to progressively segregate away from conspecifics as their joeys age.

In our study, females with young (age undefined) clearly preferred to associate in close proximity to other mothers (Fig. 1) and were more centrally positioned within social networks (Fig. 2). Other individuals, such as adult males or individuals whose sex could not be reliably determined tended to be more peripheral, generally less connected and apparently more often isolated from conspecifics. There are two nonmutually exclusive explanations for this observation: (1) mothers group together to reduce the risk of predation for their offspring; (2) mothers effectively avoid unwanted attention from males and consequently aggregate together away from males. In the first instance, dingoes, foxes and feral dogs

are predators of small adults and joeys and all were sighted at during the 6 years of this study. In the second instance, kangaroos do not form strict male-led dominance hierarchies (Caughley, 1964; Grant, 1973) and male–male aggression over females is common (Miller et al., 2010). A frequent strategy adopted by males is to increase their proximity and time spent with females (Montana et al., 2020). This can result in several males frequently inspecting the breeding status of a single female. We have observed frequent harassment of females by multiple males and, on occasion, even of females who already had pouch young or young-at-foot. Male harassment can include following, sniffing and stroking of females as well as mounting attempts by one or more males, which can displace females, interrupt their grazing and occasionally solicits ‘barks’ (aggressive growls) from females towards harassing males.

At a general level, a key hypothesis for the adaptive origin of fission–fusion sociality is the advantage conveyed through more effective management of the benefits and costs of gregarious behaviour (Sueur et al., 2011). Females in our study seem to tailor their position within social networks as a function of their reproductive state, choosing to affiliate with other mothers to potentially dilute predation risk, harassment from males, aggression towards their young, or some combination of all of these factors. Yet a female’s general sociability within any given year also predicted her tendency to form potential long-term bonds with other females. These associations tended to be among mothers but still occurred between females without young as well (Fig. 3). Unlike other species with fission–fusion social patterns, we found no evidence that a juvenile’s social position predicted later adult centrality (Gerber et al., 2019; Ilany et al., 2021; Taillon & Côté, 2006). The factors leading to both the formation of putative long-term bonds and the potential adaptive reasons for the apparent increased gregariousness of mothers and juveniles in eastern grey kangaroos, and how these factors might vary across populations (and studies), clearly warrants further investigation.

Author Contributions

N.E.C. and T.J.O. conceived the study; N.E.C. identified individuals from photographs and compiled associated data, created network graphs and conducted statistical analyses; T.J.O. completed the annual photographic surveys and contributed to statistical analyses; N.E.C. and T.J.O. wrote the paper.

Data Availability

Data are deposited in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.4f4qrfjgm>.

Declarations of Interest

None.

Acknowledgments

Funding was provided by the School of Biological, Earth and Environmental Sciences and the Science Faculty of University of New South Wales. N.E.C. was supported by an Australian Postgraduate Award from University of New South Wales.

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Appendix

Table A1

Differences in the centrality of kangaroos as a function of reproductive category, controlling for annual mean-centred adult sex ratio (females: males), its interaction with reproductive categories and annual mean-centred population size (network nodes)

Variable	Estimate (95% CI)	t	P
Intercept (females with young)	0.16 (0.11, 0.20)	7.33	<0.001
Females without young	−0.10 (−0.17, −0.04)	−3.09	0.002
Juveniles	0.02 (−0.06, 0.09)	0.48	0.635
Males	−0.07 (−0.13, −0.005)	−1.83	0.070
Unidentified sex	−0.01 (−0.10, 0.08)	−0.31	0.760
Sex ratio (mean-centred)	0.05 (−0.01, 0.10)	1.74	0.083
Population size (mean-centred)	−0.002 (−0.004, 0.001)	−1.44	0.150
Females without young*sex ratio	−0.04 (−0.12, 0.05)	−0.82	0.411
Juveniles*sex ratio	−0.03 (−0.14, 0.08)	−0.58	0.561
Males*sex ratio	−0.03 (−0.11, 0.05)	−0.71	0.481
Unidentified sex*sex ratio	−0.18 (−0.31, 0.05)	−2.77	0.006

$N_{\text{individuals, observations}}=130, 343$

CI: confidence interval.

Table A2

Differences in the centrality of kangaroos as a function of reproductive category, controlling for annual mean-centred adult sex ratio (females:males) using a compound Poisson random-effects model

Parameter	Estimate	
Dispersion	1.11	
Index	1.56	
Variable	Estimate (SE)	t
Intercept (females with young)	–1.97 (0.16)	–12.25
Females without young	–1.01 (0.29)	–3.46
Juveniles	0.07 (0.30)	0.25
Males	–0.69 (0.30)	–2.31
Unidentified sex	–0.40 (0.37)	–1.08
Sex ratio (mean-centred)	0.15 (0.14)	1.10
Population size (mean-centred)	–0.01 (0.01)	–1.33

*N*_{individuals, observations}=130, 343

The model includes a random intercept for individual identity. This model identified a compound Poisson-gamma distribution as the most appropriate error distribution for the final model (i.e. based on an index parameter sitting between 1 and 2). Confidence intervals and *P* values could not be estimated using 'jtools' because of the complexity of the model.

Table A3

Changes in the centrality of adult female kangaroos in years with and without young

Variable	Parameter estimate (95% CI)	t	P
Intercept (females with young)	0.16 (0.12, 0.21)	7.17	<0.001
Females without young	–0.10 (–0.17, –0.04)	–3.02	0.003

*N*_{individuals, observations}=70, 195

CI: confidence interval. The model applied includes a random intercept and slope for individual identity.

Table A4

Changes in the centrality of adult female kangaroos in years with and without young, with covariates of mean-centred sex ratio and mean-centred population size

Variable	Parameter estimate (95% CI)	t	P
Intercept (females with young)	0.16 (0.11, 0.20)	6.52	<0.001
Females without young	–0.10 (–0.16, –0.03)	–2.84	0.005
Sex ratio (mean-centred)	0.03 (–0.01, 0.07)	1.40	0.163
Population size (mean-centred)	–0.000 (–0.003, 0.003)	0.21	0.838

*N*_{individuals, observations}=70, 195

CI: confidence interval. The model applied includes a random intercept and slope for individual identity.

Table A5

Differences in the network centrality of kangaroos, controlling for the number of years observed and as a function of whether those kangaroos were also observed to affiliate with certain individuals across years regardless of the sex and maturity of associated individuals and among adult females only

Variable	Estimate (95% CI)	t	P
All individuals			
Intercept (no affiliations across years)	0.09 (0.03, 0.14)	2.93	0.004
Individuals exhibiting multiyear affiliations	0.14 (0.08, 0.20)	4.39	<0.001
Number of years observed	0.001 (–0.016, 0.018)	0.12	0.904
<i>N</i> _{individuals, observations} =130, 343			
Adult females only			
Intercept (no affiliations across years)	0.07 (–0.03, 0.16)	1.40	0.164
Females exhibiting multiyear affiliations	0.10 (0.01, 0.19)	2.23	0.030
Number of years observed	0.01 (–0.01, 0.04)	1.07	0.290

*N*_{females, observations}=70, 195

CI: confidence interval.

Table A6

Differences in the network centrality of kangaroos as a function of whether those kangaroos were also observed to affiliate with certain individuals across years regardless of the sex and maturity of associated individuals and among adult females only

Variable	Estimate (95% CI)	<i>t</i>	<i>P</i>
All individuals			
Intercept (no affiliations across years)	0.09 (0.06, 0.12)	6.84	<0.001
Individuals exhibiting multiyear affiliations	0.14 (0.07, 0.21)	3.80	<0.001
<i>N</i> _{individuals, observations} =119, 299			
Adult females only			
Intercept (no affiliations across years)	0.11 (0.07, 0.14)	6.01	<0.001
Females exhibiting multiyear affiliations	0.13 (0.02, 0.24)	2.23	0.031
<i>N</i> _{females, observations} =64, 174			

CI: confidence interval. This analysis focuses only on unique multiyear affiliations.

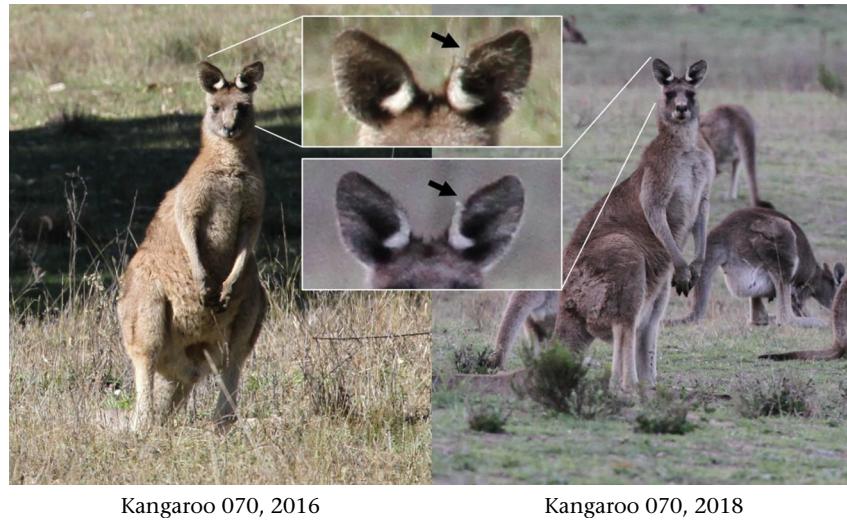


Figure A1. An example of how ear shape remains consistent through age and across years. Both images are of the same male (kangaroo 070), 2 years apart. Initially, this male was observed as a subadult in 2016 (left panel) and subsequently tracked across years to maturity in 2018 (right panel). The insets show the ears magnified to highlight the consistency in ear shape across these years and development categories. Verification of this individual can also be made based on a unique scar on the left ear, highlighted by the arrow.

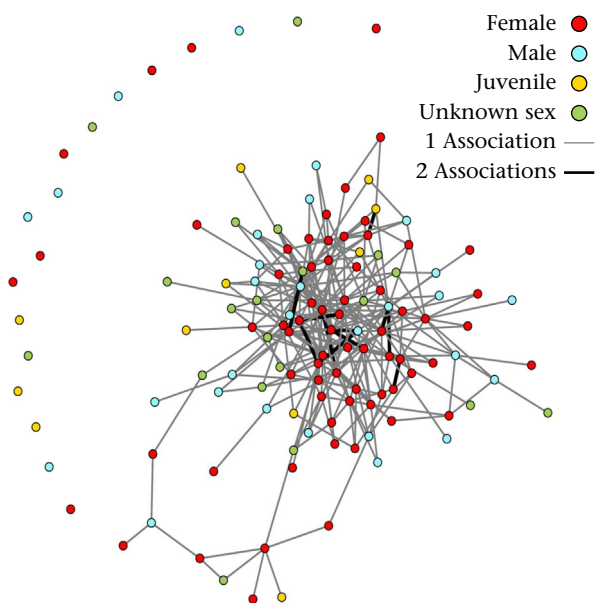


Figure A2. The proximity network graph of all 130 kangaroos observed over the 6-year study. Each node represents an individual kangaroo, with its colour corresponding to its sex and age (juvenile versus adult). Each edge is weighed according to the total number of years individuals were observed within approximately 3 m of each other. That is, those individuals seen together in separate years have edge connections of higher weight.