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ORIGINAL ARTICLE

Long-term consequences of mother-offspring associations in eastern grey kangaroos

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Abstract
Close behavioural association between mothers and offspring should enhance survival and growth of the young. Eastern grey kangaroos *Macropus giganteus* are gregarious and live in fission-fusion societies where adult females do not form strong bonds with other females but associate closely with their juvenile offspring. We aimed to determine whether the strength of these mother-offspring associations correlated with offspring size, survival and reproduction. We observed 129 marked offspring, aged 10 to 21 months, and their mothers in a high-density population at Wilsons Promontory National Park, Australia. We used half-weight indices to quantify mother-offspring associations and determined the proportion of time offspring spent with their mother, but isolated from other kangaroos, while foraging. We found strong cohort effects on size, mass, body condition, survival and reproduction. Mother-offspring sociability indices were not correlated with offspring body condition as 2-year-olds or reproduction as 3-year-olds. Juveniles that spent proportionally more time with their mothers at 18–21 months, however, were 6% larger and 19% heavier as 2-year-olds than those that did not associate closely with their mothers. In addition, juveniles that were often found alone with their mothers were more likely to survive than those that were more often found in larger groups. Stronger mother-offspring associations before weaning likely reflected nutritional maternal care in sons but non-nutritional care in daughters and had a beneficial effect on juvenile growth and survival.

Significance statement
The possible fitness consequences of mother-offspring behavioural associations can affect reproductive decisions by mothers. These fitness consequences affect population dynamics and are relevant to conservation when mothers may be harvested or killed by vehicles, as is the case for many large herbivores. We show that variability in these associations in kangaroos affects correlates of offspring fitness. Juveniles that spent proportionally more time with their mothers between 18 and 21 months of age were larger and heavier as 2-year-olds. In addition, juveniles that spent proportionally more time with their mothers but isolated from other kangaroos experienced improved survival. This study is among very few to examine the relationship between mother-offspring sociability and reproductive success in a non-primate mammal. Improved juvenile growth in sons appears to result from nutritional maternal care through prolonged nursing. Isolation of the mother with her young-at-foot occurs in all large macropod marsupials, and adaptive benefits of this behaviour should therefore occur in other species of macropods.

Keywords Half-weight index · Juvenile growth · Maternal care · *Macropus giganteus* · Survival

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Introduction

Maternal care is an important factor in early development of mammals (Maestripieri and Mateo 2009). Care of young broadly refers to any behaviours, such as nursing, food provisioning, guarding, carrying and grooming, that contribute to offspring fitness (Clutton-Brock 1991). Relationships between the care received by juveniles and their survival and growth have been shown for mammals such as spotted hyenas *Crocuta crocuta* (Hofer and East 1993), savannah baboons *Papio cynocephalus* (Altmann and Alberts 2005) and bighorn sheep *Ovis canadensis* (Festa-Bianchet et al. 2000). Although maternal effects in mammals are largely assumed to be nutritional, other maternal effects include defense and manipulation of the nest environment (Bernardo 1996). In addition to protecting young from predation, maternal defense can indirectly affect offspring growth by reducing harassment from conspecifics, which allows the young more time to feed (Clutton-Brock 1991). Environmental conditions can also affect maternal care by influencing the resources available for mothers and their ability to provision young (Monaghan 2008). Very few studies of wild mammals other than primates have examined the long-term fitness consequences of variability in mother-offspring associations and non-nutritional care (Maestripieri and Mateo 2009).

In some mammalian societies, long-term associations or social bonds among females improve their reproductive success (Silk 2007; Cameron et al. 2009). These social bonds, established through spending time in close proximity and allogrooming, often increase dominance and priority of access to food (Silk 2007), reduce harassment (Cameron et al. 2009) and may reduce the level of glucocorticoid stress hormones (Silk et al. 2012). Social bonds among females translate into improved offspring survival through maternal effects in savannah baboons (Silk et al. 2003, 2009). In contrast, in species with fluid grouping patterns such as bottlenose dolphins *Tursiops aduncus*, associations between group members are temporary but could nonetheless be beneficial (Frère et al. 2010).

Eastern grey kangaroos *Macropus giganteus* live in loose fission-fusion groups of about 3–4 individuals that form, at least partly, as an anti-predator strategy (Jarman and Coulson 1989). Dispersal is biased towards males and occurs after the age of 24 months (King et al. 2015b). Females do not form strong bonds with kin after sexual maturity at high population density (King and Goldizen 2016), but females may form weak preferential associations with other females at lower densities, with spatial overlap a more important predictor of preferential associations than relatedness (Best et al. 2014). The benefits of such associations, however, are unknown. Females usually first breed at 3 years (King et al. 2015b) and can produce a single offspring annually up to the age of 20 years (Poole 1982). Offspring are nursed for about 18 months, 10 of which are spent in the pouch (Poole 1983; King and Goldizen 2016). Mothers associate closely with offspring that have permanently emerged from the pouch but are still suckling (termed young-at-foot), with the young closely following the mother. There is considerable individual variation in mother-offspring associations, with extended associations with young daughters compared to sons in both time (King and Goldizen 2016) and space (King et al. 2015b). Because births occur annually, sequential lactations may overlap, with females carrying a pouch young aged approximately 6 months when weaning a young-at-foot of 18 months of age (Fig. S1). When mothers have an empty pouch around the normal time of weaning in winter, nursing of the young-at-foot can be extended for several months, especially for daughters (King and Goldizen 2016). Although females are gregarious, they tend to isolate themselves when accompanied by young-at-foot (Jarman 1994), perhaps to ensure that offspring correctly identify and follow their own mothers at times of sudden alarm and flight, improving survival (Croft 1981). Kangaroo mothers do not defend their offspring from aggressive conspecifics (King and Goldizen 2016) or foxes (*Vulpes vulpes*) (WJK unpubl. data).

We aimed to determine whether the strength of the relationship between mothers and offspring relates to fitness correlates in eastern grey kangaroos. We thus evaluated the effects of mother-offspring sociability patterns on limb length, mass, body condition, survival and reproduction of offspring. Social integration can be assessed as a composite measure based on proximity, approaches and allogrooming rates (Silk et al. 2003; Cameron et al. 2009). However, because foraging adult female kangaroos rarely interact with their offspring except to nurse them (King and Goldizen 2016), we initially estimated sociability as association indices between mothers and offspring based on foraging group memberships. We also measured the proportion of time offspring spent alone with the mother while foraging, because kangaroos are normally gregarious and the tendency for mothers to isolate themselves with their young has been suggested to be adaptive (Croft 1981). We predicted that these mother-offspring sociability factors would be positively correlated with offspring limb length, mass, body condition, survival and reproduction. We also compared the strength of the effects of social and non-social factors, such as cohort and body condition, on these fitness correlates.

Methods

Study area

We studied eastern grey kangaroos in Wilsons Promontory National Park, Victoria, Australia (38° 57′ S, 146° 17′ E), from April 2010 to September 2014. Kangaroos inhabited 110 ha of meadows surrounding a grassy landing strip. The area was mostly open, with scattered shrub cover of coast tea tree *Leptospermum laevigatum*, coast wattle *Acacia longifolia* and coast banksia *Banksia integrifolia* (Davis et al. 2008). Environmental conditions varied widely from 1 year to the next: spring through winter of both 2010/2011 and 2011/2012 were years of relatively high rainfall (Australian Bureau of Meteorology station no. 085163 at 38° 47′ S, 145° 11′ E), while autumn/winter forage availability was high in 2010 and 2011, reduced by one half in 2012 and by two thirds in 2013 and 2014 (D. M. Forsyth, pers. comm). There were no wild dogs, but predators on juveniles included introduced red foxes and native wedge-tailed eagles *Aquila audax*. Foxes can significantly reduce survival of young kangaroos around the time of permanent emergence from the pouch (Banks et al. 2000). Kangaroos in the study area are habituated to human presence (King and Goldizen 2016).

Captures

Annual captures to mark large pouch young (those with the head usually outside the pouch or temporarily emerged from the pouch (Jaremovic and Croft 1991b)) and to assess reproductive status of females commenced in 2008 and continued through 2014. We marked adults with plastic ear tags and collars and pouch young with small plastic ear tags for visual identification following immobilisation with Zoletil® 100 at a dose rate of 1.4 mg/kg using an extendable pole syringe (King et al. 2011). Whether a female produced a pouch young and/or was nursing a young-at-foot was established at capture through examination of her pouch and state of the teats, which can vary in length from 0 to about 10 cm (Poole and Catling 1974; Poole 1975, 1983). Loss or weaning of an earlier offspring was established through previous observations and confirmed by presence of a regressing teat (Poole 1983). The captured animals were weighed to the nearest 250 (adults and sub-adults) or 25 g (pouch young), and the foot and hind leg length were measured to the nearest 1 mm. We also measured the head length of pouch young to the nearest 0.1 mm. Yearlings (including young-at-foot) and 2-year-olds were termed sub-adults. Body condition was estimated as the standardised residual of the linear regression of the logarithm of mass on hind leg length (Schulte-Hostedde et al. 2005), with separate regressions for adult females, sub-adult females, sub-adult males, pouch young females and pouch young males (Fig. S2). Although there are alternative methods for measuring body condition of species that differ widely in size (Peig and Green 2010), our measure provided a reliable estimate of the relative body condition of animals because they were captured at about the same age and size. Residuals were normally distributed for adult females, sub-adult females, sub-adult males, pouch young females and pouch young males (Shapiro-Wilk tests, $W = 0.995, 0.974, 0.971, 0.976, 0.991$ and $P = 0.34, 0.26, 0.09, 0.06, 0.50$, respectively; Fig. S3) and randomly distributed with respect to body size (Fig. S3). Offspring birthdates were calculated as the mean of estimates from hind leg, foot and head lengths, using sex-specific growth curves (Poole et al. 1982) that provide estimates with a 95% confidence interval of about ±3 weeks at the ages pouch young were captured. We confirmed mother-offspring parentage relationships using nine highly polymorphic microsatellite markers (King et al. 2015a). There were seven cases of adoption of non-relatives over the three cohorts, but we treated adopted young as biological young because a previous study showed no apparent difference between mother-young associations for mothers with biological and adopted young (King et al. 2015a).

We marked 150 large pouch young (88 sons and 62 daughters) aged 8.4 ± 0.1 months (mean ± SE) in three cohorts between 22 August 2009 and 14 October 2011, then recaptured 57 approximately 18 months later as sub-adults (32 sons and 25 daughters) at 26.3 ± 0.2 months of age, between 7 March 2011 and 7 March 2013. Because young were born throughout the year and the time between captures varied, we did not estimate sub-adult growth but instead analysed size (hind leg length) and mass at recapture, taking age at recapture into account (range 22.0–29.9 months). We also estimated body condition of recaptured 2-year-olds using the residual index (Supplementary Figs S2, S3). We did not assess size and mass for 16 2-year-olds marked as young-at-foot, because they were first captured when much older (mean 15.1 ± 0.6 months) than pouch young, yielding a less accurate estimate of birthdate (95% confidence interval of ±2 months) (Poole et al. 1982).

Observations

We observed kangaroos at peak activity times for 2–3 h after dawn and before dusk using 8 × 32 binoculars (Leitz, Germany). Behavioural observations involved one observer (WJK) walking slowly around the study area for 10 to 12 consecutive days each month between April 2010 and June 2012 (total 1122 h). A second observer (MFB) took additional behavioural observations from July 2010 to August 2011, in October 2011 and in March 2012, providing approximately 25% of the total 17,748 groups recorded (King and Goldizen 2016). Once a group was encountered, we recorded group size, including unmarked individuals, and group composition of marked individuals using instantaneous sampling (Altmann 1974). Groups were defined as associating individuals whose most distant associate was within 10 m of another group member, using nearest neighbour distances (Clutton-Brock et al. 1982). We chose this 10-m chain rule since a pilot study showed a distinct discontinuity in nearest neighbour distances beyond 10 m (King and Goldizen 2016). We also used all occurrence sampling (Altmann 1974) to record suckling. If the mother was carrying a new pouch young, young-at-foot were last seen suckling when the pouch young averaged 3.6 ± 0.2 months of age, $n = 39$. No mother carrying a new pouch young was seen to nurse a young-at-foot beyond 18.8 months or when the pouch young was older than 6.1 months. The mean inter-birth interval was 12.7 ± 0.2 months, $n = 65$. It was not possible to record observational data blind, because our study involved marked individuals; however, size, mass and body condition of 2-year-olds were measured several months after behavioural observations took place.

Observations of mother-offspring sociability began in April 2010 when most offspring in the 2008/2009 cohort were about 15 months of age. These offspring were weaned at approximately 18 months of age; several months later in spring 2010, a second cohort (2009/2010) emerged from the pouch at around 10 months of age. A third cohort (2010/2011) emerged 1 year later in spring 2011. Observations of mother-offspring sociability ended in June 2012 (winter) when young of the third cohort averaged 17 months of age. Sometimes suckling continued to 23 months of age if the mother did not reproduce successfully the next year, but suckling by older offspring is rare and difficult to detect (King and Goldizen 2016). We examined the sociability of juveniles from 10 months of age, at which point they had permanently emerged from the pouch but continued to suckle, until 21 months of age. Because observations spanned three cohorts over 2 years, not all pairs were observed in all periods (Table 1). No offspring from the third cohort was observed at 18–21 months of age, and only two of the 3-year-old females from the first cohort were observed at 10–13 months.

Survival of the three cohorts of juveniles was monitored every 2 months from August 2009 to April 2010 and monthly from April 2010 to December 2012. We searched the study area for approximately ten consecutive days per month and noted animals as disappearing on the date last seen. Juveniles in the third cohort were at least 20 months old in December 2012. Known dispersers were 24–63 months old (King et al. 2015b), so we assumed that all disappearances before 24 months were mortalities. It is extremely unlikely that young-at-foot would disperse before weaning at 18 months of age, and we found the remains of 59% of the marked juveniles that disappeared between 19 and 23 months of age.

Table 1 Numbers of juvenile eastern grey kangaroos observed in three different cohorts from April 2010 to June 2012 at Wilsons Promontory National Park, Australia

	Cohort		
Age	2008/2009	2009/2010	2010/2011
10–13 months	4 (0)	51 (0)	29 (0)
14–17 months	35 (24)	52 (33)	11 (7)
18–21 months	41 (28)	37 (20)	0 (0)
Overall	44	55	30

Total sample size is 129 individuals. The numbers in parentheses indicate those whose mother was carrying a new pouch young

Natural mortality peaked at 10 months and again at 18 months of age, with 96% of the mortality occurring before 21 months (Fig. 1), so we chose to assess the sociability factors correlated with survival of 84 offspring from permanent pouch emergence (mean = 10.1 months) to 21 months. Thirteen daughters in the first cohort survived to 3 years of age in 2011/2012. Reproduction of these daughters was assessed as no pouch young (coded 0), produced a pouch young that died (coded 1) or carried a pouch young to permanent emergence (coded 2). Only one of 11 surviving daughters in the second and third cohorts produced a pouch young as 3-year-olds, and so reproduction in these two cohorts was not compared to previous sociability with their mothers.

Analyses

We considered two aspects of mother-offspring sociability. First, we measured the proportion of time offspring spent in foraging groups that included their mothers (group size ≥2), using the half-weight index (HWI) in SOCPROG (Whitehead 2008) for 4-month age periods from April 2010 to June 2012 (see King and Goldizen (2016)). We chose 4 months because it took several months to collect enough observations on individuals to calculate a meaningful HWI for each mother-young

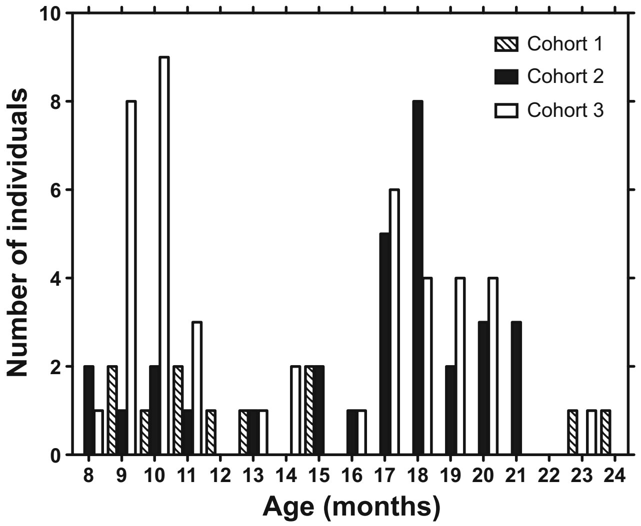

Fig. 1 Age at death or disappearance for 86 juvenile eastern grey kangaroos from three cohorts at Wilsons Promontory National Park, Australia, marked from August 2009 to December 2011 at approximately 8 months of age and followed to December 2012. Cohort 1 = 2008/2009, cohort 2 = 2009/2010 and cohort 3 = 2010/2011. Age at disappearance for 6 individuals in cohort 1 (*striped bars*) was estimated to the youngest of 2 months between the ages of 8 and 12 months, because kangaroos were only monitored every 2 months during this period

pair. We also estimated the proportion of time offspring spent foraging alone with their mothers (group size = 2) over the same time periods. The second sociability index is thus a subset of the first index. The HWI measures the likelihood of a juvenile being in a foraging group with the mother, while the second index reflects the tendency for a juvenile to follow its mother when she isolates herself. These two sociability values were calculated using a moving time window for 129 potentially suckling young-at-foot aged 10–13, 14–17 and 18–21 months, if we had at least 10 observations for both the mother and the young within these periods. We correlated HWIs with proportions of time young spent alone with the mother for each age class using Pearson correlations. We also correlated HWIs at 18–21 months with age last seen suckling for each sex, to determine whether those young-at-foot spending much time with their mothers at the oldest age class were likely still suckling. This was only possible for the first two cohorts, because observations ceased before all young-at-foot had been weaned in the third cohort. Since sample sizes were uneven across offspring ages (Table 1) and only 22 of the 57 recaptured 2-year-olds were observed at all 3 ages, we conducted analyses using mother-offspring sociability factors as predictors separately for each age class.

We first evaluated the effects of age and sex on the proportion of time young spent foraging with their mothers (HWIs) and alone with the mother using linear mixed-effects models, treating offspring identity nested within mother identity as random factors, and age class, sex, cohort and pouch status (whether or not a mother had a new suckling young in her pouch) as fixed effects. Survival of offspring from permanent pouch emergence to 21 months was analysed using generalised linear logistic regression, with offspring sex, cohort, offspring body condition as a pouch young, maternal body condition when carrying the offspring in the pouch, HWI at 10–13 months and proportion of time spent alone with the mother at 10–13 months as fixed factors. We did not examine the effect of mother-offspring sociability factors at later ages on survival because 66% of the mortality had occurred by 17 months of age (Fig. 1), and we wished to avoid a possible filtering effect that would bias HWIs to those of survivors. Factors affecting hind leg length, mass and body condition at 2 years were assessed using linear regression models and analysis of covariance (ANCOVA) and the same fixed factors as for survival, plus age at recapture, and HWIs and proportion of time spent alone with the mother at 14–17 or 18–21 months. Reproduction of 13 3-year-old daughters from the first cohort was compared with HWIs and proportion of time spent alone with the mother at 14–17 and 18–21 months using Spearman rank correlations, due to small sample sizes. Mixed-effects linear models were run using the lme function and restricted maximum likelihood (REML) in the nlme package of R version 3.3.2 (R Development Core Team 2016). The glm function with binomial error structure was used for the generalised linear logistic regression models, and the lm function was used for the linear regression models. We checked for collinearity between fixed factors using variance inflation factors (VIFs) from linear models (Quinn and Keough 2002). All VIFs were less than four. We sequentially removed the least significant parameter (based on its *P* value, threshold ≥0.05) from the model using stepwise backward selection (Crawley 2007). Initial models included interactions between offspring age and sex, between sex and the mother's pouch status and between cohort and maternal condition. We examined quartile-quartile plots of the residuals of chosen models to check for departure from normality (Crawley 2007). When sociability factors were not retained in the final model, we present the *t* and *P* values for those factors from the complete model including all fixed effects. To compare the strength of social and non-social factors, such as cohort and body condition, we calculated effect sizes as percentages.

Results

The proportion of time that young-at-foot spent in groups with their mother (HWI) was positively correlated with the proportion of time that they spent alone with her (Pearson correlation at 10–13 months: $r = 0.36$, $P = 0.001$, $n = 84$; at 14–17 months: $r = 0.64$, $P = 0.001$, $n = 90$; at 18–21 months: $r = 0.82$, $P = 0.001$, $n = 73$). Proportion of time spent with the mother (HWI) was lower at the oldest age class, in the first rather than subsequent cohorts and for sons if the mother was carrying a pouch young (Table 2, Fig. 2). Individual identity of the young-at-foot and mother each contributed 23% to the overall variance in HWIs. For sons, HWIs at 18–21 months of age were positively correlated with the age at which they were last seen suckling, whether their mother was carrying a pouch

Table 2 Coefficient estimates for the final linear mixed-effects model of the proportion of time eastern grey kangaroo offspring spent with their mothers (HWIs) while actively foraging at Wilsons Promontory National Park, Australia, $n = 246$

Coefficient	Estimate	Standard error	*t*	*P*
Intercept	0.615	0.037	16.63	0.001
Sex (female)	0.061	0.035	1.93	0.06
Age (14–17 vs. 10–13 months)	−0.008	0.030	−0.26	0.79
Age (18–21 vs. 10–13 months)	−0.290	0.033	−8.73	0.001
Cohort (2009/2010 vs. 2008/2009)	0.105	0.032	3.26	0.002
Cohort (2010/2011 vs. 2008/2009)	0.129	0.044	2.96	0.005
Pouch status (yes vs. no)	−0.155	0.036	−4.35	0.001
Sex (female) × pouch status (yes)	0.153	0.048	3.18	0.002

Mother-offspring pairs were observed between April 2010 and June 2012

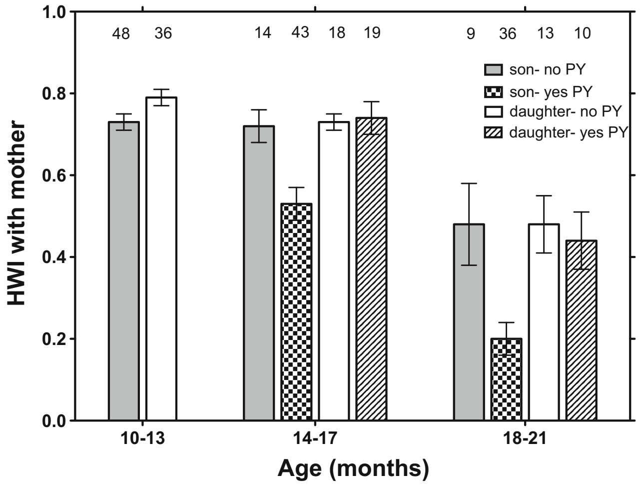

Fig. 2 Mean proportion of time (±1 SE) eastern grey kangaroo sons and daughters spent in foraging groups with their mother (HWIs) at 10–13, 14–17 and 18–21 months of age between April 2010 and June 2012 at Wilsons Promontory National Park, Australia. The *numbers above the bars* are sample sizes. *PY* new pouch young. For the youngest age class, all mothers were considered not to be carrying a new pouch young

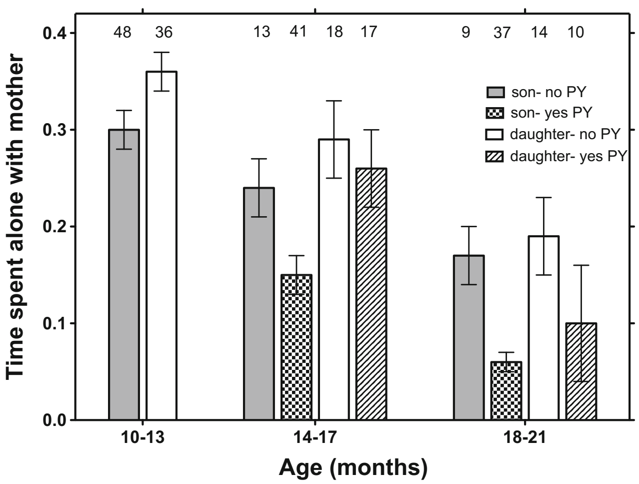

Fig. 3 Mean proportion of time (±1 SE) eastern grey kangaroo sons and daughters spent alone with their mother while actively foraging at 10–13, 14–17 and 18–21 months of age between April 2010 and June 2012 at Wilsons Promontory National Park, Australia. The *numbers above the bars* are sample sizes. *PY* new pouch young. For the youngest age class, all mothers were considered not to be carrying a new pouch young

young (Pearson correlation: $r = 0.43$, $P = 0.024$, $n = 27$) or not ($r = 0.76$, $P = 0.018$, $n = 9$). For daughters, however, these correlations were not significant (pouch young: $r = 0.24$, $P = 0.65$, $n = 6$; no pouch young: $r = 0.54$, $P = 0.06$, $n = 13$; Supplementary Fig. S4). Proportion of time spent alone with the mother decreased with offspring age and was lower for sons than daughters, lower in the first than subsequent cohorts and lower if the mother was carrying a pouch young (Table 3, Fig. 3). Individual identity of the young-at-foot and mother contributed 4 and 12% to the overall variance in proportion of time spent alone with the mother, respectively.

Measures of mother-young sociability when young were aged 10–13 ($n = 28$) and 14–17 months ($n = 47$) were not related to leg length of 2-year-old sub-adults. For proportion of time spent in groups with the mother (HWI), $t = -0.03$, $P = 0.98$ at 10–13 months and $t = 0.41$, $P = 0.68$ at 14–17 months; and for proportion of time spent alone with the mother, $t = 0.15$, $P = 0.88$ at 10–13 months and $t = -0.16$, $P = 0.87$ at 14–17 months. However, HWI at 18–21 months was positively correlated with leg length of 2-year-olds, which also varied by cohort, was larger for males and increased with age at recapture ($F_{4,\ 43} = 12.6$, $P = 0.001$, adjusted $R^2 = 0.50$, $n = 48$; Table 4). Mean leg length of 2-year-olds was 447 ± 3 mm, and an increase in HWI from 0.00 to 0.87 resulted in a 26-mm (6%) increase in leg length. Two-year-olds were 19 mm (4%) smaller in the second cohort than in the first.

Mass as a 2-year-old was independent of mother-offspring sociability at 10–13 ($n = 28$) and 14–17 months ($n = 47$) (proportion of time spent in groups with the mother (HWI), $t = 0.36$, $P = 0.73$ at 10–13 months and $t = 0.92$, $P = 0.36$ at 14–17 months; and for proportion of time spent alone with the

Table 3 Coefficient estimates for the final linear mixed-effects model of the proportion of time eastern grey kangaroo offspring spent alone with their mothers while actively foraging at Wilsons Promontory National Park, Australia, $n = 243$

Coefficient	Estimate	Standard error	*t*	*P*
Intercept	0.241	0.025	9.48	0.001
Sex (female)	0.064	0.019	3.46	0.001
Age (14–17 vs. 10–13 months)	−0.045	0.024	−1.89	0.06
Age (18–21 vs. 10–13 months)	−0.142	0.026	−5.50	0.001
Cohort (2009/2010 vs. 2008/2009)	0.051	0.020	2.49	0.017
Cohort (2010/2011 vs. 2008/2009)	0.078	0.031	2.53	0.016
Pouch status (yes vs. no)	−0.065	0.022	−2.88	0.005

Mother-offspring pairs were observed between April 2010 and June 2012

Table 4 Coefficient estimates for the final ANCOVA for length of the hind leg (mm) of 2-year-old eastern grey kangaroos first captured as large pouch young and recaptured approximately 18 months later at Wilsons Promontory National Park, Australia, between August 2009 and March 2013, $n = 48$

Coefficient	Estimate	Standard error	*t*	*P*
Intercept	288.7	42.5	6.80	0.001
Sex (female)	−28.5	5.5	−5.20	0.001
Age at recapture (in months)	6.5	1.6	4.05	0.001
Cohort (2009/2010 vs. 2008/2009)	−18.9	5.3	−3.57	0.001
HWI with mother at 18–21 months	30.5	10.5	2.90	0.006

HWI half-weight index

mother, $t = 0.29$, $P = 0.78$ at 10–13 months and $t = -0.29$, $P = 0.77$ at 14–17 months). HWI at 18–21 months, however, was positively correlated with 2-year-old mass, which varied by cohort, was higher for males and increased with age at recapture and maternal body condition ($F_{5,\ 42} = 12.61$, $P = 0.001$, adjusted $R^2 = 0.55$, $n = 48$; Table 5). Mean mass of 2-year-olds was 17.7 ± 0.4 kg, and an increase in HWI from 0.00 to 0.87 was associated with a 3.4-kg (19%) increase in mass. Two-year-olds were 3.2 kg (18%) lighter in the second cohort than in the first. An increase in maternal body condition from −0.059 to +0.090 was related to a 4.4-kg (25%) increase in mass of 2-year-olds. Maternal body condition was not correlated with the proportion of time offspring spent in groups with the mother (HWI) at any age (Pearson correlations: $r = -0.10$, $P = 0.36$, $n = 81$; $r = 0.02$, $P = 0.86$, $n = 86$; $r = 0.09$, $P = 0.47$, $n = 69$ for the three increasing age periods, respectively).

Body condition of 2-year-olds was not related to either measure of mother-young sociability at any age (proportion of time spent in groups with the mother (HWI), $t = 1.07$, $P = 0.30$ at 10–13 months, $t = 1.59$, $P = 0.12$ at 14–17 months and $t = 1.22$, $P = 0.23$ at 18–21 months; and for proportion of time spent alone with the mother, $t = 0.54$, $P = 0.60$ at 10–13 months, $t = -0.26$, $P = 0.80$ at 14–17 months and $t = -0.48$, $P = 0.64$ at 18–21 months). Two-year-old body condition was related to cohort, maternal body condition and body condition as a pouch young ($F_{6,\ 49} = 10.6$, $P = 0.001$, adjusted $R^2 = 0.51$, $n = 56$; Table 6). There was also an interaction between cohort and maternal condition, which was positively related to body condition of 2-year-olds in the first and third cohorts but not the second (Table 6). Body condition of 2-year-olds ranged between −0.061 and +0.077, decreasing by 0.008 (6% of that range) from cohort 1 to cohort 2 and by 0.026 (19% of that range) from cohort 1 to cohort 3. In comparison, as maternal body condition increased from −0.063 to +0.090, condition of 2-year-olds increased by 0.058 (42% of the range in 2-year-old condition). As pouch-young body condition increased from −0.077 to +0.116, condition as a 2-year-old increased by 0.061 (44% of the range in 2-year-old condition). Although body condition of pouch young was positively correlated with body condition of the mother at capture (Pearson correlation: $r = 0.36$, $P = 0.001$, $n = 122$), both factors contributed significantly and independently to the selected model of condition of 2-year-olds (Table 6). Mothers of the third cohort had much lower body condition than mothers of the first two cohorts (one-way ANOVA, $F_{2,\ 119} = 4.34$, $P = 0.015$), but condition of pouch young did not differ between cohorts (one-way ANOVA, $F_{2,\ 119} = 2.09$, $P = 0.13$; Fig. 4).

Table 5 Coefficient estimates for the final ANCOVA for mass (kg) of 2-year-old eastern grey kangaroos first captured as large pouch young and recaptured approximately 18 months later at Wilsons Promontory National Park, Australia, between August 2009 and March 2013, $n = 48$

Coefficient	Estimate	Standard error	*t*	*P*
Intercept	4.20	4.97	0.84	0.40
Sex (female)	−3.15	0.64	−4.94	0.001
Age at recapture (in months)	0.56	0.19	2.97	0.005
Cohort (2009/2010 vs. 2008/2009)	−3.17	0.62	−5.10	0.001
Body condition of the mother	29.32	8.62	3.40	0.001
HWI with mother at 18–21 months	3.89	1.22	3.18	0.003

HWI half-weight index

Table 6 Coefficient estimates for the final ANCOVA for body condition of 2-year-old eastern grey kangaroos first captured as large pouch young and recaptured approximately 18 months later at Wilsons Promontory National Park, Australia, between August 2009 and March 2013, $n = 56$

Coefficient	Estimate	Standard error	*t*	*P*
Intercept	−0.007	0.004	−1.75	0.08
Cohort (2009/2010 vs. 2008/2009)	−0.008	0.007	−1.08	0.28
Cohort (2010/2011 vs. 2008/2009)	−0.026	0.011	−2.41	0.020
Body condition as a pouch young	0.314	0.066	4.73	0.001
Body condition of the mother	0.377	0.105	3.59	0.001
Cohort 2009/2010 × body condition of the mother	−0.501	0.188	−2.66	0.010
Cohort 2010/2011 × body condition of the mother	−0.231	0.212	−1.09	0.28

The proportion of time offspring spent alone with mothers at 10–13 months ranged from 0 to 1, and this difference was associated with an increase in survival from permanent pouch emergence to 21 months of age from 15 to 97% ($z = 2.31$, $P = 0.021$, $n = 74$; Table 7, Fig. 5). Survival was also affected

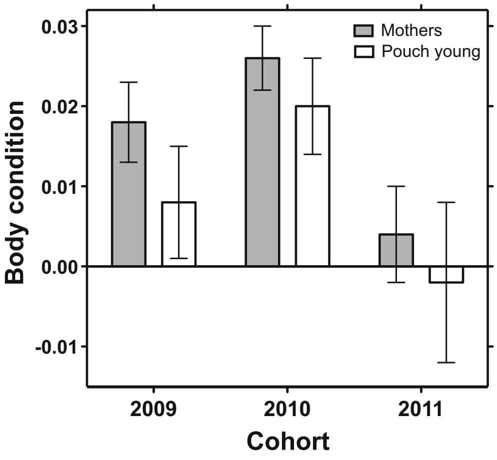

Fig. 4 Body condition (±1 SE) of female eastern grey kangaroos and their large pouch young captured at Wilsons Promontory National Park, Australia, 2009–2011. Cohorts were 2008/*2009* ($n = 42$ pairs), 2009/*2010* ($n = 48$ pairs) and 2010/*2011* ($n = 32$ pairs)

Table 7 Coefficient estimates for the final generalised logistic regression for survival from permanent pouch emergence to 21 months of age for eastern grey kangaroos first captured as large pouch young at Wilsons Promontory National Park, Australia, between August 2009 and December 2011, *n* = 74

Coefficient	Estimate	Standard error	*z*	*P*
Intercept	−1.90	0.76	−2.50	0.012
Body condition as a pouch young	12.84	5.64	2.28	0.023
Proportion of time spent alone with mother at 10–13 months	5.14	2.23	2.31	0.021

by body condition as a large pouch young ($z = 2.27$, $P = 0.023$, $n = 74$; Table 7). As pouch-young body condition increased from −0.125 to +0.139, probability of survival increased from 14 to 82%. Pouch-young body condition was not related to proportion of time spent alone with the mother at 10–13 months (Pearson correlation; $r = 0.02$, $P = 0.88$, $n = 74$). Mean survival for offspring with mother-offspring sociability measures was 46%, with no distinguishable cohort effect. There were, however, very few behavioural observations at 10–13 months for cohort 1 (Table 1), for which survival from permanent pouch emergence to 21 months was high (75%, $n = 4$; see also Fig. 1). Survival was 59% for cohort 2 ($n = 51$) and 21% for cohort 3 ($n = 29$). In a larger dataset, cohort had a measurable effect on survival when all offspring with known pouch-young body condition were examined (cohort 2 vs. cohort 1: $z = -3.26$, $P = 0.001$; cohort 3 vs. cohort 1: $z = -5.30$, $P = 0.001$, $n = 122$).

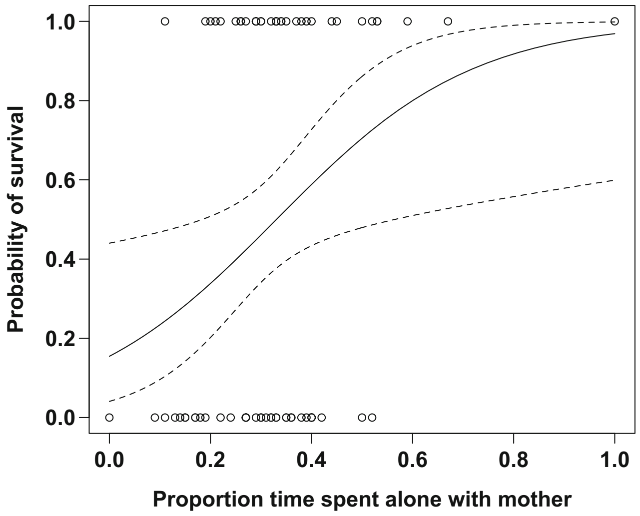

Fig. 5 Generalised linear logistic regression of proportion of time spent alone with the mother at 10–13 months on survival to 21 months for 74 eastern grey kangaroos first captured at Wilsons Promontory National Park, Australia, between August 2009 and December 2011. The *solid line* represents predicted values, and the *dotted lines* are 95% confidence intervals

Reproduction of 3-year-old daughters was not correlated with mother-offspring sociability measures (Spearman rank correlations at 14–17 months, $n = 12$, HWI: $P = 0.27$, $r_s = -0.35$; proportion of time spent alone with the mother: $P = 0.22$, $r_s = -0.39$; at 18–21 months, $n = 13$, HWI: $P = 0.30$, $r_s = 0.31$; proportion of time spent alone with the mother: $P = 0.16$, $r_s = 0.41$), despite considerable variation in HWIs (0–1.00 and 0–0.72, respectively) and proportion of time spent alone with the mother (0–0.44 and 0–0.27, respectively).

Discussion

Mother-offspring sociability was associated with differences in size, mass and survival of juveniles. Proportion of time spent with the mother at 18–21 months was positively correlated with limb length and mass of 2-year-old sub-adults. Proportion of time spent alone with the mother at 10–13 months was positively correlated with survival to weaning. These two sociability indices, however, measure different facets of the mother-offspring relationship. Because suckling juveniles follow their mothers (King and Goldizen 2016), being in the same foraging group as the mother reflects the juvenile's decision to stay with her as she moves among groups in this fission-fusion society. In contrast, being alone with the mother is a reflection of the mother's decision to leave or join groups, with the offspring following. Furthermore, proportion of time spent alone with the mother was closely correlated with suckling: both sons and daughters of 18–21 months of age whose mother had a new pouch young (and therefore must have been weaned) were less likely to be found alone with their mother than those whose mother did not have a new pouch young (Fig. 3).

We have previously shown that daughters had higher HWIs with their mothers at 14–17 and 18–21 months than did sons (King and Goldizen 2016). Here, we demonstrate that daughters whose mother had a new pouch young, thus likely to be weaned, maintained the same level of association with their mother as daughters that were likely still suckling because their mother did not have a new pouch young (Fig. 2). On the other hand, sons that were likely weaned spent proportionally much less time with their mothers than sons that were likely still suckling. Furthermore, daughters spent proportionally more time alone with their mother than did sons between the ages of 10 and 21 months. The closer sociability between mothers and their young daughters compared to sons could result from differential activity patterns of the two sexes (King and Goldizen 2016). However, the HWIs of sons with their mothers at 18–21 months and the age when sons were last seen suckling were correlated. These findings suggest that sons may benefit nutritionally more than daughters at this age, but that daughters may benefit from their stronger associations with their mothers in some as yet unknown ways.

Sons are more active than daughters in giraffes *Giraffa camelopardalis* (Pratt and Anderson 1979) and yellow baboons *Papio cynocephalus* (Nguyen et al. 2012), and the closeness of mother-offspring associations differs accordingly in these species.

We found that size of the young was related to several non-social factors. There were large differences in size (4%), mass (18%) and body condition (19%) of 2-year-olds depending on cohort. Body condition and mass of 2-year-olds were also related to their condition as pouch young and the body condition of their mother. These condition measures probably reflect nutritional maternal effects on growth of young (Mousseau and Fox 1998; Maestripieri 2009). Body condition of mothers carrying a large pouch young is likely affected by availability of resources and reflects their potential to provide maternal care from then until weaning (Lindström 1999). Transfer of resources during lactation is under greater maternal control in marsupials than in eutherians, in which there is some feedback from suckling demand (Krockenberger 2006). In kangaroos, lactation costs appear to peak when females are carrying a large pouch young (Cripps et al. 2011), before young emerge from the pouch and begin to feed on forage while still suckling. In contrast to maternal condition, body condition of large pouch young likely reflects maternal milk provisioning up to that point.

Survival of kangaroo offspring from permanent pouch emergence to 21 months was weakly influenced by body condition as a pouch young. Stochastic factors such as predation, inclement weather or poor forage availability after emergence probably have a much stronger effect on survival. In 'favourable' years for kangaroos, such as that experienced by cohort 1 where rainfall and forage availability were high in the first 2 years of life, 2-year-old size, mass and body condition were high and almost all juveniles survived. In years of relatively low forage availability, such as those experienced by cohorts 2 and 3, 2-year-old size, mass and body condition were reduced and body condition as a pouch young (indicating maternal care) was related to survival. Therefore, maternal characteristics may have a stronger effect on offspring survival when environmental resources are scarce. Similar results have been found for allied rock wallabies *Petrogale assimilis*, where maternal quality affected offspring survival from pouch emergence to weaning when conditions were poor (Delean et al. 2009). The relationship between maternal condition, lactation and offspring growth is complex, however. Under abundant resources, one expects maximum growth, early weaning and high offspring survival, while poor resources lead to slow growth and either early weaning and low survival or late weaning and high survival (Lee et al. 1991).

Social factors had a weaker effect on size and mass of young, compared to cohort and nutritional maternal effects. Indeed, 2-year-old mass was much more strongly influenced by maternal body condition than by proportion of time spent with the mother. Kangaroo mothers do not have a protective parenting style; offspring maintain contact with the mother by following her (King and Goldizen 2016). Proportion of time spent with the mother was strongly correlated with age last seen suckling for sons, so sons that spent proportionally more time with their mothers at 18–21 months of age were still suckling as well as feeding on forage. At this age, the proportion of time spent in foraging groups with the mother was correlated with leg length and mass as a 2-year-old, so the association index likely reflects nutritional maternal care, at least for sons. Mothers and their dependent offspring do not cooperate to defend resources since forage is uniformly distributed and large macropods are not territorial (Jarman and Coulson 1989), although there is some evidence for close-range interference competition (Jaremovic and Croft 1991a; Maguire et al. 2006). The effect of proportion of time spent with the mother on subsequent size and mass thus likely reflects direct care through nursing for sons. However, because weaned daughters spent proportionally as much time as unweaned daughters with their mothers at 18–21 months, the positive relationship between HWIs and size and mass could reflect non-nutritional maternal care of daughters. Yet, interaction rates between kangaroo mothers and offspring, including allogrooming, nosing and play, are low and do not differ between the sexes (King and Goldizen 2016), so it is unclear how non-nutritional mother-offspring associations could affect offspring growth.

Mothers with young-at-foot tended to isolate themselves from other adult females, and this behaviour was positively correlated with offspring survival. Female macropods may isolate themselves with their dependent offspring for several reasons. Croft (1981) suggested that the reduced locomotory ability of young-at-foot may prevent mothers from maintaining associations with other adults. Croft (1981) also proposed that mothers isolate themselves to avoid mother-young separation when a sudden disturbance causes flight (Southwell 1984; Jarman 1994), a suggestion that appeared to be upheld in this population. Separation from the mother sometimes had lethal effects for pouch young at the in-and-out stage (King et al. 2015a) and could also lead to mortality of young-at-foot. Alternatively, mothers may isolate themselves to reduce the harassment of young-at-foot by other adult females, which takes the form of growling and aggressive displacements, occurring most often when young are foraging in groups without their mother (King and Goldizen 2016). A similar situation occurs in white-tailed deer *Odocoileus virginianus* where lactating females isolate themselves and are particularly aggressive towards unrelated yearling deer (Ozoga et al. 1982). Also, isolation of the mother-young pair would likely reduce localised interference competition for forage. Kangaroo mothers spent only about one third of their foraging time isolated with young-at-foot (Fig. 4), but isolation may have been difficult in this high-density population. In addition, according to our definition, isolated meant being at least 10 m away from other kangaroos, thus anti-predator advantages could still have been obtained if other kangaroos were within sight, while isolation could both improve forage acquisition (Blumstein and Daniel 2003) and reduce harassment of young. Kangaroos appear to form groups due to predator pressure, because vigilance rates of mothers decrease with group size (King and Goldizen 2016) and fox predation can reduce juvenile survival (Banks et al. 2000). It is possible that foxes took advantage of the juveniles' poor body condition, since fox sightings were frequent (King and Goldizen 2016) and body condition appeared relatively low in the year with poorest juvenile survival. These two factors could thus affect offspring survival synergistically. The quality of the mother-offspring relationship has been found to affect offspring survival and subsequent behaviour as an adult in several species of primates (Fairbanks 1996) and rodents (Mateo 2009) and in African elephants *Loxodonta africana* (Lee and Moss 2011).

Proportion of time spent with the mother as a young-at-foot was not correlated with reproduction of 3-year-old daughters, however sample size was small. Furthermore, these data came from a cohort with very high survival and growth, so any social effects may have been masked by high resource availability. We found cohort effects in all measures of growth and survival. Cohort also affected reproduction since only 1 of 11 3-year-old daughters (9%) from the second and third cohorts reproduced, compared to 6 of 13 daughters (46%) in the first cohort. Cohort effects on offspring growth and survival have long been recognised in mammals, especially ungulates (Lindström 1999). Marsupial reproduction appears to be adapted to unpredictable environmental conditions (Tyndale-Biscoe and Renfree 1987), so one would expect strong cohort effects.

This study is among very few to have assembled the data required to examine the relationship between the mother-offspring sociability and the size, mass, body condition, survival and reproduction of offspring in a non-primate mammal. Although improved juvenile growth appears to result from maternal care through prolonged nursing rather than behavioural interactions, such as maternal defense and allogrooming, the mechanism whereby proportion of time spent alone with the mother improves juvenile survival is unclear. Isolation of the mother with her young-at-foot is common to all large macropods (Jarman and Coulson 1989), and adaptive benefits of this behaviour should therefore occur in other macropod species.

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Compliance with ethical standards

Ethical statement This study was funded by the Natural Sciences and Engineering Council of Canada and the Holsworth Wildlife Research Endowment. Captures were undertaken with ethics approval from the University of Melbourne (no. 0810628.1 and no. 0911512.1) and research permits from the Victorian Department of Sustainability and Environment (no. 1004582 and no. 1005558). Following captures, 9 of 241 pouch young were abandoned (4%); however, non-captured females also abandoned young occasionally. There was 1 death in 132 captures of sub-adults (1%; an apparent fox predation during recovery) and 1 death in 369 captures of adult females (0.3%). There were no observed capture-related injuries in the 5 years of study. Observations were conducted with animal ethics approval from the University of Queensland (no. SIB/206/09/(NF)). All applicable international, national and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted. This article does not contain any studies with human participants by any of the authors.

Conflict of interest The authors declare that they have no conflict of interest.

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