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BEHAVIORAL ECOLOGY –ORIGINAL RESEARCH

Tall young females get ahead: size-specific fecundity in wild kangaroos suggests a steep trade-off with growth

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Abstract When resources are limited, organisms face allocation conflicts. Indeterminate growth creates a persistent conflict with reproduction, as growth may enhance future reproduction, but diverts resources from current reproduction. Little is known about allocation trade-offs in mammals with indeterminate growth. We studied growth and reproduction in adult female eastern grey kangaroos (*Macropus giganteus*), an iteroparous mammal with indeterminate growth. Allocation trajectories varied with age and size: for 4-year-old females, fecundity increased from 30 to 82% from shortest to average-sized individuals. Older females had high fecundity regardless of size. The smallest females grew 30% more annually than average-sized females, but females that reached average size at an older age had lower growth rates. Environmental conditions affected allocation to size and reproduction. Rainy springs increased fecundity from 61 to 84% for females that had previously reproduced, but rainy winters reduced leg growth. Females in better relative condition grew 40% more than average, whereas most young of females below average relative condition failed to survive to 10 months of age. These results highlight an age-specific trade-off between growth and reproduction.

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Tall young females benefit from a smaller trade-off between somatic growth and early fecundity than shorter females of the same age, but older females appear to favor reproduction over growth regardless of size. Our study highlights how individual heterogeneity determines trade-offs between life-history components. We speculate that cohort effects affect age-specific reproductive success in this long-lived mammal.

Keywords Allocation · Indeterminate growth · Life history · *Macropus giganteus* · Reproductive success

Introduction

Fitness is maximized through optimal allocation to life-history components, but limited resources force allocation trade-offs between reproduction, growth, and survival (Stearns 1992; Roff 2002). As allocation decisions occur over the lifetime, fitness components may have different age-related trajectories. Large size often confers a fitness advantage for females, through larger litter size (Olsson and Shine 1996; Lardner and Loman 2003) and litter mass (Dobson and Michener 1995; Sparkman et al. 2007), higher reproductive success (Choudhury et al. 1996; Sand 1996; Festa-Bianchet et al. 1998; Pomeroy et al. 1999), greater maternal care (Landete-Castillejos et al. 2005), higher offspring survival (Beauplet and Guinet 2007; Hamel et al. 2009a), and increased longevity (Gaillard et al. 2000b). Therefore, relatively large females should enjoy increased reproductive success (Stearns and Koella 1986). Allocation to growth, however, diverts resources from reproduction (Lunn et al. 1994; Dmitriew 2011) and allocation to reproduction impedes the achievement of a large body size (Green and Rothstein 1991; Helle 2008). Allocation to one life-history component may also reduce future capacity to

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allocate. For example, rapid growth may generate long-term costs through oxidative stress and premature cellular aging (Metcalfe and Monaghan 2001; Alonso-Alvarez et al. 2007). Slow or suboptimal growth may, however, delay age at maturity (Allal et al. 2004; Rughetti and Festa-Bianchet 2011), reduce long-term reproductive success (Hayward et al. 2014), or require costly compensatory trajectories (Johnsson and Bohlin 2006; Marcil-Ferland et al. 2013). Delayed maturity may be advantageous if attaining a larger size before the first reproduction decreases offspring mortality and leads to higher lifetime reproductive success compared to maturing earlier and smaller (Stearns and Koella 1986; Lunn et al. 1994; Sand 1996). Growth, however, like reproduction, may be limited by low resource availability (Madsen and Shine 2000; Toïgo et al. 2002; Chaloupka et al. 2004), population density (Pettorelli et al. 2002), or environmental conditions such as temperature (Blanckenhorn 1999; Otterlei et al. 1999) and precipitation (Perez-Barberia et al. 1996; Servanty et al. 2009).

Most long-lived mammals stop growing shortly after sexual maturity (Karkach 2006); therefore, trade-offs between growth and reproduction only affect young individuals. Hence, the growth cost on reproduction should be higher for young mammals (Gaillard et al. 2000a; Langvatn et al. 2004) and allocation is expected to shift from growth to reproduction as animal's age (Beauplet et al. 2006; Simard et al. 2014). If growth is indeterminate, however, individuals may face persistent allocation trade-offs between growth and reproduction (Heino and Kaitala 1999). In addition, because age and size are correlated in organisms with indeterminate growth, the positive association between age and reproductive success may simply be a consequence of a size advantage (Olsson and Shine 1996), since larger individuals are usually older. If reproductive performance increases with size, reproductive success should increase with age (Beauplet et al. 2006; Sparkman et al. 2007). Furthermore, larger females may allocate more resources to progeny with higher fitness returns (Trivers and Willard 1973), and in polygynous species, this may result in size-specific differential sex allocation. Although lower male offspring survival is expected in most polygynous species (Clutton-Brock et al. 1985), larger female bridled nail-tail wallabies (*Onychogalea fraenata*) (Fisher 1999), tammar wallabies (*Macropus eugenii*), and parma wallabies (*M. parma*) (Sunnucks and Taylor 1997) produce more sons than smaller females. Female tammar wallabies that produced sons had greater weaning success in a cross-fostering experiment (Robert et al. 2010), suggesting that offspring sex may be correlated with ability to provide maternal care (Robert et al. 2010). Despite these important implications for the evolution of reproductive strategies and for population dynamics, no studies have examined the allocation decisions between growth and reproduction, and their distinct trajectories in iteroparous long-lived mammals with

indeterminate growth, and little is known about the variability in age-specific growth in these species.

We examined annual reproductive success and growth in wild female eastern grey kangaroos (*Macropus giganteus*) to understand lifetime trajectories of allocation to growth and reproduction. Kangaroos are large iteroparous herbivores, ecologically similar to ungulates; sexually dimorphic and polygynous (Fisher et al. 2002). They are marsupials, with a very short gestation and a long lactation (Tyndale-Biscoe and Janssens 1988), and can reproduce year round (Poole 1975; King and Goldizen 2016). Young remain in the pouch for about 10 months and are weaned at 16–23 months (Tyndale-Biscoe and Janssens 1988; King and Goldizen 2016). Kangaroos show indeterminate skeletal growth over their lifetime (Karkach 2006), making them ideal subjects to tease apart the effects of size, age, and environmental factors on allocation decisions between growth and reproduction. Trade-offs between growth and reproduction have already been explored in our study population (Gélin et al. 2016b), but our research now benefits from a sample of known-aged females that lived through a wide range of environmental conditions.

We first sought to quantify the relationship between reproductive success and skeletal size at different ages, to understand the relative importance of body size for reproduction in the context of indeterminate growth. Because kangaroos are monotocous, we expected an asymptotic relationship between size and reproductive success, and hypothesized that taller females would allocate more energy to reproduction than to growth. We consequently predicted that taller females would have higher fecundity and offspring survival than shorter females. In addition, we expected allocation decisions to change with age, so that for a given size, younger females would be less likely to reproduce than older females, which we expected to allocate more resources to reproduction (Sand 1996; Simard et al. 2014). Therefore, we predicted that the positive effect of size on reproductive success would decrease with female age (Langvatn et al. 2004). We also tested for sex-differential allocation and predicted that female size should affect survival of sons but not of daughters, expecting that ability to provide care would be correlated with size (Clutton-Brock et al. 1985; Robert et al. 2010). Finally, we expected that while maternal body reserves and favorable environmental conditions would increase reproductive success, the previous reproductive effort should lower success, because like many long-lived organisms, female kangaroos have a conservative reproductive strategy (Gélin et al. 2015) and may transfer the costs of reproduction to subsequent offspring (Martin and Festa-Bianchet 2010). We define reproductive effort as the proportion of energy allocated to reproduction (Tuomi et al. 1983). Body condition reflects energy stores, and changes in condition provide clues to both the previous reproductive

effort and ability to allocate to future growth and reproduction (Peig and Green 2009).

Our second aim was to investigate how adult skeletal growth varied with size and age, through annual changes in size between consecutive captures. We hypothesized that selection for continued growth would reduce allocation to reproduction, especially for small and young females. We expected indeterminate growth to act as a cost for reproduction and be an underlying mechanism for a reproductive size advantage. We quantified the age- and size-specific growth trajectories of female kangaroos, after accounting for the effects of body condition, reproductive effort, and environmental variables on annual growth. We expected females to grow more if they were in better relative body condition and predicted that environmental conditions during adult life would affect skeletal growth. We then predicted that the effect of size on annual growth would decrease with age. Females may allocate less to growth at any given size following maturity, as typically seen in organisms with indeterminate growth (Heino and Kaitala 1999; Folkvord et al. 2014), which then produces distinct size-at-age growth trajectories.

Methods

Study population and data collection

We have monitored a kangaroo population since 2008 at Wilsons Promontory National Park, Victoria, Australia (38°57′S, 146°17′E). Most marked individuals are recaptured annually (Gélin et al. 2013) in a 110-ha grassland surrounding an emergency landing strip (Davis et al. 2008), where vegetation consists primarily of grasses, herbs, sedges, and ferns (Davis et al. 2010). Between 2008 and 2016, annual rainfall ranged from 518 to 1018 mm, with 33% occurring from June to August on average. The lowest monthly mean maximum temperatures (13.4 °C) were in July [http://www.bom.gov.au/climate/data; Shallow Inlet (#085163), 38.79°S, 146.18°E; Corner Inlet (#085301), 38.63°S, 146.81°E].

To obtain reproductive and morphometric data, adult females were immobilized by Zoletil® injected with a pole syringe (King et al. 2011). They were then fitted with a unique combination of colored flexible collar and Allflex ear tags (Allflex Australia Pty Ltd., Capalaba, Australia) (Gélin et al. 2013). Females were weighed to the closest 0.25 kg with a spring scale, and their forearm, foot, and hind leg (henceforth referred to as leg) lengths measured to the nearest 1 mm using a retractable measuring tape. Leg length was used as a proxy for skeletal size. Adult females aged 3–20 years ($N = 327$) had an average ± SD leg length of 520 ± 22 mm (Fig. 1, range 456–569 mm)
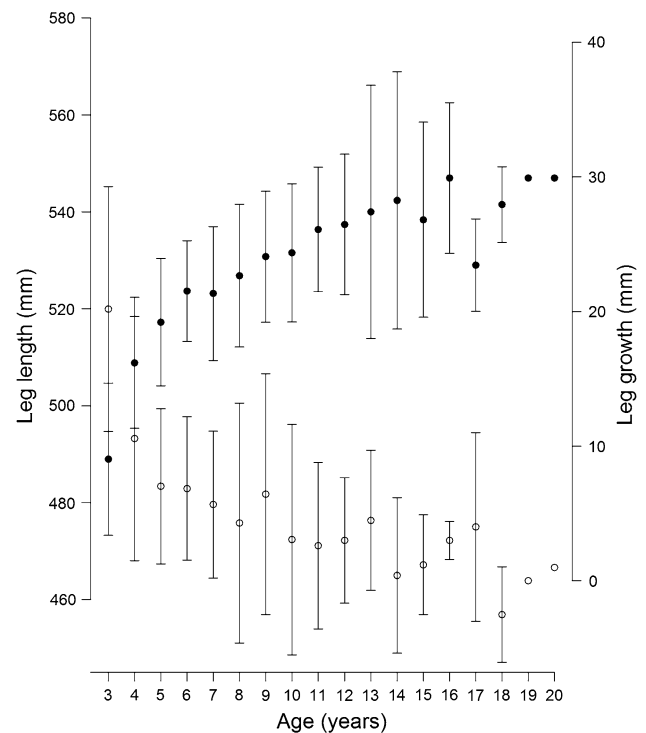

Fig. 1 Age-specific leg length and annual growth (mm) with standard deviations for eastern grey kangaroo females, Wilsons Promontory National Park, Victoria, Australia, from 2008 to 2016. Dots represent leg length and open circles annual skeletal growth

and weighed 26.25 ± 3.25 kg (range 18–34 kg). Most measurements (84%) were done by the same observer, from late July to early December each year. In this population, more than 75% of pouch young are born between November and February (King and Goldizen 2016), such that permanent emergence from the pouch (PEP) (Russell 1989) generally occurs in the Austral spring. We determined fecundity at capture by visual inspection of teats and checked for the presence of a pouch young. We considered that a female had not attempted to reproduce that year if her teats did not show signs of lactation. A female was considered fecund if she had an elongated or regressing teat, whether the pouch held a young at capture or not. Because females were monitored over multiple years, we were also able to detect cases where the female was still nursing a young produced the previous year. Observation of teats at capture revealed if the female had produced a young in the current year. Fecundity was scored as a binomial trait (0 = no lactation, 1 = lactation). For the < 10% of females not recaptured in a year, we considered that they had reproduced if a distended pouch was noted during field observations. At capture, pouch young were marked with colored Leader ear tags (Leader Products Pty Ltd., Craigieburn, Australia) if they weighed at least 0.9 kg. Following capture, mother–young pairs were monitored

almost daily from August to December, in March, and then located again at the end of the following winter (August). Date of PEP was recorded for all marked young surviving to that stage. Offspring survival was also scored as a binomial trait (0 = died before PEP, 1 = successful PEP).

Other maternal characteristics documented included age and relative body condition. Age was known if the female had first been captured in the pouch or weighing less than 15 kg (aged l year). For females first caught as adults that were found dead, age at death was estimated by the Molar Index, based on the anterior progression of the upper molars with age. The 95% confidence interval of this index has a range of 16% of the estimated age (Kirkpatrick 1965). Age was then retroactively calculated to first capture (see Fig. S1 in ESM for sample distribution). Maternal relative body condition was the ratio of body mass-to-mass predicted by an ordinary least-squares regression of log mass on log leg length (Le Cren 1951). This index ranged 0.93–1.07 (SD = 0.02). The residuals of this regression were normally (Shapiro–Wilk normality test: $W = 0.997$, $P = 0.13$; ESM Appendix S2, Fig. S2) and randomly distributed (ESM Appendix S2, Fig. S3). The body condition estimates were not correlated to leg length ($r_p = 0.01$, $df = 246$, $P = 0.82$). The condition index was, therefore, independent of skeletal size and appropriate for organisms with indeterminate growth. We calculated the relative body condition index using leg length, because it best represented skeletal size. In a principal component analysis including leg, forearm, and foot measurements, leg length had a component loading of 51.8% on the first principal component, which explained 94.9% of variability in female size (see ESM Appendix S3 for details). To represent inter-annual variability in environmental conditions during a reproductive attempt or a growth interval throughout the study (2008–2016), we used precipitation data from the closest Australian Bureau of Meteorology's station at Shallow Inlet station, 17.5 km from the study area. Rainfall data provided a density-independent environmental factor linked to primary productivity and known to influence population dynamics of large herbivores

through the body condition of females (Gaillard et al. 2000a; Forchhammer et al. 2001).

Statistical analyses

To test the hypothesis of a size advantage in female kangaroos, we studied their annual probability of fecundity as well as the probability of a juvenile surviving to PEP (about 10 months). A total of 309 captures (or female-years) of females aged 3–20 years were used to analyze fecundity (ESM; Fig. S1). To investigate the probability of PEP, we used a subset of 212 captures of 88 lactating females. The explanatory variables considered for both reproductive stages were four maternal traits: age, leg length, relative body condition, and reproductive status the previous year, to account for possible costs of the previous reproduction on the current attempt (Pomeroy et al. 1999; Hamel et al. 2009a). The previous reproductive status was recorded as whether or not a female carried a pouch young the previous year until it was large enough to tag, about 7–8 months. Rainfall during the season prior to the reproductive stage considered was included in each model set (Table 1), to account for environmental conditions. We examined the age-size allocation trajectory by testing for an interaction of size and age. Because the effect of the previous reproductive status on current reproduction may vary with leg length, age, and total rainfall, we tested for those interactions, as well. We considered the possibility of sex-differential survival and compared annual juvenile sex ratio of the entire marked population with that of known-aged females to check for a possible bias. Twenty generalized linear-mixed logistic regressions with a logit link function were compared, investigating the two reproductive stages through two model sets (ESM Appendix S4; Tables S1–S2).

We then examined how growth may involve a reproductive cost. Our 327 captures of females aged 3–20 years provided 243 growth intervals from 79 individuals. The pattern of indeterminate growth was investigated through the difference in leg length (mm) between consecutive annual captures, and we adjusted annual growth to a 365-day interval for all females. Average inter-capture interval was

Table 1 Seasonal rainfall variables that were compared to two stages of eastern grey kangaroo reproduction at Wilsons Promontory National Park, Victoria, Australia

Stage of reproduction (sample size in female-years)	Precipitation data	Period	Mean ± SD	Min–Max
Evidence of lactation ($n = 309$)	Total rainfall (mm) during spring prior to breeding season	September–November (t)	224.5 ± 65.5	145–322
Permanent emergence from the pouch (PEP) (10 months, $n = 212$)	Total rainfall (mm) during winter of pouch life	June–August ($t + 1$)	277.1 ± 70.5	144–400

Rainfall data were available from the Australian Bureau of Meteorology repository, at the Shallow Inlet station. 't' refers to the year

356 days (SD = 59 days) and 269 of 327 (82%) captures occurred in late winter or early spring (mean = 24 August, SD = 36 days). A model set of 20 linear-mixed candidate models with a Gaussian link function was formulated to explain annual leg growth, with female age, leg length, relative body condition, and reproductive status (large pouch young or not) at the first capture of each growth interval as explanatory variables (ESM Appendix S5; Table S3). Winter rainfall (June to August) prior to the growth interval was included to represent climatic conditions just before the measured growth increment. Age-specific changes in the allocation trajectory were tested using an interaction between age and leg length. We also tested if winter rainfall and age modulated the effect of current reproductive status on annual growth.

In all models, female identity was included as a random factor to account for repeated measurements of the same individuals. The significance of year of capture as a random factor was tested using a log-likelihood ratio test. We also tested for potential observer effects by considering observer identity as a random factor. We evaluated the relative support of multiple biological hypotheses that could explain skeletal growth, fecundity, and PEP (Burnham and Anderson 2002) with three sets of candidate models, using the second-order Akaike's information criterion (AIC_c) (Burnham and Anderson 2002). For each hypothesis, the relative strength of evidence of each candidate model was established and we ranked the models by Δi values relative to the model with the lowest AIC_c. Akaike weights (w_i) and evidence ratios were computed to indicate the probability that a model was the best among those compared and the ratio of w_i of the best model to the w_i of the next-best model, respectively (Burnham and Anderson 2002). Models with $w_i \geq 0.05$ were considered to have support. When more than one model was within a Δi value of two or if no model had a $w_i > 0.9$, model selection uncertainty existed. Under these circumstances, we calculated model-averaged parameter estimates (Burnham and Anderson 2002) to obtain average effect sizes for variables of interest. Model-averaged estimates for variables that best described leg growth and reproductive success had 95% unconditional confidence intervals that did not overlap zero (Burnham et al. 2011).

All model-averaged parameters were obtained from regressions fit to rescaled explanatory variables, accounting for untransformed binary operators ($\mu = 0$, SD = 0.5) (Gelman 2008). The Pearson's product-moment correlation coefficient r_p was calculated between age, body mass, leg length, and relative body condition to assess the strength of association between these variables. In full models including all explanatory variables, all generalized variance inflation factors (GVIF) were less than 2, the highest being 1.82 (age). We used R version 3.2.5 and the *lmer* and *glmer* functions from the *lme4* package (Bates et al. 2015). To obtain AIC_c

values, perform model averaging and estimate model parameters, we used the *aictab* and *modavg* functions in the *AICcmodavg* package (Burnham et al. 2011).

Results

Maternal relative body condition index varied among years ($F = 10.24$, $df = 7$, $P < 0.001$) and was not correlated with age ($r_p = 0.06$, $df = 246$, $P = 0.17$). Although leg length was correlated with both age ($r_p = 0.66$, $df = 246$, $P < 0.001$) and mass ($r_p = 0.78$, $df = 246$, $P < 0.001$), the relative body condition index was independent of leg length ($r_p = 0.02$, $df = 246$, $P = 0.80$).

In all four model selections, no single candidate model had clear support, because at least another model was within two AIC_c units of the best model (Tables 2, 3). Therefore, multi-model inference was performed to estimate effect sizes.

Size-specific fecundity and offspring survival

Rainfall prior to the reproductive stage varied substantially among years (Table 1). We included year as a random factor in models for PEP, as it significantly improved the global model fit, but year did not improve the fit for the fecundity models (log-likelihood ratio tests; Fecundity: $\chi^2 = 0.08$, $P = 0.79$; PEP: $\chi^2 = 26.34$, $P < 0.001$).

There was no significant yearly variability in the proportion of females that attempted to reproduce (Fig. 2a, ANOVA: $F = 1.32$, $df = 8$, $P = 0.26$), but there were differences for successful PEP (Fig. 2b, ANOVA: $F = 411$, $df = 1$, $P < 0.001$). Fecundity increased with leg length, although this effect was much greater for younger females (Table 4, Fig. 3a). Maternal relative body condition increased fecundity (Table 4, Fig. 3b). Furthermore, the effect of rainfall on fecundity was affected by the previous reproductive status (Table 4), since spring precipitation increased fecundity only for females that had produced a large pouch young the previous year (Fig. 3c).

Sex of the pouch young was known for 62% (131/212) of reproductive attempts of known-aged females, compared to 76% (471/616) of all marked females. The proportion of sons did not differ between the two subsets (all females: 252/471 (53.5%), known-age females: 65/131 (49.6%); $\chi^2 = 0.18$, $df = 1$, $P = 0.67$). Model selection and model averaging for known-aged females with known-sex pouch young suggested no effect of sex on survival to PEP (model-averaged β, 0.6; 95% CI – 0.3 to 1.5) and neither leg length (model-averaged β, 1.2; 95% CI – 0.7 to 3.0) nor maternal body condition (model-averaged β, 2.6; 95% CI – 0.3 to 4.9) modulated this effect. Therefore, to increase sample size, our final model sets did not include sex of the young. Maternal

Table 2 Model selection for the effects of leg length, age, relative body condition, previous reproductive status, and seasonal rainfall on the probability of fecundity for female kangaroos and survival of their young to permanent emergence from the pouch

Model[a]	K	AIC$_c$	Δi	w$_i$	Evidence ratio
Fecundity for all females ($n = 309$)					
Age + Size + pRS + Cond + Rain + Age × Size + pRS × Rain +1|ID	9	329.21	0.00	0.56	2.5
Age + Size + pRS + Cond + Rain + Age × Size +1|ID	8	331.12	1.91	0.22	6.2
Age + Size + pRS + Cond + Rain + Age × Size + Age × pRS +1|ID	9	332.85	3.64	0.09	7.0
Age + Size + pRS + Cond + Rain + Age × Size + Size × pRS +1|ID	9	333.19	3.98	0.08	
Permanent pouch emergence, only females that produced a young ($n = 212$)					
Cond + 1| ID + 1|Year	4	195.39	0.00	0.60	2.2
Cond + pRS + 1|ID + 1|Year	5	196.96	1.57	0.27	

Maternal identity (1|ID) was included as a random factor in both model selections, whereas year of reproductive attempt (1|Year) was included in fecundity models

[a]*K* number of estimated parameters (with intercept and error terms), *AIC$_c$* Akaike's second-order information criterion, *Δi* difference between model AIC$_c$ and the lowest AIC$_c$ in the model set, *w$_i$* Akaike model weight, *Evidence ratio* ratio of *w$_i$* of the best model to the *w$_i$* of the subsequent models. Models are ranked in descending order of support and models with weak support (*w$_i$* < 0.05) are omitted from the table but listed in Appendix 1 of the Electronic supplementary material. *Age* female age at capture, *Size* initial leg length (mm), *pRS* previous reproductive status, *Cond* initial relative body condition, *Rain* total rainfall during the season (3 months) prior to the reproductive stage tested, *1|ID and 1|Year* maternal identity and year of reproductive attempt, respectively, that were included as a random intercept

Table 3 Model selection for the effects of leg length, age, relative body condition, reproductive status, and winter rainfall on annual leg growth (mm) of female kangaroos ($n = 79$)

Model[a]	K	AIC$_c$	Δi	w$_i$	Evidence ratio
Age + Size + Cond + RS + Rain + Age × Size + Age × RS + 1|ID	10	1543.13	0.00	0.64	2.8
Age + Size + Cond + RS + Rain + Age × Size + Age × RS + RS × Rain + 1|ID	11	1545.12	1.99	0.23	8.0
Age + Size + Cond + RS + Rain + Age × Size + RS × Rain +1|ID	10	1547.34	4.21	0.08	

Maternal identity (1|ID) was included as a random factor

[a]*K* number of estimated parameters (with intercept and error terms), *AIC$_c$* Akaike's second-order information criterion, *Δi* difference between model AIC$_c$ and the lowest AIC$_c$ in the model set, *w$_i$* Akaike model weight, *Evidence ratio* ratio of *w$_i$* of the best model to the *w$_i$* of the subsequent models. Models are ranked in descending order of support and 17 models with weak support (*w$_i$* < 0.05) are omitted from the table but listed in Appendix 1 of the Electronic supplementary material. *Age* female age at capture, *Size* initial leg length (mm), *RS* reproductive status at the initial capture, *Cond* initial relative body condition, *Rain* total winter rainfall prior to growth, *1|ID* maternal identity included as a random intercept

relative body condition was a strong predictor of survival to PEP (Table 4, Fig. 3d). Rainfall, previous reproductive status, and leg length alone or in interaction with age did not yield effects different from zero (Table 4).

Intrinsic and extrinsic determinants of annual growth

Recorded changes in leg length ± SD over 365 days decreased from 20.2 ± 9.1 mm for females aged 3 years to 3.1 ± 4.7 mm for females aged 12 and older (Fig. 1). At capture, 69% of females (168/243) showed signs of lactation. Winter rainfall prior to the growth interval averaged 279 ± 73 mm (range 144–400). Final models of growth did not include year of capture as a random variable, because it did not improve the global model fit (Log-likelihood ratio test: $\chi^2 = 2.94$, $P = 0.09$). A likelihood ratio test comparing

mixed models with and without observer identity as a random factor did not detect significant observer effects on recorded leg growth ($\chi^2 = 0.87$, $P = 0.35$).

Annual leg growth was mostly determined by leg length at the beginning of the growth interval (Table 4), but this effect varied with age (Table 4, Fig. 4a). At the average age of 8 years, females that were one standard deviation (22 mm) shorter than average grew 57% more (10.8 mm year^{-1}) than the average-sized female growth of 6.9 mm year^{-1}. Moreover, average-sized females aged 4 years grew more than twice as much (10.0 mm year^{-1}) as average-sized females aged 12 years (3.8 mm year^{-1}). Maternal relative body condition was positively correlated with leg growth; females whose body condition was one standard deviation (0.02) above average grew 3.2 mm more per year compared to females of average condition (Table 4). In addition, every
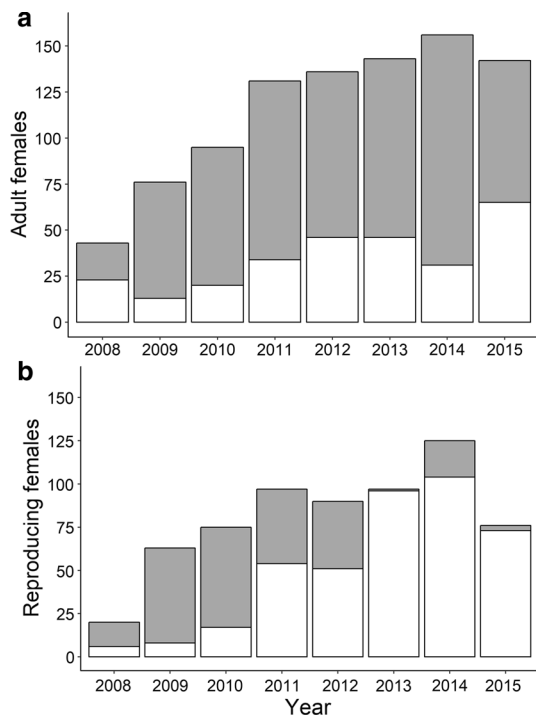
Fig. 2 a Marked female kangaroos aged 3 years and older that did (grey bars) and did not (white bars) reproduce at Wilsons Promontory National Park, Victoria, Australia, from 2008 to 2015. For females that reproduced, **b** grey bars show number of females whose young survived to permanent emergence from the pouch (PEP)

additional standard deviation of winter rainfall (73 mm) reduced leg growth by 2 mm (Table 4). While the effect of female reproductive status did not differ from zero, age modulated this effect (Table 4). Reproduction reduced leg growth for females younger than 9 years and affected the youngest females most (Fig. 4b): at age 4, breeding females grew 3.4-mm year^{-1} less than non-breeding females; this difference was reduced to 1.7-mm year^{-1} at age 7.

Discussion

Fecundity of female eastern grey kangaroos increased with body size, but this effect weakened with age. Young and short females were less fecund, but being short later in life did not affect fecundity as much, suggesting that as females aged, they switched resource allocation from growth to reproduction, regardless of their size. We detected costs of the previous reproduction on current fecundity but only during harsh environmental conditions, confirming that reproductive costs fluctuate in variable environments (Tuomi et al. 1983; Toïgo et al. 2002). Both fecundity and offspring survival to PEP were strongly affected by maternal condition. Annual growth of adult females was mostly explained by their size and age, although annual

differences in winter rainfall and interindividual variation in body condition also explained variability in individual growth. Environmental conditions and habitat quality can influence the growth of adult kangaroos, especially for young females whose growth is faster. Although older females had lower growth rates than younger females, young females that attempted to reproduce had reduced growth, whereas older females maintained similar growth whether they lactated or not. These results suggest that the fitness benefit of size in kangaroos emerges from reduced trade-offs between growth and reproduction at a larger size (Green and Rothstein 1991; Folkvord et al. 2014), but also highlight a flexible age-dependent allocation between these two life-history components (Heino and Kaitala 1999; Lardner and Loman 2003), since both short and tall females had high fecundity later in life.

Longitudinal monitoring of known-age females revealed that fecundity remained high and stable across all years. Juvenile survival to PEP (10 months), however, fluctuated substantially. In 2013, only 1% of females (1/97) carried their young until PEP, compared to 87% (55/63) in 2009. Annual variation was partly explained by maternal relative body condition, as expected, and maternal condition was a strong predictor for both fecundity and offspring survival to PEP. In kangaroos, gestation is very short and its costs are negligible compared to lactation (Tyndale-Biscoe and Janssens 1988; Cripps et al. 2011). Accordingly, we found that maternal condition was most important in mid lactation: all lactating females one standard deviation below average relative condition failed that reproductive attempt, while young born to females that were two standard deviations above average had a 75% probability of PEP. This suggests that lactating kangaroos need to maintain condition to sustain reproduction. Indeed, lactating females must also carry their young, which can weigh up to one quarter of maternal mass by the end of pouch life (Poole et al. 1982; Tyndale-Biscoe and Janssens 1988). In long-lived mammals such as large herbivores, females adopt a conservative reproductive strategy (Gaillard et al. 1998; Gélin et al. 2015; Rughetti et al. 2015), favoring their own survival and transferring the cost of reproduction to their young (Martin and Festa-Bianchet 2010). Among marsupial herbivores, maternal condition has been linked to juvenile survival in the agile wallaby (*Macropus agilis*) (Bolton et al. 1982), and in our study population, low forage production was associated with lower maternal condition and lower milk energy content in mid lactation (Quesnel et al. 2017). Kangaroos are partly income breeders (Gélin et al. 2016b) and may experience highly variable environmental conditions. Our results suggest that most females attempted to reproduce, because gestation involves negligible energy costs, but after parturition, females in poor condition terminated their reproductive attempt, probably to favor their own survival.

Table 4 Model-averaged parameter estimates with their unconditional 95% confidence intervals explaining variation in annual fecundity, offspring survival to permanent emergence of the pouch, and skeletal growth in female eastern grey kangaroo, using rescaled variables (reduced and centered to 2 × mean)

Terms	Parameter value	95% unconditional confidence interval
Fecundity (N = 309)		
Female age	− 0.17	− 1.0, 0.6
Female leg length	**1.7**	**0.8, 2.6**
Relative body condition	**1.7**	**0.9, 2.5**
Rainfall during conception period	0.4	− 0.1, 1.0
Previous reproductive status (reference = no lactation)	− 0.7	− 1.4, 0.1
Female age × leg length	**− 2.1**	**− 3.6, − 0.6**
Female age × previous reproductive status	0.4	− 0.9, 1.7
Leg length × previous reproductive status	− 0.2,	− 1.6, 1.2
Rainfall × previous reproductive status	**1.2**	**0.02, 2.4**
Permanent emergence from the pouch (N = 212)		
Female age	− 0.5	− 1.5, 0.5
Female leg length	0.6	− 0.4, 1.6
Relative body condition	**2.0**	**0.6, 3.4**
Rainfall during winter of pouch life	0.7	− 2.5, 3.9
Previous reproductive status (reference = no lactation)	0.3	− 0.5, 1.1
Female age × leg length	− 0.9	− 2.7, 0.9
Female age × previous reproductive status	− 0.7	− 2.4, 0.9
Leg length × previous reproductive status	0.04	− 1.7, 1.8
Rainfall × previous reproductive status	1.3	− 1.7, 4.2
Annual skeletal growth (N = 243)		
Female age	− 1.8	− 4.4, 0.9
Female leg length	**− 11.9**	**− 14.6, − 9.3**
Female relative body condition	**3.2**	**1.3, 5.2**
Total winter rainfall	**− 1.9**	**− 3.6, − 0.3**
Current reproductive status (reference = no lactation)	− 2.4	− 4.3, 0.1
Female age × leg length	**9.1**	**5.3, 12.9**
Female age × reproductive status	**3.8**	**0.3, 7.4**
Winter rainfall × reproductive status	− 0.8	− 4.6, 2.9

Values in bold have unconditional 95% confidence intervals that differ from zero

Our results reveal that fecundity followed an age- and size-specific trajectory in kangaroos. After accounting for body condition, taller females were more fecund, highlighting the importance of skeletal size for reproduction. Although 83% of average-sized females aged 8 years attempted to reproduce, those shorter by one or two standard deviations (SD = 22 mm) were 10 or 25% less likely to reproduce, respectively. This size effect was strongest for younger females. In moose (*Alces alces*) (Sand 1996) and red deer (*Cervus elaphus*) (Langvatn et al. 2004), increases in mass had stronger positive effects in the probability of ovulation in younger females. In addition, heavier young female bison (*Bison bison*) calved earlier than lighter females (Green and Rothstein 1991). Female chamois (*Rupicapra rupicapra*) with rapid early horn growth achieved higher pre-reproductive body mass and were primiparous at a younger age than females with slow early horn growth (Rughetti and Festa-Bianchet 2011). Our results suggest that

in a context of indeterminate growth, age-specific skeletal size is also of paramount importance in determining age-specific allocation decisions. As fecundity increases with size, selection may favor a delay in allocation to reproduction until females reach a threshold size (Heino and Kaitala 1999; Dmitriew 2011; Simard et al. 2014). Thus, females that enjoy favorable early growth may enjoy a longer reproductive lifespan, because their initially greater size gives them a permanent advantage over smaller females (Madsen and Shine 2000). Other studies of large mammals reported that the early reproduction both increased reproductive lifespan and was positively correlated with later reproductive success (Green and Rothstein 1991; Hayward et al. 2014), suggesting that early growth may be related to phenotypic quality. Because most females from our sample with known age and pre-reproductive growth are still alive, we cannot yet investigate the effect of early growth on lifetime reproductive success.
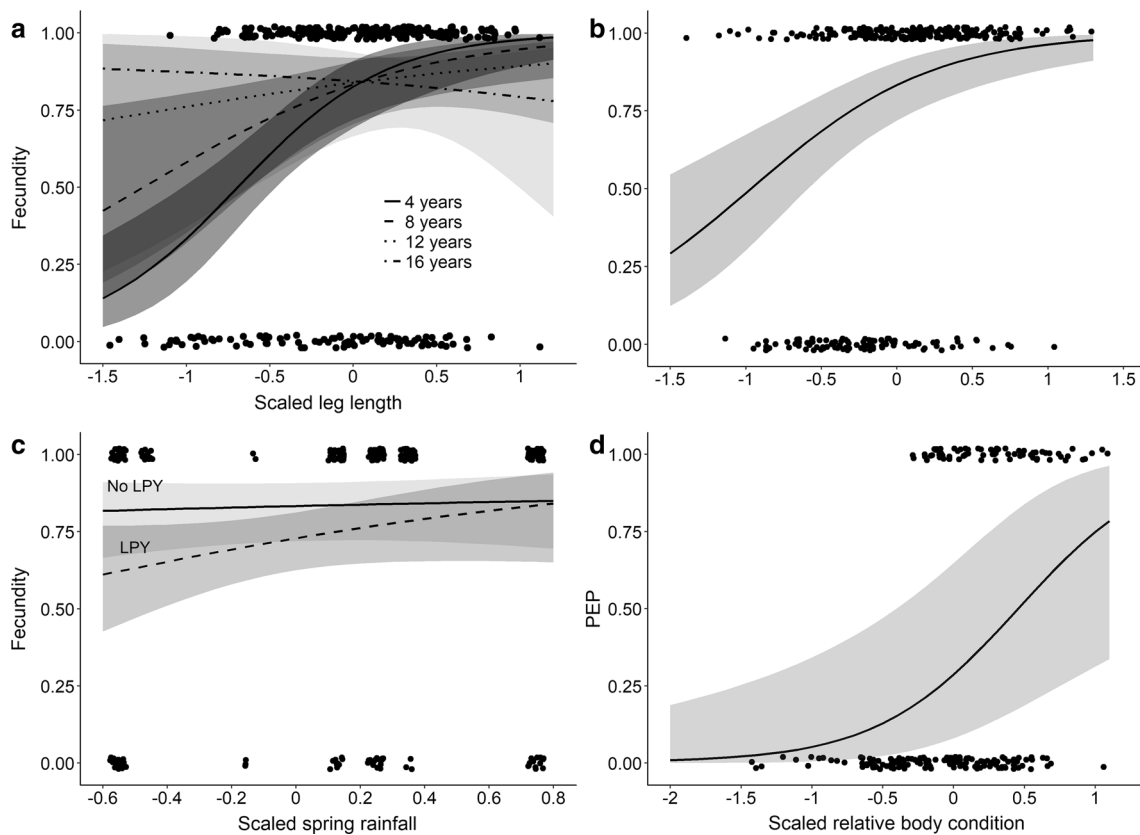
Fig. 3 Model-averaged effects of maternal and environmental variables on reproductive performance in female kangaroos at Wilsons Promontory National Park, Victoria, Australia, 2008 to 2015. Estimates are shown by lines and 95% CIs are represented by darkened bands. Dots show raw data. **a** Effect of scaled leg length as a function of four female ages on fecundity. **b** Effect of scaled maternal relative condition on fecundity. **c** Effect of scaled spring rainfall as a function of previous reproductive status on fecundity. LPY = juvenile survived to the Large pouch young stage, about 7 months. **d** Effect of scaled maternal relative condition on the probability of permanent emergence from the pouch (PEP)

The size effect on fecundity decreased with increasing age, suggesting that the optimal allocation changed as females aged, as predicted for organisms with indeterminate growth (Heino and Kaitala 1999; Folkvord et al. 2014). Older females allocate more to reproduction even if they are small. The greater experience or better foraging skills of older females may allow greater reproductive success despite a smaller size (Lunn et al. 1994).

We did not find sex effects on survival to PEP, despite predictions that sons should be more affected than daughters by a poor environment or lower maternal care in sexually dimorphic mammals (Clutton-Brock et al. 1985). Our sample of known-sex juveniles, however, included mostly young that had survived to 7–8 months, and thus, we could not account for the early mortality. In addition, only mothers in good condition successfully brought their young to PEP and in this population, and heavier mothers tend to produce sons (Le Gall-Payne et al. 2015), potentially contributing to the apparent lack of sex bias in juvenile survival. Other factors are likely responsible for the highly variable PEP between

years (King et al. 2017), suggesting a considerable role of environmental stochasticity, including weather and predation (Banks et al. 2000; King and Goldizen 2016).

We quantified the indeterminate skeletal growth pattern in kangaroos and explored some of its endogenous and exogenous determinants. The previous work on the same population found increased allocation to somatic functions for smaller females (Gélin et al. 2016b), supporting a pattern of size-dependent growth common in most organisms, likely due to larger individuals reducing allocation to growth because of higher biomass maintenance costs (Pomeroy et al. 1999; West et al. 2001; Lardner and Loman 2003). Thus, as expected, short females grew 30% more than females of average leg length. This size-dependent skeletal growth trajectory was, however, considerably influenced by age, suggesting that growth is a higher priority for young females, as expected for animals with indeterminate growth (Folkvord et al. 2014). Because annual growth in female kangaroos is mostly explained by their body size, the lower fecundity of short females may partly involve a greater allocation to
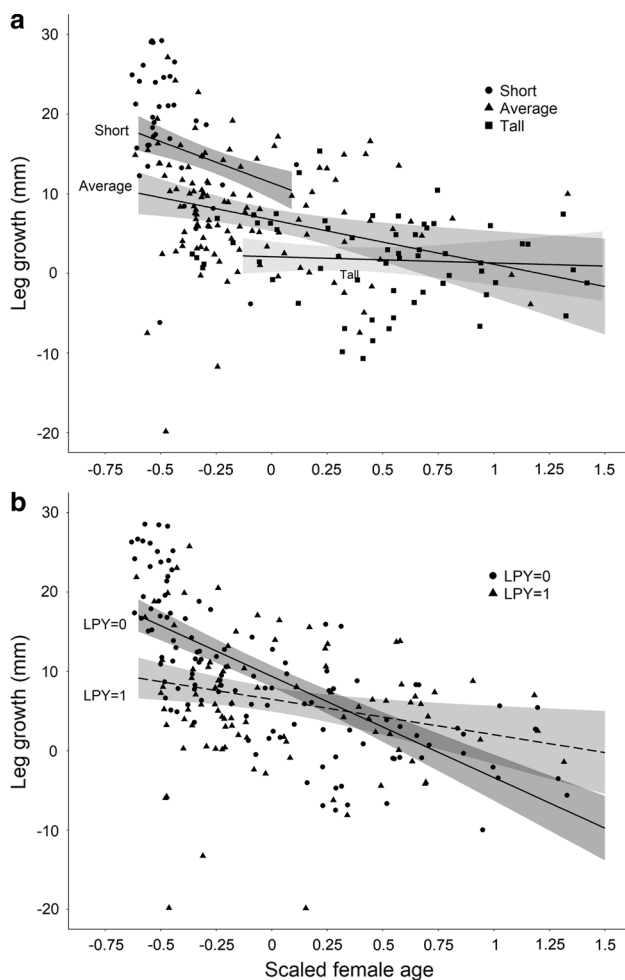
Fig. 4 Model-averaged effect of age as a function of **a** initial body size and **b** reproductive status on annual leg growth (mm) in female kangaroos at the Wilsons Promontory National Park, Victoria, Australia, from 2008 to 2016. Estimates for average leg length ± 1 SD and current reproductive status (LPY = juvenile survived to the Large pouch young stage, about 7 months) are shown by lines and 95% CIs are represented by darkened bands. Scaled female age 0 = 8 years

early conditions prolonged their growth as a strategy to compensate for their initial size deficit and consequently weaned a smaller proportion of their lambs. It is likely that size differences between individual kangaroos were maintained throughout life and resulted at least partly from poor conditions during early ontogeny (Madsen and Shine 2000; Hamel et al. 2009b), impacting other life-history traits. Indeed, shorter adult females could have survived harsher early conditions and, consequently, have reduced the early somatic growth (Sæther 1997; Pettorelli et al. 2002). We found that adult growth rates were affected by climatic factors, since winter rainfall appeared to reduce subsequent leg growth and that shorter females had lower reproductive effort through decreased fecundity. Winter rain likely increased thermoregulatory costs (Parker et al. 2009), reducing the proportion of resources available for growth.

Interindividual variation in relative body condition also explained differences in growth increments. Females in a better condition had higher leg growth in the following year than females in poor condition, after accounting for age, size, and inter-annual environmental differences. A greater amount of acquired resources allows more energy to be allocated to various functions and variable resource acquisition may partly account for changes in allocation to somatic functions (van Noordwijk and de Jong 1986; Parker et al. 2009). In the same population, females that had faster bites rates also had higher mass gain (Gélin et al. 2016a), suggesting heterogeneity in ability to acquire resources. Skeletal growth may be a reliable index of resource acquisition and be associated with other fitness-related traits (Beauplet and Guinet 2007; Gélin et al. 2016b).

Growth rates of older females appeared independent of reproductive status, but growth of younger females decreased by up to 34% if they reproduced, suggesting a short-term allocation trade-off between growth and reproduction for females with the fastest growth. In female common frogs *Rana temporaria*, no trade-offs between growth and reproduction were identified (Lardner and Loman 2003), whereas short-term trade-offs between these traits were identified in young female bison (Green and Rothstein 1991) and in wild Atlantic cod (*Gadus morhua*) (Folkvord et al. 2014). In our study population, Gélin et al. (2016b) found positive long-term correlations of reproduction with leg growth; however, they did not account for age. They also showed that contracepted females gained more mass and grew more than females that could reproduce. Our results suggest an age-specific trade-off between growth and reproduction, after accounting for individual heterogeneity (van Noordwijk and de Jong 1986; Heino and Kaitala 1999), resulting in a size advantage for the early reproduction. Further investigation is needed to understand why older females apparently do not face this trade-off. Growth increments of older females

skeletal growth, leaving fewer resources for reproduction (Lunn et al. 1994; Festa-Bianchet et al. 1998; Simard et al. 2014). Growth may also be costlier for older females, as it diverts energy from metabolic maintenance, including antioxidant protection (Alonso-Alvarez et al. 2007). Indeterminate growth results in prolonged elevated cellular activity that may also be responsible for oxidative stress. As oxidative damage accumulates, its costs may select for decreased growth of older individuals (Metcalfe and Monaghan 2001; Smith et al. 2016).

Being short as a young adult resulted in greater allocation to growth during the remaining lifetime, with shorter females growing more than taller ones at any age. Marcil-Ferland et al. (2013) found that in bighorn sheep (*Ovis canadensis*), females that had experienced poor

are small, however, limiting the power to detect differences in this age group.

In conclusion, we identified a positive effect of body size on growth and a steep trade-off between skeletal growth and reproduction, with the highest reproductive costs of somatic growth occurring for young and short females. We suggest that strong cohort effects are likely to explain differences in age-specific reproductive effort, since the early life conditions may have long-term consequences on future age-specific growth rates of female kangaroos. Females with rapid early growth could start to reproduce earlier and possibly maintain that advantage over the lifetime. A test of this hypothesis will require continued monitoring of known-aged individuals.

Author contribution statement All conducted fieldwork and collected data; LQ analyzed and interpreted the data, and wrote the manuscript; LQ and MFB designed and executed the study; WJK, GC, and MFB provided editorial advice during the writing of the manuscript.

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