



# Forage availability and maternal characteristics affect costs of reproduction in a large marsupial

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## Abstract

Life history theory predicts trade-offs in allocation between survival, maintenance, growth, and reproduction, especially when resources are scarce. Individual variation in resource acquisition can affect trade-offs, but is often unaccounted for. We quantified the fitness costs of reproduction, accounting for environmental conditions, maternal characteristics and individual variation. We analyzed 10 years of data from marked kangaroos to evaluate how reproductive allocation affected annual mass change and skeletal growth, subsequent fecundity and weaning success, and survival, accounting for maternal mass or size and forage availability. Through repeated measurements of 76–91 females, we investigated how trade-offs varied within and between individuals, assessing whether individual variation could mask population-level trade-offs. In poor environments, females that weaned an offspring lost mass. Females that nursed an offspring for > 7 months had reduced skeletal growth. Females that did not gain mass over the previous 12 months rarely reproduced, especially if they had nursed an offspring for > 7 months the previous year. Reproductive allocation had no effect on weaning success, which was very low, and did not affect maternal survival, suggesting a conservative strategy. Disentangling within- and between-individual responses revealed trade-offs within individuals, but because individuals did not vary in their responses to earlier effort, these trade-offs did not drive population trends. The interacting effects of environmental conditions, maternal characteristics and individual variation on allocation trade-offs demonstrate the importance of long-term monitoring for understanding life history variations in changing environments.

**Keywords** Eastern grey kangaroo · Environmental effects · Individual variation · Life history · Reproductive tactics

## Introduction

Life history theory predicts that individuals will allocate their limited energy to survival, growth, maintenance, and current or future reproduction, in ways that maximize fitness (Stearns 1992). The resulting trade-offs in allocation are often interpreted as costs of one function or trait over another. Trade-offs are often forced by resource scarcity,

and are therefore affected by forage availability and population density (Therrien et al. 2008; Hamel et al. 2010). When resources are abundant, some individuals may have enough energy to avoid some trade-offs. Individuals also vary in ability to obtain resources, and differences in resource acquisition affect trade-offs (Hamel et al. 2010). How forage availability and predictability affect allocation trade-offs likely depends upon a species position along the income–capital breeding gradient (Jönsson 1997). In mammals, the costliest phase of reproduction is lactation (Clutton-Brock et al. 1989; Cork and Dove 1989). Income breeders, such as roe deer (*Capreolus capreolus*, Andersen et al. 2000), rely solely on current environmental resources to sustain reproduction, while strict capital breeders like southern elephant seals (*Mirounga leonina*, Costa 1993) fast during lactation and rely on stored resources (Jönsson 1997). Trade-offs are likely more affected by current environmental conditions in income than in capital breeders (Heesen et al. 2013), and

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should be more affected by female body condition in capital than in income breeders (Andersen et al. 2000).

In iteroparous mammals, lactation costs vary with both the rate of milk delivery and the duration of lactation (Green et al. 1980). Reproduction can therefore have a large, but variable, impact on structural growth (Helle 2008), mass change (Hamel and Côté 2009; Morano et al. 2013), future reproduction (Hamel et al. 2010; Morano et al. 2013), and survival (Leivesley et al. 2019). Maintenance of body reserves is important for future reproduction, as females in poor condition seldom reproduce successfully (Festa-Bianchet 1998; Morano et al. 2013). Growth, on the other hand, stops at or shortly after primiparity in most species. In species where growth continues past sexual maturity; however, females face the reproduction–growth trade-off over several reproductive episodes, not only at primiparity (Boretto et al. 2015). Trade-offs between survival and current reproduction in iteroparous species are rare. Because survival of adult females is usually much higher and stable over time than offspring survival, mothers have a higher reproductive value than offspring and should favour their own body condition and survival over that of their offspring (Festa-Bianchet and Jorgenson 1998).

Despite theoretical predictions, several observational studies of wild mammals failed to detect trade-offs (Toïgo et al. 2002). Trade-offs can be hidden by differences in resource acquisition abilities. Individuals may have different total amounts of energy to allocate, partly explaining variation in reproductive success (Lang et al. 2009). When individual variation in resource acquisition are greater than differences in allocation, there may be a null or positive relationship between allocations to different traits (van Noordwijk and de Jong 1986; Hamel et al. 2009a). To quantify allocation trade-offs, it is therefore essential to account for resource availability.

Here, we used long-term data to analyse the fitness costs of reproduction in eastern grey kangaroos (*Macropus giganteus*), first at the population level, then within individuals. Kangaroos are iteroparous mammals with indeterminate growth (Karkach 2006), and are in the middle of the income–capital breeding gradient (Gélin et al. 2015a). The study area has a seasonal climate, but forage availability and population density vary substantially and unpredictably (Fig. S1), providing an opportunity to study how environment affects reproductive costs. With many repeated measures on marked known-age females and data collected over a wide range of environmental conditions, we first tested how trade-offs between reproduction and other traits vary between individuals and ecological conditions (Festa-Bianchet et al. 2017). We tested the prediction that allocation to reproduction reduces mass gain, skeletal growth, future reproduction, and survival, accounting for resource availability by considering maternal traits that affect reproductive performance:

mass, mass change, and skeletal size. We expected reproductive costs to increase with allocation to current reproduction (Green et al. 1980), as earlier research on the same population, limited to years with relatively abundant resources, revealed allocation trade-offs between current reproduction and growth (Quesnel et al. 2018), future reproduction, and body condition (Gélin et al. 2015b, 2016). These studies also suggested that allocation trade-offs may vary with female age and size, with a stronger trade-off between growth and early fecundity for short females than for tall ones, but a size-independent prioritization of reproduction over growth for old females (Quesnel et al. 2018). Previous work also found that at high forage availability, females that did not reproduce were in better body condition and more likely to reproduce the following year than females that reproduced (Gélin et al. 2015b). We therefore expected a stronger negative fitness impact of reproduction for light females, and at low forage availability. Between 2008 and 2012, differences between individuals hid most costs of reproduction (Gélin et al. 2015a, 2016). A greater number of repeated measurements of marked known-age individuals allowed us to distinguish population-level mean effects of reproductive allocation from effects within individuals. We thus investigate how individuals may vary in allocation trade-offs, as determined by individual variation in response slope and intercept, and how individual responses may differ from population trends.

## Methods

### Study area

We monitored habituated, individually marked kangaroos at Wilsons Promontory National Park (38° 570 S, 146° 170 E), Victoria, Australia. The climate is temperate, with average monthly temperature from 13.4 (July; austral winter) to 26.2 °C (January; summer) (Yanakie Corner Inlet Station, Australian Bureau of Meteorology 2019). Vegetation includes a variety of grasses, sedges, herbs and ferns (details in Davis et al. 2010). During our study, population density and seasonal pasture biomass varied both yearly and seasonally (Fig. S1).

### Study species

Eastern grey kangaroos are sexually dimorphic marsupial grazers. Females can attain sexual maturity at 2 years (Poole 1973), with gestation lasting ~36 days (Poole 1975). In the study population, ~85% of births occur between November and February (Fig. S2). Until the offspring reaches ~7 months, lactation costs are relatively low (Tynedale-Biscoe and Janssens 1988). For older offspring, costs increase as milk composition changes, milk consumption

and the weight to be carried increase (Tyndale-Biscoe and Janssens 1988). The offspring leaves the pouch permanently at ~10 months (Poole 1975), but continues to suckle until 16–20 months (King and Goldizen 2016; see Fig. S3 for the steps of a reproductive event). After the offspring leaves the pouch, the female can give birth again and can nurse two offspring simultaneously. Marsupial young grow outside the uterus from a very early stage (Poole 1975). Compared to eutherians, females can more easily control allocation to reproduction and, if environmental conditions are unfavourable, terminate a reproductive attempt during lactation with little cost. Moreover, kangaroos show indeterminate growth (Fig. S4, Karkach 2006). Compared to most other mammals, where structural growth ends near primiparity, kangaroo females face a potential trade-off between reproduction and growth for most of their reproductive life.

### Data collection

We captured adult females annually in August–December since 2008 by Zoletil injection into the hind limb muscle mass, using a pole syringe (see King et al. 2011 for details), and marked them with ear tags and visual collars. We weighed kangaroos with a spring scale (0.25 kg precision for adults, 0.025 kg for pouch young) and measured leg length (Poole et al. 1982) within 1 mm. We assessed reproductive status by examination of the teats at capture and presence of a dependent offspring. About 90% of marked adult females were recaptured yearly and their pouch young tagged. We sampled vegetation four times a year since April 2009 by clipping to the height where kangaroos graze within 50–54 exclosures of 0.56 m-diameter that exclude grazers rabbit sized or larger. Samples were sorted into vegetation palatable and not palatable to kangaroos, dried and weighed. Kangaroo population density was estimated four times annually since January 2009 using DISTANCE (Thomas et al. 2010) by twice walking each of six transects located systematically throughout the study area (Fig. S5, Glass et al. 2015).

### Variable description

*Response traits* We considered females measured between August and December. Yearly mass change and skeletal growth were continuous variables, while fecundity and weaning success, the two levels of reproductive success assessing increasing allocation to reproduction, and female survival, were binary factors.

- Yearly mass change (kg,  $n=374$  female-years) was the difference between mass in year 1 and in year 2, both adjusted to median capture date, as females lose mass in late winter (Aug.), but gain mass in spring (Sept.–Dec.) (Fig. S6).
- Yearly skeletal growth (mm,  $n=372$  female-years) was the difference in leg length from year 1 to year 2.
- Fecundity ( $n=374$  female-years) compared females that did and did not show evidence of lactation.
- Weaning success ( $n=287$  female-years) excluded non-lactating females and compared those whose offspring did and did not survive to 21 months. Age of weaning is variable (King and Goldizen 2016), and for most offspring our field season included their 21st month.
- Female survival ( $n=440$  female-years) was measured from August 1st in year 1 to October 1st in year 2, therefore for survivors it partly overlapped the next reproductive opportunity. August 1st was the usual start of the field season, and the earliest when we evaluated female survival relative to their previous reproduction. Most births occur after we leave the study area in mid-December. We considered October 1st in year 2 as cutoff for survival estimation, as it approximates weaning age for young born at the birth peak (December–January) and represents the end of maternal allocation for year 1. Females ( $n=15$ , 3.3% of the dataset) that died of unnatural causes (mostly hit by vehicles) were excluded from survival analyses.

### Explanatory variables and covariates:

- We limited analyses to females of known age, either first captured as juveniles or subadults, or found dead and aged by the molar index (Kirkpatrick 1965).
- Mass (kg) was mass adjusted to the median date of capture.
- Mass change ( $\Delta$ Mass, kg) was the difference between adjusted mass in years 1 and 2.
- Leg length (mm) was used as skeletal size.
- Reproductive allocation in year 1 was a four-level factor, with 0=no reproduction, 1=young died before 7 months (as until the young reaches ~7 months, lactation costs are relatively low), 2=young died between 7 months and weaning, 3=young weaned.
- We estimated vegetation biomass every 3 months as the average dry mass of palatable vegetation from 54 exclosures. We divided the mean value by the number of days from the previous sample to obtain an estimate of daily growth. Daily growth was divided by kangaroo density at the closest sampling session, providing a daily value of per capita available forage ( $\text{kg kangaroo}^{-1} \text{day}^{-1}$ ). We summed those daily estimates over periods of time of interest, depending on the response trait. Forage over 12 months before the date of capture in year 2 was included as a predictor of mass change and skeletal growth, corresponding to the time over which these response variables were calculated. We used forage over the 12 months before October 1st, date of sur-

vival estimation, for female survival. For year 2 fecundity and weaning success, we assessed the effect of forage availability over 2, 4, 6, 8, 10 and 12 months before parturition date for fecundity or capture date in year 2 for weaning success, using generalized linear mixed models (GLMMs) compared by Akaike information criterion (AIC) (Burnham and Anderson 2002). We only included females measured from August 2010 onwards in all analyses as forage availability over 12 months was not available before that.

## Data handling and analyses

For each response variable, we tested three main hypotheses, assessing whether each trait was affected by (1) only forage availability; (2) only maternal characteristics (including reproductive allocation); or (3) both maternal characteristics and forage availability. We fitted GLMMs with the ‘lme4’ R package (Bates et al. 2015), or the ‘blme’ R package (Chung et al. 2013) when encountering convergence or fit problems (Bolker 2019). We tested a quadratic effect of age on yearly mass change, skeletal growth and reproductive success, as the effect of increasing age could be positive for young females and negative for old females. We selected the most appropriate polynomial structure using AICc (Hurvich and Tsai 1989; Burnham and Anderson 2002). We tested for significance of year and female identity as random effects with likelihood ratio tests. After selecting the random effect structure, we used AICc to determine the most appropriate model based on fixed effects (Hurvich and Tsai 1989; Burnham and Anderson 2002). AICc is particularly relevant when confronting models that correspond to different biological hypotheses (Burnham et al. 2011). When several nested models were within 2  $\Delta$ AIC, we used model averaging on the entire candidate model set using the ‘MuMIn’ R package (Barton 2018). As parameter estimates from model averaging were similar to those from the model with the lowest AIC, we present estimates of that model and report estimates from model averaging in Supplementary Materials. When an independent factor with more than two levels had a significant effect, we ran a Tukey post hoc test to assess which levels were statistically different, using the ‘emmeans’ R package (Lenth 2018). All continuous independent variables were scaled (mean = 0, variance = 1) to facilitate model convergence and interpretation of effect sizes; none were multicollinear (variance inflation factor < 3; Graham 2003).

**Yearly mass change and skeletal growth** We performed two analyses to quantify the influence of explanatory variables on yearly mass change and skeletal growth. For both response variables, we developed ten candidate models with different combinations of variables that included maternal effects such as age and mass in year 1 for mass change, as mass change is expected to be negatively correlated with

initial mass (Bårdsen et al. 2014), or an interaction between size and age in year 1 for skeletal growth, as initial size has an age-dependent negative relationship with growth (Quesnel et al. 2018); reproductive allocation in year 1; forage availability per capita 12 months prior to year 2 capture. We also tested two-way interactions between reproductive allocation and mass (for mass change) or size (for skeletal growth) in year 1, reproductive allocation and available forage, mass or size in year 1 and available forage, and a three-way interaction (Tables S1 & S2).

**Year 2 reproductive success** **Fecundity:** we developed ten candidate models including different combinations of maternal effects such as age in year 1, mass change (Gélin et al. 2016), mass at capture in year 1 (the nearest capture to conception); reproductive allocation in year 1; available forage per capita 2 months prior to parturition, two-way interactions between reproductive allocation in year 1 and female mass, reproductive allocation in year 1 and available forage, mass and available forage, and a three-way interaction (Table S3). **Weaning success:** we assessed whether the response trait was affected (a) near conception (year 1), (b) near permanent pouch exit (year 2), and (c) over 12 months before pouch exit by (1) environmental characteristics; (2) maternal characteristics; and (3) a combination of both. To quantify the effects of explanatory variables on weaning success, we developed 22 candidate models that included maternal effects such as age, mass in year 1, and in year 2, mass change from year 1 to year 2; reproductive allocation the previous year; and available forage per capita 2 months prior to parturition (year 1), 8 months prior to capture in year 2, two-way interactions between year 1 reproductive allocation and female mass or mass change, year 1 reproductive allocation and available forage, mass or mass change and available forage, and a three-way interaction (Table S4).

**Female survival** We developed 14 candidate models of female survival, including different combinations of variables with maternal allocation and available forage, two-way interactions between female mass and age, reproductive allocation and female mass, reproductive allocation and available forage, mass and available forage, and a three-way interaction (Table S5).

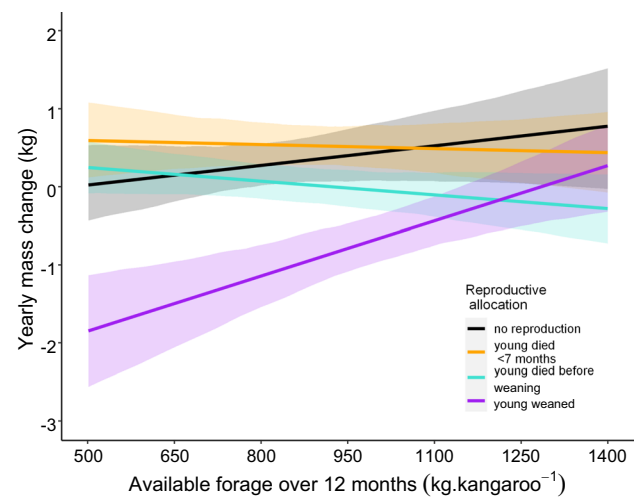
**Decomposing fixed effects into between- and within-individual components** Because life history trade-offs can be masked by individual variation (van Noordwijk and de Jong 1986), we used a within-subject centering technique for the explanatory variable reproductive allocation, to disentangle individual variation from population variation in mass change, skeletal growth, subsequent year fecundity ( $n = 348$  female-years) and subsequent year weaning success ( $n = 257$  female-years) (van de Pol and Wright 2009). To simplify interpretation, we considered two levels of reproductive allocation: low = no reproduction or offspring died before 7 months; high = offspring survived to at least 7 months.

Reproductive allocation was then decoupled into within- ( $\beta_W$ , reflecting intra-individual variation) and between- ( $\beta_B$ , describing population trend) individual components.  $\beta_B$  is the mean value of a variable across all observations for one individual.  $\beta_W$  is, for each observation of that individual, the deviation from its mean value  $\beta_B$ . For each response variable, we used the best model, selected as mentioned above but without interactions, and incorporated the within- and between-individual components (van de Pol and Wright 2009) as fixed effects (Table S6). When there was between-individual variation ( $\beta_B$ ), we investigated if it was driven by within-individual variation ( $\beta_W$ ), by including the between-individual component  $\beta_B$  and the non-decoupled variable (reproductive allocation) instead of its within-individual component ( $\beta_W$ ). This technique assesses the effect of the difference between between- and within-individual components effect ( $\beta_W - \beta_B$ ): if within-individual variation drives between-individual (populational) variation in a trait, their effect size should be similar, hence the difference ( $\beta_W - \beta_B$ ) should be  $\sim 0$ . Finally, we tested for variation in the within-individual component ( $I \times E$ , sensu Nussey et al. 2007) by testing its significance as a random slope of reproductive allocation by individual identity using likelihood ratio tests. We generated best linear unbiased predictors (BLUPs) for each female (i.e. individual intercept and slope, when relevant) from the final model to graphically represent within individual response. The analysis was restricted to females with at least two measurements of the response variable (91 for mass change, skeletal growth and fecundity, 76 for weaning success).

## Results

We analysed 287 observations of 105 females for weaning success, 372 and 374 observations of 115 females for skeletal growth, and mass change and fecundity respectively, and 440 female-years from 125 females for survival, between 2010 and 2017. Mass change ranged from  $-5.00$  to  $+5.45$  kg (mean =  $-0.02$ , SD = 1.41), skeletal growth from  $-9$  to  $+30$  mm (mean = 6.5, SD = 9.0), overall fecundity was 76.7%, weaning success 15.3%, and survival 84.1%.

**Mass change** Females that did not reproduce or whose offspring died before 7 months gained more mass over the subsequent year than females whose offspring survived past 7 months. Females that weaned an offspring lost mass (Fig. 1, Table 1). Forage availability had a strong positive effect on mass change for females that weaned an offspring, as their mass loss was near zero in years of highest forage availability. Forage availability had a weak positive effect for females that did not reproduce and a weak negative one on females whose offspring died between 7 months and weaning (Fig. 1, Table 1, Table S7). Young



**Fig. 1** Interaction between available forage per capita over the 12 months when mass change was measured and female reproductive allocation (black = no reproduction, orange = offspring died before 7 months, blue = offspring died before weaning, purple = offspring was weaned), on yearly mass change for 115 female eastern grey kangaroos at Wilsons Promontory, Victoria, Australia, 2010–2017 ( $n = 374$  female-years). Shaded areas are 95% CIs. Colored version of the figure is available online

or light females tended to gain mass, while older or heavier females tended to lose mass (Table 1, Fig. S7a, b).

**Leg growth** Females that weaned an offspring grew less than other females and taller females grew less than shorter ones. The negative effect of initial size on growth was stronger for females with lower allocation to reproduction (Fig. 2, Table 2, Tables S8 & S9) and for young females. Older females, however, had lower skeletal growth than younger females (Table 2, Fig. S8a). Forage availability had no effect on skeletal growth (Table 2, Fig. S8b).

**Year 2 fecundity** Females whose offspring survived over 7 months had lower fecundity in year 2 than other females (Fig. 3, Table 3); their fecundity increased with mass gain. Yearly mass change had a weaker positive effect on the fecundity of females whose offspring died before 7 months (Fig. 3, Tables 3, S10). Old females had lower fecundity than younger females (Table 3, Fig. S9a). Forage availability and female mass increased fecundity (Table 3, Fig. S9b & c).

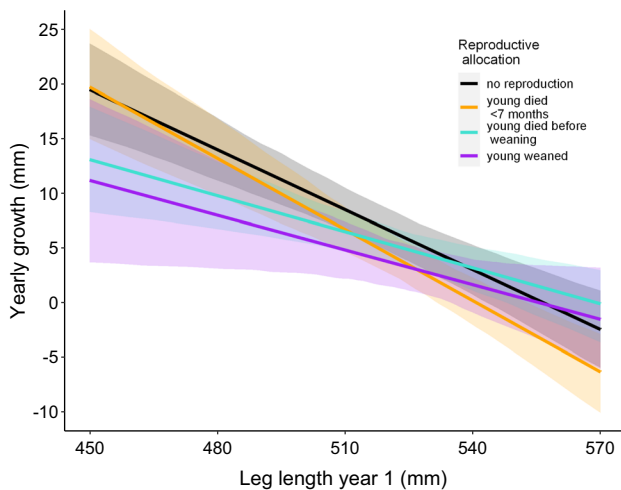
**Year 2 weaning success** Only 15.3% of known-aged females weaned an offspring in year 2 (Fig. S10, Table S11). Reproductive allocation in year 1 had little effect on weaning success, which was lowest for females that either did not reproduce or nursed an offspring for at least 7 months in year 1 (Table 4, Fig. S10, Table S12). Weaning success increased with forage availability over the first 8 months of lactation (Table 4, Fig. S10, Table S12), especially for females that lost their previous offspring before 7 months. Weaning success decreased with age (Table 4, Fig. S11a, Table S12),

**Table 1** Effect of age, mass in year 1, reproductive allocation, per capita available forage over the previous 12 months, and the interaction between reproductive allocation and daily available forage over 12 months, on yearly mass change in 115 female eastern grey kangaroos at Wilsons Promontory, Victoria, Australia, 2010–2017 ( $n = 374$  female-years)

Fixed effects	$\beta$	SE	95% CI	
			Lower limit	Upper limit
Intercept	0.16	0.15	-0.13	0.45
Age	-1.17	1.14	-3.42	1.08
Age <sup>2</sup>	<b>-3.68</b>	<b>1.19</b>	<b>-6.02</b>	<b>-1.34</b>
Mass year 1	<b>-0.62</b>	<b>0.07</b>	<b>-0.76</b>	<b>-0.48</b>
Repro—lost young < 7 months	0.20	0.18	-0.15	0.56
Repro—lost young > 7 months	-0.30	0.19	-0.67	0.07
Repro—weaned young	<b>-1.29</b>	<b>0.25</b>	<b>-1.77</b>	<b>-0.80</b>
Available forage per capita 12 months	0.20	0.15	-0.09	0.50
Repro—lost young < 7 months $\times$ available forage	-0.25	0.19	-0.63	0.12
Repro—lost young > 7 months $\times$ available forage	<b>-0.35</b>	<b>0.17</b>	<b>-0.69</b>	<b>-0.01</b>
Repro—weaned young $\times$ per available forage	0.36	0.21	-0.06	0.78

Parameter estimates are from bold model in Table S1. ‘No reproduction’ is the reference level for reproductive allocation (Repro) in year 1. All numerical variables were scaled. Coefficients for which 95% CIs exclude 0 are in bold

CI confidence interval



**Fig. 2** Interaction between leg length in year 1 and reproductive allocation (black=no reproduction, orange=offspring died before 7 months, blue=offspring died before weaning, purple=offspring was weaned), on skeletal growth to year 2 for 115 female eastern grey kangaroos at Wilsons Promontory, Victoria, Australia, 2010–2017 ( $n = 372$  female-years). Shaded areas are 95% CIs. Colored version of the figure is available online

and increased with maternal mass in year 2 (Table 4, Fig. S11b, Table S12).

**Female survival** Female survival increased with mass for prime-aged and old females (Table 5, Fig. S12). The best model did not include reproductive allocation or forage availability (Table S5).

**Decomposition of fixed effects into between- and within-individual components** Random regression analyses indicated no individual variation (non-significant random

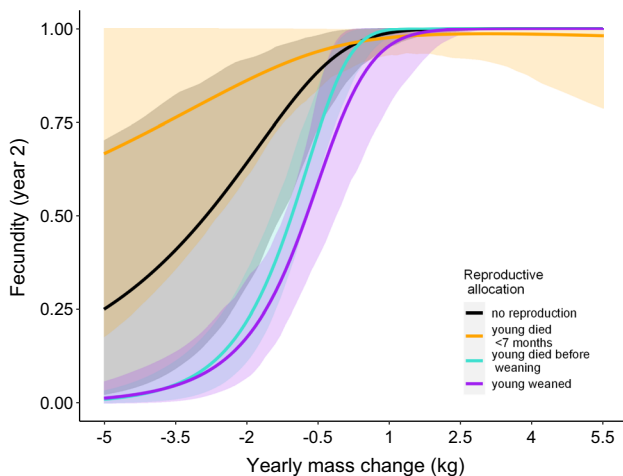
slope) in the relationship between reproductive allocation and any of the traits tested (LRT mass = 0,  $P = 1$ ; LRT growth = 0,  $P = 1$ ; LRT fecundity = 0,  $P = 1$ ; LRT wean = 1.59,  $P = 0.45$ ). Only the estimate of the within-individual ( $\beta_W$ ) component of reproductive allocation had a significant negative effect on mass change to year 2 ( $\beta_W = -0.37$ ,  $SE_W = 0.09$ ,  $P_W < 0.005$ ,  $\beta_B = -0.008$ ,  $SE_B = 0.12$ ,  $P_B = 0.98$ , Fig. 4a), suggesting that reproductive allocation reduced mass change for each individual, but that the effect was similar between individuals. Estimates of the within-individual ( $\beta_W$ ) and between-individual ( $\beta_B$ ) components of reproductive allocation had no significant effect on skeletal growth ( $\beta_W = -0.42$ ,  $SE_W = 0.44$ ,  $P_W = 0.33$ ,  $\beta_B = 0.58$ ,  $SE_B = 0.66$ ,  $P_B = 0.37$ , Fig. 4b). The negative effect of within-individual ( $\beta_W$ ) component of reproductive allocation ( $\beta_W = -0.64$ ,  $SE_W = 0.16$ ,  $P_W < 0.005$ ) suggested that reproductive allocation reduced year 2 fecundity for each individual. The between-individual ( $\beta_B$ ) component of reproductive allocation had a significant positive effect on year 2 fecundity ( $\beta_B = 0.43$ ,  $SE_B = 0.17$ ,  $P_B = 0.01$ , Fig. 4c), suggesting between-individual variation in reproductive allocation. Because the difference in slopes between within- and between-individual components ( $\beta_W - \beta_B$ ) was positive and significant ( $\beta = 1.07$ ,  $SE = 0.22$ ,  $P < 0.005$ ), however, the between-individual variation mean response was likely not driven by intra-individual variation in reproductive allocation. The estimates of the within-individual ( $\beta_W$ ) and between-individual ( $\beta_B$ ) components of reproductive allocation indicate that these variables had no effect on year 2 weaning success ( $\beta_W = -0.22$ ,  $SE_W = 0.24$ ,  $P_W = 0.37$ ,  $\beta_B = -0.38$ ,  $SE_B = 0.35$ ,  $P_B = 0.27$ , Fig. 4d).

**Table 2** Effect of age, size in year 1, reproductive allocation, forage production per capita over the previous 12 months, and the interaction between reproductive allocation and size in year 1, on yearly skeletal growth in 115 female eastern grey kangaroos at Wilsons Promontory, Victoria, Australia, 2010–2017 ( $n = 372$  female-years)

Fixed effects	$\beta$	SE	95% CI	
			Lower limit	Upper limit
Intercept	<b>7.10</b>	<b>1.16</b>	<b>4.82</b>	<b>9.38</b>
Age	<b>-2.19</b>	<b>0.46</b>	<b>-3.11</b>	<b>-1.28</b>
Size year 1	<b>-4.33</b>	<b>0.66</b>	<b>-5.63</b>	<b>-3.03</b>
Age $\times$ size year 1	<b>1.70</b>	<b>0.39</b>	<b>0.93</b>	<b>2.45</b>
Repro—lost young < 7 months	<b>-2.28</b>	<b>0.97</b>	<b>-4.18</b>	<b>-0.38</b>
Repro—lost young > 7 months	-1.41	0.92	-3.21	0.39
Repro—weaned young	<b>-3.07</b>	<b>1.21</b>	<b>-5.43</b>	<b>-0.70</b>
Available forage per capita 12 months	-0.49	0.78	-2.02	1.04
Size year 1 $\times$ Repro—lost young < 7 months	-0.73	0.86	-2.42	0.95
Size year 1 $\times$ Repro—lost young > 7 months	<b>1.65</b>	<b>0.83</b>	<b>0.01</b>	<b>3.28</b>
Size year 1 $\times$ Repro—weaned young	1.71	1.22	-0.68	4.10

Parameter estimates from bold model in Table S2. ‘No reproduction’ is the reference level for reproductive allocation (Repro) in year 1. All numerical variables were scaled. Coefficients for which 95% CIs exclude 0 are in bold

CI confidence interval



**Fig. 3** Interaction between mass change between years 1 and 2, and reproductive allocation (black = no reproduction, orange = offspring died before 7 months, blue = offspring died before weaning, purple = offspring was weaned) in year 1, on fecundity in year 2 for 115 female eastern grey kangaroos at Wilsons Promontory, Victoria, Australia, 2010–2017 ( $n = 374$  female-years). Shaded areas are 95% CIs. Colored version of the figure is available online

## Discussion

Costs of reproduction on crucial life-history traits in a large marsupial herbivore were modulated by forage availability and maternal characteristics. The greatest costs were associated with weaning success and involved lower mass change, growth and subsequent reproduction. Maternal survival, however, appeared independent of reproductive effort.

Trade-offs should be more evident in poor than in rich environments (Therrien et al. 2008; Hamel et al. 2010), as high resource availability may provide enough energy to allocate to many traits. Our results support this prediction, with a strong trade-off between reproductive allocation and subsequent mass gain in years of poor forage availability, but not in years of greater food abundance. At higher forage availability, female mass change was independent of reproductive effort. The impact of environmental conditions suggests that kangaroo females have a flexible resource allocation, typical of income breeders (Jönsson 1997; Heesen et al. 2013). Females needed to gain mass to reproduce, especially if they had reproduced the previous year, indicating that they combine aspects of both income and capital breeding (Gélin et al. 2015a).

In most iteroparous species, adult females, whose survival is high and stable (Gaillard et al. 1998), adopt a conservative reproductive strategy, prioritizing their own survival over that of their offspring, whose survival is low and variable (Festa-Bianchet and Jorgenson 1998; Hamel et al. 2010). Kangaroo females also adopted a conservative reproductive strategy, especially when available forage was more limited. Females had much lower fecundity if they did not gain mass, especially if the previous year they had nursed an offspring for more than 7 months: those females likely allocated all available resources to self-maintenance and survival. The positive effect of mass and mass gain on fecundity, weaning success and survival suggested that some females obtain sufficient resources to allocate much energy to different traits. Our results indicate that kangaroo females prioritize allocation to traits that will ensure their survival, and only allocate to reproduction when

**Table 3** Effect of age, mass in year 1, mass change between years 1 and 2, reproductive allocation in year 1, available forage per capita over 2 months prior to parturition (median parturition date for nonreproductive females), and the interaction between mass change and reproductive allocation, on year 2 fecundity of 115 female eastern grey kangaroos at Wilsons Promontory, Victoria, Australia, 2010–2017 ( $n=374$  female-years)

Fixed effects	$\beta$	SE	95% CI	
			Lower limit	Upper limit
Intercept	<b>0.96</b>	<b>0.28</b>	<b>0.40</b>	<b>1.51</b>
Age	<b>-0.24</b>	<b>0.09</b>	<b>-0.43</b>	<b>-0.06</b>
Mass	<b>0.64</b>	<b>0.13</b>	<b>0.39</b>	<b>0.90</b>
$\Delta$ Mass between years 1 and 2	<b>0.65</b>	<b>0.24</b>	<b>0.18</b>	<b>1.13</b>
Repro—lost young < 7 months	0.08	0.29	-0.50	0.65
Repro—lost young > 7 months	-0.25	0.32	-0.89	0.39
Repro—weaned young	<b>-0.66</b>	<b>0.44</b>	<b>-1.52</b>	<b>0.21</b>
Available forage per capita 2 months	<b>0.20</b>	<b>0.10</b>	<b>0.01</b>	<b>0.39</b>
$\Delta$ Mass $\times$ Repro—lost young < 7 months	-0.39	0.33	-1.03	0.25
$\Delta$ Mass $\times$ Repro—lost young > 7 months	<b>0.77</b>	<b>0.36</b>	<b>0.06</b>	<b>1.47</b>
$\Delta$ Mass $\times$ Repro—weaned young	0.65	0.41	-0.15	1.45

Parameter estimates from bold model are in Table S3. ‘No reproduction’ is the reference level for reproductive allocation (Repro) in year 1. All numerical variables were scaled. Coefficients for which 95% CIs exclude 0 are in bold

CI confidence interval

**Table 4** Effect of age, mass in year 2, available forage per capita over the 8 first months of lactation, and reproductive allocation in year 1, on weaning success in year 2 for 105 female eastern grey kangaroos at Wilsons Promontory, Victoria, Australia, 2010–2017 ( $n=287$  female-years)

Fixed effects	$\beta$	SE	95% CI	
			Lower limit	Upper limit
Intercept	<b>-4.11</b>	<b>0.79</b>	<b>-5.66</b>	<b>-2.57</b>
Age	<b>-1.18</b>	<b>0.41</b>	<b>-1.99</b>	<b>-0.37</b>
Mass year 2	<b>1.52</b>	<b>0.31</b>	<b>0.91</b>	<b>2.13</b>
Available forage per capita 8 months	<b>1.70</b>	<b>0.63</b>	<b>0.45</b>	<b>2.95</b>
Repro—lost young < 7 months	-3.44	1.90	-7.16	0.28
Repro—lost young > 7 months	0.33	0.82	-1.28	1.93
Repro—weaned young	1.72	1.39	-1.00	4.44
Repro—lost young < 7 months $\times$ available forage	<b>4.34</b>	<b>1.74</b>	<b>0.94</b>	<b>7.74</b>
Repro—lost young > 7 months $\times$ available forage	-0.10	0.81	-1.69	1.49
Repro—weaned young $\times$ available forage	-1.84	1.28	-4.36	0.67

Parameter estimates from bold model in Table S4. ‘No reproduction’ is the reference level for reproductive allocation (Repro) in year 1. All numerical variables were scaled. Coefficients for which 95% CIs exclude 0 are in bold

CI confidence interval

**Table 5** Effect of age and mass on survival to October 1st for 125 female eastern grey kangaroos at Wilsons Promontory, Victoria, Australia, 2010–2017 ( $n=440$  female-years)

Fixed effects	$\beta$	SE	95% CI	
			Lower limit	Upper limit
Intercept	0.75	0.45	-0.14	1.64
Age	<b>-0.24</b>	<b>0.12</b>	<b>0.01</b>	<b>0.47</b>
Mass	<b>0.66</b>	<b>0.11</b>	<b>-0.88</b>	<b>-0.44</b>
Age $\times$ mass	<b>0.57</b>	<b>0.15</b>	<b>0.28</b>	<b>0.85</b>

Parameter estimates from bold model are in Table S5. All numerical variables were scaled. Coefficients for which 95% CIs exclude 0 are in bold

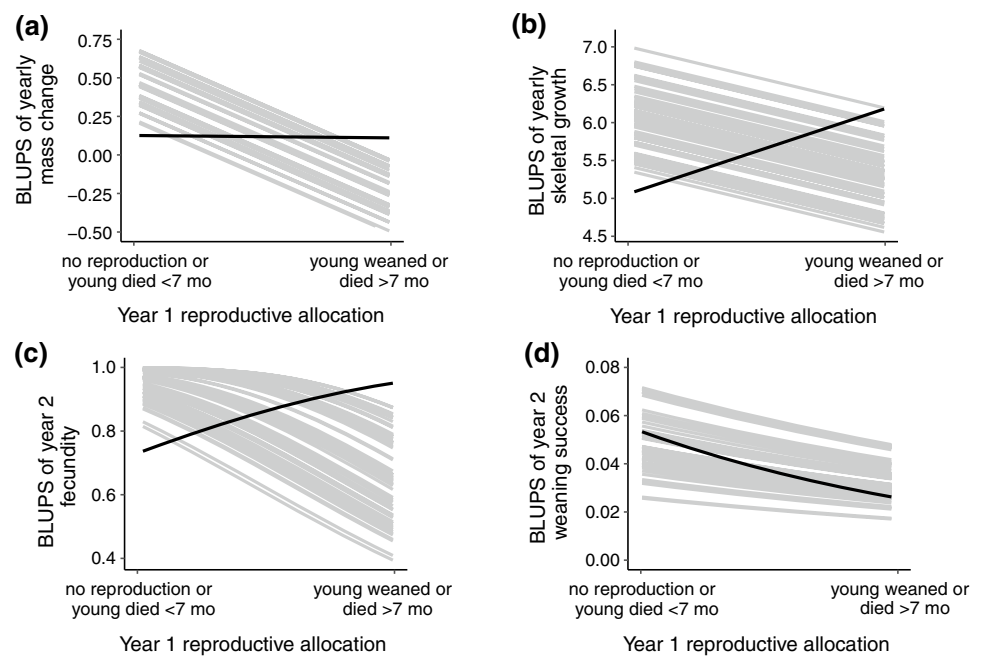
CI confidence interval

additional resources are available, as in other iteroparous mammals (Martin and Festa-Bianchet 2010).

Surprisingly, we detected no costs of reproductive allocation on weaning success the subsequent year. Because overall weaning success was very low, however, our statistical power was limited. Only 2.1% of females weaned an offspring in consecutive years, 15% weaned an offspring in year 2 and 11% in year 1 (Table S11), leaving little variability to analyse. Only females able to acquire sufficient resources can wean an offspring, so that individual variation in acquisition may mask reproductive costs (van Noordwijk and de Jong 1986; Hamel et al. 2009a; Lang et al. 2009). The importance of variation in resource acquisition is underlined by the effect of female size on the trade-off between



**Fig. 4** Between- ( $\beta_B$ , black line) and within-individual responses ( $\beta_W$ , grey lines) of reproductive allocation, on **a** yearly mass change, **b** yearly skeletal growth, **c** subsequent year fecundity, and **d** subsequent year weaning success, for 76 (weaning success) to 91 (mass change, skeletal growth, fecundity) female eastern grey kangaroos (best linear unbiased predictors, or BLUPs) at Wilsons Promontory, Victoria, Australia, 2010–2017 ( $n = 257$  (weaning success) to 348 (mass change, skeletal growth, fecundity) female-years)



reproduction and growth. Short females grew less if they lactated for 7 months or more, while reproductive effort did not affect the growth of taller females. After decoupling reproductive allocation into within- and between-individual components (van de Pol and Wright 2009), we found significant trade-offs within individuals between reproduction and mass gain and between reproduction and subsequent fecundity. Moreover, for all traits investigated, individual intercepts varied, but there was no variation in individual responses (i.e. no random slope), suggesting that some individuals may perform better in several traits, such as mass gain and fecundity, regardless of their previous allocation to reproduction.

Partitioning the effect of reproductive allocation into within- and between-individual components (van de Pol and Wright 2009) revealed no variation in reproductive trade-offs between individuals for any trait, as within-individual variation as a random slope never improved model fit. Individual variation may thus be due to consistent differences in traits such as mass, size or condition that affect reproductive potential (Hamel et al. 2009b). We found positive effects of mass and mass gain on fecundity, and of mass on weaning success. The negative impact of lactating for more than 7 months on skeletal growth was especially strong for short females. In most species, larger females have higher reproductive success (Brooks et al. 2008), hence rapid growth would confer greater benefits to short than to tall females, and greater allocation to growth may explain why short females are less likely to reproduce. Traits such as body mass may reflect differences in resource acquisition and in reproductive potential that could explain differences in performance, but we found no variation in allocation trade-offs involving reproduction between individuals.

Our study took advantage of repeated measurements of marked known-age individuals under a range of environmental conditions, as per capita forage availability varied substantially. Detailed individual monitoring allowed us to better understand fitness costs of reproduction by revealing changes in allocation trade-offs according to forage availability and maternal characteristics (Hamel et al. 2010). Our results advance previous work on the population (Gélin et al. 2015a, b, 2016; MacKay et al. 2018; Quesnel et al. 2018). They encompass a wider range of environmental conditions, and the many repeated measurements allow the use of statistical methods to separate individual from population variation in allocation trade-offs. Only a few studies of mammals have empirically investigated the costs of reproduction on multiple life history traits (Clutton-Brock et al. 1983; Festa-Bianchet et al. 2019), including skeletal growth (Helle 2008). Even fewer have examined the interacting effects of both environmental and individual characteristics on such trade-offs (Clutton-Brock et al. 1983; Hamel et al. 2010). Very few studies address the impact of individual variation in reproductive potential on reproductive costs, and most define individual variation as “quality”, correlated with maternal characteristics (Weladji et al. 2008; Hamel et al. 2009a; Moyes et al. 2011). This notion of “quality” is redundant as one cannot distinguish if maternal characteristics are a cause or a result of differences in acquisition (Bergeron et al. 2011). By statistically differentiating within- and between-individual effects of reproductive allocation on other traits, we demonstrated the importance of considering a panoply of characteristics to understand how life history varies in changing environments.

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**Author contribution statement** PT conceived the idea; PT, DMF and MFB collected the data; PT analysed the data and wrote the first draft; all authors contributed substantially to revisions.

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