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BEHAVIORAL ECOLOGY –ORIGINAL RESEARCH

Individual heterogeneity and offspring sex affect the growth–reproduction trade-off in a mammal with indeterminate growth

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Abstract Reproduction can lead to a trade-off with growth, particularly when individuals reproduce before completing body growth. Kangaroos have indeterminate growth and may always face this trade-off. We combined an experimental manipulation of reproductive effort and multi-year monitoring of a large sample size of marked individuals in two populations of eastern grey kangaroos to test the predictions (1) that reproduction decreases skeletal growth and mass gain and (2) that mass loss leads to reproductive failure. We also tested if sex-allocation strategies influenced these trade-offs. Experimental reproductive suppression revealed negative effects of reproduction on mass gain and leg growth from 1 year to the next. Unmanipulated females, however, showed a positive correlation between number of days lactating and leg growth over periods of 2 years and longer, suggesting that over the long term, reproductive costs were masked by individual heterogeneity in resource acquisition. Mass gain was necessary for reproductive success the subsequent year. Although mothers of daughters generally lost more mass than females nursing sons, mothers in poor condition experienced greater mass gain and arm growth if they had daughters than if they had sons. The strong links between individual mass changes and reproduction suggest that reproductive tactics are strongly resource-dependent.

Keywords Reproductive costs · Manipulation · *Macropus giganteus* · Sex allocation · Environmental effects

Introduction

A central assumption of life-history theory is that reproduction involves trade-offs with growth, subsequent reproduction and survival (Roff 2002). Assuming energy is limited, allocation of resources to reproductive functions occurs at the expense of somatic ones, resulting in negative correlations between fitness-related traits (Stearns 1992), such as reduced resistance to parasites in bighorn ewes, *Ovis canadensis* (Festa-Bianchet 1989), and reproductive success the following year for mountain goats, *Oreamnos americanus* (Hamel et al. 2010a). Trade-offs in allocation can at times be reduced by increasing resource acquisition: for example, female eastern grey kangaroos, *Macropus giganteus*, increase foraging effort when lactating and particularly when carrying a large pouch young (Cripps et al. 2011).

Resource allocation theory has been experimentally investigated in birds (Gustafsson and Sutherland 1988), lizards (Sinervo and DeNardo 1996) and small mammals (Koivula et al. 2003) through the manipulation of reproductive effort by modifying litter size. Few experimental studies, however, have explored reproductive allocations in free-ranging large mammals (but see Tavecchia et al. 2005) because of logistical difficulties. That is unfortunate because the reproductive allocation strategy of large mammals is of great interest for life-history theory, as traits such as long lactation, small litter size and breeding strategies

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often include an important capital component of reliance on stored body reserves. Previous research on wild mammals showed that reproduction tended to reduce mass gain (Clutton-Brock et al. 1983; Gallant et al. 2001; Nilsen et al. 2010), but few studies have examined the potential impacts of reproduction on skeletal growth. In women, Helle (2008) found an increase in adult height when primiparity was delayed. Most mammals have determinate growth, so that trade-offs between growth and reproduction affect only young females, which often suffer greater costs of reproduction than fully-grown adults (Green and Rothstein 1991; Hamel and Côté 2009). Mammals with indeterminate growth, such as most Macropodidae (Jarman 1983), including eastern grey kangaroos (Poole et al. 1982), are therefore interesting models to examine potential trade-offs between reproduction and both mass and growth for all ages. In eastern grey kangaroos, lactation lasts over 18 months (Poole 1975). Females may carry in their pouch a young weighing up to a quarter of their mass, increasing the energetic costs of reproduction. This trade-off is likely to be important because large females often have high reproductive success, as has been reported for fur seals, *Arctocephalus tropicalis* (Beauplet and Guinet 2007), caribou, *Rangifer tarandus* (Gerhart et al. 1997) and Gambian women (Allal et al. 2004).

Despite theoretical expectations, trade-offs are not always observed among wild animals, often because of individual variation in resource acquisition (van Noordwijk and de Jong 1986). Several studies have shown that individual heterogeneity can hide the fitness costs of reproduction (Beauplet et al. 2006; Weladji et al. 2008). Individual resource acquisition is usually correlated with allocation to somatic functions (van Noordwijk and de Jong 1986), so that mass gain can be used as an index of individual heterogeneity (Glazier 1999). Females that gain more mass are expected to have higher reproductive success than females less able to accumulate resources. Therefore, theory predicts both a negative correlation between reproduction and mass gain, and a positive correlation between mass gain and subsequent reproduction.

Trivers and Willard (1973) suggested that in polygynous, sexually dimorphic species, mothers in good condition should provide greater care to offspring of the sex with more variable reproductive success and that there should be a greater fitness benefit of additional maternal care. Studies of sexually dimorphic mammals often report greater fitness costs of sons than of daughters (Clutton-Brock et al. 1981; Bérubé et al. 1996; Rickard et al. 2007). Few studies, however, have examined the effects of offspring sex on maternal mass (Birgersson 1998; Martin and Festa-Bianchet 2010), and to date there have been no attempts to determine if offspring sex affects skeletal growth. Adult male eastern grey kangaroos can have twice the mass of

females (Weckerly 1998), and males grow faster than females (Poole et al. 1982). Consequently, mothers of sons may need more resources than mothers of daughters during lactation, as suggested by their higher bite rate (Gélin et al. 2013). If sons require more investment than daughters, they should also have a greater negative impact on maternal growth. Trivers and Willard (1973) predicted that females in poor condition may benefit from producing the cheaper sex, but evidence for adaptive offspring sex ratio manipulation in mammals remains equivocal (Cameron et al. 2008). In eastern grey kangaroos, heavier mothers tend to produce more sons (Le Gall-Payne et al. 2015). The aim of our study was, therefore, to explore whether sex allocation varies according to individual and environmental conditions. We predicted that mothers in poor condition should be particularly affected by the higher fitness costs of sons.

The manipulation of reproductive effort is a powerful approach to control for heterogeneity in reproductive potential and for environmental stochasticity (Reznick 1985; Sinervo and DeNardo 1996; Koivula et al. 2003; Bårdsen et al. 2008), but it has rarely been attempted in free-ranging large mammals (Tavecchia et al. 2005; Cripps et al. 2011; Gélin et al. 2013). Long-term studies of marked individuals can partly control for individual and environmental variation that may affect reproductive costs (Clutton-Brock and Sheldon 2010) and are a useful complementary approach to experimental manipulations of reproductive effort. We monitored marked female eastern grey kangaroos from 2007 to 2012 in a population where some were experimentally prevented from reproducing and in an unmanipulated population. We investigated the trade-off between reproduction and growth by testing the prediction that the number of days spent lactating would negatively affect the mass and limb growth of mothers. Given the ambiguity of theoretical expectations, we also tested the non-directional prediction that mass change and limb growth of mothers over two successive reproductive episodes were related to survival of the young in both years. Finally, we tested the prediction that for both current and previous offspring, sons would have a greater negative effect on mass gain and skeletal growth than daughters.

Methods

Study areas and data collection

We studied kangaroos in two populations at different locations in Victoria, Australia: (1) Anglesea Golf Club (referred to as 'Anglesea'; 38°24′S, 144°10′E; 2007–2012) and (2) Wilsons Promontory National Park (referred to as 'Wilsons Promontory'; 38°57′S, 146°17′E; 2008–2012). Population densities were 4 and 6 individuals/

ha, respectively. Vegetation was mostly grass at Anglesea (Inwood et al. 2008), where the golf course was regularly watered and fertilized, and grasses, sedges, herbs and ferns at Wilsons Promontory (Davis et al. 2010).

A total of 393 captures of 219 marked adult females (169 at Wilsons Promontory; 50 at Anglesea) provided morphometric data. We immobilized kangaroos by Zoletil injection with an extendable pole syringe (King et al. 2011) and marked individuals with a unique combination of colored ear tags and collars. We usually captured females a few weeks before conception (average capture date 28 November $\pm$ 112 days; parturition date: 15 January $\pm$ 61 days) and weighed them with a spring scale. We measured leg, foot and arm length (Poole et al. 1982) using a flexible tape. Leg measurements at Wilsons Promontory showed significant observer effects, and analyses were performed on data adjusted for this effect using mixed models (Martin and Pelletier 2011), although one observer collected 72 % of the measurements. Data from Anglesea could not be similarly adjusted as the names of observers were not systematically recorded. However, analyses using corrected and uncorrected measurements from Wilsons Promontory led to similar results, suggesting that observer effects were minor. The mass of lactating females ranged from 18 to 35.5 kg, the leg length from 425 to 554 mm, the foot length from 296 to 349 mm and the arm length from 163 to 245 mm. Because foot growth was minimal (mean 0.9 ± 5.4 mm/year, or <0.3 %), we analyzed only leg and arm measurements.

Reproductive status of marked individuals at each reproductive cycle was determined at capture or through visual observations. For each reproductive cycle, we classified females as unsuccessful (acronym NPY for No Pouch Young) if they did not appear to reproduce or if their young disappeared before the large pouch young stage at about 7–8 months of age (Poole et al. 1982; Jaremovic and Croft 1991) and as successful (LPY for Large Pouch Young) if their young survived to the 'large' stage, with a fully furred head that regularly protruded outside the pouch. At that point, we usually recaptured the female and measured and tagged the young. Tests of the effects of offspring sex were limited to young that survived to the large pouch young stage, as we seldom knew the sex of young that died before capture. Analyses of sex effects were limited to the Wilsons Promontory population because the sex of most young was unknown at Anglesea due to fewer recaptures of females carrying a pouch young. Only females weighing at least 18 kg were considered in our analyses as that was the minimum mass of a lactating female. At capture, we estimated the birthdate of the young from its skeletal measurements (Poole et al. 1982) and the lactation status of females by examining the teats. We recorded the duration of association between mothers and their nursing young-at-foot and

survival of the young during regular population surveys. We estimated the number of days each female was lactating between successive captures by combining information on lactation and juvenile survival. Although females can give birth as soon as their young leaves the pouch at about 10 months of age (Poole 1975), during our study >90 % of females gave birth to 1 young/year or fewer. We considered three age classes: 'Young' females, 'Prime-age' females and 'Old' females. 'Young' females were known-age individuals first caught as pouch young or subadults (20 kg or less) and nulliparous at first capture. These females were aged 3–5 years while reproductively active during our study. 'Prime-age' or 'Old' females were classified by incisor wear, with the latter either missing or having incisors which were worn within 1–2 mm of the gum line.

Experimental manipulation and statistical analyses

We analyzed individual growth over the long term and between two successive reproductive events. Long-term growth was measured between the first and last capture of each female, over a minimum of 2 years [mean $\pm$ standard deviation (SD); Anglesea 3.33 ± 0.81 years, Wilsons Promontory 2.98 ± 0.74 years]. We measured changes in body mass, leg and arm length over two successive reproductive events at intervals ranging from 200 to 550 (average 364 ± 71) days when females were potentially involved in two subsequent reproductive events. The young of mothers in poor body condition may have lower survival, potentially leading to shorter inter-birth intervals. Thus, for the analysis of the effect of offspring sex on growth per reproductive episode, we also included 15 females with inter-capture intervals of 159–199 days in order to avoid excluding mothers with low body condition. As our data were normally distributed, we used linear models with Gaussian error distribution. Growth was defined as the difference in body mass and in leg and arm length between two captures.

The analysis of long-term growth sought to test the effect of lactation and offspring sex ratio on mass change and skeletal growth, using only one measurement per individual. Sample size was 109 females (Anglesea 50, Wilsons Promontory 59). An earlier study tested the efficacy of two hormonal contraceptive implants, deslorelin and levonorgestrel, in female kangaroos at Anglesea (Wilson 2012; Wilson et al. 2013). In these studies, at first capture, nine females received deslorelin (a gonadotropin-releasing hormone agonist) implants (9.4 mg, Suprelorin; Peptech Animal Health, Macquarie Park, NSW, Australia), which is effective for 2–3 years. Eight females received levonorgestrel (progestin) implants (210 mg, Norplant II; Leiras Pharmaceutical, Turku, Finland), which is effective for at least 3 years (Wilson 2012). As controls, ten females of the same population (Anglesea) had one small pouch young (mostly <2 months

old) removed, and these females did not re-conceive until the following year (Wilson et al. 2013). One female had very small pouch young removed in 2 years of monitoring. Therefore, the time spent lactating was experimentally reduced for these 28 manipulated female-years compared to 22 unmanipulated females monitored as controls. 'Days lactating' between captures was the time spent nursing offspring and ranged from 0 (for some manipulated females) to 1673 days at Anglesea (mean ± SD: 539 ± 470 days) and from 300 to 1445 days at Wilsons Promontory (885 ± 284 days). In addition to the effect of days lactating, we also compared growth between manipulated and unmanipulated females. Proportion of sons for each female was the number of males divided by the number of offspring of known sex that reached the large pouch young stage between first and last capture ($N = 58$ offspring). Arm growth was not considered in these analyses as it was not measured for manipulated females at Anglesea.

The aim of the analysis of growth between two reproductive episodes was to quantify the effects of having a large pouch young in year 1 or in year 2 and of sex of young in years 1 and 2 on changes in mass and size of unmanipulated females. For this analysis, we recaptured 87 females at Wilsons Promontory (average of 1.9 recaptures each after the initial capture). The sample size of unmanipulated females was insufficient to conduct this analysis using data from Anglesea, where females were recaptured less frequently, and thus pouch young sex could not be determined. We first tested the significance of individual as a random effect by comparing models with and without the random effect using a likelihood ratio test (Steele and Hogg 2003). Although, female identification as a random effect was not significant (likelihood ratio test, $P > 0.05$), we used linear mixed models to avoid any bias due to pseudoreplication. For multiple comparisons between categories, we used Tukey's post-hoc test ['library(multcomp)']. We also tested whether female body condition (assessed

using the scaled mass index; Peig and Green 2009) in year 1 interacted with sex of young in year 1 and year 2 to influence mass gain and leg and arm growth from year 1 to year 2. When the effect of sex of young was significant, we repeated the analysis for females in the lowest quartile of the distribution of body condition. To highlight the importance of mother body condition on growth according to sex of young, we present here results including and excluding the interaction between these variables.

All analyses were performed with R version 2.14.1 R Foundation for Statistical Computing, Vienna, Austria) and user interface Rstudio version 0.97.551 (Rstudio Integrated Development Environment, Boston, MA). We controlled for factors known to affect reproductive costs and growth, such as inter-capture interval, age class, year of study, capture and recapture date (McNamara and Houston 1996; Glazier 1999). Capture dates were coded as Julian days with 1 August as day 1 to test for possible seasonal effects on mass gain. August 1st best separated successive reproductive seasons: in both populations, <3 % of births occurred in July and August (winter in Australia). Growth rates are typically size-dependent (Hector and Nakagawa 2012), and therefore female size at first capture was also accounted for. We used backward stepwise elimination of non-significant variables to reach the minimal adequate model (Crawley 2007; Zuur et al. 2009). Only significant covariates and interactions are reported.

Results

Long-term growth

At Anglesea (manipulated population), mass gain decreased with the number of days lactating between captures when controlling for inter-capture interval, initial mass and capture date (Table 1; $R^2 = 0.48$). Manipulated

Table 1 Linear models of mass change (kg) for eastern grey kangaroo females with inter-capture intervals of at least 2 years at two sites in Victoria State, Australia, 2007–2012

Variable	Anglesea including manipulated females[a]				Wilsons promontory			
	Estimate	SE	F value	P	Estimate	SE	F value	P
Intercept	15.291	3.325	21.16	<0.001	19.715	5.024	15.40	<0.001
Days lactating	−0.002	0.001	6.46	0.015	−0.010	0.005	4.18	0.046
Inter-capture interval (years)	1.161	0.502	5.35	0.026	−4.368	1.639	7.10	0.010
Initial mass (kg)	−0.653	0.103	40.20	<0.001	−0.293	0.082	12.86	<0.001
Capture date	0.011	0.005	5.68	0.022				
Days lactating × inter-capture interval					0.004	0.002	5.57	0.022

The analysis was based on 49 females at Anglesea and 58 at Wilsons Promontory

SE standard error

[a] At Anglesea, 'manipulated' females included 17 with contraceptive implants and 10 whose small pouch young was removed

Table 2 Linear models of leg growth (mm) for eastern grey kangaroo females at two sites in Victoria State, Australia, 2007–2012

Variable	Anglesea including manipulated females[a]				Wilsons promontory			
	Estimate	SE	*F* value	*P*	Estimate	SE	*F* value	*P*
Intercept	373.464	40.459	9.2	<0.001	215.696	31.251	47.64	<0.001
Days lactating	−0.011	0.005	−2.49	0.017	−0.048	0.019	6.15	0.016
Inter-capture interval (years)	1.213	2.700	0.45	0.656	−17.375	6.707	6.71	0.012
Initial leg length (mm)	−0.690	0.078	−8.88	<0.001	−0.294	0.052	32.30	<0.001
Days lactating × inter-capture interval					0.018	0.006	8.73	0.005

The analysis was based on 50 females at Anglesea and 59 at Wilsons Promontory

[a] At Anglesea, manipulated females included 18 with contraceptive implants and 10 whose small pouch young was removed

females gained 1.8 ± 0.8 kg more than unmanipulated ones ($F_{1,46} = 5.24$; $P = 0.027$). At Wilsons Promontory (unmanipulated population), an interaction between inter-capture interval and days lactating (Table 1) suggested a long-term positive correlation between lactation and mass gain. The model integrating this interaction explained 22 % of variation in mass gain, which was independent of the proportion of sons produced ($F_{1,54} = 0.08$, $P = 0.78$) or of capture date ($F_{1,52} = 0.74$, $P = 0.39$). We found no quadratic effects of capture date (Anglesea: $F_{1,42} = 0.30$, $P = 0.58$; Wilsons Promontory: $F_{1,51} = 0.46$, $P = 0.50$) nor linear effects of recapture date (Anglesea: $F_{1,43} = 1.74$, $P = 0.19$; Wilsons Promontory: $F_{1,53} = 1.21$, $P = 0.28$).

At Anglesea, leg growth decreased with days spent lactating when controlling for inter-capture interval and initial leg length (Table 2; $R^2 = 0.61$). Leg growth was greater (by 8.3 ± 4.1 mm) in manipulated than unmanipulated females ($F_{1,47} = 4.07$, $P = 0.049$). At Wilsons Promontory, the best model explained 43 % of variability in leg growth and included an interaction between days lactating and inter-capture interval (Table 2). There seemed to be no effect of days lactating on leg growth for inter-capture intervals of <3 years, and a positive effect for longer intervals. The proportion of sons produced did not affect leg growth ($F_{1,55} = 0.40$, $P = 0.53$).

Growth between two successive reproductive events

Mass gain at Wilsons Promontory ($N = 157$ recaptures) decreased for females whose young survived to the large pouch young stage in year 1 (Fig. 1; Table 3), but it increased with reproductive success in year 2 (Fig. 1; Table 3) when controlling for age class, mass and capture date in year 1 and year of first capture. This model explained 62 % of the variability in mass change. Females unsuccessful in year 1 and successful in year 2 tended to gain more mass than those successful in both years (mean difference ± SE: 0.74 ± 0.31 kg; $t_{146} = 2.42$, $P = 0.074$; Fig. 1). Heavy females gained less mass than light ones
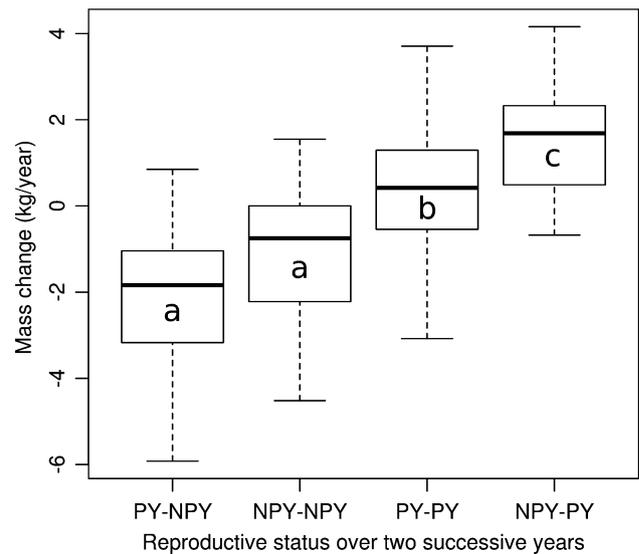

Fig. 1 Mass change as a function of reproductive status over 2 successive years for 87 eastern grey kangaroo females at Wilsons Promontory, VIC, Australia, 2008–2012. *LPY* years when the pouch young survived to at least 7 months of age, *NPY* years when the female did not reproduce or the pouch young disappeared before 7 months of age. *Dark horizontal line in box* Median, *different letters in boxes* indicate significant differences at $P < 0.05$. Sample sizes ranged from 14 to 76 mass change measurements for each category. *Error bars:* standard deviation of the mean

(Table 3). In 2011, females lost almost 750 g more than in other years (Table 3). For reproducing females, sex of the young in year 2 did not affect mass gain [daughters compared to sons, mean difference ± standard error (SE): 0.20 ± 0.25 kg; $\chi^2_1 = 0.62$, $P = 0.43$, $N = 108$], but females that had a daughter in year 1 lost more mass than mothers of sons (-0.57 ± 0.26 kg; $\chi^2_1 = 4.91$, $P = 0.026$, $N = 151$) in a model not including interactions. However, mass gain was also affected by an interaction between female body condition and sex of young in year 1 ($\chi^2_1 = 5.23$, $P = 0.022$). Females in very poor initial condition gained more mass if they had a daughter compared to

Table 3 Linear mixed models using 157 datasets on mass change and 160 datasets on arm growth according to reproductive status over 2 successive years for up to 86 eastern grey kangaroos females at Wilsons Promontory in Victoria State, Australia, 2008–2012

Variables	Mass change (kg)				Arm growth (mm)			
	Estimate	SE	χ^2 value (df)	P	Estimate	SE	χ^2 value (dff)	P
Young survival to LPY in year 1	−0.747	0.242	9.49 (1)	0.002	−2.7	0.9	9.80 (1)	0.002
Young survival to LPY in year 2	2.175	0.208	109.68 (1)	<0.001	0.8	0.7	1.16 (1)	0.282
Age—*compared to young*			7.21 (2)	0.027				
Prime age	−0.825	0.361						
Old	−1.189	0.447						
Initial measurement (kg or mm, as appropriate)	−0.170	0.038	20.03 (1)	<0.001	−0.2	0.0	27.82 (1)	<0.001
Capture date in year 1	−0.002	0.001	5.95 (1)	0.015	−0.0	0.0	5.32 (1)	0.021
(Capture date in year 1)^2					0.0	0.0	5.57 (1)	0.018
Year of recapture—*compared to 2009*			17.60 (3)	<0.001			7.05 (3)	0.070
2010	0.026	0.330			−0.6	1.2		
2011	−0.740	0.359			2.0	1.3		
2012	0.295	0.312			0.3	1.1		

Categorical effects are presented in italics

LPY indicates a year when the female had a young that survived to the 'large' stage, or about 7 months of age; *df*, degrees of freedom

those that had a son in year 1 (mean ± SD: 1.16 ± 2.62 vs. −0.23 ± 2.28 kg, respectively; $\chi_1^2 = 5.36$, $P = 0.021$, $N = 39$).

At Wilsons Promontory ($N = 159$), a model explaining 16 % of leg growth revealed an interaction between reproductive effort in year 1 and inter-capture interval ($\chi_1^2 = 3.91$, $P = 0.047$) and one between reproductive success in year 2 and leg length at first capture ($\chi_1^2 = 4.88$, $P = 0.027$) when controlling for year of recapture ($\chi_3^2 = 11.62$, $P = 0.009$). Leg growth increased with inter-capture interval for females that had a large pouch young in year 1, but not for those reproductively unsuccessful in year 1. Leg growth was negatively correlated with initial leg length only for females that had a large pouch young in year 2. Sex of young in either year 2 ($\chi_1^2 = 1.73$, $P = 0.19$, $N = 109$) or year 1 ($\chi_1^2 = 0.12$, $P = 0.72$, $N = 153$) did not affect leg growth.

At Wilsons Promontory, a model ($R^2 = 0.24$; Table 3) which included capture date in year 1, the square of capture date (quadratic effect), year of recapture and arm length at first capture suggested that reproductive status in year 1 decreased arm growth but that reproduction in year 2 had no effect. Arm growth was independent of sex of young in either year 1 ($\chi_1^2 = 0.11$, $P = 0.74$, $N = 153$) or year 2 ($\chi_1^2 = 2.52$, $P = 0.11$, $N = 109$). There was a significant interaction between body condition in year 1 and sex of young in year 2 ($\chi_1^2 = 4.43$, $P = 0.035$, $N = 109$) affecting arm growth. Females in very poor initial condition had greater arm growth if they had a daughter than a son in year 2 (mean ± SD: 5.9 ± 5.3 vs. 2.1 ± 2.8 mm, respectively; $\chi_1^2 = 4.35$, $P = 0.037$, $N = 27$).

Discussion

To our knowledge, this is the first study of any wild mammal to experimentally quantify a trade-off between structural growth and reproduction and to show an effect of offspring sex on skeletal growth. By combining experimental manipulation and multi-year monitoring of a large sample of marked kangaroos, we revealed a somatic cost of reproduction, a link between individual ability to gain mass and reproductive success and an interplay between female body condition and somatic cost of offspring of different sex.

Our study provides valuable insights into the trade-offs between life-history traits, despite substantial individual differences in reproductive potential (Reznick 1985; Clutton-Brock and Sheldon 2010). Females whose reproductive effort was experimentally reduced had greater long-term mass gain and skeletal growth than unmanipulated females, revealing growth costs of reproduction. Reproduction also reduced the mass gain of unmanipulated females, but not leg growth, suggesting that females may prioritize skeletal growth over mass accumulation when resources are scarce. The analysis of growth per reproductive episode also showed reproductive costs in unmanipulated females. Females that had a large pouch young in year 1 decreased mass gain and arm growth, but not leg growth, leading to a reduction in body condition. Our results are consistent with other long-term correlative studies reporting that reproductive effort reduces body condition (Clutton-Brock et al. 1983), mass of primiparous females (Green and Rothstein 1991), mass gain of young females (Hamel and Côté 2009) or asymptotic height in women (Helle 2008). No study,

however, has reported reproductive costs on skeletal growth for wild mammals, a trade-off that is likely more explicit in species with indeterminate growth.

Individual differences in age class and initial size affected growth and, consequently, the amount of energy available for reproduction. Younger, smaller and lighter individuals generally allocated more resources to somatic than to reproductive functions, leading to faster growth compared to older and larger females. In large herbivores, body mass and mass gain are often positively correlated with reproductive success (Gaillard et al. 1992; Festa-Bianchet et al. 1998; Stewart et al. 2005). Strategies to reduce the impacts of reproduction on maternal body condition are also important because poor condition can lower maternal survival (Tavecchia et al. 2005), reduce future reproduction (Persson 2005) and lower growth and survival of offspring (Martin and Festa-Bianchet 2011). The ability of individuals to accumulate resources appears to increase with body size and may influence reproductive costs, as reported in bighorn ewes (Festa-Bianchet et al. 1998). Aggressive interactions are rare in eastern grey kangaroos (Maguire et al. 2006), suggesting that our results were probably not affected by individual differences in dominance status, a factor which may affect resource acquisition for other mammals (Clutton-Brock and Huchard 2013). Independently of size, age and current reproductive effort, mass gain appeared necessary to allow female kangaroos to reproduce successfully in the following year (Fig. 1), underlining the pivotal role of resource acquisition. Leg growth increased with inter-capture interval for mothers that were successful in year 1, but not for unsuccessful females, suggesting an association between individual heterogeneity in growth and reproductive success.

Mass gain increased reproductive success, and successful females had higher leg growth during the subsequent year, suggesting that mass gain in 1 year could have a positive effect on both reproduction and leg growth the following year. However, reproductive effort also decreased mass gain, suggesting that the ability to acquire resources over the long term plays a major role in the reproductive performance of individuals. The positive interaction between days lactating and inter-capture interval on leg growth over the longer term (Table 2) suggests that, while each reproduction involved short-term somatic costs, over multiple years females with greater growth also reproduced at a higher rate. When resource allocation is less variable than its acquisition, the cost of reproduction should affect females according to individual capacity to acquire resources rather than individual reproductive effort (Hamel et al. 2010b). Gittleman and Thompson (1988) underlined the importance of behavior in compensating for the energy costs of reproduction. Female eastern grey kangaroos increase foraging to cope with reproductive costs (Cripps et al. 2011) and

show wide individual variation in foraging behavior (Gélin et al. 2013). Individual foraging strategies may reduce the immediate somatic costs of reproduction, as reported by Hamel and Côté (2009) for prime-aged female mountain goats. Young female kangaroos had greater mass gain and bite rates than older ones, after controlling for reproductive effort (Gélin et al. 2013). Although our analyses are concerned with the 'capital' aspect of their breeding strategy, kangaroos clearly show evidence of both 'capital' and 'income' breeding effects. The strong effect of changes in foraging behavior on growth may suggest that, compared to ungulates in seasonal environments, kangaroos have a more 'income breeder' strategy (Stearns 1992). Yearly changes in foraging behavior and mass further reinforce the link between foraging strategy and reproductive success. A higher bite rate in 2011 at Wilsons Promontory suggests an increase in reproductive cost (Gélin et al. 2013). The lower mass gain in 2011 compared to other years (Table 3) may imply that, despite increased foraging effort, low resource availability decreased reproductive success in that year.

Lactation of large pouch young is likely the most energetically costly aspect of kangaroo reproduction because females have to both increase milk production and carry a young up to a quarter their own mass. Milk is also more energetically costly to produce in late than in early lactation because its composition changes (Green et al. 1980). Most females unable to gain sufficient resources abandoned their reproductive attempt before this stage of lactation, leading to a positive correlation between inter-year mass gain and reproductive success in year 2.

Most studies of sexually dimorphic mammals report higher reproductive costs of sons than of daughters (Clutton-Brock et al. 1981; Bérubé et al. 1996). Kangaroo mothers nursing sons increased foraging effort compared to mothers of daughters, also suggesting a higher energy requirements of sons (Gélin et al. 2013). Therefore, we were surprised to find that overall production of sons was associated with lower mass loss. However, if females that conceive sons had higher reproductive potential than females that conceived daughters, as reported for tammar wallabies (*Macropus eugenii*; Robert et al. 2010), they may also be better at maintaining their mass than mothers of daughters. Therefore, individual differences in body condition could obscure differential sex allocation. Indeed, among mothers in poor condition in year 1, those that had daughters in year 1 gained more mass, and those that had daughters in year 2 had greater arm growth compared to those that had sons, while leg growth was not affected by offspring sex. The proportion of sons produced did not affect maternal growth, possibly because kangaroo females manipulated offspring sex ratio (Le Gall-Payne et al. 2015) or sex-specific maternal effort according to their body condition to limit the somatic costs of lactation. Those results

suggest that producing daughters rather than sons decreases reproductive effort and allows mothers in poor body condition to increase their condition.

Our analyses suggest that reproduction at times led to substantial somatic costs, to a point where some females were unable to reproduce the following year. Although we did not directly measure energy allocation to lactation, the experimental manipulation strongly suggests that allocation to reproduction led to a trade-off with somatic growth. Leg growth, however, showed no short-term negative effects of reproduction, and over the longer term, it was positively associated with reproductive effort in unmanipulated females. Therefore, leg length could be an important trait for long-term fitness (Gerhart et al. 1997; Beauplet and Guinet 2007) because females able to sustain more skeletal growth were also reproductively successful. Skeletal growth may be an index of resource acquisition that could be correlated with reproductive potential. These complex results underline the importance of collecting varied morphological traits and monitoring marked individuals over multiple years to understand life-history patterns in changing environments (Clutton-Brock and Sheldon 2010).

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