Behavioral Ecology and Sociobiology (2018) 72:7
https://doi.org/10.1007/s00265-017-2419-9

FEATURED STUDENT RESEARCH PAPER

Maternal resource allocation adjusts to timing of parturition in an asynchronous breeder

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Received: 6 June 2017 / Revised: 29 November 2017 / Accepted: 4 December 2017

Abstract

Environmental variation affects foraging decisions and resources available for allocation among competing life-history traits. In seasonal environments, variation in breeding phenology leads to differences in relative timing of resource intake and expenditure, which can lead to variation in maternal allocation tactics. Monitoring maternal allocation to fetal growth in wild mammals is challenging, however, and few studies have linked seasonal effects of forage and maternal condition to early offspring development. Asynchronous parturition and short gestation make kangaroos ideal for studying phenological effects on very early growth, since pouch young born in different seasons can be measured during stages equivalent to in utero development for eutherian mammals. Over 4 years, we recaptured 68 eastern grey kangaroo mother-young pairs with parturition dates spanning 5 months to evaluate how birthdate affects maternal allocation to offspring growth before pouch exit. Structural equation modeling revealed that mothers that gave birth in autumn gained mass during lactation, and their young grew faster than young born in early summer. When later lactation coincided with poor winter forage and cold temperatures, mothers prioritized maintenance of their own mass over offspring growth. Differences in maternal mass change and allocation to early and late-born young suggest that seasonal resource availability influenced tactics of resource storage and expenditure. Our results provide a mechanistic link between reproductive phenology, seasonal forage, and allocation trade-offs in wild mammals, and demonstrate a clear effect of maternal mass change on growth of young during a phase that occurs in utero for eutherian mammals.

Significance statement

Capital and income breeding are often presented as opposing tactics of resource provisioning. Many species, however, use a combination of stored and concurrent resources to reproduce. In seasonal environments, reproductive phenology should affect the relative timing of resource acquisition and expenditure, which could affect maternal allocation to offspring. We used repeated captures of mother-young kangaroo pairs and path analysis to explain how maternal allocation tactics adjust to season of parturition. Mothers that timed later lactation with cold weather and low winter forage relied more heavily on stored resources for reproduction and allocated less to offspring growth. Flexibility in foraging tactics may explain the variability in kangaroo parturition date by allowing mothers to use stored energy to sustain reproduction during periods of scarce forage.

Keywords Early growth rate · Income or capital breeding · Life-history theory · Maternal effects

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Communicated by C. Soulsbury

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00265-017-2419-9) contains supplementary material, which is available to authorized users.

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Introduction

Resource allocation among competing traits controls the life history of individuals, and therefore demography (Boggs 1992). When resource pools are restricted, different allocation tactics can prioritize survival or reproduction according to the residual reproductive value of parents and offspring (Hirshfield and Tinkle 1975; Brommer et al. 2000). For herbivores in seasonal environments, plant phenology affects foraging decisions and the quality and availability of resources to be allocated to successive stages of reproduction (Forchhammer 1995). When the season of high resource acquisition is shorter than an organisms' period of reproductive expenditure, stored "capital" resources can sustain reproduction during periods of restricted resource intake (Jönsson 1997; Oftedal 2000; Stephens et al. 2009). Hence, variation in reproductive phenology should affect the relative timing of resource intake and expenditure, leading to variation in resource storage and allocation.

To maximize lifetime fitness, most iteroparous mammals prioritize allocation of resources to survival over reproduction, by reducing maternal care when resources are scarce (Therrien et al. 2008). Hence, the survival of adult females should be canalized against environmental variation by a risk-avoidance reproductive strategy (Gaillard and Yoccoz 2003). Reduced allocation to offspring may, however, decrease pre- and post-natal growth rates, decreasing offspring fitness independently of post-weaning conditions (Boltnev et al. 1998; Lummaa and Clutton-Brock 2002; Beauplet et al. 2005). Faster post-natal growth is associated with higher fitness (Festa-Bianchet et al. 2000; Marcil-Ferland et al. 2013), but can be costly if it requires diversion of resources from somatic maintenance and reproduction (Dmitriew 2011), reducing lifespan (Metcalfe and Monaghan 2003).

Despite its probable fitness consequences, there are no longitudinal studies of maternal allocation during fetal development in wild free-ranging mammals, likely because it is extremely difficult to measure prenatal growth. Several studies made population-level inferences using cross-sectional data from culled pregnant animals (Skogland 1984; Reimers 1997; Christiansen et al. 2014), but none measured fetal growth directly. Others found that timing of birth relative to seasonal resources affected environment and maternal condition during gestation (Albon et al. 1983; Ceesay et al. 1997; Strand et al. 2011), which can affect size at birth (Lummaa and Clutton-Brock 2002), a possible proxy for fetal growth rate. Size at birth, however, is also dependent on gestation length, which is usually unknown. Mothers that adjust gestation length in response to timing of conception (Morel et al. 2002), forage availability (Holst and Allan 1992; West 1996), or to time birthdate with a local environmental optimum (Hogg et al. 2017), can affect offspring size at birth independently of fetal growth rate. The causal relationships (Pearl 2012) between reproductive phenology, foraging decisions and maternal allocation to early offspring growth, have not been examined.

Here, we use structural equation modeling (SEM) (Bollen and Pearl 2013; Shipley 2016) and repeated captures of wild eastern grey kangaroo (*Macropus giganteus*) mother-young pairs to uncover mechanisms explaining how reproductive phenology affects maternal allocation to offspring growth while young are completely dependent on maternal care. We expected a faster juvenile growth rate when mothers had access to more resources. We predicted that mothers with different reproductive phenologies would adopt different tactics of resource allocation.

Methods

Study species

Eastern grey kangaroos have a 36-day gestation and a 10-month pouch life period (Poole et al. 1982; King and Goldizen 2016), minimizing the effects of environment during gestation (Clements et al. 2011) and allowing measurement of young at very early stages of development. In marsupials, a long, maternally controlled lactation (Trott et al. 2003; Nicholas et al. 2012) accounts for the majority of maternal energy allocation to reproduction (Atramentowicz 1995; Kuruppath et al. 2012). Pouch young are protected from weather and consume only milk until first pouch exit (~ 9 months), when they resemble a newborn ungulate in size and development (Tyndale-Biscoe and Renfree 1987). Thus, environmental effects on early growth are transmitted solely through the mother, similar to fetal growth in eutherians. Despite the different schedules of allocation to gestation and lactation, weaning mass does not differ between the two infraclasses for similar-sized species (Hayssen et al. 1985). Kangaroos also share ecological and life-history traits with ungulates: they are herbivorous, long-lived and iteroparous (Jarman 1991). Growth during pouch life in marsupials is therefore likely to affect early survival and lifetime reproductive success similarly to fetal growth in eutherian ungulates.

Kangaroos likely exhibit a combination of income and capital breeding tactics (Stephens et al. 2009), as do some other mammals (Broussard et al. 2005; Lewis and Kappeler 2005; Wheatley et al. 2008). While fecundity may depend on prebreeding mass gain (Gélin et al. 2016), females also increased resource intake during lactation (Gélin et al. 2013). Finally, male pouch young grow faster than female pouch young (Poole et al. 1982), which may make males more susceptible to reduced maternal care in a poor environment (Byers and Hogg 1995; Garel et al. 2006).

Study area, population and environment

The study area is 1.5 km^2 of coastal grassland around an emergency landing strip in Wilsons Promontory National Park, southern Victoria (38° 56′ S, 146° 17′ E). The shrub-encroached grassland comprises sedges, herbs, ferns and grasses (Davis et al. 2010). The study population declined from 5.6 kangaroos/ha in spring 2013 (Glass et al. 2015) to 2.8 kangaroos/ha in autumn 2015; the lowest since quarterly monitoring began in 2009. For this study, we used data from the 2013 to 2016 cohorts.

Palatable forage was harvested from 50 systematically distributed, circular, wire-mesh 0.25 m^2 exclusion cages every January, April, July and October. We used clippers to cut the forage to ground level. Samples were combined to give the mean palatable forage growth per 1 m^2 since the previous sample. We calculated total forage growth between birthdate and capture as a large pouch young (LPY) for each mother-young pair using a forage accumulation curve (Online Resource 1; Fig. S1). To control for variability in intervals between birthdate and capture as an LPY, we divided the total forage accumulated since birth by the capture interval, obtaining a mean daily rate of forage growth.

Southern Victoria has a temperate climate (Stern et al. 2000). We used meteorological data from the Shallow Inlet (38° 47′ S, 146° 10′ E) and Corner Inlet (38° 48′ S, 146° 19′ E) weather stations of the Australian Government Bureau of Meteorology (http://www.bom.gov.au/climate/data/), 17 km and 19 km NW from our study area, respectively. Rainfall was the mean of both stations, but only temperature from Corner Inlet was used because Shallow Inlet lacked temperature data for some periods. Despite high yearly variability, summer is drier (median January rainfall = 42.5 mm) and warmer (median daily minimum temperature = 13.2 °C) than winter (median July rainfall = 97.2 mm; median daily minimum temperature = 7.5 °C). We calculated mean daily minimum temperature and mean daily rainfall between birthdate and date of LPY capture for each mother-young pair.

Captures

Mothers ($n = 54$) were immobilized by injection of Zoletil using a pole syringe (King et al. 2011), then marked with Allflex ear tags and collars (Gélin et al. 2016). Mothers were first captured when young in the pouch ($n = 68$) averaged 75 days old (SD = 32) and again when young were nearing first pouch exit (LPY mean age = 231 days, SD = 16). At each capture, we measured maternal mass to the nearest 0.25 kg. We also measured head, leg and foot length of the pouch young to the nearest millimeter following Poole et al. (1982). We compared body measurements of pouch young to growth models for captive kangaroos (Poole et al. 1982) to estimate age at each capture. Mother-young pairs were measured and weighed on location and released with the young in the pouch. It was not possible to record capture data blind because our study involved marked wild animals.

Growth curves from captive eastern grey kangaroos

Congruence between growth rates of captive and wild marsupials has previously been documented (Wood et al. 1983; Atramentowicz 1995) and may be explained by a buffered pouch environment (Delaney and De'ath 1990) or by high mortality of slow-growing young. Poole et al. (1982) constructed sex-specific hyperbolic growth models from weekly body measurements of 25 male and 22 female captive eastern grey kangaroos from multiple genetic lineages whose birthdates were exactly known. Age estimates derived from these models were used to construct latent variables of birthdate and pouch young growth.

Latent variables: birthdate and pouch young growth

Because we did not directly observe births, birthdate is a latent variable estimated with error (Shipley 2016). We estimated age of small pouch young (SPY) using non-linear growth models for captive young (Poole et al. 1982) for head, leg and foot length. We then subtracted these age estimates from the capture date to obtain three indicators of birthdate per pouch young. Birthdate was expressed in Julian days with 1 August as day 1, because only 2% of births in this population occur between June and September (King and Goldizen 2016).

Pouch young growth is also a latent variable because it can be measured in different ways (Shipley 2016). Growth is usually represented by change in length of body parts over time; here we investigated increases in head, leg and foot lengths from SPY to large pouch young (LPY) stages. We could not, however, simply use a linear rate of change of body size between captures, because growth during pouch life is non-linear and the rate of change is age-dependent. Instead, we relied on growth trajectories for captive young (Poole et al. 1982) to establish an expected pattern of growth and measured how much individual age estimates at capture as LPY deviated from the mean trajectory. A difference of 1 mm in head length is not comparable to a 1 mm difference in leg or foot length. Therefore, we used differences in ages estimated from size measurements to express all three indicators in the same unit, age in days:

$$\text{Growth Indicator}_{(i,j)} = \left(\text{age from length}_{(i)}\ \text{LPY}_{(j)}\right) - \left(\text{age from length}_{(i)}\ \text{SPY}_{(j)} + \text{interval}\right).$$

Hence, each indicator of latent growth was the difference between ages estimated from body length i for individual j

when captured as an LPY and as an SPY. Interval was the number of days between captures and was added to age estimated at SPY to obtain the age that we expected to estimate at LPY if the pouch young had followed the growth trajectory perfectly. Positive values indicated that young grew faster than predicted by the growth curves, while negative values indicated slower growth. A similar method, although not with a latent variable approach, was used to estimate pouch young growth in wild brushtail possums (*Trichosurus vulpecula*) (DeGabriel et al. 2009). Variance for both latent variables was set to one, allowing all indicators to load freely on the latent constructs (Shipley 2016).

Statistical analyses

We used structural equation modeling (SEM) and the package *lavaan* (Rosseel et al. 2015) in R version 3.2.4 (R Core Team 2016) to test effects of birthdate on growth from small pouch young (SPY) to large pouch young (LPY), nearing the age of pouch exit. SEM is ideal for testing complex directional hypotheses as it can measure chains of causal effects and indirect effects (Pearl 2012; Bollen and Pearl 2013), and permits the inclusion of latent variables (Lowry and Gaskin 2014). All variables were standardized (mean = 0, SD = 1).

Our path models tested the general prediction that resources available in the environment affected, through foraging decisions, the resources available for reproduction (Boggs 1992). We added an effect of timing of parturition on seasonal environmental resources, and measured allocation to reproduction as offspring growth between captures. The timing of birthdate determines the seasonal weather and forage production experienced during lactation. Mothers that time lactation with more favorable spring weather and greater forage availability should allocate more to pouch young growth, compared to mothers that time lactation with restricted winter plant growth. We included temperature, rainfall and forage independently in path models instead of using them as indicators of a latent variable “environment” because we were interested in their individual effects. We considered interaction effects between environmental variables by multiplying their standardized values and including the product as a new variable (Little et al. 2007). Models including rainfall and control variables of age at first capture and year were not coherent with the covariance structure of the data and were rejected ($\alpha = 0.05$). Seven alternate nested path models were coherent with the data, and included maternal mass change during lactation and an interaction between temperature and forage (Online Resource 1; Fig. S2). We compared models by Akaike’s information criterion corrected for sample size (AICc) (Shipley 2013) using the *AICcmodavg* package (Mazerolle 2015). Nested models were designed to test if indirect effects of birthdate on pouch young growth were transferred either sequentially through a chain of effects of environment on maternal mass change, or by a parallel direct effect of environment on pouch young growth. A parallel model structure suggests a risk-avoidance strategy, as environmental effects are passed directly by the mother to the young. We then used the highest-ranked model to investigate whether unmeasured maternal attributes affected parturition date, maternal mass changes and pouch young growth. We again performed model selection using AICc selection to test different patterns of free covariance between variables (Shipley 2016, pp. 103–104) while maintaining the causal structure selected for in the previous analysis. Finally, we used a multigroup approach (Shipley 2016) to investigate whether the expected faster growth rates of sons (Poole et al. 1982) made them more vulnerable than daughters to maternal mass loss or poor environment.

Data availability All data analyzed during this study are included in this published article and its supplementary information files (Online Resource 2).

Results

We recaptured 69 female-young pairs over 4 years (2013 to 2016), including 33 daughters and 36 sons. There were no recorded instances of multiple births. One mother-son pair was excluded, despite conforming to the tendencies of the path model, because the mother was the only primiparous female sampled. Hence, her mass increase was likely influenced more by size growth due to her young age than by seasonal variability, and inexperience could explain her late parturition, 45 days later than the next latest mother. Mean age of young did not differ by sex at SPY (*t* test, overall mean = 75 days, $t = -1.08$, df = 61, $P = 0.28$) or at LPY capture (*t* test, overall mean = 231 days, $t = -0.85$, df = 67, $P = 0.39$). Birthdate estimates at SPY capture ranged from 1 December to 15 May (mean = 9 January, SD = 35 days), and did not vary by year (ANOVA, $F(3, 68) = 1.4$, $P = 0.25$), and were 17 days later for daughters than for sons (*t* test, $t = 2.04$, df = 50, $P = 0.04$). Mean maternal mass at SPY capture was 28.2 kg (SD = 2.4) and mass change between captures ranged from − 4.0 to 2.0 kg (mean ± SD = − 0.6 ± 1.1 kg), with no year effect (ANOVA, $F(3, 68) = 1.6$, $P = 0.19$). Overall, 47 mothers lost mass, 6 maintained mass, and 15 gained mass. The mean (± SD) interval between captures was 156 ± 33 days. Pouch young growth did not vary with year (ANOVA, $F(3, 68) = 1.1$, $P = 0.38$) and was not correlated with interval between captures ($r_{\mathrm{Pearson}} = -0.18$, $P = 0.15$), age at SPY ($r_{\mathrm{Pearson}} = 0.16$, $P = 0.19$), or age at LPY capture ($r_{\mathrm{Pearson}} = -0.05$, $P = 0.68$).

The mean (± SD) difference between measured and expected age at LPY capture was 0.16 ± 11.36 days. Birthdate indirectly explained 30.5% of variance in growth between captures through parallel effects of maternal mass change and forage, moderated by temperature, during lactation (Fig. 1).

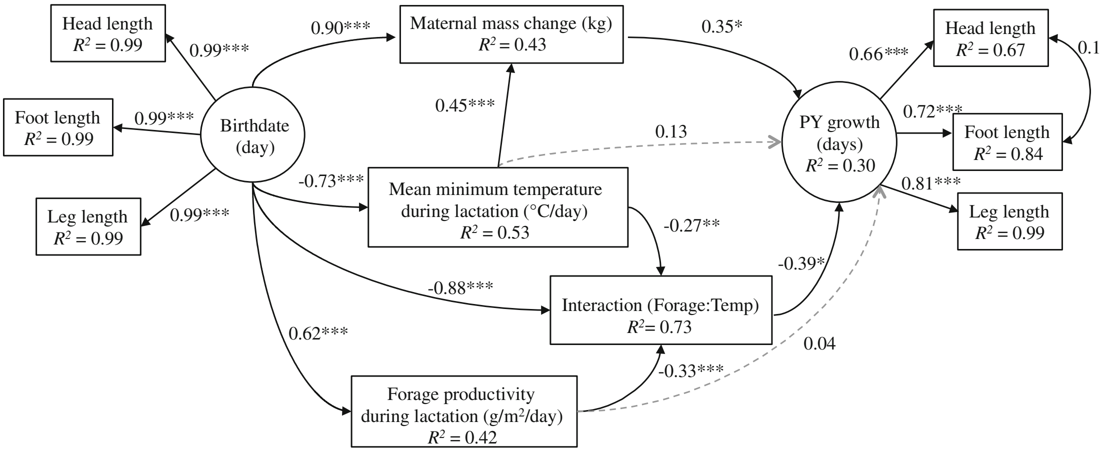

Fig. 1 Confirmatory structural equation model of the effect of birthdate on growth of eastern grey kangaroo pouch young (PY) through maternal and environmental effects. Birthdate and PY growth are latent variables (circles), each with three observed indicator variables. Birthdate was constructed from the age estimated at small pouch young (SPY) capture from measures of head, leg, and foot lengths applied to growth models for captive kangaroos. PY growth is the difference between measured and expected age at large pouch young (LPY) capture according to head, leg, and foot length measurements. Boxes represent observed variables and R^2 values show the variance explained by the effects of all causal parent variables. Solid black arrows indicate significant paths ($*P \leq 0.05$; $**P \leq 0.01$; $***P \leq 0.001$); grey, dashed arrows indicate paths that were not significant ($\alpha = 0.05$). Numbers on arrows are standardized effect coefficients. The double-headed arrow indicates a free covariance between PY growth as estimated from head and foot length. The structural model was the best supported of seven path models tested using Akaike's information criterion corrected for sample size (AICc) (Table 1) and is coherent with the data ($\chi^2 = 31.65$, df = 27, $P = 0.24$, $n = 68$)

Most mothers that gave birth later than 30 January gained mass during lactation (Fig. 2a) and their young grew faster than those born earlier (Fig. 2b). However, only 20.5% of mothers gave birth after 30 January, so most did not time parturition to favor seasonal mass increases that maximize pouch young growth. Furthermore, mothers that experienced relatively warmer temperatures for similarly-timed lactation periods (i.e., relatively warmer winter) also lost less mass (Online Resource 1; Fig. S2). In parallel, the increased forage availability associated with later summer and autumn birthdates improved pouch young growth independently of maternal mass change, but only when seasonal conditions were cooler (Fig. 3). The total indirect mean (± SE) standardized effect of birthdate on pouch young growth was 0.63 ± 0.19 ($Z = 3.3$, $P = 0.001$). The mean (± SE) effect of birthdate transmitted through maternal mass change was 0.20 ± 0.09 ($Z = 2.2$, $P = 0.03$), while that acting through forage was 0.43 ± 0.20 ($Z = 2.2$, $P = 0.03$).

The full model without the effect of the environmental interaction on maternal mass change (Online Resource 1 Fig. S2d) also had support (Table 1). However, the added effect of daily forage production on maternal mass change was not statistically significant. Furthermore, adding free covariance between parturition date, maternal mass change and pouch young growth did not improve model fit (Table 2).

Growth of sons was no more susceptible to harsh environment than that of daughters (Online Resource 1; Table S1). Multi-group models with effects allowed to vary according to pouch young sex did not explain more variance than the fully constrained model.

Discussion

Timing of parturition determined the food resources available to lactating mothers, and affected maternal mass change dynamics, which in turn affected maternal resource allocation to pouch young growth. The variation in reproductive phenology of eastern grey kangaroos allowed us to measure the effects of a difference in relative timing of resource intake and expenditure on resource storage and allocation to reproduction. All mother-young pairs were measured during the same reproductive stage: from undeveloped altricial young until near pouch exit. Yet, maternal mass change dynamics differed dependent on parturition date.

Mothers that gave birth in early summer moved into the costlier phase of lactation for older pouch young (Trott et al. 2003; Nicholas et al. 2012) in late winter, when forage was scarce. Nearly all of these early-timed mothers lost mass, suggesting that they relied on stored "capital" resources to sustain lactation (Bowen et al. 1992; Oftedal 2000). Conversely, late summer and autumn parturitions resulted in a net maternal mass gain during lactation, likely due to an alternative tactic of compensatory feeding (Jönsson 1997) on abundant spring forage. Indeed, kangaroo mothers with later-stage young increased foraging efforts compared to females without, or with younger, pouch young (Gélin et al. 2013). Food availability affects growth rate in juvenile primates (Altmann and Alberts 2005), and some ungulates (Andersen et al. 2000; Kerby and Post 2013) and other macropodid marsupials (Schwanz and Robert 2012) also rely on concurrent resources to offset the costs of lactation. The young of late-timed mothers that gained

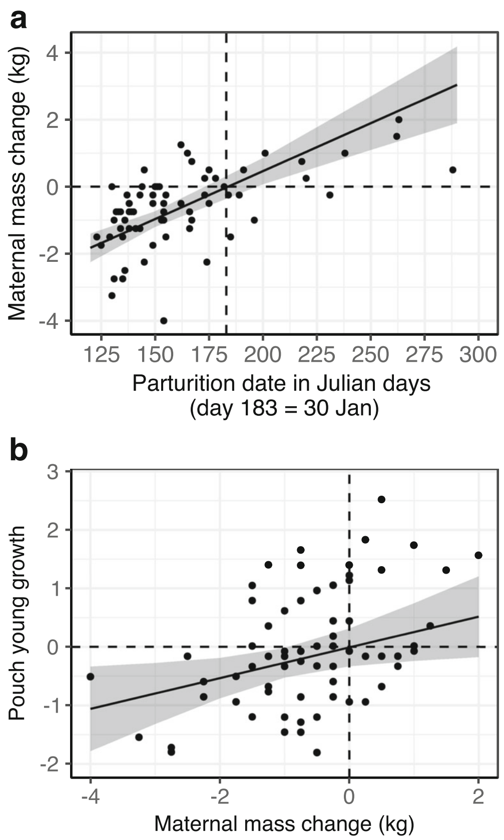

Fig. 2 Indirect effect of parturition date on growth of eastern grey kangaroo pouch young (PY) until first pouch exit via changes in maternal mass during lactation. Effects are unstandardized and taken from the path analysis (Fig. 1). **a** Maternal mass change during lactation as a function of parturition date, controlled for mean minimum temperature during lactation (shaded area, 95% CI). Horizontal dashed line indicates no net change in maternal mass during lactation. Vertical dashed line indicates 30 January, after which mothers tended to gain mass during lactation. **b** Effect of maternal mass change on PY growth (shaded area, 95% CI), controlled for direct environmental effects. Horizontal and vertical dashed lines indicate no deviation from growth as predicted by models derived from captive PY, and no net change in maternal mass during lactation, respectively. Latent PY growth is the difference in mean age estimates from leg, foot, and head measurements at large PY capture and expected age estimates according to age at small PY capture and days elapsed between captures

body mass also showed faster age-specific growth. This effect, however, was moderated by temperature, since for a given parturition date, mothers lost less mass in warmer years, leading to faster pouch young growth. Mothers that timed costly late lactation with abundant spring resources apparently allocated more to offspring growth than early-birthing mothers that used capital body stores to sustain lactation. Greater allocation may be expressed through better quality milk. For same-aged young, milk produced later in the spring has higher concentrations of lipids and protein, which are essential for offspring growth (Quesnel et al. 2017). Our study revealed different tactics of relative timing of resource acquisition and expenditure among individuals experiencing the same seasonal environment.

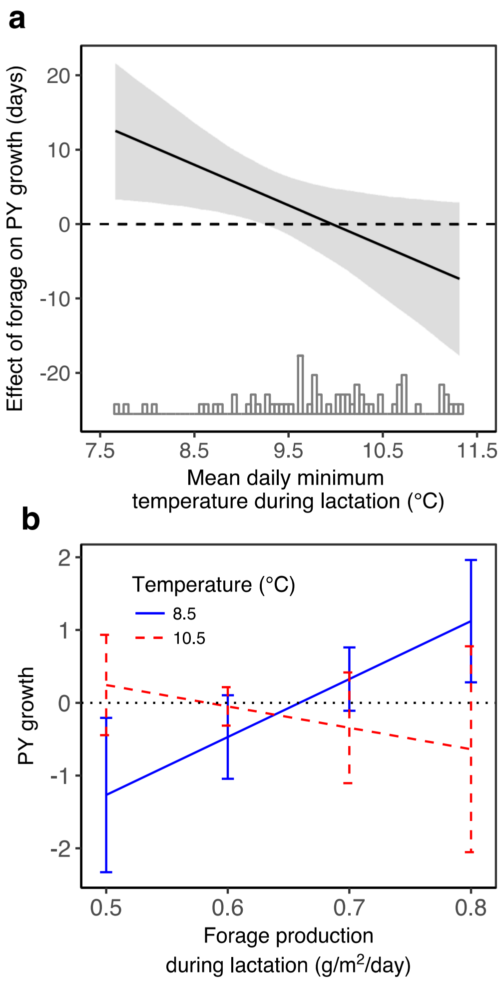

Fig. 3 Effect of daily forage production during lactation, moderated by mean daily minimum temperature, on growth of eastern grey kangaroo pouch young (PY). **a** Declining effect of forage on PY growth (measured – expected age at large PY capture) with increasing mean daily minimum temperature during lactation (shaded area, 95% CI). The histogram displays the distribution of mean minimum daily temperatures during lactation. **b** Effect of daily forage production during lactation on PY growth (a standardized latent construct) for high and low mean daily minimum temperatures, bars are 95% confidence intervals. Mean deviation from growth predicted by models derived from measures of captive kangaroos was 0.16 days (horizontal dotted line). One standard deviation of PY growth is 11.36 days

Parturition date explained 43% of the variance in maternal mass change. Unexplained variance could be due to individual differences in foraging strategies or nutrient gain efficiency (Boggs 1992). Greater net allocation to offspring growth does not necessarily indicate greater reproductive effort since late-born young may receive a smaller proportion of the overall resource pool (Brommer et al. 2000). Therefore, more information about total available resources and physiological efficiency of energy transfer to young (Boggs 1992) is required before drawing conclusions about differential reproductive effort for young with varying birthdates.

Table 1 Ranking of candidate models for effects of birthdate on growth of eastern grey kangaroo pouch young using Akaike's information criterion corrected for sample size (AICc), their number of estimated model parameters (*K*), and weights (*Wt*). The sequential models included indirect effects of birthdate (BD) that cascaded through mean minimum daily temperature (T) and mean daily forage produced during lactation (F) affecting maternal mass change (M), which in turn affected pouch young growth. In parallel models, the effects of birthdate passed independently through parallel paths of maternal and environmental variables. Full models included all possible effects found in sequential and in parallel models. Additional effects were added to the corresponding model base. The top-ranked model (Fig. 1) had a parallel base structure with an additional effect of temperature on maternal mass change. All models maintain the same latent variable structure as shown in Fig. 1. For the complete list of illustrated models and effects, see Online Resource 1 (Fig. S2)

Model base	Additional effects	*K*	AICc	ΔAICc	AICc *Wt*	Log likelihood
Parallel	(M~T)	38	818.06	0.00	0.63	− 364.05
Full		39	820.53	2.47	0.18	− 363.35
Sequential	(M~BD)	37	821.16	3.10	0.13	− 367.46
Full	(M~T:F)	40	824.57	6.51	0.02	− 363.35
Parallel	Base model	37	824.81	6.75	0.02	− 369.29
Parallel	(M~F)	38	826.14	8.08	0.01	−368.09
Sequential	Base model	36	837.31	19.25	0.00	− 377.32

Forage productivity directly affected pouch young growth, suggesting that kangaroo mothers exhibit a risk-avoidance reproductive strategy similar to that reported for ungulates (Gaillard and Yoccoz 2003; Therrien et al. 2008). Forage productivity interacted with seasonal temperature dynamics to influence resource allocation. During colder winters, maternal energy requirements for thermoregulation appeared to have priority over milk production, since the combination of low temperature and low forage directly reduced pouch young growth. The direct effect of forage on pouch young growth, not acting through maternal mass change, suggests that mothers allocated resources to body condition at the expense of maternal care, as reported for bighorn ewes (*Ovis canadensis*) (Festa-Bianchet and Jorgenson 1998; Martin and Festa-Bianchet 2010). By restricting allocation to reproduction in a harsh environment, female eastern grey kangaroos might maximize energy available for future reproduction (Hirshfield and Tinkle 1975; Brommer et al. 2000), should conditions improve. In primates, mothers that reconceived sooner invested less in their current infant's growth (Bowman and Lee 1995). Trade-offs between current and future reproduction are also expected in kangaroos, which must maintain or gain mass to successfully reproduce in the subsequent year (Gélin et al. 2016), and where the use of energy stores for reproduction establishes a common resource pool linking breeding attempts (Jönsson 1997). Our results support the hypothesis that highly iteroparous mammals should canalize adult survival against environmental variation to maximize fitness (Gaillard and Yoccoz 2003). Hence, the convergence of life-history traits between species could result in the convergence of reproductive strategies.

Allowing free covariance between pouch young growth and either birthdate or maternal mass change did not improve model fit (Table 2), but these models were equivalent and had essentially the same amount of support as the null model (Fig. 1). It is therefore likely that there remain unmodelled causal relationships between these three variables, possibly due to unmeasured maternal traits that affect both timing of parturition and pouch young growth. Despite the better understanding we have achieved through relatively simple path models, the unresolved covariance highlights the complexity of seasonal effects on aseasonal reproduction and resource allocation tactics.

Table 2 Ranking of candidate models for free covariance structures of the top-ranked path model (Fig. 1) for indirect effects of birthdate on growth of pouch young (PY) in eastern grey kangaroos using Akaike's information criterion corrected for sample size (AICc), their number of estimated model parameters (*K*), and weights (*Wt*). The null model does not allow covariance between residuals. Candidate models test free covariance between PY growth, maternal mass change (M), and birthdate (BD). All models maintain the same structural and latent variable models

Covariance structure	*K*	AICc	ΔAICc	AICc *Wt*	Log likelihood
Null	38	818.06	0.00	0.33	− 364.05
PYgrowth~~M	39	818.36	0.30	0.29	− 362.26
PYgrowth~~BD	39	818.36	0.30	0.29	− 362.26
M~~BD	39	821.93	3.87	0.05	− 364.05
PYgrowth~~M + BD	40	822.40	4.34	0.04	− 362.26
PYgrowth~~M + BD and M~~BD	41	826.61	8.55	0.00	− 362.26

The use of path analysis was essential to understand how reproductive phenology affected maternal allocation to reproduction, because it included indirect effects of birthdate on offspring growth. Strong indirect effects of birthdate on the growth rate of maternally dependent young were conveyed through maternal mass change and forage availability during lactation. Most females, however, gave birth earlier than expected if the timing of parturition was selected to maximize growth during pouch life, which is comparable to fetal growth in eutherians. We predict, therefore, that early parturition is likely to benefit other components of reproduction that outweigh the fitness costs of slower growth in the pouch. Synchronizing post-pouch lactation, which is comparable to lactation in eutherians, with spring forage could improve juvenile survival, and warrant the stored energy expenditure we observed in early-timed mothers (Hogg et al. 2017). Despite slower growth while in the pouch, early-born young may benefit from more time to grow prior to the subsequent winter, or from faster growth as young-at-foot, analogous to post-partum growth in young ungulates (Côté and Festa-Bianchet 2001; Feder et al. 2008). Hence, parturition cannot be timed to maximize growth at all stages of juvenile development, and future studies should focus on how birth timing leads to potential trade-offs between growth stages.

We used a latent variable for birthdate to reduce the potentially biasing influence of imperfect estimates. The high congruence between loadings of the three indicators for birthdate estimates at SPY capture reinforces our confidence in the accuracy of the estimates at this age. Higher precision in measurements of smaller pouch young, and a more constrained error in the growth model at younger ages (Poole et al. 1982), likely contribute to the congruence between indicators. Age estimates obtained from foot, leg, and head lengths at SPY capture were very similar (mean difference = 0.45 days). The short time between birth and capture likely restricted divergence from the predicted growth rate. Very early growth could also be less variable among individuals due to the lower energy required to carry and suckle the very small young in the first few months after birth (Trott et al. 2003; Nicholas et al. 2012), making environmental and maternal effects less likely to cause variation in growth at this stage. Eutherian mammals also exhibit low variability in early fetal development. In both reindeer (*Rangifer tarandus*) and red deer (*Cervus elaphus*), variation in fetal growth rate and effects of environment on birth mass were apparent only in the last third of gestation (Albon et al. 1983; Skogland 1984).

The use of sex-specific growth prediction models may explain why path coefficients were similar for both sexes, since the faster male growth rate was accounted for when predicting age at large pouch young (LPY) capture. The growth models were accurate in predicting the age of LPY nearing pouch emergence, particularly for young born near the mean parturition date of 9 January. The mean deviation between measured and expected age at LPY capture was 0.16 (95% CI: −2.64, 2.96) days. However, since parturition date explained a significant part of the variance in growth between captures, birthdate estimates of older pouch young from this population should be corrected to account for seasonal effects on growth.

Asynchronous parturition and a short gestation in kangaroos provided novel insight into the effects of phenology on tactics of maternal resource allocation to reproduction. Seasonal timing of birth strongly influenced growth indirectly through maternal mass changes and forage availability. Female eastern grey kangaroos exhibited flexibility in the use of income-capital resources to sustain reproductive efforts dependent on season of parturition. Kangaroo mothers used a risk-avoidance reproductive strategy, prioritizing body condition and opportunity for future reproduction over current reproduction in colder conditions. Our results provide a clear link between maternal resources and growth of young during a phase that occurs in utero for eutherian mammals.

Acknowledgements We acknowledge the important contributions of students and field assistants. We thank two anonymous reviewers for their insightful suggestions. L. Quesnel and W. King provided constructive comments on an earlier draft of the manuscript and helped with fieldwork. N. Davis assisted with vegetation monitoring, and B. Shipley provided guidance with analyses. This research was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC), the Australian Research Council (ARC) Linkage Program (LP0560344), the Ministère de l'Éducation, du Loisir et du Sport of Québec (MELS), Parks Victoria, the Quebec Center for Biodiversity Science, the University of Melbourne and the Université de Sherbrooke. We also acknowledge the logistical support provided by Parks Victoria.

Project funding This research was supported financially by the Natural Sciences and Engineering Research Council of Canada (NSERC), the Australian Research Council (ARC) Linkage Program (LP0560344), the Ministère de l'Éducation, du Loisir et du Sport of Québec (MELS), Parks Victoria, the Quebec Center for Biodiversity Science, the University of Melbourne and the Université de Sherbrooke. We appreciate the logistic support of Parks Victoria.

Compliance with ethical standards

Ethical approval All procedures involving animals were authorized by The University of Melbourne Animal Ethics Committee (protocol no.: 1312902.1) and by the Université de Sherbrooke Animal Care Committee (protocol no.: MFB2012-02), affiliated with the Canadian Council on Animal Care. All applicable institutional, national, and international guidelines for the care and use of animals were followed.

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

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