Experimental manipulation of female reproduction demonstrates its fitness costs in kangaroos

Uriel Gélin[1]*, Michelle E. Wilson[2], Graeme Coulson[2] and Marco Festa-Bianchet[1,2]

[1]Département de biologie, Université de Sherbrooke, 2500 boulevard de l'université, Sherbrooke, QC J1K 2R1, Canada; and [2]Department of Zoology, The University of Melbourne, Melbourne, Vic. 3010, Australia

Summary

1. When resources are scarce, female mammals should face a trade-off between lactation and other life-history traits such as growth, survival and subsequent reproduction. Kangaroos are ideal to test predictions about reproductive costs because they may simultaneously lactate and carry a young, and have indeterminate growth and a long breeding season.

2. An earlier study in three of our five study populations prevented female eastern grey kangaroos (*Macropus giganteus*) from reproducing during one reproductive season by either inserting contraceptive implants or removing very small pouch young. We explored how individual and environmental variables affect the costs of reproduction over time, combining this experimental reduction of reproductive effort with multi-year monitoring of 270 marked females. Experimental manipulation should control for individual heterogeneity, revealing the costs of reproduction and their likely sources. We also examined the fitness consequences of reproductive effort and offspring sex among unmanipulated individuals to test whether sex allocation strategies affected trade-offs.

3. Costs of reproduction included longer inter-birth intervals and lower probability of producing a young that survived to 7 months in the subsequent reproductive event. Weaning success, however, did not differ significantly between manipulated and control females. By reducing reproductive effort, manipulation appeared to increase individual condition and subsequent reproductive success.

4. Effects of offspring sex upon subsequent reproductive success varied according to year and study population. Mothers of sons were generally more likely to have a young that survived to 7 months, compared to mothers of daughters.

5. The fitness costs of reproduction arise from constraints in both acquisition and allocation of resources. To meet these costs, females delay subsequent parturition and may manipulate offspring sex. Reproductive tactics thus vary according to the amount of resource available to each individual, promoting a wide range in reproductive performance within and among individuals and populations.

Key-words: body condition, environmental effects, individual heterogeneity, *Macropus giganteus*, mammal, marsupial, reproductive costs, reproductive rate, sex allocation, trade-off

Introduction

The substantial energy costs of lactation (Robbins 1983; Oftedal 1985) should force a trade-off between current reproduction and other life-history traits such as growth, survival and subsequent reproduction (Roff 2002). Yet, correlative studies of wild animals often produce ambiguous results (Reznick 1985), probably because reproductive

costs are obscured by individual heterogeneity (Van Noordwijk & de Jong 1986; Beauplet *et al.* 2006; Weladji *et al.* 2008). Experimental manipulation is a powerful approach to examine fitness trade-offs while controlling for individual differences (Partridge & Harvey 1988; Reznick, Nunnev & Tessier 2000; Oksanen *et al.* 2001). Reproductive effort of birds, reptiles and small mammals can be manipulated by modifying clutch or litter size (e.g. Slagsvold 1984; Sinervo & DeNardo 1996; Koivula *et al.* 2003; Skibiel, Speakman & Hood 2013), but logistic difficulties have limited the number of manipulative studies of

wild large mammals (Tavecchia *et al.* 2005; Bårdsen *et al.* 2009; Cripps *et al.* 2011), which tend to be long-lived, highly iteroparous and often rely on body reserves to meet reproductive costs (Jönsson 1997). Large herbivores have a conservative reproductive strategy, favouring maternal over juvenile survival (Gaillard, Festa-Bianchet & Yoccoz 1998) contrary to small mammals (Koivula *et al.* 2003). Therefore, they may not show the same fitness trade-offs as other species and may respond differently to experimental manipulations (Partridge & Harvey 1988). For example, contraception of young feral sheep, *Ovis aries* (Tavecchia *et al.* 2005), did not reveal clear fitness trade-offs, possibly because it allowed some females in poor condition to survive. Furthermore, experimental manipulations of reproduction in wild animals can rarely attain the sample size required to examine how fitness trade-offs vary in response to individual and environmental changes (Partridge & Harvey 1988). In large mammals, female reproductive allocation is typically age-specific (Hamel & Côté 2009): reproductive strategies differ among individuals and over time, as resource availability or population density change (Schaik & van Noordwijk 1985; Ezard, Becker & Coulson 2007). Manipulative experiments under different environmental conditions are needed to better understand fitness trade-offs in species with conservative reproductive strategies (Clutton-Brock & Sheldon 2010). Longitudinal studies of marked individuals can also partly account for individual or environmental effects that may hide reproductive costs, through statistical control of confounding variables (Partridge & Harvey 1988; McNamara & Houston 1996; Clutton-Brock & Sheldon 2010). Few studies of large mammals, however, have monitored enough individuals to perform these analyses, and those studies have mostly concerned temperate ungulates or pinnipeds (Clutton-Brock & Sheldon 2010).

We explored the costs of reproduction in female eastern grey kangaroos (*Macropus giganteus*), combining experimental contraception with multi-year monitoring of hundreds of marked individuals in five populations. Kangaroos present several characteristics that make them attractive to test predictions about the cost of reproduction. First, they have an extended lactation and face the additional energy cost of carrying a young, which can be over a quarter of maternal mass, during lactation (Poole, Carpenter & Wood 1982). Two main stages can be used as a reference to measure reproductive success: survival to 7–8 months ('LPY' for 'large pouch young') and to weaning at 18 months of age (Poole 1982). Lactation until both reference points requires substantial energy expenditure: mothers nursing LPYs ingested 49% more forage in daylight (Cripps *et al.* 2011), and weaning a young led to increased bite rates 1 year later (Gélin *et al.* 2014). Survival to these two stages is likely affected by different factors: until the LPY stage, young are protected in the pouch, but between permanent pouch exit at about 11 months and weaning, the effects of environmental

conditions should increase. Secondly, unlike most mammals, female kangaroos have indeterminate growth (Poole, Carpenter & Wood 1982; Jarman 1983). The fitness cost of reproduction for eutherians is often more evident for small and growing females, which sustain the combined costs of reproduction and growth (Hamel & Côté 2009). Kangaroos, however, face a growth-reproduction allocation trade-off during each reproductive episode. Thirdly, kangaroos may breed all year, even though most births occur in summer (Poole 1982; 50; % of births were in December–January in our study), whereas most large mammals studied so far have a short breeding season, for example 2 weeks in bighorn sheep, *Ovis canadensis* (Feder *et al.* 2008). A longer breeding season may allow flexibility in the timing of reproduction, adjusting for previous reproductive effort. With highly seasonal reproduction, females cannot adjust reproductive timing according to individual resource acquisition. A delay of the next reproductive event in response to reproductive effort is common in species where births are not strictly seasonal (Cheney *et al.* 2004).

The source of variation in fitness trade-offs is of particular interest for understanding reproductive strategies of large mammals with long breeding seasons. These trade-offs have been investigated in correlative studies while controlling for individual and environmental characteristics to detect the cost of reproduction (Festa-Bianchet, Gaillard & Jorgenson 1998; Martin & Festa-Bianchet 2011; Hamel, Craine & Towne 2012). Very few experimental studies have been conducted to identify the possible sources of changes in reproductive performance of females (Bårdsen *et al.* 2009). No manipulative study has detected costs on subsequent reproduction in free-ranging mammals, and experimental evidence for fitness trade-offs remains scarce. Mass of breeding females that we monitored varied twofold, suggesting strong heterogeneity in individual reproductive potential. In addition, contracepted females gained more mass than controls (Gélin 2014). Body condition is an important determinant of reproductive success in many mammals (Gaillard *et al.* 2000). The cost of reproduction can also be affected by age-specific constraints in resource allocation (Martin & Festa-Bianchet 2011). Young individuals that need to grow generally allocate more resources to somatic functions than older individuals, leading to greater costs of reproduction (Hamel & Côté 2009). Reproductive costs may also increase with poor environmental conditions (Festa-Bianchet, Gaillard & Jorgenson 1998), which reduce resource acquisition (Gélin *et al.* 2013).

In polygynous and dimorphic mammals, sons usually carry a greater fitness cost than daughters (Bérubé, Festa-Bianchet & Jorgenson 1996; Rickard, Russell & Lummaa 2007; but see Byers & Moodie 1990). Male eastern grey kangaroos grow faster than females (Poole, Carpenter & Wood 1982), and as adults are more than twice as heavy (Weckerly 1998). Consequently, mothers of sons may need more resources than mothers of daughters, as suggested

by their higher bite rate (Gélin *et al.* 2013). The ability to provide greater care to sons may depend on maternal condition and environmental resources (Kruuk *et al.* 1999; Robert, Schwanz & Mills 2010), so that the higher cost of sons becomes obvious only when resources are limited. If mothers in poor condition tended to conceive daughters, however, they may show reduced subsequent reproductive success. Evidence of adaptive offspring sex-ratio manipulation remains inconsistent in sexually dimorphic mammals (Cameron *et al.* 2008), and its fitness consequences are seldom documented using longitudinal data in the wild (Clutton-Brock & Iason 1986; Bercovitch, Widdig & Nürnberg 2000; Martin & Festa-Bianchet 2010).

We sought to test the consequences of reproductive effort on success during the subsequent reproductive event and on inter-birth interval according to body condition, age and possible environmental variability related to study population and year. We predicted that previous reproductive effort would reduce subsequent reproductive success and increase inter-birth interval and that these effects would be stronger for mothers of sons compared to mothers of daughters. We also expected that the fitness costs of reproduction would be increased by poor body condition, young age and unfavourable environmental conditions.

Materials and methods

STUDY AREAS AND DATA COLLECTION

We monitored kangaroos in five populations in Victoria, Australia: Anglesea Golf Club (38°24′S, 144°10′E), Wilsons Promontory National Park (38°57′S, 146°17′E), Serendip Sanctuary (38°00′S, 144°24′E), Plenty Gorge Parklands (37°37′S, 145°06′E) and Yan Yean Reservoir (37°32′S, 145°09′E). The climate at all sites is temperate, with average annual rainfall ranging from 447 mm at Serendip to 1097 mm at Wilsons Promontory (Australian Bureau of Meteorology). Vegetation includes mostly grass at Anglesea (Wilson *et al.* 2013), grassy woodland at Serendip and Plenty Gorge (Wilson *et al.* 2013), a variety of grasses, sedges, herbs and ferns at Wilsons Promontory (Davis, Coulson & Forsyth 2008) and open forest and disturbed open woodland at Yan Yean (Ramp & Coulson 2002). According to ecological characteristics, Anglesea, Serendip and Plenty Gorge presented better environmental conditions than Yan Yean and Wilsons Promontory (Table 1).

We caught kangaroos by Zoletil injection, using a pole syringe (King *et al.* 2011) or in a draw-string trap (Coulson 1996). We marked individuals with a unique combination of coloured ear tags and collars and measured leg length and body mass (Poole, Carpenter & Wood 1982) at each capture. Females were usually captured a few weeks before conception (average capture date: November 28 ± 112 days, average parturition date: January 15 ± 61 days). The mass of breeding females ranged from 16 to 37·5 kg and leg length from 419 to 563 mm. We measured body condition using the 'scaled mass index' (Peig & Green 2009), a regression of individual mass and leg length controlling for the average leg length of each population (Table S1, Supporting information). We defined three age classes: 'young' females were

known-age individuals first caught as pouch young or subadults (≤20 kg), aged 2–6 years while reproductively active during our study. Other females were classified by incisor wear as 'old' (teeth missing or worn within 1–2 mm of the gum line) or 'prime-age' (Gélin *et al.* 2013). We documented up to 90 reproductive episodes by young females, 585 by prime-aged and 93 by old females, combining Anglesea, Promontory and Serendip where we monitored all age classes.

Presence, sex and survival of the young were determined at capture or through pouch observations. Birth date was estimated using growth curves from Poole, Carpenter & Wood (1982) for head, leg and foot measurements of pouch young and averaging the results. We coded date as Julian days with August 1 as day 1, because <5% of births were recorded in July or August. Nearly all females in our study populations had one reproductive cycle per year. Inter-birth intervals averaged 373 ± 52 days for females whose young were caught and aged in successive years.

We measured success at each reproductive episode according to whether or not a female had a young that survived to the LPY stage, with a fully furred head that often protruded from the pouch. We attempted to recapture the female at this stage to mark the young with small ear tags. For each reproductive episode, we classified females as unsuccessful (acronym NPY for 'no pouch young') if they did not reproduce or if their young disappeared before the LPY stage. We classified young as weaned if they survived to 18 months, about 5–7 months after permanent pouch exit (Poole 1982). For weaning success, unsuccessful females included those whose young died before weaning and those that did not reproduce. Our overall sample comprised 593 reproductive events by 270 females (Table 1).

EXPERIMENTAL MANIPULATION

An earlier study tested the effectiveness of contraceptives in female kangaroos in three of our study populations (Wilson 2012; Wilson *et al.* 2013; Table 1). Females considered in this study received deslorelin implants (2 × 4·7 mg, Suprelorin, a GnRH agonist; Peptech Animal Health, Macquarie Park, NSW, Australia), which were effective for about a year. Contracepted females did not differ from control females in sexual activity, social group structure (Wilson 2012), vigilance or foraging behaviour (Gélin *et al.* 2013). To ensure that contracepted females were capable of reproducing, implants were inserted only in females carrying a very small pouch young (mostly <2 months old) that was removed and euthanized at capture (Wilson 2012). To provide a control group to compare to contracepted females, a sample of females also had their very small pouch young euthanized. Among these females, we considered as 'manipulated' those that did not conceive again for at least 4 months (average 10 months), so that removal of pouch young had a similar effect to the contraceptive, as both groups of females did not conceive again until the following breeding season. We built upon those experimental manipulations of reproductive effort to test hypotheses about the cost of reproduction. We defined as manipulated all females that skipped at least one reproductive opportunity because their pouch young was removed, regardless of whether or not they received a contraceptive implant. Our analyses included only contracepted females that reproduced again after being treated. At Anglesea, we used data from three females with subcutaneous implants and 18 whose very small pouch young was removed. At Serendip, six females were implanted with deslorelin or their very

Table 1. Characteristics of the 5 kangaroo study sites in Victoria, Australia. Numbers of marked females and female years indicate site-specific total sample size. Sample sizes for each analysis are indicated in the text

Study areas	Years of monitoring	Marked females	female years	Manipulation	Density (kangaroos/ha)	Other characteristics
Anglesea Golf Club	2007–2012	85	201	Yes	4	Irrigated
Plenty Gorge Park	2007–2008	20	44	Yes	0·6	Abundant forage. Predators* removed by park management
Wilsons Promontory National Park	2008–2012	121	274	Yes	6	Predators* removed
Serendip Sanctuary	2007–2012	25	47	Yes	0·8	Culls to maintain low density. Predators* removed
Yan Yean Reservoir	1992–1998	19	27	No	2·2	Predators* removed

*Potential predators include dogs, *Canis familiaris*, and red foxes, *Vulpes vulpes*.

small pouch young was removed. At Plenty Gorge, 13 of 44 females were treated with deslorelin or had a very small pouch young removed. At Wilsons Promontory, six females that abandoned their large pouch young at capture were considered as manipulated. No females were manipulated at Yan Yean.

STATISTICAL ANALYSES

In a first step, we compared survival to LPY and to weaning of the young produced by manipulated females in the first year they reproduced after manipulation and by control females at their subsequent reproductive opportunity. We also compared inter-birth interval of females that had their young removed with that of control females, excluding one manipulated female whose inter-birth interval was much shorter (124 days) than for other manipulated females (average 333 ± 56 days). We monitored females with young-at-foot only at Anglesea and Wilsons Promontory and therefore restricted analysis of weaning success to those populations.

In a second step, we compared subsequent reproductive success 1 year (year 2) of unmanipulated females whose young reached the LPY stage and of females whose young failed to reach that stage or that had no young the previous year (year 1). We also compared subsequent reproductive success and inter-birth interval of unmanipulated mothers that weaned a young to females that failed to do so. The effect of survival to LPY on inter-birth interval could not be tested because successive birth dates were known only for five females whose young died before the LPY stage. We did not analyse weaning success in 2012 at Anglesea, because young from that cohort had not reached 18 months of age when data collection ended.

In a third step, we tested specific predictions about how the costs of reproduction were affected by environment-dependent constraints in resource acquisition at Wilsons Promontory, by testing for potential effects of years of study.

In a fourth step, we investigated the costs of reproduction according to offspring sex. We tested specific predictions about allocation and acquisition of resources by including the interactions between offspring sex in year 1 and year of study in affecting reproductive success in year 2 at Wilsons Promontory. We also present an analysis of an interaction between weaning success in year 1 and offspring sex in year 2 on bite rate of mothers, based on 316 focal observations of 49 individuals in 2010–2011 at Wilsons Promontory. Bite rate was measured during 10-min focal

samples, controlling for foraging time while the head was visible (Gélin *et al.* 2013).

We used generalized linear models for reproductive success, coded as a binary variable (LPY or not; weaning or not), and linear models for inter-birth intervals. Individual as a random effect was not significant in linear mixed models and was removed from subsequent analyses (Zuur *et al.* 2009). All analyses were performed with R version 3.0.3 (R Foundation for Statistical Computing, Vienna, Austria) and user interface Rstudio, version 0.98.501 (Rstudio Integrated Development Environment, Boston, MA, USA). Analyses accounted for variables known to affect reproduction, including pre-conception body condition, previous parturition date and study population. For each variable of interest, we began with a saturated model and then used reduced data sets excluding missing values to assess the influence of each independent variable by backward stepwise elimination of non-significant variables, leading to a minimal adequate model (Crawley 2007; Zuur *et al.* 2009). To control for seasonal effect on body condition, we used the residuals of the regression of a linear mixed models of scaled mass index as a function of capture date and the square of capture date with individual as random effect. We did not include results for unmanipulated females at Plenty Gorge because there was no variation in reproductive success; all females had an LPY in year 1. Only significant interactions were included.

Results

Compared to control females, manipulated females had a higher probability of having an LPY in year 2 and a shorter inter-birth interval, but their weaning success in year 2 did not differ (Tables 2 and 3). For control females, the effect of survival of the young in year 1 on the probability of having an LPY in year 2 differed between populations (survival to LPY: $N = 340$, $\chi_3^2 = 12·79$, $P = 0·005$; survival to weaning: $N = 258$, $\chi_1^2 = 6·51$, $P = 0·011$). Weaning success in year 2 was also affected differently by reproductive effort in year 1 according to population (survival to LPY: $N = 249$, $\chi_1^2 = 5·10$, $P = 0·024$; survival to weaning: $N = 221$, $\chi_1^2 = 5·33$, $P = 0·021$). These interactions, however, did not suggest a trade-off in reproductive success in consecutive years (Table 2). Instead, at Anglesea and Serendip, reproductive success in successive years was

Table 2. Proportion of eastern grey kangaroos females with a young that survived to the LPY stage and to weaning in year 2, and mean inter-birth interval according to reproductive effort in year 1. Panels report results according to (a) whether or not females were prevented from reproducing, (b) excluding manipulated ones, whether or not females had an LPY and (c) excluding manipulated ones, whether or not females weaned a young. Statistics are from GLM models (binomial distribution) controlling for pre-conception body condition and capture date in four populations (Anglesea, Wilsons Promontory, Serendip and Yan Yean), Victoria, Australia. Bold numbers indicate significant population-specific effects. The column 'Cost' reports the results of models including all populations (see text for details): 'Yes' indicates a cost of reproduction in year 1 on reproductive success in year 2 and 'No' an absence of cost. The number of female years is indicated in parentheses

| | Reproductive effort in year 1 | | | | | | | |
| | Anglesea | | Promontory | | Serendip | | | |
	No	Yes	No	Yes	No	Yes	Yan Yean	Cost
(a) Manipulation, %								
Survival to LPY in year 2	74 (86)	86 (21)	**55** (179)	**100** (6)	86 (22)	83 (6)	(no data)	Yes
Survival to weaning in year 2	20 (46)	20 (10)	34 (168)	33 (6)	(no data)			No
Birth interval (days)	368 (24)	331 (5)	384 (88)	352 (5)				Yes

| | Anglesea | | Promontory | | Serendip | | Yan Yean | | |
	No	Yes	No	Yes	No	Yes	No	Yes	Cost
(b) Survival to LPY, %									
Survival to LPY in year 2	**44** (16)	**78** (68)	59 (63)	55 (153)	**50** (8)	**90** (20)	75 (4)	63 (8)	No
Survival to weaning in year 2	**0** (11)	**23** (35)	34 (58)	34 (145)	(no data)		(no data)		No

| | Anglesea | | Promontory | | | | |
	No	Yes	No	Yes	Serendip	Yan Yean	Cost
(c) Weaning success, %							
Survival to LPY in year 2	**62** (34)	**93** (14)	56 (107)	59 (103)	(no data)	(no data)	No
Survival to weaning in year 2	**5** (20)	**38** (8)	34 (99)	37 (98)			No
Birth interval (days)	343 (8)	384 (3)	376 (28)	387 (59)			No

Table 3. Effects of reproductive effort in year 1 on reproduction in year 2 in female eastern grey kangaroos, controlling for pre-conception body condition and site effects in three populations (Anglesea, Wilsons Promontory and Serendip), Victoria, Australia. Estimates are based on GLM (binomial distribution) for survival to LPY and weaning success and LM for inter-birth interval

| | Reproductive success in year 2 | | | | | | | | |
| | Survival to LPY ($N = 320$) | | | Weaning ($N = 230$) | | | Inter-birth interval (days) | | |
Variables	Estimate (SE)	X^2 (df)	P	Estimate (SE)	X^2 (df)	P	Estimate (SE)	F (df)	P
Control compared to manipulated	−1·04 (0·57)	4·05 (1)	0·044	0·05 (0·62)	0·01 (1)	0·940	37·0 (15·5)	5·68 (1117)	0·019
Pre-conception body condition	0·24 (0·09)	7·99 (1)	0·005	0·14 (0·10)	2·04 (1)	0·153	−7·6 (4·8)	2·50 (1117)	0·117
Sites compared to Anglesea		16·03 (2)	< 0·001		3·06 (1)	0·080		2·07 (1117)	0·153
Wilsons Promontory	−0·94 (0·29)			0·66 (0·39)			14·5 (10·1)		
Serendip	0·50 (0·60)			NA			NA		
Previous birth date							−0·3 (0·1)	14·28 (1117)	< 0·001

positively correlated and there was no correlation at Wilsons Promontory and Yan Yean (Table 2). Survival of the young to weaning in year 1 did not affect the subsequent inter-birth interval (mean difference ± SE: 11 ± 10 days; $F_{1,94} = 1·11$, P = 0·29; Table 2). For unmanipulated females at Wilsons Promontory, survival of young to LPY ($N = 216$) was lower in 2011 (36%) compared to 2009,

2010 and 2012 ($\chi^2_3 = 17·43$, P < 0·001; respectively, 76%, 74% and 51%, Table S2, Supporting information) and increased with pre-conception body condition ($\chi^2_1 = 10·54$, P = 0·001), but was unaffected by age class ($\chi^2_2 = 4·38$, P = 0·11) or by survival of young to LPY the previous year ($\chi^2_1 = 0·14$, P = 0·70). Survival to weaning was lower for young born in 2011 and 2012 (13% and 26%) compared to

2009 and 2010 ($N = 203$; $\chi_3^2 = 20\cdot76$, $P < 0\cdot001$; 63% and 48%, Table S2, Supporting information) and tended to decrease for old compared to young and prime-aged females ($\chi_2^2 = 5\cdot07$, $P = 0\cdot079$; Fig. 1), while neither pre-conception body condition ($\chi_1^2 = 2\cdot06$, $P = 0\cdot15$) nor survival of young to LPY in year 1 ($\chi_1^2 = 0\cdot36$, $P = 0\cdot55$) had significant effects. The effect of weaning success on inter-birth interval varied among years ($F_{3,79} = 4\cdot72$, $P = 0\cdot004$) in a model including birth date of young in year 1. Inter-birth interval increased for females that weaned a young in 2011 and 2012, while in other years, the very few females that failed to wean their young had longer inter-birth interval (Fig. 2).

Considering only unmanipulated females at Anglesea and Wilsons Promontory, sex of young in year 1 had no effect on survival to weaning in year 2 ($N = 244$, $\chi_1^2 = 0\cdot50$, $P = 0\cdot48$) or on inter-birth interval ($F_{1,141} = 0\cdot28$, $P = 0\cdot60$) in a model accounting for pre-conception body condition in year 1 and population. Survival to the LPY stage in year 2, however, tended to be greater for females that had a son rather than a daughter in year 1 ($N = 310$, $\chi_1^2 = 3\cdot59$, $P = 0\cdot058$) when accounting for an interaction between population and pre-conception body condition ($\chi_1^2 = 7\cdot34$, $P = 0\cdot007$). Although the interaction between population and sex of young in year 1 did not have a significant effect on survival to LPY ($\chi_1^2 = 2\cdot72$, $P = 0\cdot099$), when populations were considered separately, mothers of daughter in year 1 had lower reproductive success in year 2 compared to mothers of sons at Wilsons Promontory (46% vs. 59%; $\chi_1^2 = 2\cdot89$, $P = 0\cdot004$). There was no effect of offspring sex at Anglesea (63% for both; $\chi_1^2 = 0\cdot01$, $P = 0\cdot94$).

At Wilsons Promontory, the effect of sex on survival of young to LPY ($N = 172$, $\chi_3^2 = 16\cdot30$, $P < 0\cdot001$; Fig. 3) and to weaning ($N = 161$, $\chi_2^2 = 8\cdot28$, $P = 0\cdot041$; Table S3,

Supporting information) in year 2 varied among years: mothers that had sons in 2008 had lower weaning success the following year than mothers of daughters, while the reverse occurred in 2009 and 2010. There was no apparent effect of offspring sex in 2011. Years 2008 and 2011 were characterized by low reproductive success and substantial mass loss by females (Gélin 2014; Table S2, Supporting information).

Fig. 2. Inter-birth interval as a function of weaning success in year 1 for 54 unmanipulated female eastern grey kangaroos monitored in 2008–2012 at Wilsons Promontory, Victoria, Australia.

Fig. 3. Probability to produce a young that survived to the Large Pouch Young (LPY) stage in year 2 as a function of sex of young born in 2008–2011 for 100 unmanipulated female eastern grey kangaroos of three age classes at Wilsons Promontory, Victoria, Australia.
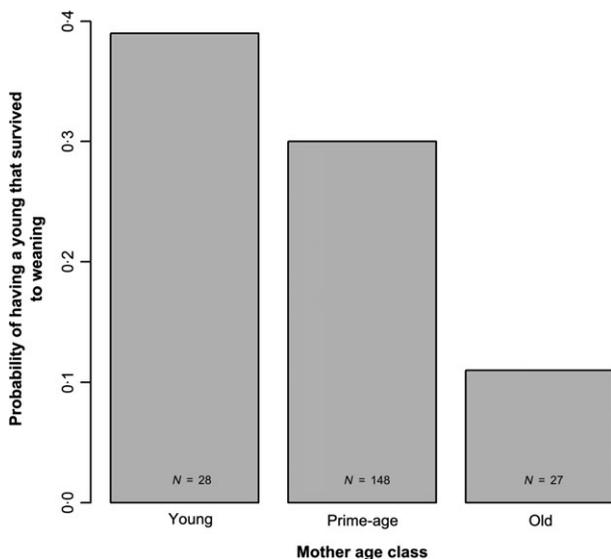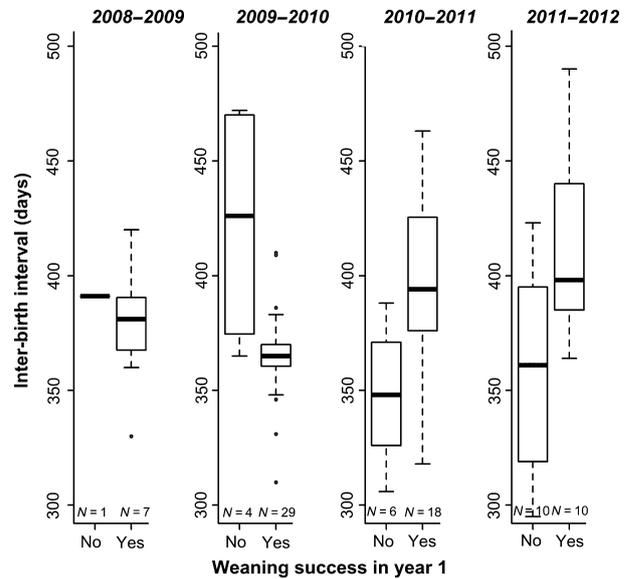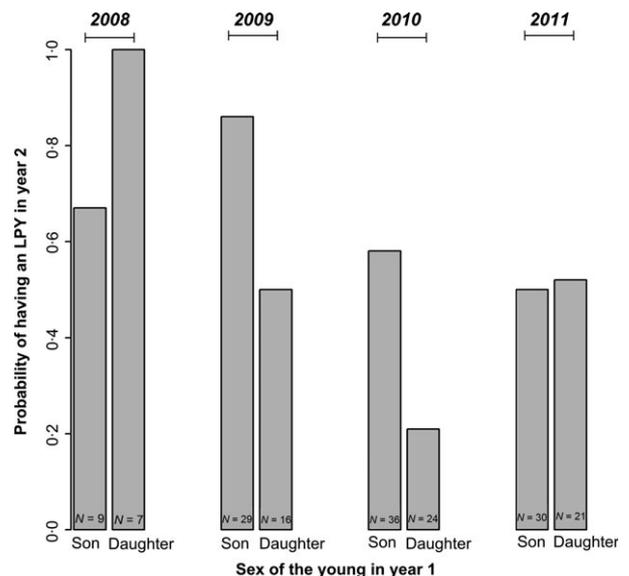

Fig. 1. Probability of having a young that survived to weaning in year 2 as a function of age class for 112 unmanipulated female eastern grey kangaroos at Anglesea, Victoria, Australia.

Bite rate of females at Wilsons Promontory was affected differently by weaning success in year 1 according to sex of current young ($F_{1,309} = 6.56$, $P = 0.010$), in a model including year (2010–2011), time of the day (A.M. or P.M.), duration of the observation and individual female as random effect. Compared to females that failed to wean a young, mothers whose young survived to weaning in year 1 increased bite rate in year 2 by 8% if nursing a sons but reduced it by 9% if nursing a daughter.

Discussion

By combining experimental manipulation of reproductive effort with long-term monitoring of multiple populations, we were able to quantify the fitness consequences of reproduction in a wild large mammal. Compared to control females, those whose reproductive effort was experimentally reduced had a higher probability of producing a young that survived to 7–8 months and a shorter inter-birth interval, but did not show increased weaning success. A comparison of subsequent reproductive success between control and manipulated females among populations, controlling for body condition pre-conception, suggested that the fitness cost of reproduction varied according to environmental conditions and operated by reducing individual condition, impairing the ability to reproduce in the subsequent year. Therefore, our experimental study identified improved body condition, resulting from reduced reproductive effort, as a source of the higher reproductive success of manipulated females, particularly under less favourable environmental conditions such as in the high-density population at Wilsons Promontory.

We also detected reproductive costs among unmanipulated females by accounting for individual characteristics and inter-annual differences. Our research identifies kangaroos as both income and capital breeders (Jönsson 1997), as reproductive success 1 year was affected by body condition the previous year only when resources appeared scarce. The effect of offspring sex on subsequent reproductive success varied according to population and year. Mothers of sons in year 1 were generally more successful in year 2 compared to mothers of daughters at Wilsons Promontory, but not in years where reproductive success was generally low.

EXPERIMENTAL MANIPULATION REVEALED FITNESS COSTS OF REPRODUCTION

Compared to manipulated females, control females were less likely to have an LPY in year 2 and had a lower reproductive rate, reflected in a longer inter-birth interval, consistent with correlative studies in other species (Albon, Mitchell & Staines 1983; Feder *et al.* 2008 but see Plard *et al.* 2014). Inter-birth interval was partly explained by the positive effect of body condition before conception, as reported in roe deer, *Capreolus capreolus* (Plard *et al.*

2014). Lactation generally lowers mass gain (Arnbom, Fedak & Boyd 1997), and our experimental manipulation of reproductive effort provided strong evidence of a negative effect of lactation on body condition (Gélin 2014). Direct hormonal effects of contraceptive implants on metabolism were unlikely because manipulated females did not differ in mass gain from those successful over two successive reproductive events (Gélin 2014). In addition, skipping one reproductive event may allow females to increase mass (Pomeroy *et al.* 1999), and mass gain is necessary to ensure reproductive success in female kangaroos (Gélin 2014). The effect of experimental manipulation on reproductive success was absent at Serendip, where most individuals were in good condition, and was weak at Anglesea, where irrigation may have increased grass availability (Tables 1 and 2; Table S1, Supporting information). The effect of manipulation on survival to LPY was more evident at Wilsons Promontory, where kangaroos were living at very high density and were in poor condition (Tables 1 and 2; Table S1, Supporting information), likely because reproductive effort lowered body condition and increase energetic requirements that could not be readily compensated by increased resource acquisition. Therefore, our results strongly suggest that the higher survival to LPY of young produced by manipulated females was due to an increase in maternal body condition resulting from a release from lactation the previous year. Nonetheless, in populations where resources were abundant because of low density or artificial irrigation (Table 1), some lactating females could compensate for the energy costs of reproduction without depleting their body condition. Substantial ecological differences among populations (Table 1) correlated with differences in body condition (Table S1, Supporting information) and reproductive success (Table 2, Tables S2 and S3, Supporting information), which also varied among years (Table S2, Supporting information), suggesting that costs of reproduction were affected by resource availability. Environmental stochasticity should favour a conservative maternal strategy in long-lived mammals if maternal care has limited effects on juvenile survival (Gaillard & Yoccoz 2003), possibly explaining the lower importance of body condition on weaning success and in populations with greater resource availability. The fitness costs of reproduction appear weak when body condition and resource availability are high, allowing most females to cope with the energetic costs of lactation (Festa-Bianchet, Gaillard & Jorgenson 1998).

Weaning success was not significantly affected by previous reproductive effort, perhaps because the smaller sample size decreased statistical power. Survival of juveniles after pouch exit may also depend less on maternal care and more on environmental effects, as implied by the strong yearly variability in survival to weaning (Table S2, Supporting information). In addition, factors such as predation by foxes (Banks, Newsome & Dickman 2000) may affect survival after pouch emergence independently of

maternal characteristics. We documented fox predation at both Anglesea and Wilsons Promontory, but could not quantify it.

Reproductive success among unmanipulated females was either not affected by or increased with previous reproductive effort. In correlative studies, individual heterogeneity often explains the apparent absence of trade-offs among life-history traits, as some individuals maintain a high reproductive rate independently of previous effort (Beauplet *et al.* 2006; Weladji *et al.* 2008). In addition, mass gain of female kangaroos was strongly correlated with subsequent reproductive success (Gélin 2014) as shown in other species (Glazier 1999). Hence, some mothers were able to maintain high reproductive success in successive years despite the costs of lactation, possibly by greater foraging skills or resistance to parasites and to other sources of mass loss (Illius *et al.* 1995). This could lead to positive or null correlation between successive reproductive events, respectively, in more (Anglesea and Serendip) or less (Wilsons Promontory and Yan Yean) favourable sites.

REPRODUCTIVE STRATEGIES: FLEXIBILITY IN SUBSEQUENT REPRODUCTION TO RECOVER BODY CONDITION

Gittleman & Thompson (1988) and Parker, Barboza & Gillingham (2009) showed that increase foraging effort may compensate for reproductive costs. Female kangaroos had a higher bite rate and increased time spent foraging when lactating (Cripps *et al.* 2011). Increased foraging effort is likely to partly satisfy the immediate energetic requirements for lactation, which may also vary across years (Gélin *et al.* 2013). By adjusting food intake, individuals may recover body condition and reduce the fitness costs of reproduction. Recovering body condition could, however, take substantial time. In eastern grey kangaroos, the energetic cost of successive reproductive events can overlap; for example, weaning success leads to an increase in bite rate the following year (Gélin *et al.* 2013). The substantial effect of reproductive costs on inter-birth interval and the importance of pre-conception body condition on reproductive success suggest that females delay subsequent reproduction to recover body condition. This hypothesis is also supported by the greater increase in inter-birth intervals in less favourable years (Table S2, Supporting information) with low reproductive success (2008 and 2011), lower mass gain (2011, Gélin 2014) and higher bite rate (2011, Gélin *et al.* 2013). A direct test of the effect of individual foraging strategy on mass gain and reproductive success, as suggested by Pianka (1976), is required to confirm this hypothesis. A reproductive strategy involving flexibility in inter-birth interval is likely widespread among mammals in moderately seasonal environment (Cheney *et al.* 2004). Species in highly seasonal environments face drastic changes in resource availability and cannot delay reproduction to

acquire more resources (Feder *et al.* 2008). Eastern grey kangaroos in our study areas can breed all year, but about 50% of births occur in December–January, suggesting that flexibility in birth timing is not unlimited. Thus, females unable to recover sufficient body condition may be forced to skip an annual reproductive opportunity, as shown in young mountain goats, *Oreamnos americanus* (Hamel, Côté & Festa-Bianchet 2010), and grey seals (Pomeroy *et al.* 1999).

REPRODUCTIVE STRATEGIES: FROM SEX ALLOCATION TO SEX-RATIO MANIPULATION

Contrary to our expectations based on results from other sexually dimorphic ungulates (Clutton-Brock, Albon & Guinness 1981; Bérubé, Festa-Bianchet & Jorgenson 1996), mothers of sons generally had higher subsequent reproductive success than mothers of daughters at Wilsons Promontory, consistent with the greater mass loss of mothers of daughters (Gélin 2014). The effect of previous offspring sex, however, disappeared in more limiting years and did not affect inter-birth interval. Therefore, the difference in reproductive success in year 2 probably did not arise from a higher investment in daughters than in sons in year 1. Instead, we suggest that mothers of sons have a higher reproductive potential (Robert, Schwanz & Mills 2010), which may be less evident in less favourable years when the costs of reproduction cannot be compensated through increased foraging effort. Cameron & Linklater (2007) showed that change in maternal body condition was a good predictor of offspring sex ratio in mammals. In eastern grey kangaroos, females in poor condition gained more mass if they had a daughter than a son (Gélin 2014). Females may manipulate offspring sex (Trivers & Willard 1973) based on their body condition to reduce the costs of reproduction, as shown for senescent bighorn ewes (Martin & Festa-Bianchet 2011). Poor environmental conditions decreased the proportion of sons produced by bridled nail-tail wallabies, *Onychogalea fraenata* (Fisher 1999), and red deer, *Cervus elaphus* (Kruuk *et al.* 1999). A similar manipulation may occur in kangaroos. Females unable to recover condition may produce a daughter to limit the cost of reproduction. In support of this hypothesis, mothers that weaned a young in year 1 had lower bite rate in year 2 if they had a daughter compared to a son.

In this large marsupial, reproductive effort decreased subsequent reproductive success by lowering body condition. Flexibility in timing of inter-birth interval suggests that kangaroos can recover body condition by increasing foraging effort. The seasonality of births, however, limits this tactic, probably because resource availability varies seasonally. Non-lactating females showed a decrease in bite rate from early to late spring, while lactating females maintained a high bite rate (Gélin *et al.* 2013). An increase in food intake may allow lactating females to recover or maintain body condition (Hamel & Côté 2009), which in large mammals is strongly linked to reproductive success

(Côté & Festa-Bianchet 2001). Therefore, to limit the mismatch between energetic requirements and food availability, females may vary resource allocation to reproduction by delaying subsequent parturition and producing the less costly sex. These complex patterns provide important insights into the reproductive strategies of large free-ranging mammals with long breeding seasons.

Acknowledgements

Data accessibility

Data available from the Dryad Digital Repository http://dx.doi.org/10.5061/dryad.58d51 (Gélin *et al.* 2014).

References

Albon, S.D., Mitchell, B. & Staines, B.W. (1983) Fertility and body weight in female red deer: a density-dependent relationship. *Journal of Animal Ecology*, **52**, 969–980.

Arnbom, T., Fedak, M.A. & Boyd, I.L. (1997) Factors affecting maternal expenditure in southern elephant seals during lactation. *Ecology*, **78**, 471–483.

Banks, P.B., Newsome, A.E. & Dickman, C.R. (2000) Predation by red foxes limits recruitment in populations of eastern grey kangaroos. *Austral Ecology*, **25**, 283–291.

Bårdsen, B.-J., Fauchald, P., Tveraa, T., Langeland, K. & Nieminen, M. (2009) Experimental evidence of cost of lactation in a low risk environment for a long-lived mammal. *Oikos*, **118**, 837–852.

Beauplet, G., Barbraud, C., Dabin, W., Küssener, C. & Guinet, C. (2006) Age-specific survival and reproductive performances in fur seals: evidence of senescence and individual quality. *Oikos*, **112**, 430–441.

Bercovitch, F.B., Widdig, A. & Nürnberg, P. (2000) Maternal investment in rhesus macaques (*Macaca mulatta*): reproductive costs and consequences of raising sons. *Behavioral Ecology and Sociobiology*, **48**, 1–11.

Bérubé, C.H., Festa-Bianchet, M. & Jorgenson, J.T. (1996) Reproductive costs of sons and daughters in Rocky Mountain bighorn sheep. *Behavioral Ecology*, **7**, 60–68.

Byers, J. & Moodie, J. (1990) Sex-specific maternal investment in pronghorn, and the question of a limit on differential provisioning in ungulates. *Behavioral Ecology and Sociobiology*, **26**, 157–164.

Cameron, E.Z. & Linklater, W.L. (2007) Extreme sex ratio variation in relation to change in condition around conception. *Biology Letters*, **3**, 395–397.

Cameron, E.Z., Lemons, P.R., Bateman, P.W. & Bennett, N.C. (2008) Experimental alteration of litter sex ratios in a mammal. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **275**, 323–327.

Cheney, D.L., Seyfarth, R.M., Fischer, J., Beehner, J., Bergman, T., Johnson, S.E. *et al.* (2004) Factors affecting reproduction and mortality among baboons in the Okavango Delta, Botswana. *International Journal of Primatology*, **25**, 401–428.

Clutton-Brock, T.H., Albon, S.D. & Guinness, F.E. (1981) Parental investment in male and female offspring in polygynous mammals. *Nature*, **289**, 487–489.

Clutton-Brock, T.H. & Iason, G.R. (1986) Sex ratio variation in mammals. *The Quarterly Review of Biology*, **61**, 339–374.

Clutton-Brock, T. & Sheldon, B.C. (2010) Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Special Issue: Long-Term Ecological Research*, **25**, 562–573.

Côté, S.D. & Festa-Bianchet, M. (2001) Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. *Oecologia*, **127**, 230–238.

Coulson, G. (1996) A safe and selective draw-string trap to capture kangaroos moving under fences. *Wildlife Research*, **23**, 621–627.

Crawley, M.J. (2007) *The R Book*. John Wiley & Sons, Chichester, UK.

Cripps, J.K., Wilson, M.E., Elgar, M.A. & Coulson, G. (2011) Experimental manipulation of fertility reveals potential lactation costs in a free-ranging marsupial. *Biology Letters*, **7**, 859–862.

Davis, N.E., Coulson, G. & Forsyth, D.M. (2008) Diets of native and introduced mammalian herbivores in shrub-encroached grassy woodland, south-eastern Australia. *Wildlife Research*, **35**, 684–694.

Ezard, T.H.G., Becker, P.H. & Coulson, T. (2007) Correlations between age, phenotype, and individual contribution to population growth in common terns. *Ecology*, **88**, 2496–2504.

Feder, C., Martin, J.G.A., Festa-Bianchet, M., Bérubé, C. & Jorgenson, J. (2008) Never too late? Consequences of late birthdate for mass and survival of bighorn lambs *Oecologia*, **156**, 773–781.

Festa-Bianchet, M., Gaillard, J.-M. & Jorgenson, J.T. (1998) Mass and density-dependent reproductive success and reproductive costs in a capital breeder. *The American Naturalist*, **152**, 367–379.

Fisher, D.O. (1999) Offspring sex ratio variation in the bridled nailtail wallaby, *Onychogalea fraenata*. *Behavioral Ecology and Sociobiology*, **45**, 411–419.

Gaillard, J.-M., Festa-Bianchet, M. & Yoccoz, N.G. (1998) Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology and Evolution*, **13**, 58–63.

Gaillard, J.-M. & Yoccoz, N.G. (2003) Temporal variation in survival of mammals: a case of environmental canalization? *Ecology*, **84**, 3294–3306.

Gaillard, J.M., Festa-Bianchet, M., Delorme, D. & Jorgenson, J. (2000) Body mass and individual fitness in female ungulates: bigger is not always better. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **267**, 471–477.

Gélin, U. (2014) *Stratégies de reproduction des femelles du kangourou géant (Macropus giganteus)*. PhD thesis, Université de Sherbrooke, Sherbrooke.

Gélin, U., Wilson, M.E., Coulson, G.M. & Festa-Bianchet, M. (2013) Offspring sex, current and previous reproduction affect feeding behaviour in wild eastern grey kangaroos. *Animal Behaviour*, **86**, 885–891.

Gélin, U., Wilson, M.E., Coulson, G.M. & Festa-Bianchet, M. (2014) Data from: Experimental manipulation of female reproduction demonstrates its fitness costs in kangaroos. *Dryad Digital Repository*. http://dx.doi.org/10.5061/dryad.58d51

Gittleman, J.L. & Thompson, S.D. (1988) Energy allocation in mammalian reproduction. *American Zoologist*, **28**, 863–875.

Glazier, D.S. (1999) Trade-offs between reproductive and somatic (storage) investments in animals: a comparative test of the Van Noordwijk and De Jong model. *Evolutionary Ecology*, **13**, 539–555.

Hamel, S. & Côté, S.D. (2009) Foraging decisions in a capital breeder: trade-offs between mass gain and lactation. *Oecologia*, **161**, 421–432.

Hamel, S., Côté, S.D. & Festa-Bianchet, M. (2010) Maternal characteristics and environment affect the costs of reproduction in female mountain goats. *Ecology*, **91**, 2034–2043.

Hamel, S., Craine, J.M. & Towne, E.G. (2012) Maternal allocation in bison: co-occurrence of senescence, cost of reproduction, and individual quality. *Ecological Applications*, **22**, 1628–1639.

Illius, A.W., Albon, S.D., Pemberton, J., Gordon, I.J. & Clutton-Brock, T.H. (1995) Selection for foraging efficiency during a population crash in Soay sheep. *Journal of Animal Ecology*, **64**, 481–492.

Jarman, P. (1983) Mating system and sexual dimorphism in large, terrestrial, mammalian herbivores. *Biological Reviews*, **58**, 485–520.

Jönsson, K.I. (1997) Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos*, **78**, 57–66.

King, W.J., Wilson, M.E., Allen, T., Festa-Bianchet, M. & Coulson, G. (2011) A capture technique for free-ranging eastern grey kangaroos

(*Macropus giganteus*) habituated to humans. *Australian Mammalogy*, **33**, 47–51.

Koivula, M., Koskela, E., Mappes, T. & Oksanen, T.A. (2003) Cost of reproduction in the wild: manipulation of reproductive effort in the bank vole. *Ecology*, **84**, 398–405.

Kruuk, L.E.B., Clutton-Brock, T.H., Albon, S.D., Pemberton, J.M. & Guinness, F.E. (1999) Population density affects sex ratio variation in red deer. *Nature*, **399**, 459–461.

Martin, J.G.A. & Festa-Bianchet, M. (2010) Sex ratio bias and reproductive strategies: what sex to produce when? *Ecology*, **92**, 441–449.

Martin, J.G.A. & Festa-Bianchet, M. (2011) Age-independent and age-dependent decreases in reproduction of females. *Ecology Letters*, **14**, 576–581.

McNamara, J.M. & Houston, A.I. (1996) State-dependent life histories. *Nature*, **380**, 215–221.

Oftedal, O.T. (1985) *Pregnancy and Lactation. Bioenergetics of Wild Herbivores*, pp. 215–236. CRC Press, Boca Raton, Florida, USA.

Oksanen, T.A., Jonsson, P., Koskela, E. & Mappes, T. (2001) Optimal allocation of reproductive effort: manipulation of offspring number and size in the bank vole. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **268**, 661–666.

Parker, K.L., Barboza, P.S. & Gillingham, M.P. (2009) Nutrition integrates environmental responses of ungulates. *Functional Ecology*, **23**, 57–69.

Partridge, L. & Harvey, P.H. (1988) The ecological context of life history evolution. *Science*, **241**, 1449–1455.

Peig, J. & Green, A.J. (2009) New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. *Oikos*, **118**, 1883–1891.

Pianka, E.R. (1976) Natural selection of optimal reproductive tactics. *American Zoologist*, **16**, 775–784.

Plard, F., Gaillard, J.-M., Coulson, T., Hewison, A.J.M., Delorme, D., Warnant, C. *et al.* (2014) Long-lived and heavier females give birth earlier in roe deer. *Ecography*, **37**, 241–249.

Pomeroy, P.P., Fedak, M.A., Rothery, P. & Anderson, S. (1999) Consequences of maternal size for reproductive expenditure and pupping success of grey seals at North Rona, Scotland. *Journal of Animal Ecology*, **68**, 235–253.

Poole, W.E. (1982) *Macropus giganteus*. *Mammalian Species*, **1887**, 1–8.

Poole, W.E., Carpenter, S.M. & Wood, J.T. (1982) Growth of grey kangaroos and the reliability of age determination from body measurements. I. The eastern grey kangaroo, *Macropus giganteus*. *Australian Wildlife Research*, **9**, 9–20.

Ramp, D. & Coulson, G. (2002) Density dependence in foraging habitat preference of eastern grey kangaroos. *Oikos*, **98**, 393–402.

Reznick, D. (1985) Costs of reproduction: an evaluation of the empirical evidence. *Oikos*, **44**, 257–267.

Reznick, D., Nunnev, L. & Tessier, A. (2000) Big houses, big cars, superfleas and the costs of reproduction. *Trends in Ecology & Evolution*, **15**, 421–425.

Rickard, I.J., Russell, A.F. & Lummaa, V. (2007) Producing sons reduces lifetime reproductive success of subsequent offspring in pre-industrial Finns. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **274**, 2981–2988.

Robbins, C.T. (1983) *Wildlife Feeding and Nutrition*. Academic Press, New York City, New York, USA.

Robert, K.A., Schwanz, L.E. & Mills, H.R. (2010) Offspring sex varies with maternal investment ability: empirical demonstration based on cross-fostering. *Biology Letters*, **6**, 242–245.

Roff, D.A. (2002) *Life History Evolution*. Sinauer Associates, Sunderland, Massachusetts, USA.

Schaik, C.P. & van Noordwijk, M.A. (1985) Interannual variability in fruit abundance and the reproductive seasonality in Sumatran Long-tailed macaques (*Macaca fascicularis*). *Journal of Zoology*, **206**, 533–549.

Sinervo, B. & DeNardo, D.F. (1996) Costs of reproduction in the wild: path analysis of natural selection and experimental tests of causation. *Evolution*, **50**, 1299–1313.

Skibiel, A.L., Speakman, J.R. & Hood, W.R. (2013) Testing the predictions of energy allocation decisions in the evolution of life-history trade-offs. *Functional Ecology*, **27**, 1382–1391.

Slagsvold, T. (1984) Clutch size variation of birds in relation to nest predation: on the cost of reproduction. *Journal of Animal Ecology*, **53**, 945–953.

Tavecchia, G., Coulson, T.N., Morgan, B.J.T., Pemberton, J.M., Pilkington, J., Gulland, F.M.D. *et al.* (2005) Predictors of reproductive cost in female Soay sheep. *Journal of Animal Ecology*, **74**, 201–213.

Trivers, R.L. & Willard, D.E. (1973) Natural selection of parental ability to vary the sex ratio of offspring. *Science*, **179**, 90–92.

Van Noordwijk, A.J. & de Jong, G. (1986) Acquisition and allocation of resources: their influence on variation in life history tactics. *The American Naturalist*, **128**, 137–142.

Weckerly, F.W. (1998) Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. *American Society of Mammalogists*, **79**, 33–52.

Weladji, R.B., Loison, A., Gaillard, J.M., Holand, O., Mysterud, A., Yoccoz, N.G. *et al.* (2008) Heterogeneity in individual quality overrides costs of reproduction in female reindeer. *Oecologia*, **156**, 237–247.

Wilson, M.E. (2012) *Fertility Control for Managing Eastern Grey Kangaroos (Macropus Giganteus)*. The University of Melbourne, Melbourne.

Wilson, M.E., Coulson, G., Shaw, G. & Renfree, M.B. (2013) Deslorelin implants in free-ranging female eastern grey kangaroos (*Macropus giganteus*): mechanism of action and contraceptive efficacy. *Wildlife Research*, **40**, 403–412.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G. (2009) *Mixed Effects Models and Extensions in Ecology With R*. Springer, New York City, New York, USA.

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Average body mass and body condition ± SD of breeding eastern grey kangaroo females in different study populations, Victoria, Australia. Body condition was estimated by the scaled mass index (Peig & Green 2009).

Table S2. Survival of the young to LPY stage, to weaning, interbirth interval, annual mass gain and bite rate as function of year in female eastern grey kangaroos at Wilsons Promontory, Victoria, Australia.

Table S3. Survival of the young to weaning in years 2009–2012 as function of year and sex of young the previous year in female eastern grey kangaroos at Wilsons Promontory, Victoria, Australia.