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Offspring sex, current and previous reproduction affect feeding behaviour in wild eastern grey kangaroos

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In mammals, lactation is the most energetically demanding component of female reproduction. Theory predicts an increase in food intake by lactating females, but very few studies have used contraceptives to experimentally test the influence of reproduction on foraging behaviour of wild mammals. From 2009 to 2011, we observed 182 individually marked female eastern grey kangaroos, *Macropus giganteus*, in two populations, including 29 that received an experimental contraceptive treatment. We sought to determine whether lactating females increase their foraging rate compared to contracepted and naturally nonlactating females. The proportion of time spent foraging during 10 min focal samples did not vary according to reproductive status in one population. In the other, lactating females spent 4% less time feeding than nonlactating females. Day and midday activity and bite and chewing rates were higher in lactating than in nonlactating females. Bite rate increased with the size of the pouch young and was higher for mothers of sons than for mothers of daughters. Bite rate was also affected by reproductive effort in the previous year, being higher for females that had weaned a young. Foraging behaviour was independent of body mass and group size, but bite rate appeared to decrease with female age. In one population, we found strong effects of date and year on foraging behaviour. Our study is a rare experimental manipulation of reproduction in free-ranging large mammals. We found that foraging behaviours were affected by both previous and current reproductive effort and varied with individual characteristics and environmental conditions.

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Life history theory predicts trade-offs between survival, growth and reproduction when resources are limited (Stearns 1992). In mammals, lactation is very demanding (Oftedal 1985), increasing energy expenditure four to seven times over basal metabolic rate (Robbins 1983). For example, allocation of resources to reproduction has been shown to reduce female mass in red deer, *Cervus elaphus* (Clutton-Brock et al. 1982) and bighorn sheep, *Ovis canadensis* (Festa-Bianchet et al. 1995). These energetic costs could have fitness consequences, because body mass also increases reproductive success and longevity in these species (Festa-Bianchet 1998; Nussey et al. 2011). To compensate for the energetic demands of reproduction, mothers usually increase feeding (Jönsson 1997), possibly forcing trade-offs with other activities, such as vigilance (Illius & Fitzgibbon 1994). Lactating females may increase their foraging time (MacWhirter 1991; Hamel & Côté 2008), forage more intensively (Ruckstuhl & Festa-Bianchet 1998; Cripps et al.

2011), increase their chewing rate (Hamel & Côté 2009) or select high-quality food (Neuhaus & Ruckstuhl 2002).

Most studies of foraging behaviour of reproducing and non-reproducing wild female mammals, however, have relied on natural variation, so have been potentially confounded by individual differences in reproductive potential (Tavecchia et al. 2005). Experimental manipulation of reproductive effort may control for this variability, but only two studies have used contraception to investigate how foraging behaviour in free-ranging mammals is affected by reproductive status: MacWhirter (1991) on Columbian ground squirrels, *Spermophilus columbianus*, and Cripps et al. (2011) on eastern grey kangaroos, *Macropus giganteus*. These short-term studies, however, had small sample sizes and could not account for the effects of several potentially important individual characteristics and environmental factors. Therefore, we know very little about how females may alter foraging behaviour to compensate for the energetic costs of reproduction. To overcome these limitations, we undertook 3 years of intensive observations of a large sample of individually marked female eastern grey kangaroos, including some that had experimentally been prevented from reproducing. We sought to investigate how current and previous reproduction affected foraging behaviour.

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Kangaroos are gregarious marsupial herbivores that are particularly suitable for the study of foraging behaviour, because they graze in open habitat and are easily observable (Coulson 2009). Gestation lasts 36 days, but lactation can be up to 18 months (Poole 1975), and the development of the young is easily observable in the pouch and after pouch exit (Cripps et al. 2011). Lactating marsupials typically increase feeding. Cork (1991) found that food and energy intake of tamar wallaby, *Macropus eugenii*, mothers were similar to those of nonlactating females while the pouch young was small, but as the growth rate and size of the young increased, so did food intake by mothers, keeping pace with requirements for milk production. These results were supported by observations in free-ranging eastern grey kangaroos (Cripps et al. 2011). Therefore, we predicted an increase in foraging with the presence of a pouch young and as its size increased.

In addition to its size, sex of the current young may influence foraging behaviour. Trivers & Willard (1973) suggested that in polygynous and sexually dimorphic species, mothers should provide greater care to sons than to daughters (Clutton-Brock et al. 1981). If mothers of sons need more resources than mothers of daughters, they may increase foraging effort. In mammals, the evidence for effects of offspring sex on maternal feeding behaviour is equivocal. Lamb sex does not affect foraging behaviour of bighorn ewes (Ruckstuhl & Festa-Bianchet 1998). In Antarctic fur seals, *Arctocephalus gazella*, sex-biased differences were found in the duration of maternal foraging trips in only one of 3 years (Lunn & Arnould 1997). In mountain goats, *Oreamnos americanus*, however, mothers of sons spend more time foraging than mothers of daughters (Hamel & C t  2008). Because male kangaroos grow faster than females during the pouch stage (Poole et al. 1982), we predicted that mothers of sons would display greater foraging effort than mothers of daughters.

In large herbivores, the cost of reproduction generally involves a reduction in future reproduction rather than a reduction in maternal survival (Martin & Festa-Bianchet 2010). No study, however, has examined how one reproductive event may affect foraging behaviour during the subsequent event. We therefore examined whether the foraging behaviour of kangaroo females differed according to both current and previous reproduction.

METHODS

Study Areas and Data Collection

We monitored eastern grey kangaroos at two sites in Victoria, Australia: Anglesea Golf Club (38°24'S, 144°10'E) and Wilsons Promontory National Park (38°57'S, 146°17'E). Population densities were, respectively, approximately four and six individuals/ha. The climate is temperate, with an annual range of mean maximum monthly temperatures of 13–23 °C and 12–21 °C, respectively, and annual rainfall of 814 mm and 1097 mm (<http://www.bom.gov.au/climate/data/>). Vegetation includes mostly grass at Anglesea (Inwood et al. 2008), and a variety of grasses, sedges, herbs and ferns at Wilsons Promontory (Davis et al. 2010). Potential predators included domestic dogs, *Canis familiaris*, at Anglesea and red foxes, *Vulpes vulpes*, at both sites.

We captured kangaroos by Zoletil injection using a pole syringe (King et al. 2011). We marked 511 sexually mature individuals with a unique combination of coloured eartags and collars, and collected standard morphometric measurements including mass at each capture. We also gave animals an incisor wear score of 0 (severely worn and/or missing) to 3 (almost no wear) at each capture. At Anglesea, 29 females had received subcutaneous implants of either deslorelin (2 × 4.7 mg, Suprelorin, a GnRH agonist, Peptech Animal Health, Australia) or levonorgestrel (3 × 70 mg,

Norplant II, a progestin, Leiras, Finland) contraceptives to prevent them from breeding (Wilson 2012; Wilson et al. 2013). No females were manipulated at Wilsons Promontory, and environmental conditions were different; therefore, the two sites were analysed separately. Sex of the young was determined at capture. We assigned females to three age classes: 'young' females were known-age individuals first caught as pouch young or subadults; others were classified by incisor wear as 'prime-age' (score 1–2.5) or 'old' (score 0–0.5). We defined 1 August as day 1 for 'date of observation'.

Observations lasted from late August to early December in 2009–2011, corresponding to the Austral late winter to early summer. We observed the behaviour of marked females through binoculars (10 × 42). We recorded 10 min focal samples on a tape recorder in 2009 and by video camera in 2010–2011. If the focal animal disappeared or was interrupted for more than 1 min by interspecific interactions, we discarded the observation and resampled the animal. Observations that lasted less than 10 min were not used in analysis. We calculated total time spent feeding, vigilant, number of bites, chews and steps during samples (Martin & Bateson 1993). We recorded chewing when individuals stopped foraging and started to chew mouthfuls of forage. A female was considered vigilant when she raised her head. Following Jaremovic & Croft (1991), we classified young as small pouch-young (SPY), medium pouch-young (MPY), large pouch-young (LPY), and young-at-foot (after permanent emergence from the pouch, YAF). Females with SPY, MPY, LPY and YAF are referred to as lactating females. These stages of young development are easily distinguished, allowing us to test whether foraging behaviours changed with the size of young. Nonlactating females included contracepted as well as unmanipulated females that had lost their young (no pouch young, NPY). Nine females that showed no evidence of reproduction for a given year and for which we had behavioural observations were excluded from analyses. At Anglesea, most mothers were expected to be at the peak of lactation because they had large pouch-young or recent young-at-foot during observations. Young that survived to 18 months were considered weaned. Although females can give birth as soon as their current young leaves the pouch at about 10 months of age, during our study most females gave birth to one young/year. The correlation between mass measurements of the same female collected 10–15 months apart was >0.80 at both sites.

We conducted observations over one session/year between October and early December at Anglesea and over three sessions at Wilsons Promontory: late August to mid-September (late winter), late September to mid-October (early spring) and late October–November (late spring). We defined a group as two or more individuals within 10 m of each other (Carter et al. 2009). Group size varied from 2 to 100. At both sites, we collected focal observations during daytime, from 0500 to 1000 hours and from 1600 to 2200 hours, when most kangaroos were active. Kangaroos were habituated to people and were observed at distances of 10–100 m. Foraging and chewing were coded as two independent behaviours. We could measure bite and chewing rates only when the kangaroo's head was visible. For the analysis of bite rate, we only considered observations with at least 3 min of feeding while the head was clearly visible, and for the analysis of chewing rate, we only considered observations with at least 30 s of chewing with the head clearly visible. As the length of time visible for both behaviours varied among observations, it was included in statistical models. As a result, bite and chewing rates were defined as the number of chews and bites statistically controlling for the amount of time when they could be observed. There was no difference between the number of steps taken by lactating and nonlactating females, so the results are not reported. We did not look for an

effect of offspring sex at Anglesea because in many cases the sex was unknown as few females were recaptured.

In 2009 and 2010, we surveyed the 73 ha Anglesea golf course 7–27 times/day between 0630 and 2015 hours. One observer walked slowly over half of the golf course, noting the identity and activity of every individual seen. Activity was a binomial variable, foraging or not. Scans lasted 15–60 min. We divided the day into five periods of 2.75 h each for analysis.

Statistical Analyses

We coded focal observations using JWatcher v.1.0 (Blumstein et al. 2006). We used linear mixed models (LMM) to analyse the data for feeding and vigilance duration and bite and chewing rate. We used generalized linear mixed models (GLMM) to analyse foraging activity. In both cases, we included individual as a random effect to control for pseudoreplication because we had repeated observations of the same animal (on average, at least three observations/individual depending on the type of behaviour). We investigated intraindividual variation in bite rate between lactating and nonlactating females, or according to the size of the young, using a reduced data set of females observed in both the first and the last session at Wilsons Promontory. Linear models allowed us to control for factors known to affect reproductive costs and foraging behaviours in large mammals. Intrinsic factors included age and body mass of breeding females. Extrinsic factors were year of observation, session, date, time of day, temperature and group size. These factors were included in models as appropriate based on expectations from the literature (intrinsic factors: Ruckstuhl 1998; Kamilar & Pokempner 2008; Bårdsen et al. 2009; Hamel & Côté 2009; extrinsic factors: Southwell 1987; McCullough & McCullough 2000; Banks 2001; Ramp & Coulson 2002). Multiple comparisons used Tukey's post hoc test for bite rate at Wilsons Promontory (see Results, Table 2) for factors with more than two categories. *P* values are reported with two decimals for nonsignificant variables and with three decimals for variables included in the final model.

Chewing rate was square-root transformed to meet normality. We performed all analyses with R v.2.14.1 (R Foundation for Statistical Computing, Vienna, Austria) and user interface Rstudio v.0.97.551 (RStudio Integrated Development Environment, Boston, MA, U.S.A.). The effect of lactation on vigilance was tested independently of confounding factors and restricted to comparing lactating and nonlactating females. For every other behavioural variable of interest, we began with a saturated model, then used reduced data sets, excluding missing values, to assess the influence of each independent variable by backward stepwise elimination of nonsignificant variables, leading to the minimal adequate model (Crawley 2007; Zuur et al. 2009). Because not all parameters included in models were available for all observations, as some nonsignificant variables were progressively excluded, sample size for each tested variable could increase. Bite rate was included in the final models explaining variability in chewing rate to distinguish between the effects of increased food intake and other possible consequences of lactation.

From maximal models including all categories of reproductive status (NPY, pooling contracepted and females that lost their young, SPY, MPY, LPY, YAF), we selected a smaller number of categories when standard errors of the means of different categories overlapped and pooling did not increase residual deviance as tested by ANOVA (Crawley 2007). Thus, differences between categories were more likely to reflect actual biological consequences of different levels of reproductive expenditures, rather than the somewhat arbitrary stages of development we initially selected. Results of the pooling exercise (Supplementary material, Tables S2–S8) differed

according to the type of comparison, although typically our analyses either compared lactating and nonlactating females, or mothers of large young (LPY and YAF) to nonlactating females pooled with mothers of small young (SPY and MPY). We investigated the significance of individual as a random effect by comparing models with and without the random effect using a likelihood ratio test (Steele & Hogg 2003; Supplementary Table S1).

RESULTS

Anglesea: Experimental Manipulation of Reproduction

Daily activity

The probability that a female was seen feeding during scan samples ($N = 2415$ sightings) was independent of her mass ($X^2_1 = 1.00$, $P = 0.32$) or group size ($X^2_1 = 1.56$, $P = 0.21$). It was also not affected by interactions between year and reproductive status ($X^2_1 = 1.66$, $P = 0.20$) or between temperature and reproductive status ($X^2_1 = 0.40$, $P = 0.53$). The best model (Table 1) included female reproductive status (LPY/YAF compared to all others: $X^2_1 = 77.20$, $P < 0.001$), maximum daily temperature (range 15–31 °C; $X^2_1 = 2.40$, $P = 0.121$), year of observation (2009–2010; $X^2_1 = 39.88$, $P < 0.001$), categories of time (1–5; $X^2_4 = 60.53$, $P < 0.001$), the interaction between time and temperature ($X^2_4 = 59.97$, $P < 0.001$), and individual as a random effect ($X^2_1 = 60.80$, $P < 0.001$; Supplementary Table S1). Controlling for temperature, time and year, females with large pouch-young and young-at-foot were more likely to be foraging (80%) than were nonreproducing females or females with small/medium pouch-young (64%) (Table 1). Females reduced foraging activity between 0915 and 1730 hours. On hot days, they reduced activity even further between 1200 and 1730 hours (Table 1).

Feeding and vigilance

The best model of variability in feeding duration ($N = 478$ observations), which included year (2009–2011), was not improved by the addition of number of steps ($F_{1,126} = 0.07$, $P = 0.80$), female mass ($F_{1,130} = 0.85$, $P = 0.36$), period of the day (morning or evening: $F_{1,301} = 0.56$, $P = 0.56$), female age class ($F_{2,304} = 4.76$, $P = 0.09$) or group size ($F_{1,349} = 1.84$, $P = 0.17$). Controlling for year ($F_{1,392} = 27.25$, $P < 0.001$), date ($F_{1,392} = 3.77$, $P = 0.052$) and individual random effects ($X^2_1 = 2.81$, $P = 0.09$; Supplementary Table S1), lactating females spent 4% less time feeding than nonlactating females ($F_{1,392} = 4.37$, $P = 0.04$). Vigilance duration ($N = 478$) was not affected by lactation ($F_{1,395} = 1.89$, $P = 0.17$). Females spent on average 20% of the focal being vigilant.

Table 1

Probability of being seen feeding during 202 scans and 3806 sightings for 97 female eastern grey kangaroos at Anglesea, Victoria, in 2009–2010, based on GLMM

Variables	Estimate	SE	Z	P
Intercept	1.61	0.5	3.22	0.001
Reproductive status: LPY/YAF	1.12	0.13	8.79	<0.001
Temperature	−0.03	0.02	−1.55	0.121
Time 2: 0915–1200 hours	−1.67	0.62	−2.7	0.007
Time 3: 1200–1445 hours	−4.62	0.71	−6.51	<0.001
Time 4: 1445–1730 hours	−3.38	0.59	−5.77	<0.001
Time 5: >1730 hours	1.25	1.49	0.84	0.4
Year 2010	0.79	0.13	6.32	<0.001
Temperature*time2	−0.04	0.03	−1.28	0.2
Temperature*time3	0.11	0.03	3.32	<0.001
Temperature*time4	0.14	0.03	5.5	<0.001
Temperature*time5	−0.02	0.05	−0.36	0.72

Females with large pouch-young (LPY) or young-at-foot (YAF) were compared to females with no, small or medium pouch-young. The different classes of time were compared to 'Time 1' (0630–0915 hours).

Bite rate

Bite rate was independent of female mass ($F_{1,60} = 0.01, P = 0.91$), group size ($F_{1,164} = 0.22, P = 0.64$), age class ($F_{2,196} = 2.37, P = 0.31$) and of the interactions between reproductive status and number of steps ($F_{1,243} = 1.02, P = 0.31$), reproductive status and time of day ($F_{1,242} = 2.42, P = 0.12$). The best model ($N = 318$) explaining variability in bite rate included reproductive status (lactating versus nonlactating: $F_{1,243} = 27.93, P < 0.001$), date (25 September–21 November: $F_{1,243} = 9.28, P = 0.002$), year of observation (2010–2011: $F_{1,243} = 22.91, P < 0.001$), number of steps (2–73: $F_{1,243} = 5.97, P = 0.015$), time of day (morning or evening: $F_{1,243} = 17.25, P < 0.001$), duration of feeding when head was visible (173–593 s: $F_{1,243} = 493.54, P < 0.001$), an interaction between reproductive status and year ($F_{1,243} = 19.51, P < 0.001$) and individual random effects ($X^2_1 = 9.11, P = 0.003$; [Supplementary Table S1](#)). Although mothers had similar bite rates in both years, they took 13% more bites in 2011 and 31% more bites in 2012 than nonlactating females.

Females that fed less during the day could compensate by increasing feeding rate in the evening. Therefore, we examined how feeding (proportion of scans when each female was foraging) and presence (proportion of scans when each female was seen) on the golf course affected bite rate between 1630 and 2030 hours of the same day.

Bite rate of females that were seen the least frequently during the day increased by up to 20% in the evening compared to females that were seen the most ($F_{1,15} = 5.58, P = 0.032$). The best model ($N = 51$ observations) explaining variability in bite rate in the evening included female reproductive status (lactating or not), proportion of scans when each female was seen on the golf course earlier that day (0.18–1), and the duration of feeding when the head was visible (256–572 s). Individual as a random effect was significant ($X^2_1 = 4.41, P = 0.04$; [Supplementary Table S1](#)). Neither date of observations ($F_{1,13} = 0.04, P = 0.84$) nor number of steps ($F_{1,14} = 3.17, P = 0.08$) affected bite rate in this model.

Chewing rate and reproductive status

Neither group size ($F_{1,51} = 0.42, P = 0.52$), year ($F_{1,67} = 2.73, P = 0.10$), time of day (morning or evening: $F_{1,66} = 0.87, P = 0.35$) nor date of observation ($F_{1,50} = 0.18, P = 0.67$) improved the model ($N = 113$ observations) explaining chewing rate. Controlling for female mass (21–36.5 kg), duration of chewing when the head was visible (31–274 s) and individual random effects ($X^2_1 < 0.01$,

$P = 0.99$; [Supplementary Table S1](#)), nonlactating females and females with small or medium pouch-young had a 6% lower chewing rate than females with large pouch-young or young-at-foot ($F_{1,74} = 5.51, P = 0.022$). Young females had a 12% higher chewing rate than prime-aged and old females ($F_{1,34} = 5.81, P = 0.022$). Chewing rate was independent of bite rate ($F_{1,73} = 0.03, P = 0.86$).

Wilsons Promontory: Unmanipulated Population

Feeding and vigilance

Females spent on average 87% of the focal observation foraging. Sex of the young ($F_{1,337} = 0.02, P = 0.90$), age ($F_{2,403} = 0.71, P = 0.71$), number of steps ($F_{1,408} = 0.92, P = 0.34$) and time of the day (morning or evening: $F_{1,410} = 2.57, P = 0.11$) did not affect the proportion of time feeding. The best model ($N = 667$ observations) included session (late winter or late spring: $F_{2,426} = 2.85, P < 0.001$), year (2009–2011: $F_{1,426} = 37.16, P < 0.001$), mass ($F_{1,426} = 3.57, P = 0.059$), group size ($F_{1,426} = 4.08, P = 0.043$) and individual as a random effect ($X^2_1 = 1.38, P = 0.239$; [Supplementary Table S1](#)). Controlling for these variables, reproductive status did not affect the proportion of time spent feeding (NPY/SPY/MPY/LPY versus YAF: $F_{1,426} = 2.85, P = 0.091$). Females spent 11% of their time vigilant regardless of reproductive status ($F_{1,580} = 0.18, P = 0.672$).

Bite rate and reproductive status

Mass ($F_{1,263} = 0.18, P = 0.68$), number of steps ($F_{1,355} = 1.13, P = 0.29$), group size ($F_{1,340} = 0.29, P = 0.59$) and the interactions between current reproductive status and previous weaning success (NPY versus SPY/MPY or LPY/YAF: $F_{2,356} = 4.99, P = 0.08$), reproductive status and number of steps ($F_{3,355} = 6.14, P = 0.11$) or reproductive status and time of day ($F_{2,356} = 3.47, P = 0.18$) did not affect bite rate in this model. The best model ($N = 427$ observations) explaining variability in number of bites ([Table 2](#)) included reproductive status (nonlactating versus lactating: $F_{2,356} = 40.85, P < 0.001$), survival of the previous young to weaning (0 or 1: $F_{1,356} = 7.56, P = 0.006$), age class ($F_{2,356} = 7.47, P = 0.024$), time of day (morning or evening: $F_{1,356} = 16.96, P < 0.001$), session (late winter–late spring: $F_{2,356} = 9.15, P = 0.010$), year (2010–2011: $F_{1,356} = 0.42, P = 0.518$), duration of feeding while the head was visible (128–595 s: $F_{1,356} = 907.89, P < 0.001$), the interaction between reproductive status and year ($F_{2,356} = 11.34, P = 0.003$), and individual as a random effect ($X^2_1 = 46.97, P < 0.001$;

Table 2
Effects of current and previous reproductive success on bites taken during 10 min focal observations by 59 eastern grey kangaroo females (427 observations) feeding at Wilsons Promontory, Victoria in 2010–2011, based on LMM (356 degrees of freedom)*

Variables	Estimate (number of bites)	SE (number of bites)	t	P
Intercept	–93	27	–3.41	<0.001
Reproductive status: SPY	67	18	3.74	<0.001
Reproductive status: MPY	95	17	5.71	<0.001
Reproductive status: LPY	138	12	11.70	<0.001
Reproductive status: YAF	149	15	9.77	<0.001
Wean a young the previous year	35	11	3.26	0.001
Prime-aged	–44	18	–2.43	0.039
Old	–48	23	–2.10	0.087
Morning/evening	30	7	4.14	<0.001
Session: early spring	–17	13	–1.30	0.390
Session: late spring	–25	8	–3.02	0.007
Year 2011	59	10	6.03	<0.001
Duration of feeding	1.21E-003	4.00E-005	29.91	<0.001

The sample included 46 females that weaned a young the previous year. Prime-aged and old females were compared to young females. SPY: small pouch-young; MPY: medium pouch-young; LPY: large pouch-young; YAF: young-at-foot (after permanent emergence from the pouch). Females with SPY, MPY, LPY and YAF are referred to as lactating females.

* Multiple comparisons used Tukey's post hoc test for factors with more than two categories.

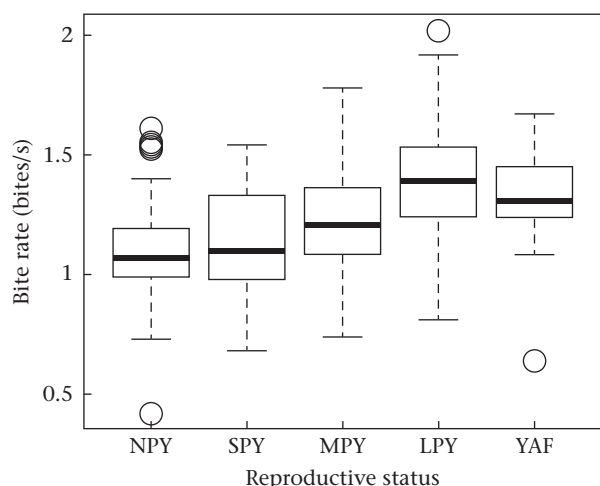


Figure 1. Bite rate as a function of reproductive status for 59 female eastern grey kangaroos during 427 observations at Wilsons Promontory, Victoria, 2010–2011. NPY: no pouch young; SPY: small pouch-young; MPY: medium pouch-young; LPY: large pouch-young; YAF: young-at-foot.

Supplementary Table S1). Lactating females took 18% more bites/min ($F_{1,359} = 62.84, P < 0.001$) than nonlactating females, and bite rate increased with the size of the young (Table 2, Fig. 1). Over one reproductive season, females that lost their pouch young showed a stronger decline in bite rate than females that had no young or females that had a pouch young in both observation sessions (Table 3). Nonlactating females and females with young-at-foot did not change their bite rate between 2010 and 2011. Females with small, medium and large pouch-young increased their bite rates by 29%, 14% and 12%, respectively. Females that had weaned a young the previous year increased their bite rate by 7%. Bite rate decreased as females aged, by 9% between young and prime-age females and by 11% between young and old females (Table 2, Fig. 2).

Effect of offspring sex

Sex of previous young ($F_{1,245} = 0.64, P = 0.42$), number of steps ($F_{1,341} = 0.51, P = 0.48$), observation session ($F_{2,342} = 4.95, P = 0.08$), and the interactions between offspring sex and maternal age ($F_{2,343} = 0.60, P = 0.74$) and between sex of the current and previous offspring ($F_{1,247} = 2.78, P = 0.10$) did not affect bite rate. In a model ($N = 420$ observations) including offspring sex, age class (young/prime-age/old), year (2010–2011), period of the day (morning or evening), time feeding when the head was visible (128–595 s) and individual random effects ($X^2_1 = 96.24, P < 0.001$; Supplementary Table S1), the 29 mothers of daughters had a bite rate that was 6% lower than that of the 38 mothers of sons ($F_{1,344} = 6.57, P = 0.010$).

Chewing rates and reproductive status

Mass ($F_{1,98} = 0.07, P = 0.80$), group size ($F_{1,131} = 1.42, P = 0.23$), time of day (morning or evening: $F_{1,128} = 1.14, P = 0.29$), or the

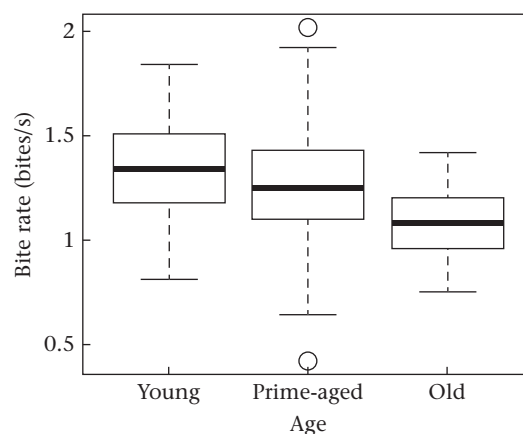


Figure 2. Bite rate as a function of age class for 59 female eastern grey kangaroos during 427 observations at Wilsons Promontory, Victoria, 2010–2011.

interaction between reproductive status and year (nonlactating females compared to SPY/MPY and LPY/YAF: $F = 1.58, P = 0.45$) did not improve the model. Offspring sex did not influence chewing rate ($F_{1,125} = 0.05, P = 0.82$). The most parsimonious model to explain variability in chewing rate included reproductive status (nonlactating, SPY/MPY and LPY/YAF: $F_{2,148} = 21.15, P < 0.001$), session (late winter or late spring: $F_{2,148} = 19.52, P < 0.001$), age class, year (2010–2011: $F_{1,148} = 17.49, P < 0.001$), the duration of chewing when the head was visible (30–138 s: $F_{1,148} = 619.59, P < 0.001$) and individual as a random effect ($X^2_1 = 4.03, P = 0.045$; Supplementary Table S1). In contrast with the results at Anglesea, chewing rate increased with bite rate ($F_{1,149} = 21.76, P < 0.001$), so that the effects of small/medium pouch-young and large pouch-young/young-at-foot were similar (mean \pm SD: 0.12 ± 0.16 ; $t_{149} = 0.78, P = 0.72$). The chewing rate of lactating females was 4% higher than that of nonlactating females ($F_{1,148} = 4.71, P = 0.030$) when controlling for bite rate. The chewing rate of young and prime-aged females was 11% higher than that of old females ($F_{1,148} = 16.32, P < 0.001$).

DISCUSSION

Our research is among a handful of studies of behaviour in free-ranging mammals to use contraceptives to control for individual differences in reproductive potential. By experimentally manipulating reproduction and monitoring a large number of marked females in two sites over 3 years, we found that lactating female eastern grey kangaroos modified their foraging behaviour in response to the energy costs of reproduction. This is the first study of wild mammals to reveal that foraging behaviour of females is affected by both current and previous reproduction, and the first to show an effect of previous reproduction and offspring sex on bite rate. Compared to nonreproductive females, lactating females spent more time foraging during the middle of the day (higher bite rate and chewing rate), but they did not change or slightly

Table 3

Changes in bite rate during 10 min focal observations between late winter and late spring according to session-specific reproductive status (NPY vs PY) of female eastern grey kangaroos at Wilsons Promontory in 2010–2011, Victoria in 2010–2011, based on LMM

Reproductive status	Late winter (bites/s)	Late spring (bites/s)	Change in bite rate	N females (N observations)	t (df)	P
NPY → NPY	1.1	1.04	–5%	20 (105)	–2.04 (83)	0.044
PY → NPY	1.57	1.12	–29%	6 (35)	–9.74 (27)	<0.001
PY → PY	1.34	1.33	<1%	54 (316)	–0.79 (260)	0.430

NPY: females with no pouch young (females that had a pouch young earlier on, then lost it); PY: females with a pouch young.

decreased the proportion of time spent feeding during focal samples, presumably to maintain an adequate level of vigilance.

At Anglesea, the foraging behaviour of contracepted and unmanipulated females that lost their young was similar, suggesting that foraging was not strongly affected by intrinsic differences between females or early costs of reproduction. There was also no evidence that foraging changed as a side effect of the contraceptive (Gray & Cameron 2010). At Wilsons Promontory, bite rate increased with offspring development, suggesting that females modified their behaviour in response to short-term changes in energy requirements as reported by Cripps et al. (2011). This interpretation is reinforced by the decrease in foraging effort by females at Wilsons Promontory after they lost their young (Table 3). Therefore, it appears that, in kangaroos, females that lose their young during early lactation are an acceptable 'control' group to examine how reproduction affects foraging behaviour.

Combining differences in the probability of feeding during different times of the day and differences in bite rate, females at the peak of lactation (with a large pouch-young or a young-at-foot) increased daylight food intake by 53% compared with nonlactating females, assuming that bite rate remained constant throughout the day and that bite size was independent of reproductive status. Cripps et al. (2011) found an increase of 49% in another study population. The consistency among studies and sites demonstrates that these estimates are robust and underlines the substantial difference in foraging effort according to reproductive status. Much of the difference appears to originate from continued feeding of lactating females during the day, when warm temperatures may make foraging behaviour more costly. Most nonlactating and some lactating females retreated to cover at this time. We found some of these females by searching in wooded areas around both study sites, and all were resting. Moreover, females not seen on the golf course on a given day increased their bite rate that evening, suggesting that they had not been feeding elsewhere. As previously reported for some eutherian herbivores (Gross et al. 1995; Hamel & C  t   2009), chewing rate was higher for lactating females than it was for nonlactating females, presumably to further break down vegetation and increase digestive efficiency after the food bolus was swallowed (Pond et al. 1984). Lower vegetation quality might explain why chewing rate was affected by bite rate only at Wilsons Promontory. Both food intake and chewing rate increased with the presence of a pouch young, consistent with the mounting energy requirement of lactation, as reported in captive tamar wallabies (Cork 1991).

We found no evidence of a trade-off between foraging and vigilance (Ruckstuhl et al. 2003). Compared to nonlactating females, lactating females did not increase the proportion of time spent feeding during focal samples at Wilsons Promontory and decreased it at Anglesea. Anecdotal evidence suggests that foxes were more common at Anglesea than at the Promontory. Foxes are an effective predator of juvenile kangaroos (Banks 2001), possibly forcing lactating females to maintain a high level of vigilance. This result suggests that vigilance was important, forcing females to attempt to satisfy the energetic cost of reproduction through more time spent feeding at midday and greater biting and chewing rates. Cripps et al. (2011) showed that vigilance did not vary with reproductive effort in another population of the same species, suggesting that the cost of reproduction could be risk dependent (P  riquet et al. 2012).

This is the first study of wild mammals to demonstrate that mothers of sons increase their bite rate compared with mothers of daughters. We expected this because kangaroos are among the most dimorphic of terrestrial mammals (Weckerly 1998). It is also consistent with previous reports describing higher reproductive

costs of sons in sexually dimorphic mammals. In bighorn sheep, for example, mothers of sons experienced decreased survival of the lamb produced the following year (B  rub   et al. 1996) compared with mothers of daughters. By increasing foraging rates, mothers of sons may partly compensate for a greater energy cost of lactation.

To our knowledge, no study of wild mammals has reported an effect of previous reproduction on current foraging behaviour. In other large mammals, current reproduction is often compromised by earlier reproductive effort (Martin & Festa-Bianchet 2011). Our results suggest that previous reproduction also imposes a reproductive cost in kangaroos, because previously successful mothers appear forced to increase their forage intake. Similarly to the effect of offspring sex on foraging behaviour, this result indicates that reproductive females can to some extent counter both the short- and the long-term energetic costs of reproduction by modifying their foraging behaviour.

In addition to the multiple underlying effects of reproductive status, our study shows how energy requirements vary with individual characteristics. When significant, individual effects explained between 10 and 31% of variation in feeding behaviours. Individual variation could partly arise from differences in metabolic rate (Nkrumah & Okine 2006) and may limit the short-term negative effect of reproduction on body condition, possibly decreasing the fitness cost of reproduction upon future reproductive success or survival. Unexpectedly, female mass did not affect the feeding behaviours we examined, contrary to earlier studies of wild mammals (Kamilar & Pokempner 2008) and despite wide variation in mass (20–36.5 kg) of adult females. This suggests that foraging behaviour was mainly driven by the energetic costs of reproduction, making any residual effects of maternal mass difficult to detect.

We found some differences between sites and between years, possibly related to habitat quality. For example, age class affected bite and chewing rates at Wilsons Promontory but only affected chewing rate at Anglesea, where the golf course was regularly watered and fertilized, and population density was lower. Bite rate was lower at Anglesea, possibly making age differences more difficult to detect. At the Promontory, bite rate by lactating females, excluding mothers with young-at-foot, was higher in 2011 than in 2010, possibly reflecting an increase in reproductive cost, as suggested by their lower reproductive success in 2011. These examples show the importance of long-term monitoring to account for how variability of resource availability affects life-history patterns (Clutton-Brock & Sheldon 2010).

In conclusion, the combination of intensive observations of two populations and experimental manipulation of reproduction in one population allowed us to quantify how females partly compensate for reproductive costs by modifying their foraging behaviour. Differences between study areas and between years may have been due to variation in predation risk or forage availability, suggesting that foraging behaviour can be affected by extrinsic factors that may also affect the costs of reproduction.

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Supplementary Material

Supplementary material associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2013.08.016>.

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