



Original Article

# Heterogeneity in reproductive success explained by individual differences in bite rate and mass change

Uriel Gélín,<sup>a,b</sup> Graeme Coulson,<sup>c</sup> and Marco Festa-Bianchet<sup>a,c</sup>

<sup>a</sup>Département de Biologie, 2500 boul. de l'Université, Université de Sherbrooke, Sherbrooke, Québec J1K2R1, Canada, <sup>b</sup>Laboratoire de Physiologie de la Reproduction et des Comportements, CNRS-UMR 7247—Université de Tours, 37380 Nouzilly, France, and <sup>c</sup>School of Biosciences, The University of Melbourne, Royal Parade, Melbourne, Victoria 3010, Australia

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Allocation of resources to current reproduction may reduce future reproduction, growth, and survival, but individual heterogeneity in resource acquisition may obscure this fitness cost. In capital breeders, heterogeneity in reproductive success is often related to body mass or condition, underlining the importance of stored reserves for reproduction. Heterogeneity in the rate of resource acquisition could also affect reproduction. Resource acquisition depends on food intake, but the effects of individual foraging rate on mass gain and reproductive success in wild herbivorous mammals are unknown. We measured how individual bite rate affected mass change and reproductive success of 55 female eastern gray kangaroos (*Macropus giganteus*) over 2 years. Females with faster bite rate had greater subsequent mass gain, leading to greater offspring survival. In one of 2 years, bite rate directly increased juvenile survival to 8 months. Bite rate appeared to have a direct effect on survival to weaning for young born to females with above-average mass gain, particularly for females in better body condition. Independent of bite rate, individual mass change explained most of the variation in offspring survival. We found a weak positive effect of body condition on reproductive success, suggesting that condition affected reproductive success through its effect on mass change and bite rate. Kangaroos appeared to combine income and capital breeding strategies to deal with internal and external constraints on resource allocation. Our study underlines the importance of accounting for different sources of individual heterogeneity that may affect trade-offs among life-history traits, with important consequences for population dynamics and the evolution of reproductive strategies.

**Key words:** body condition, environmental effects, foraging, *Macropus giganteus*, reproductive costs, trade-off.

## INTRODUCTION

A central concept in life-history theory is that resource scarcity will force trade-offs between reproduction, growth, and survival (Stearns 1992), affecting vital rates and population dynamics (Frederiksen et al. 2014). Although manipulative studies have reported fitness costs of reproduction, leading to trade-offs with subsequent reproductive success, growth, and survival in insects (Fowler and Partridge 1989), reptiles (Sinervo and DeNardo 1996), birds (Gustafsson and Sutherland 1988), and mammals (Koivula et al. 2003), numerous observational studies have found no or positive correlations between life-history traits (reviewed in Lim et al. 2014). van Noordwijk and de Jong (1986) suggested that positive correlations among fitness components occur when individual

variation in resource acquisition exceeds variation in resource allocation. Reznick et al. (2000) predicted that individuals better able to acquire resources would show both greater growth and greater reproductive success. Many studies have since explored individual heterogeneity in resource allocation to life-history traits (e.g., in mammals, Beuplet et al. 2006; Weladji et al. 2008; Hamel et al. 2009; Chambert et al. 2013). A recent meta-analysis reported a consistent negative correlation between number and size of offspring after accounting for individual reproductive potential (Lim et al. 2014), confirming the importance of quantifying sources of individual heterogeneity, notably because heterogeneity in vital rates can affect demography (Kendall et al. 2011).

Lim et al. (2014) used body mass to quantify individual ability to allocate energy. Other studies used different indices (Wilson and Nussey 2010), including life-history (subsequent reproductive success; Chambert et al. 2013) or morphological traits such as horn length (Bergeron et al. 2008). The energy used for somatic and

Address correspondence to U. Gélín. E-mail: gelinuriel@gmail.com.

reproductive functions may be provided by accumulated reserves, in capital breeders, or by resource acquisition through feeding, in income breeders (Jönsson 1997). This distinction between breeding strategies has important implications for reproductive trade-offs because the relative influence of environmental conditions at the time of breeding should decrease as reliance on stored resources increases (Jönsson 1997). In many cases, however, reliance on each strategy may vary according to environmental resources, even within the same individual (Fletcher et al. 2013; Stephens et al. 2014). Therefore, future allocation to reproduction should be affected by the ability to acquire resources (foraging skills or intake rate), the capacity to store energy (body condition), and the rate of energy restoration (mass gain rate).

Many studies investigated the effect of individual mass or condition on reproduction (Boggs 1992; Morse and Stephens 1996; Festa-Bianchet et al. 1998), but few have tested the effect of individual mass gain (Glazier 1999; Hamel and Côté 2009; Gélín et al. *In press*). In general, studies have found that heavier females and those with limited mass loss had greater reproductive success and lower fitness costs of reproduction than females that were small or lost more mass (Festa-Bianchet et al. 1998; Gélín et al. *In press*). Earlier studies (Pianka 1976; Boggs 1981) highlighted the important link between foraging and allocation to life-history traits. Availability and spatio-temporal distribution of resources affect foraging behavior (Boggs 1992; Frey-Roos et al. 1995; Iason et al. 1999) and life-history traits (Clutton-Brock et al. 1989; Scrimgeour and Culp 1994; Ballesteros et al. 2013). Foraging activities have been widely investigated within the context of optimal foraging theory (Perry and Pianka 1997; Houston and McNamara 2014), considering trade-offs against predation risk (Scrimgeour and Culp 1994) or energy expenditure (Parker et al. 1996). Recent studies have underlined the importance of individual heterogeneity in reproductive success (Chambert et al. 2013), strong phenotypic plasticity in mass changes (Pelletier et al. 2007), and individual differences in foraging behavior (Bergvall and Leimar 2005), suggesting that individual variability may affect the ability to store, replenish, and acquire resources, possibly explaining variation in reproductive success. Energy intake varies with bite size and food quality (Shipley et al. 1999), but no study has attempted to relate individual foraging rate to life-history traits in large herbivores.

We investigated the relationships between bite rate, mass gain, body condition, and reproductive success in female eastern gray kangaroos, *Macropus giganteus*, which present several characteristics that make them attractive for this research. First, they have an extended lactation and face the additional energy cost of carrying their young, which can be up to a quarter of maternal mass, during midlactation (Poole et al. 1982). Two main stages can be used as reference to measure reproductive success: survival of the young 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 (Gélín et al. 2013). Survival to these 2 stages may require different allocation strategies, because maternal body condition improves juvenile survival to the LPY stage but not weaning success (Gélín et al. 2015). Heterogeneity in mass gain is linked to reproductive success (Gélín et al. *In press*). Second, females show substantial differences in foraging behavior, with individual explaining up to 25% of variation in bite rate (Gélín et al. 2013). Third, kangaroos are easily observed as they graze and their abundance in our study area facilitated observation of a large sample of individuals.

We investigated how individual bite rate affected female mass change and explored the effects of bite rate, mass change, and body condition on juvenile survival to LPY and to weaning. We predicted that mass gain would increase for individuals with faster bite rate and that reproductive success would show independent positive effects of mass change, body condition, and bite rate.

## MATERIALS AND METHODS

### Study areas and data collection

We monitored marked females at Wilsons Promontory National Park (38°57'S, 146°17'E), Victoria, Australia. We caught kangaroos by Zoletil injection (King et al. 2011), marked individuals with colored ear tags and collars, and measured body mass and leg length (Poole et al. 1982) at each capture. Leg measurements showed significant observer effects, so before analyses the data were adjusted for this effect using mixed models (Martin and Pelletier 2011), although 81% of measurements were collected by 1 observer. We measured body condition using the “scaled mass index” (Peig and Green 2009), a regression of individual mass and leg length controlling for the average leg length of the population. Analyses of reproductive success in year 2 include our estimate of body condition in year 1. Mass change was the difference in mass between first and second capture controlling for recapture interval. We defined 3 age classes. Known-age females were 2–6 years old during our study and were classed as “young.” Other females were classified by incisor wear as “old” (teeth missing or worn within 1–2 mm of the gum line) or “prime age” (Gélín et al. 2013). We determined the presence, sex, and survival of the young at capture and through observations. We measured 2 levels of individual success at each reproductive season: Whether a female had a young that survived to LPY stage, at about 7–8 months of age, with a fully furred head often protruding from the pouch and whether a female had a young that survived to weaning. Mass gain, survival of young to LPY stage and to weaning were higher in 2012 than in 2011 (Gélín et al. 2015). Bite rate by lactating females was higher in 2011 than in 2010 (Gélín et al. 2013).

We observed feeding behavior of 55 marked females from late August to early December 2010 and 2011, corresponding to the Austral late winter to early summer. We videotaped 10-min focal samples, then calculated the number of bites using J-Watcher 1.0 (Blumstein et al. 2006). Bite rate was the number of bites divided by the time when the head was visible. For each female, we calculated an annual individual bite rate per second for each year separately.

### Statistical analyses

We sought to test how annual individual bite rate affected mass change and reproductive success after accounting for independent variables that we had earlier shown to be important, including reproductive effort the previous year (Gélín et al. 2013, 2015; Table 1). We investigated the effects of annual individual bite rate on mass change over 2 successive reproductive episodes, referred to as year 1 and year 2, and on whether the young survived to LPY stage or to weaning in year 2. Intercapture interval averaged  $361 \pm 52$  (standard deviation) days. Analyses controlled for reproductive effort, age class, and year. Preliminary analyses showed that annual individual bite rate was independent of the number of observations (range 1–9) used to calculate it. Five mothers who lost their young between 2 observation sessions within the same year were excluded from analyses. Bite rate could be influenced

**Table 1**

**Models used to test the effects of bite rate on mass change and survival of 55 female eastern gray kangaroos (*Macropus giganteus*) from 2010 to 2013 at Wilsons Promontory, Victoria, Australia**

Response variable	Explanatory variables	<i>N</i>	Models
Mass change	Individual bite rate, survival of young to LPY stage in year 1, age class, recapture interval, <i>initial body mass</i> , and <i>year</i>	84	Linear
Survival of young to LPY in year 2	Individual bite rate, annual mass change, body condition of the mother a few weeks before conception, <i>survival of young to LPY stage in year 1</i> , year, recapture interval, and <i>age class</i>	84	Generalized linear (binomial distribution)
Survival of young to weaning in year 2	Individual bite rate, annual mass change, body condition of the mother a few weeks before conception, survival of young to LPY stage in year 1, year, recapture interval, and <i>age class</i>	81	Generalized linear (binomial distribution)

Variables in italics were removed from minimal adequate models. *N* is the number of female-years.

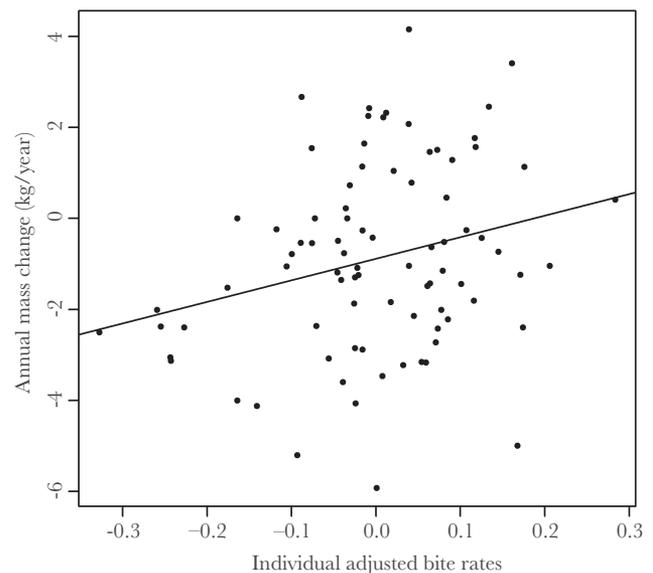
by several variables (Gélin et al. 2013) that could also affect mass change and reproduction: reproductive status (lactating or not), female age class, and year of observation. Initial body mass also affects mass change (Gélin et al. In press). Therefore, we included all these factors in multiple regressions (Freckleton 2002).

We used linear models and generalized linear models with a binomial distribution to investigate mass change and offspring survival. We did not use mixed models because we had fewer than 2 observations per individual on average, and individual as random effect did not significantly improve our models (likelihood-ratio test, Zuur et al. 2009). All analyses were performed with R version 3.0.2 (R Foundation for Statistical Computing, Vienna, Austria) and user interface Rstudio, version 0.98.501 (Rstudio Integrated Development Environment, Boston, MA). For each analysis, we began with a saturated model, then assessed the influence of each independent variable by backward stepwise elimination of nonsignificant variables, leading to a minimal adequate model (Crawley 2007; Zuur et al. 2009). We centered and standardized continuous variables as suggested by Schielzeth (2010), using the `scale()` function in R. Only significant interactions are reported. Global fit of the models was provided by  $R^2$  in the “stats” package (Pinheiro and Bates 2000) and by pseudo- $R^2$  calculated with the “lmer” function in the “rms” package (Harrell 2014). Here, we present models with the greatest AIC weight (“AICcmodavg” package; Supplementary Material). The AIC weight of all of these top models was at least twice greater than for the second-ranked model.

## RESULTS

Bite rate ranged from 0.7 to 1.7 bites/s and was associated with subsequent mass gain for young and prime-age females (Figure 1; Table 2). One more bite per second increased mass gain by 0.46 kg/year. Mass gain was independent of year ( $F_{1,74} = 0.01$ ,  $P = 0.89$ ) and initial mass ( $F_{1,75} = 0.42$ ,  $P = 0.37$ ). Mass gain ranged from -6 to 4 kg/year, decreased with previous reproductive effort and increased with recapture interval (Table 2).

The probability to produce a young that survived to the LPY stage increased with maternal mass gain and maternal condition in a model including recapture interval (Table 3). Independently of its effect on mass gain, bite rate increased survival to LPY in 2012 (increasing bite rate by 0.5 bite/s increased offspring survival by 10%) but not in 2011 (Table 3). Survival to LPY was independent of survival of previous young to LPY ( $\chi^2_1 = 0.05$ ,  $P = 0.82$ ) and of female age class ( $\chi^2_2 = 0.53$ ,  $P = 0.77$ ). When mass gain was not included, bite rate increased survival to LPY ( $\chi^2_1 = 7.74$ ,  $P = 0.005$ ) in a model including survival of previous young to LPY, year, and recapture interval.

**Figure 1**

Annual mass change as a function of adjusted bite rate for 55 female eastern gray kangaroos (*Macropus giganteus*) monitored during 84 female-years at Wilsons Promontory, Victoria, Australia, 2010–2012.

Maternal bite rate increased juvenile survival to weaning only for females with higher mass gain and recapture interval of less than a year (Table 3). We also found a complex effect of bite rate on survival to weaning (Table 3): Bite rate had no effect for females with low mass gain, but increased survival to weaning for the offspring of females that gained more mass. In addition, this positive effect was stronger for females already in good body condition in year 1 (Supplementary Material). Increasing bite rate by 0.5 bite/s increased offspring survival by 25% for females in below-average condition and by 35% for females in above-average condition. The positive effect of mass gain on survival to weaning was stronger for females that did not have an LPY in year 1 (Table 3). Survival to weaning was greater in 2011 than in 2012 (Table 3). Female age class ( $\chi^2_2 = 0.11$ ,  $P = 0.95$ ) had no effect on survival to weaning. If mass gain was not included in the model, bite rate increased survival to weaning ( $\chi^2_1 = 7.34$ ,  $P = 0.007$ ; model including survival of previous young to LPY stage).

## DISCUSSION

To our knowledge, this is the first study to quantify the effect of individual foraging rate on mass change and reproductive success

**Table 2**

**Factors affecting mass gain between successive reproductive events for 84 female-years of observations of 55 female eastern gray kangaroos (*Macropus giganteus*) at Wilsons Promontory, Victoria, Australia**

Variables	Mass change (kg)		
	Estimate (SE)	F value (df)	P
Intercept	1.67 (0.33)		
Bite rate	0.69 (0.33)	4.52 (1.76)	0.037
LPY in year 1	-1.50 (0.24)	40.03 (1.76)	<0.001
Age class compared with young	Prime age: -0.66 (0.32) Old: -1.13 (0.42)	3.67 (1.76)	0.030
Intercapture interval (days)	0.20 (0.08)	5.81 (1.76)	0.018
Bite rate × age class compared with young	Prime age: -0.23 (0.33) Old: -1.02 (0.42)	4.28 (2.76)	0.017

Because the independent variables are centered and standardized, the value of the estimate indicates the importance of its effect on the response variable for simple variable and interactions (Schielzeth 2010). Estimates are based on linear models. df, degrees of freedom; SE, standard error.

**Table 3**

**Effects of bite rate on survival of young to LPY stage and to weaning for 55 female eastern gray kangaroos (*Macropus giganteus*) at Wilsons Promontory, Victoria, Australia**

Variables	Survival to LPY (N = 84; pseudo-R <sup>2</sup> = 65%)			Survival to weaning (N = 81; pseudo-R <sup>2</sup> = 65%)		
	Estimate (SE)	χ <sup>2</sup>	P	Estimate (SE)	χ <sup>2</sup>	P
Intercept	0.75 (0.55)			0.22 (1.84)		
Bite rate (bites/second)	-0.22 (0.50)	0.19	0.664	2.73 (1.04)	10.77	0.001
Mass change (kg)	2.94 (0.73)	40.41	<0.001	7.68 (2.62)	20.73	<0.001
Maternal condition (kg)	0.99 (0.45)	5.54	0.019	0.81 (0.50)	1.12	0.094
LPY in year 1				-2.21 (2.02)	1.12	0.289
Year	-2.24 (0.97)	6.41	0.011	-4.13 (1.61)	9.79	0.002
2012 compared with 2011						
Intercapture interval (days)	1.17 (0.44)	8.85	0.003	-0.39 (0.52)	0.58	0.446
Bite rate × year	1.82 (0.94)	4.52	0.034			
Bite rate × mass change				3.44 (1.21)	14.83	<0.001
Bite rate × intercapture interval				-2.09 (0.79)	10.70	0.001
Mass change × LPY in year 1				-6.50 (2.57)	10.00	0.002
Bite rate × mass change × maternal condition				1.33 (0.74)	5.06	0.025

df = 1 for all χ<sup>2</sup> tests. Because the independent variables are centered and standardized, the value of the estimate indicates the importance of its effect on the response variable for simple variable and interactions (Schielzeth 2010). Estimates are based on generalized linear models (binomial distribution). df, degrees of freedom; SE, standard error.

in a wild mammalian herbivore. We simultaneously assessed 3 possible sources of heterogeneity (bite rate, body condition, and mass change) on reproductive success. We found a direct positive effect of bite rate on mass gain for young and prime-aged females and an indirect positive effect on juvenile survival the following year, which appeared mostly due to the positive relationship between bite rate and mass gain. Bite rate also directly increased survival to LPY after a year of high juvenile mortality. The effect on survival to weaning resulted from a complex interaction between 3 possible sources of heterogeneity. Independently of maternal body condition, bite rate had no effect on survival to weaning for females with low mass gain. However, bite rate increased survival to weaning for females that had high mass gain, and this effect was stronger for females in good body condition. Reproductive success also increased with mass gain. When controlling for individual bite rate and mass change, female condition increased offspring survival to LPY. According to model estimates (Schielzeth 2010), the most important variable affecting reproductive success was the rate of replenishment of energy (mass gain), followed either by the ability to acquire resources (bite rate) for offspring survival to weaning, or storage of energy (body condition) for survival to LPY stage. This study confirmed that kangaroos are both capital and income

breeders (Gélin et al. *In press*) because they use both stored and current resources for reproduction. Our results underline the central role of behavior in modulating life-history trade-offs and have implications for population dynamics because they directly link maternal foraging behavior with juvenile survival. They also suggest that foraging behavior is likely to be under selective pressure.

The strong effect of bite rate on mass change revealed that individual foraging rate partly explains heterogeneity in mass gain, which then affects reproductive success (Table 3). Females with faster bite rates increased their reproductive success the following year, independently of body condition, current reproductive effort, year, or age class, suggesting that foraging rate is an important source of heterogeneity in reproductive success. Reproductive effort depletes body reserves, but females must maintain mass to reproduce the following year (Gélin et al. *In press*). Bite rate increased survival of young mainly through its effect on mass gain: Females with greater intake rate were better able to recover or maintain their mass. Bite rate also directly increased survival to LPY stage following a less favorable year. Both 2011 and 2012 were less favorable than 2010, with lower mass change and lower juvenile survival, and increased bite rate for lactating females in 2011 (Gélin et al. 2013, 2015). Females that were able to cope with current reproductive effort

through greater bite rate in 2011 were likely better able to allocate resources to reproduction in 2012 because they maintained their mass despite low resource availability. As suggested by Taillon et al. (2013), energy stores acquired through higher food intake may allow females to attenuate the mismatch between environmental resources and lactation effort. Most females lost mass in 2011 (Gélin et al. *In press*) and presumably were forced to allocate resources to their own survival, lowering offspring survival. Therefore, only females with greater ability to acquire resources could maintain both body condition and reproductive success. Bite rate also had a positive effect on survival to weaning for females with greater ability to replenish energy (mass gain), and this effect was stronger for females with greater capacity for energy storage (body condition), suggesting that a combination of both mass gain and good initial body condition was required to sustain the 18-month lactation. No effect of bite rate was found for females with lower rate of mass gain, suggesting that the ability to stock acquired resources was crucial for reproduction. Our results confirm the need to account for both income and capital resources, and individual ability to use them to fully understand individual variation in reproductive success. Longer time series are required to assess the relative importance of income and capital strategies according to environmental variations (Fletcher et al. 2013). We controlled for possible confounding effects such as age class and body condition on bite rate and observed a grazer that mostly feeds on an apparently evenly distributed resource within a fairly homogeneous habitat (Woolnough and Johnson 2000). Therefore, our study system was likely not affected by competition for better food patches. Aggressive interactions are rare in eastern gray kangaroos (Maguire et al. 2006). Individual differences in forage selection could affect foraging rate and mass gain, but because a previous study found no effect of the number of steps on bite rate, we suspect that individual diets may not play an important role in this species (Gélin et al. 2013).

Individual foraging ability may play an important role in species where, for instance, locomotory ability (yellow bellied marmots, *Marmota flaviventris*, Blumstein et al. 2004), cognition (great tits, *Parus major*, Cole et al. 2012), or size (California sea lions, *Zalophus californianus*, Weise et al. 2010) are crucial for food acquisition because resources vary spatially and/or temporally. Our study system shows that unselective grazers may also vary in foraging abilities, although no allometric relationship was found between body size and bite rate (female mass, Gélin et al. 2013; leg length, Gélin U, unpublished data). Individual differences in metabolic rate may, however, affect allocation of metabolic resources to reproduction (Harshman and Zera 2007), although the direction of causality between feeding rate and metabolic rate is unclear (Glazier 2014). Neural circuits and hormones such as neuropeptides also affect appetite and ingestive behavior (Volkoff et al. 2005; Schneider et al. 2013). Integrating other measurements such as individual hormone levels or heart rate may point to the physiological sources of heterogeneity in foraging rate.

A rapid bite rate may also imply costs. For instance, it may increase tooth wear (Galbany et al. 2011), which can decrease longevity (Ozaki et al. 2010 but see Nussey et al. 2007) and lower future foraging efficiency (McArthur and Sanson 1988; Skogland 1988), possibly leading to faster senescence (Carranza et al. 2004). In our study, bite rate did not affect mass gain for older females. In addition to lower chewing rate in old females kangaroos (Gélin et al. 2013), increased tooth wear could lower digestive efficiency by increasing the size of ingested food particles. Heterogeneity in foraging intensity could be a source of reproductive senescence. A faster bite rate may also decrease vigilance (Favreau et al. 2014), increasing the risk

of predation. Individuals with higher bite rates may be favored only in the absence of predators capable of killing adults, as is the case in our study population. Individuals with greater food intake may also increase their parasite load. Eastern gray kangaroos avoid food patches contaminated with feces, presumably to reduce parasite infection (Garnick et al. 2010). Alternatively, females that feed more rapidly or require more resources because of a higher metabolic rate may be selected against when resources are scarce (Turbill et al. 2013). This hypothesis, however, seems unlikely to apply to our study population, which had the highest reported density for this species. Finally, a genetic trade-off (Johnston et al. 2013) may lead to a negative correlation between foraging rate and other life-history traits. All these hypotheses still need to be investigated.

Recent findings in nutritional ecology show a major impact of nutrient intake on allocation to life-history traits (Parker et al. 2009). The efficiency of food assimilation is particularly important, as we found a strong effect of mass change on reproductive success. Possibly, individual foraging rate may be linked to differences in nitrogen absorption and allocation. By increasing food intake, females could store more body nitrogen to support milk production. In caribou, *Rangifer tarandus*, maternal nitrogen stores affected calf mass and may influence juvenile survival (Taillon et al. 2013). Our results suggest that mass change is the main source of heterogeneity in reproductive success, consistent with previous studies (Glazier 1999; Hamel and Côté 2009; Martin and Festa-Bianchet 2012; Gélin et al. *In press*). The positive effect of mass gain on survival to weaning was stronger when lactating effort was lower the previous year, suggesting that energy not used for reproduction was stored to increase subsequent reproductive success. The effect of foraging behavior on reproductive success varied according to body condition, reproductive status, and environmental resources, corroborates the suggestion that while foraging behavior maximize reproductive value, it has different consequences according to female state (Houston and McNamara 2014).

In conclusion, food intake in female eastern gray kangaroos is both a source of individual heterogeneity and a response to energetic needs (Shipley et al. 1994; Glazier 2014). The simultaneous effects of bite rate, body condition, and mass change on offspring survival indicate that they are independent sources of heterogeneity and that females relied on both capital and income strategies to reproduce. This study underlines the importance of different sources of individual heterogeneity affecting trade-offs among life-history traits, with possible consequences for population dynamics and the evolution of reproductive strategies.

## SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>

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U.G. and M.F.-B. conceived, designed, and executed this study. U.G. analyzed the data and wrote the manuscript. M.F.-B. read and provided advice on earlier version of the manuscript. U.G., M.F.-B., and G.C. conducted fieldwork and provided advice on the last version of the manuscript.

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