



Original Article

Determinants of offspring sex in kangaroos: a test of multiple hypotheses

Pauline Toni,^{a,●} David M. Forsyth,^b and Marco Festa-Bianchet^{a,c}

^aUniversité de Sherbrooke, 2500 boulevard de l'Université, J1K2R1 Sherbrooke, Quebec, Canada,

^bVertebrate Pest Research Unit, New South Wales Department of Primary Industries, 1447 Forest Road, Orange, NSW 2800, Australia, and ^cResearch School of Biology, 46 Sullivans Creek Road, The Australian National University, Canberra, ACT 2600, Australia

Received 14 April 2020; revised 2 October 2020; editorial decision 28 October 2020; accepted 12 November 2020; Advance Access publication 22 February 2021.

When the fitness costs and benefits of sons and daughters differ, offspring sex ratio manipulation could be an important reproductive tactic. We explored the effects of environment and maternal caring ability on offspring sex to test four adaptive sex ratio modification hypotheses: the extrinsic modification hypothesis (EMH), carrying capacity hypothesis (CCH), Trivers-Willard hypothesis (TWH), and cost-of-reproduction hypothesis (CRH). The EMH and CCH propose that environmental conditions shape offspring sex ratios, directly or in interaction with maternal condition. The TWH and CRH predict a positive relationship between maternal condition and production of the costlier sex. The TWH predicts that mothers with superior caring ability should produce more of the sex that can provide the greatest fitness returns from additional maternal allocation, and the CRH proposes that females with limited caring ability should reduce fitness costs by producing the cheaper sex. Repeated measures on 83 known-age eastern gray kangaroos, polygynous marsupials with strong sexual dimorphism, revealed that offspring sex ratio was independent of per capita forage, supporting neither the EMH nor CCH, but was dependent on maternal mass, consistent with the TWH and CCH. Our results, however, cannot clearly identify the ultimate cause of the relationship between maternal mass and greater production of sons. One of the three assumptions of the TWH could not be verified, and mothers of sons suffered only marginal additional fitness costs. Sex ratios in higher vertebrates are likely not solely explained by factors dependent on maternal control.

Key words: adaptive sex ratio manipulation, carrying capacity hypothesis, cost-of-reproduction hypothesis, environmental effects, extrinsic modification hypothesis, Trivers-Willard hypothesis

INTRODUCTION

At conception, vertebrate sex ratio is usually fixed near parity (Stearns 1992). When the fitness costs and benefits of male and female offspring differ, however, parental fitness could benefit from altering offspring sex ratio (Trivers and Willard 1973; Clutton-Brock and Iason 1986; Post et al. 1999; Cockburn et al. 2002).

Males and females often differ in size, weapons, or ornaments. In many species, sons grow faster (Case 1978; Georgiadis 1985) and are heavier than daughters at birth or hatching (San José et al. 1999; Bercovitch et al. 2000; Rutkowska and Cichoń 2002) and at the end of parental care (Bowen et al. 2001; Magrath et al. 2007; Foster and Taggart 2008). In these sexually dimorphic species, the faster growth of juvenile males may be partly due to differences in parental care (Clutton-Brock and Albon 1982; Gendreau et al. 2005), sometimes leading to sons having greater fitness costs than daughters (Gomendio et al. 1990; Cockburn et al. 2002; Merkling

et al. 2015). Parents may provide more food to sons (Magrath et al. 2007) or mothers may provide milk richer in proteins to sons than to daughters (Robert and Braun 2012; Galante et al. 2018). In some mammals, mothers provide more care to sons than to daughters and have lower growth, mass gain, or reproductive success the year after they wean a son (Douhard 2017 and references therein). Other studies have found that raising a son has higher costs only for parents in poor condition or in years of poor environmental conditions, implying that fitness costs vary with individual and environmental characteristics (Arnbom et al. 1994; Nager et al. 2000).

Mammalian and avian eggs are few and large, while sperm are numerous and small. Consequently, in species with little or no paternal care, males, whose reproductive success is linked to the number of partners, attempt to inseminate as many females as possible. Females, limited by both the number of eggs and resource availability, should exert mate choice (Bateman 1948). In many mammals, body size and mass are stronger determinants of reproductive success for males than for females (Arak 1988; Clutton-Brock 1988), since large size is advantageous in male–male

Address correspondence to P. Toni. E-mail: pauline.toni@usherbrooke.ca.

competition (Clutton-Brock 1983; Székely et al. 2014; Toni 2018). In polygynous species, males can have higher reproductive variance than females, as a few successful males could sire many offspring, whereas females are constrained to a few (Trivers 1972; Clutton-Brock et al. 1988). In polygynous and sexually dimorphic species, the fitness benefits of sons and daughters are expected to differ according to environmental conditions and maternal body mass and condition that reflect caring ability. Hence, such species are good candidates for sex ratio manipulation. Sex ratio manipulation studies, however, have produced inconsistent results in many higher vertebrate species (Cockburn et al. 2002; Douhard 2017; Liu et al. 2019), possibly because sex ratio is influenced by both extrinsic factors (Post et al. 1999; Delean et al. 2009) and parental characteristics (Krackow 2002; Cameron 2004).

Many theories have been proposed to explain how sex ratio manipulation could be adaptive. Sex ratio could be biased in response to environmental conditions. For instance, it could be modified by environmental factors independently of parental allocation (the extrinsic modification hypothesis [EMH]). Resource availability could affect female body condition during pregnancy, biasing birth sex ratio if the impact of adverse conditions differs according to fetal sex (Post et al. 1999; Weladji and Holand 2003). Although harsh environmental conditions could bias sex ratios, under favorable conditions sex ratio could be under parental control (Forchhammer 2000; Delean et al. 2009). Kruuk et al. (1999) proposed that parents can adjust offspring sex ratio according to their allocation abilities only when the population is below carrying capacity and resources are abundant (the carrying capacity hypothesis [CCH]). Two other hypotheses, the Trivers-Willard hypothesis (TWH) and the cost-of-reproduction hypothesis (CRH), state that sex ratio should vary with the potential of parents to provide care (Trivers and Willard 1973; Myers 1978; Cockburn et al. 2002). The TWH predicts that if parental care affects offspring fitness, rearing a son (often the costlier sex) rather than a daughter may be more demanding, but could be more rewarding if the son had high reproductive success. Parents with the ability to provide superior care should therefore produce more sons (Trivers and Willard 1973; Douhard, Festa-Bianchet, and Pelletier 2016). The TWH relies on three assumptions. First, offspring condition at the end of parental care should be correlated with parental condition during care. Second, differences in offspring condition at the end of parental care should persist until adulthood. Third, an increase in parental care should result in higher fitness benefits for sons than for daughters. If these assumptions are met, parents in good condition that produce sons should have higher fitness (Trivers and Willard 1973; Delean et al. 2009). Alternatively, the CRH proposes that parents with limited parental care abilities could reduce reproductive costs by producing more offspring of the cheaper sex (Myers 1978; Cockburn et al. 2002). The inherent assumption to this hypothesis is that sons and daughters impose different costs to parents.

We tested multiple maternal sex ratio manipulation hypotheses using long-term data from eastern gray kangaroos (*Macropus giganteus*), an iteroparous marsupial with strong sexual dimorphism (Jarman 1989). Females produce a single offspring, carry it in the pouch for about 10 months, and wean it at about 16–20 months (King and Goldizen 2016). In contrast, males are polygynous (Montana et al. 2020), suggesting greater reproductive variance for males than for females.

We first investigated population offspring sex ratio at three ages: 1–4 months (early lactation), 7–10 months (pouch exit), and 21 months (weaning). In species exhibiting strong sexual

dimorphism, offspring of the larger sex have a faster growth rate and are more affected by poor environmental conditions during parental care, resulting in higher mortality (Clutton-Brock et al. 1985; Kahn et al. 2015). Fisher (1930) predicted that mothers should on average allocate equally to each sex over their lifetime. He suggested that birth sex ratio is often slightly biased toward males, but this bias disappears at later ages due to differential preweaning mortality (Fisher 1930). Previous studies of the study population, however, found no effect of sex on juvenile mortality (King et al. 2017; MacKay 2019). If birth sex ratio was biased toward males and there was no differential mortality, sex ratio should be male-biased (Clutton-Brock and Albon 1982) at all developmental stages. We investigated the effects of maternal mass and per capita forage availability (a proxy for environmental conditions) on offspring sex ratio, to test the four hypotheses. Both the TWH and the CRH predict a positive relationship between maternal condition and the production of sons. The EMH predicts that in years with limited forage during gestation, offspring sex ratio would be biased toward females regardless of maternal mass. The CCH predicts that population sex ratio would be at parity in years of low forage availability, while in years of high forage availability heavy females would be more likely to have sons, as previously reported (Le Gall-Payne et al. 2015). During the first 6 years of our study, heavy mothers, but not those with high body condition, produced more sons (Le Gall-Payne et al. 2015), in apparent support of the TWH or the CRH. For this sex ratio bias to be adaptive sensu the TWH, the species must also fit the three assumptions of the hypothesis. We examined the relationship between maternal reproductive potential and offspring mass in early adulthood by quantifying the correlation between maternal mass at mid-lactation and offspring mass at 2 years of age. We investigated the relationship between offspring mass at age 2 and at adulthood (age 3 for females, 4 for males). We then explored whether an increase in maternal effort, measured as a negative effect on mass change from mid-lactation to the end of lactation a year later, led to a larger increase in mass at age 2 for sons than for daughters. Due to polygyny, strong sexual dimorphism, and the likely higher variance in reproductive success of males than of females (Rioux-Paquette et al. 2015; Montana et al. 2020), we expected eastern gray kangaroos to fulfill the three assumptions and be a good candidate to test the TWH.

Alternatively, an increase in the production of sons with increasing maternal mass could result from differential costs of sons and daughters, as predicted by the CRH. We thus tested for sex-differential costs by analyzing the effect of offspring sex on maternal yearly mass change, skeletal growth, and subsequent reproduction. The strong sexual dimorphism of eastern gray kangaroos, the faster growth rate of males than females after permanent exit from the pouch (Poole et al. 1982) and previous work showing that in the study population mothers of sons had a faster bite rate and experienced higher reproductive costs when in poor body condition than mothers of daughter (Gélin et al. 2013; Gélin et al. 2016), suggest potentially higher fitness costs of sons than of daughters.

METHODS

Study site

We monitored habituated, individually marked kangaroos at Wilsons Promontory National Park (38°57'S, 146°17'E), Victoria, Australia. The climate is temperate, with annual rainfall of 518 to 1149 mm in 2008–2018 (Australian Bureau of Meteorology 2019) and mean monthly temperatures of 13.4 °C (July; austral winter)

to 26.2 °C January; summer) in 2013–2018 (Australian Bureau of Meteorology 2019). The vegetation comprises grasses, sedges, herbs, ferns, and shrubs (Davis et al. 2010). During our study, there were substantial yearly and seasonal variations in kangaroo density and pasture biomass (Figure 1).

Study species

Eastern gray kangaroos are sexually dimorphic marsupial grazers that can live for 12–20 years (Poole 1973). Males grow more rapidly than females (Poole et al. 1982, Supplementary Figure S1). In the study population, males and females aged >5 years weighed 24–75 kg and 21–35 kg, respectively. Kangaroos have indeterminate skeletal growth (Karkach 2006), unlike most other mammals where structural growth ends near primiparity. Kangaroos may therefore face a trade-off between reproduction and growth for most of their life. Most females breed for the first time at 3 or 4 years (King et al. 2015). Males do not reproduce before 4 years (Poole and Catling 1974). Gestation lasts 36 days (Poole 1975), and ~85% of births in the study population occur between November and February (Supplementary Figure S2). Lactation costs are relatively low until the offspring reaches ~7 months (Tyndale-Biscoe and Janssens 1988). Past 7 months, changes in milk composition, greater milk consumption, and weight of the offspring in the pouch increase reproductive costs (Tyndale-Biscoe and Janssens 1988). Young suckle until 16–20 months (King and Goldizen 2016), past permanent pouch exit which occurs at ~10 months. For a detailed description of eastern gray kangaroo reproduction, see King et al. (2017). Females can give birth immediately after an offspring has left the pouch, and nurse two young simultaneously. As marsupial offspring grow outside the uterus from a few weeks after conception, comparable to very early fetal development in eutherian mammals (Poole 1975), marsupial mothers can more easily control allocation to reproduction than eutherian mothers. As a result, marsupial mothers can terminate a reproductive attempt during early lactation with little cost should environmental conditions be unfavorable (Tyndale-Biscoe and Janssens 1988).

Data collection

Since 2008, we captured adult kangaroos annually in August–December by Zoletil injection (King et al. 2011) and marked them

with visual collars and ear tags. At capture, we weighed kangaroos with spring scales with a 0.25 kg precision for adults and 0.025 kg for pouch young, and measured the length of the tibia (“leg length”) to the nearest mm (details in Poole et al. 1982). We assessed female reproductive status by examining the teats at capture and by the presence of a suckling offspring. The yearly recapture rate for marked females was >90%. We tagged and measured pouch young at 7–10 months of age, when their mothers were caught. We recaptured surviving juveniles at 22–30 months in February–March, then every subsequent year in August–December. We also captured and measured a subset of adult females in February–March, when their pouch young were 1–4 months old; surviving offspring were recaptured at 7–10 months.

Since summer 2009, we estimated population density (individuals/ha) four times annually using Program DISTANCE (Thomas et al. 2010) by twice walking six transects located systematically throughout the study area (Glass et al. 2015). Since autumn 2009, we sampled vegetation four times annually by clipping it to ~2 mm within 45–54 exclosures of 0.56 m-diameter that exclude large grazers (MacKay et al. 2018). We sorted the samples into vegetation palatable and unpalatable to kangaroos. Due to the large volume of clipped vegetation, we dried and weighed subsamples to a 0.01 g accuracy, then divided the subsamples wet weights by their dry weights, to calculate a correction factor. This correction factor was then applied to all wet weights to obtain dry weights for each exclosure. We estimated vegetation biomass every 3 months as the average dry mass of palatable vegetation from all exclosures. We then divided the mean biomass by the number of days since the previous sampling, to obtain a daily estimate of forage availability. Daily forage availability was further divided by mean kangaroo density at the closest sampling session, providing a daily value of available forage per individual, hereafter termed per capita forage availability. We then summed those daily estimates over periods of time of interest, depending on the response trait. To determine the number of days prior to parturition to use in the analysis of each response trait, we compared models with different time windows (36, 60, 120, 180, 240, 300, or 360 days) and selected the most informative model using AICc (Hurvich and Tsai 1989; Burnham and Anderson 2002; Supplementary Table S1). Because all models had similar AICc values (Supplementary Table S1), and per capita forage availability was highly correlated across temporal windows,

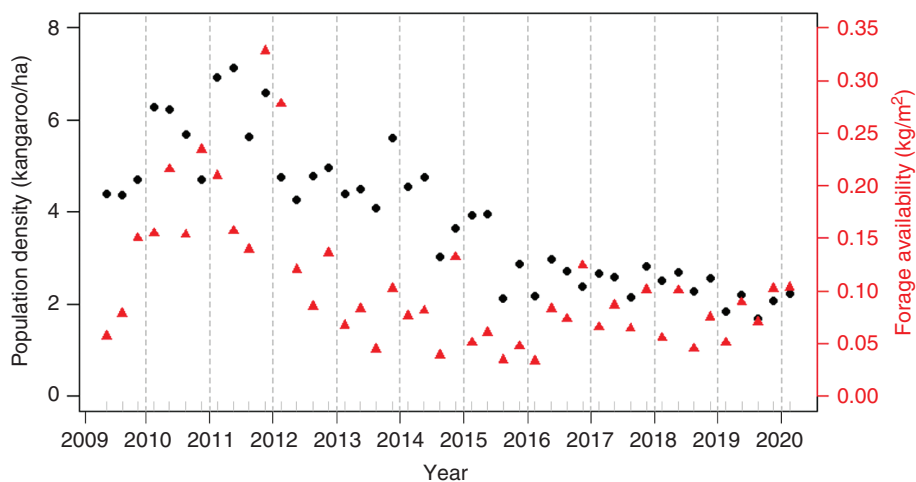


Figure 1

Quarterly estimates of kangaroo population density (black dots) and forage availability (red triangles) at Wilsons Promontory National Park, January 2009 to February 2020. See main text for sampling methods.

we used a single window of 36 days, corresponding to average gestation duration, for all models to make results easier to interpret.

Data analysis

Because individual characteristics are strongly age dependent in species with indeterminate growth, we limited analyses to females of known age, either first captured as juveniles (before weaning) or subadults (between weaning and sexual maturity) or found dead and aged by the molar index (Kirkpatrick 1965).

Sex ratio

We used χ^2 tests to compare the numbers of sons and daughters at 1–4 months (163 offspring, 2010–2018), 7–10 months (622 offspring including 98 survivors from the 1–4 months dataset, 2008–2019), and 21 months (224 survivors from the 7–10 months dataset, 2008–2018). We used generalized linear models (GLM) to investigate variation in the probability that a female would have a son (149 observations from 83 females). We compared 4 models to determine whether the probability of having a son varied with maternal age and mass circa conception only (sensu the TWH and CRH), with per capita forage availability during gestation (36 days prior to parturition) (sensu the EMH), or with an interaction between maternal mass circa conception and per capita forage availability (sensu the CCH) (Supplementary Table S2a). We used maternal mass in August–December, providing it was either within 4 months before or 2 months after conception, as mass circa conception; this excluded 113 offspring from analyses. We repeated the analysis replacing mass with maternal condition, calculated as the ratio of measured mass to mass predicted by an ordinary least-squares regression of log mass on log leg length (Le Cren 1951; Supplementary Table S2b).

Testing the assumptions of the TWH

We compared a linear mixed model (LMM) with offspring mass at age 2 (postweaning; King and Goldizen 2016) as a function of offspring age at capture in days, sex, and maternal mass when the offspring was 7–10 months, with a model that did not include maternal mass (Supplementary Table S2c; 114 offspring from 98 females). We also compared a model with offspring condition at age 2 as a function of age at capture in days, sex, and maternal condition when the offspring was 7–10 months, with a model excluding maternal condition (Supplementary Table S2d). Maternal ID and offspring capture year were included as random factors in both cases. We compared a linear model (LM) with mass at adulthood as a function of mass at age 2 (representing mass at the end of maternal care) and age at “adult” capture in days, to a model without mass at age 2 (Supplementary Table S2e). We performed this analysis for sons (14 from 11 mothers) and daughters (45 from 44 mothers) separately. Mass at adulthood was at 3 years for females and 4 years for males. Finally, we calculated maternal effort as the change in maternal mass, adjusted to median capture date, from when the offspring was caught at 7–10 months to 1 year later. We tested for an interaction between maternal effort and offspring sex on offspring fitness by comparing a LMM with offspring mass at age 2 as a function of maternal mass change in interaction with offspring sex, age at capture as a 2-year-old and maternal reproductive status in year 2 as a two-level factor according to whether or not the female reproduced, with a model that did not include the interaction (Supplementary Table S2f; 90 offspring from 77 females). We included maternal reproductive status in year 2 to control for potential confounding effects of allocation to a new offspring.

Sex-differential costs of year 1 offspring (CRH assumption)

These analyses were limited to females with a young of known sex in year 1 that were caught and measured between August and December. Maternal yearly mass change (208 observations from 96 females) was the difference between mass in years 1 and 2, both adjusted to median capture date (August 27) to account for seasonal mass changes. To adjust mass to median capture date, we used the residuals of a regression of capture date to the power of 3 (in Julian days), in interaction with reproductive status (reproduced or not), against measured mass. Maternal skeletal growth from year 1 to year 2 (207 observations from 96 females) was the difference in leg length. Reproductive success in year 2 was evaluated at four levels: fecundity, weaning success, offspring sex, and offspring mass at 7–10 months. Fecundity (206 observations from 96 females) compared females that did and did not show evidence of lactation. Weaning success (148 observations from 75 females) compared lactating females whose offspring did and did not survive to 21 months (King and Goldizen 2016). Analyses of offspring sex included 94 observations from 49 females, those of offspring mass included 74 observations from 44 females whose offspring in year 2 was measured at 7–10 months. Reproductive allocation as an explanatory variable had four levels: 0 = no evidence of reproduction, 1 = offspring died before 7 months, 2 = offspring died between 7 and 21 months, 3 = offspring survived to 21 months. We fitted LMs (when no random variable was selected) and LMMs using a gaussian link function for continuous response variables (yearly mass change, skeletal growth and offspring mass at 7–10 months), and GLMs (when no random variable was selected) or generalized linear mixed models (GLMMs) with a binomial link function for binary response variables (year 2 fecundity, weaning success and offspring sex). To investigate variability in yearly mass change, skeletal growth, year 2 fecundity and weaning success, we included covariates known to influence the response variables in this population (Toni et al. 2020a; Supplementary Table S2g–j). We compared these models to models including offspring sex in year 1, an interaction between offspring sex in year 1 and maternal mass, and between offspring sex and maternal reproductive allocation, unless models failed to converge (Supplementary Table S2g–j). To investigate variation in offspring sex in year 2, we compared a model including maternal age, mass and reproductive allocation in year 1 with models including also offspring sex in year 1, and interactions between offspring sex in year 1 and maternal mass or reproductive allocation in year 2 (Supplementary Table S2k). To investigate variation in mass at 7–10 months of the offspring born in year 2, we compared a model controlling for offspring sex and age and including maternal mass at the capture nearest to its conception, per capita forage availability over the previous 7 months and maternal reproductive allocation in year 1 with models also including offspring sex in year 1, and interactions between offspring sex in year 1 and maternal mass or reproductive success (Supplementary Table S2l).

Model comparisons

For all analyses using GLMMs, LMMs, and GLMs or LMs, we used the “lme4” (Bates et al. 2015) and “stats” (R Core Team 2020) packages, respectively. We used likelihood ratio tests (LRT) to determine the significance ($P < 0.05$) of random effects. After selecting the random effect structure, we compared nested models using F -statistics to determine if variables of interest improved model fit (Zuur et al. 2009). The difference in deviance between two models follows a χ^2 distribution with

degrees of freedom corresponding to the difference in degrees of freedom between the two models. Independent variables were not multicollinear (variance inflation factor < 3; [Graham 2003](#)). All analyses were performed using software R version 3.6.3 ([R Core Team 2020](#)).

RESULTS

Sex ratio

A slight male bias in offspring sex ratio (1–4 months 55.2% males; 7–10 months 53.7%; 21 months 54.9%) was never statistically different from parity (1–4 months $\chi^2_1 = 1.77$, $P = 0.18$, $n = 163$; 7–10 months $\chi^2_1 = 3.40$, $P = 0.07$, $n = 622$; 21 months $\chi^2_1 = 2.14$, $P = 0.14$, $n = 226$). The interaction between per capita forage availability and maternal mass or maternal condition did not improve model fit (mass: $F_{144,145} = -0.62$, $P = 0.43$; condition: $F_{144,145} = -1.40$, $P = 0.24$). Per capita forage availability also failed to improve the model (mass: $F_{145,146} = -2.25$, $P = 0.13$; condition: $F_{145,146} = -2.41$, $P = 0.12$). The probability of having a son depended only on maternal body mass or condition circa conception, after accounting for maternal age (mass: $F_{145,146} = -6.68$, $P = 0.01$, $\beta = 0.49 \pm 0.19$, $n = 149$; condition: $F_{145,146} = -10.20$, $P = 0.001$, $\beta = 0.57 \pm 0.19$, $n = 149$).

Testing the three assumptions of the TWH

In the analysis of offspring mass or condition at the end of maternal care, maternal mass ($\chi^2_1 = 3.56$, $P = 0.06$) and condition ($\chi^2_1 = 3.02$, $P = 0.08$) tended to improve the model fit. Offspring mass at 2 years and maternal mass in mid-lactation tended to be positively correlated ($\beta = 0.41 \pm 0.22$, $n = 114$, [Table 1](#)). In the analysis of offspring mass at adulthood, offspring mass at 2 years (end of maternal care) improved the model fit for both sexes (daughters: $F_{41,42} = 27.6$, $P < 0.00001$, sons: $F_{10,11} = 12.3$, $P = 0.006$), and was significantly correlated with mass at adulthood (daughters: $\beta = 0.75 \pm 0.14$, $n = 45$, sons: $\beta = 1.27 \pm 0.36$, $n = 14$, [Table 2](#)). The interaction between offspring sex and maternal effort, however, did not improve the fit of a model of offspring mass at 2 years ($F_{9,10} = 1.23$, $P = 0.27$, [Figure 2](#)).

Differential costs (CRH assumption)

Mass change and skeletal growth

Model fits were not improved by interactions between offspring sex in year 1 and maternal mass (mass change: $F_{197,198} = 0.13$, $P =$

0.72; skeletal growth: $\chi^2_2 = 1.12$, $P = 0.57$) or reproductive allocation (mass change: $F_{196,198} = 0.01$, $P = 0.99$; skeletal growth: $\chi^2_2 = 2.90$, $P = 0.23$). A model including offspring sex in year 1 did not explain variation in yearly mass change ($F_{198,199} = 0.24$, $P = 0.63$; [Figure 3a](#)) better than a model without this variable, but offspring sex tended to improve the model fit for skeletal growth ($\chi^2_1 = 2.86$, $P = 0.09$). Mothers of sons tended to grow less than mothers of daughters ($\beta = 1.46 \pm 0.86$, $n = 207$; [Figure 3b](#)).

Subsequent reproduction

In analyses of reproductive success in year 2, the interactions between offspring sex in year 1 and maternal mass (fecundity: $\chi^2_1 = 0.003$, $P = 0.95$; weaning success: $\chi^2_1 = 1.09$, $P = 0.30$; offspring sex: $\chi^2_1 = 1.12$, $P = 0.29$; offspring mass: $\chi^2_1 = 0.01$, $P = 0.92$) or reproductive allocation (offspring sex: $\chi^2_2 = 1.94$, $P = 0.38$; offspring mass: $\chi^2_2 = 2.59$, $P = 0.27$) did not improve model fits. A model including offspring sex in year 1 did not explain variation in year 2 fecundity ($\chi^2_1 = 1.00$, $P = 0.32$; [Figure 3c](#)) better than a model without this variable. Offspring sex, however, tended to improve the model fit for variation in subsequent weaning success ($\chi^2_1 = 2.78$, $P = 0.095$) or offspring sex ($\chi^2_1 = 2.87$, $P = 0.09$). Mothers of sons tended to have a lower probability of weaning an offspring ($\beta = 1.20 \pm 0.74$, $n = 148$; [Figure 3d](#)) or producing a son ($\beta = 0.84 \pm 0.56$, $n = 94$; [Figure 3e](#)) the following year. A model including offspring sex in year 1 did not explain variation in offspring mass ($\chi^2_1 = 0.14$, $P = 0.71$; [Figure 3f](#)) better than a model without this variable.

DISCUSSION

Adaptive sex ratio theory predicts when offspring sex ratio should differ from parity, but many empirical studies do not support those predictions ([Douhard 2017](#); [Liu et al. 2019](#)). Prewaning sex ratio in wild eastern gray kangaroos showed a nonsignificant trend toward a higher proportion of males. Data on the sex ratio at conception or birth were unavailable, hence we could only analyze sex ratio of offspring aged ≥ 1 month. Juvenile males often suffer greater mortality than females in sexually dimorphic mammals and birds ([Clutton-Brock et al. 1985](#); [Kahn et al. 2015](#); [Edwards et al. 2019](#)), but we found no decline in sex ratio from 4 to 21 months of age. Offspring sex depended on maternal mass or condition circa conception, but not on per capita forage availability. We did not identify significant sex-differential costs of reproduction, and found limited evidence that any adaptive effects of increased maternal effort varied with offspring sex.

Models including per capita forage availability, either as an independent variable (testing the EMH, [Post et al. 1999](#); [Weladji and Holand 2003](#)) or in interaction with maternal mass (testing the CCH, [Kruuk et al. 1999](#)), did not explain offspring sex better than a model without per capita forage availability. Our data therefore do not support the sex ratio manipulations predicted by the EMH or the CCH. The CCH requires population density to be below carrying capacity so that females would have extra energy to allocate to the costlier sex ([Kruuk et al. 1999](#)). The EMH predicts that harsh environmental conditions will reduce maternal condition so that fewer offspring of the costlier sex are born ([Post et al. 1999](#); [Weladji and Holand 2003](#)). Iteroparous females such as kangaroos are expected to adopt a conservative strategy, favoring their own survival and body condition over that of their offspring ([Clutton-Brock 1991](#); [Festa-Bianchet and Jorgenson 1998](#)). In our study, forage availability did not significantly affect female

Table 1

Effects of sex, age, capture date, and maternal mass in mid-lactation on mass at 2 years (end of maternal care) for 114 eastern gray kangaroos, Wilsons Promontory National Park, 2011–2019

Fixed effects	β	95% CI	
		Lower limit	Upper limit
Intercept	-2.32	-16.89	12.25
Sex = Female	-2.23	-2.96	-1.50
Age (days)	0.01	0.00	0.02
Maternal mass	0.41	-0.01	0.83
Capture date (Julian day)	-0.01	-0.04	0.02

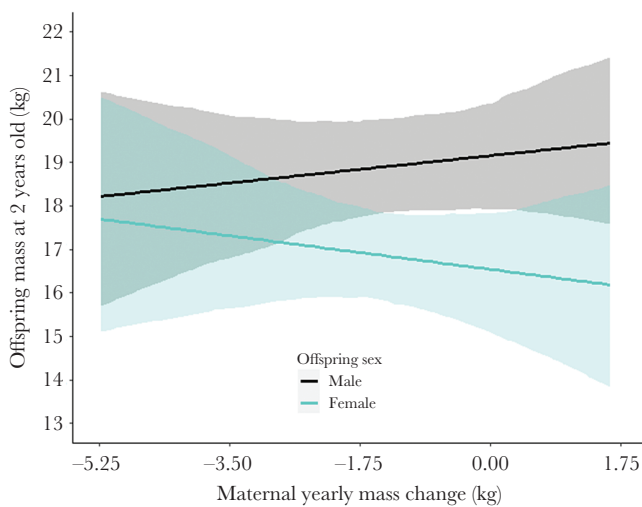
CI, confidence interval. “Male” is the reference level for offspring sex.

Table 2

Effect of mass at 2 years (end of maternal care) on mass at age 3 for 45 female and at age 4 for 14 male eastern gray kangaroos at Wilsons Promontory National Park, 2012–2019

Fixed effects	Females			Males		
	β	95% CI		β	95% CI	
		Lower limit	Upper limit		Lower limit	Upper limit
Intercept	-0.28	-13.36	12.80	35.11	-143.31	213.54
Mass at 2 years	0.75	0.46	1.03	1.27	0.46	2.07
Age (days)	-0.00	-0.01	0.01	-0.02	-0.14	0.09
Capture date (Julian day)	0.04	0.02	0.06	0.03	-0.06	0.13

CI, confidence interval.

**Figure 2**

Interaction of maternal effort, measured as mass change, and offspring sex, on mass at age 2 for 90 offspring born to 77 female eastern gray kangaroos at Wilsons Promontory National Park, 2011–2019. Shaded areas are 95% confidence intervals.

mass (Supplementary Figure S3). Our monitoring included three years (2013, 2014, and 2015) with very low forage (Figure 1), when weaning success was near zero (MacKay 2019). These environmental conditions could be defined as extreme (Moreno and Møller 2011; Wingfield et al. 2011); eastern gray kangaroo females thus appear to maintain body condition at the expense of offspring survival, rather than produce offspring of the less costly sex, consistent with a conservative strategy.

We confirmed that heavier eastern gray kangaroo females (Le Gall-Payne et al. 2015), and females in relatively better condition, produce more sons, supporting either the TWH or the CRH. Our results, however, cannot distinguish which of the two hypotheses better explains offspring sex variation. Kangaroos meet the first two assumptions of the TWH (Trivers and Willard 1973), but our test of the third assumption did not allow us to confirm the adaptive value of offspring sex ratio manipulation. Offspring mass at the end of parental care tended to be correlated with maternal mass, and was correlated with offspring mass near adulthood, but maternal effort, measured as mass change from mid-lactation to a year later, did not have a higher impact on mass of sons than of daughters near adulthood, our proxy for offspring fitness. Studies of short- and long-lived birds have tested all three assumptions of

the TWH (Komdeur 1998; Bowers et al. 2015; Liu et al. 2019), but few studies have fully tested them in wild mammals. The third assumption is difficult to verify, especially in long-lived species, requiring long-term monitoring of male and female offspring. Our measure of offspring fitness was imperfect. At age 3, females have reached close to 80% of asymptotic mass (Festa-Bianchet, unpublished data), and can, rarely, first reproduce at age 2 (Poole 1973; Poole et al. 1982), although only one 2-year-old female reproduced during our study, out of 99 females of known age at primiparity (King et al. 2015). At age 4, males weighed on average 32.75 kg. Large adult males weighed >60 kg, and most reproductive males are older than 4 years (Montana et al., unpublished data). Mass at a later age, or lifetime reproductive success would have been better measures of offspring fitness, but they could not be estimated with the available data.

We found limited evidence of a greater cost of sons than of daughters on skeletal growth and subsequent weaning success or any effects on subsequent offspring sex, providing limited support for the CRH. Many studies of sexually dimorphic species found sex-differential costs of parental care (Merkling et al. 2015; review for mammals in Douhard 2017), including some on macropodids (Schwanz and Robert 2016), but other studies of sexually dimorphic species found that sons and daughters led to similar fitness costs, despite a greater birth mass for one sex (Bowen et al. 2001). We confirmed that offspring sex is affected by maternal mass (Le Gall-Payne et al. 2015), suggesting that individual heterogeneity in reproductive potential could mask differential costs. After controlling for age, heavier females are more likely than lighter females to have sons. If heavy females have more resources to allocate to reproduction, then they could mitigate the greater cost of having a son, compared to light females. G elin et al. (2013) found that mothers of sons had a higher bite rate (a commonly used proxy for foraging intake in herbivores; Hudson 1985; Shipley et al. 1994) than mothers of daughters, suggesting that mothers partly compensate for the higher costs of sons by increasing energy acquisition. Moreover, in 2008–2012, mothers of daughters lost more mass than mothers of sons, and females in poor condition incurred less severe costs of reproduction if they nursed a daughter than a son (G elin et al. 2016). These earlier results suggested that mothers of sons may have greater acquisition and allocation abilities than those raising daughters. Those effects, however, nearly disappeared in our analysis, perhaps because our analyses included years with low per capita forage availability that may have reduced differences in reproductive potential. Some studies suggest that costs may only be detectable in parents with fewer resources to allocate, such as those

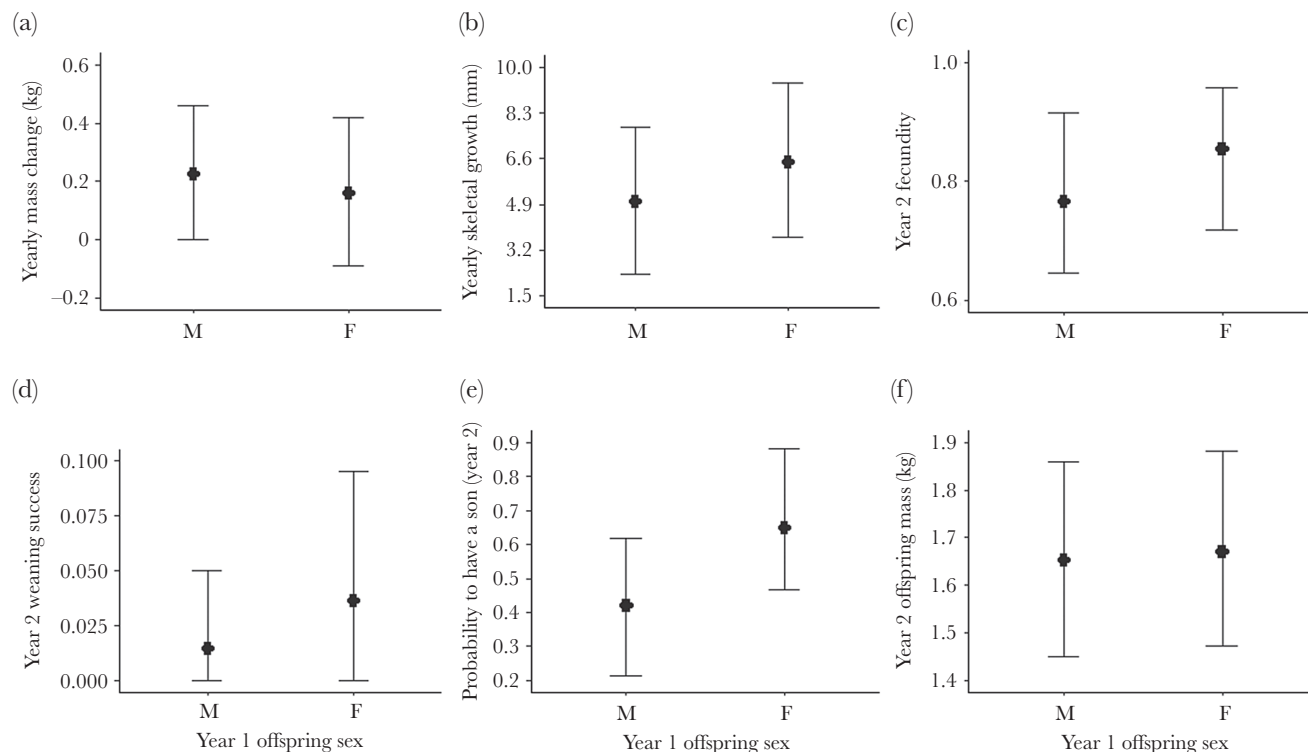


Figure 3

Effect of offspring sex in year 1 on (a) maternal yearly mass change, (b) maternal yearly skeletal growth, (c) year 2 fecundity, (d) year 2 weaning success, (e) year 2 offspring sex, and (f) year 2 offspring mass at 7–10 months, for eastern gray kangaroos at Wilsons Promontory National Park, 2010–2017. Bars are 95% confidence intervals.

in poor condition (Nager et al. 2000; Gélin et al. 2016) or in mammalian females that reproduce before reaching asymptotic mass (Landete-Castillejos et al. 2004). The interaction between offspring sex and maternal mass on mass change, skeletal growth, subsequent year fecundity, weaning success, offspring sex and offspring mass, however, never improved the models, ruling out this possibility. Offspring sex could have a stronger impact on reproductive costs over the longer term. Female bighorn sheep (*Ovis canadensis*) that weaned more sons during early life experienced faster reproductive senescence than females that weaned more daughters (Douhard et al. 2020). In preindustrial Finnish women, mothers of sons produced a subsequent offspring with lower survival and lifetime reproductive success, thus decreasing maternal lifetime reproductive success (Rickard et al. 2007).

Sex ratio in eastern gray kangaroos depended on maternal mass, but increased effort measured as maternal mass change did not translate into a higher increase in fitness for sons than for daughters. Females that can provide superior maternal care may do so as a response to differential offspring demand, but not as an allocation tactic to enhance their own fitness (Krackow 2002; Sikes et al. 2007). Given the many empirical studies that found no support for adaptive sex ratio manipulation (Hewison and Gaillard 1999; Sikes et al. 2007), it is likely that sex ratios are not explained by factors dependent only on maternal control. Recent studies have explored paternal effects on offspring sex ratio (Edwards and Cameron 2014; Bookmythe et al. 2017; Douhard 2018). In birds, females are the heterogametic sex, but in mammals offspring sex depends on fertilization of the oocyte by a X- or Y-chromosome bearing sperm. Mechanisms allowing mammalian females to manipulate offspring

sex remain poorly understood: hormonal concentrations at different times of the reproductive cycle can affect the propensity of an oocyte to be fertilized by a Y-chromosome bearing sperm, or influence sex-specific embryo mortality (Cameron 2004; Ryan et al. 2012; Schwanz and Robert 2014). In mammalian males, the ratio of X/Y-chromosome bearing sperm is influenced by reproductive potential (Edwards et al. 2016), suggesting that offspring sex ratio manipulation by mothers may partly be dependent on sire traits (Mainguy et al. 2009; Douhard, Festa-Bianchet, Coltman, et al. 2016; Douhard 2018). Paternal effects should ideally be considered in studies of adaptive sex ratios manipulations resulting from selection for differential maternal tactics.

FUNDING

Funding was provided by the Natural Sciences and Engineering Research Council of Canada (Discovery Grant to M.F.-B.) and by Bishop's University (Senate Research Committee grant to Wendy King).

We thank Graeme Coulson, Naomi Davis, Wendy King, and all students and field assistants who helped with fieldwork. We are grateful to W. King and G. Coulson for their dedicated work to age kangaroo skulls. We acknowledge Parks Victoria, Wilsons Promontory National Park staff, and the University of Melbourne for logistic support. W. King, as well as two anonymous reviewers provided detailed comments on previous versions of the manuscript. Animal handling was approved by the Animal Care Committee of the Université de Sherbrooke (protocol MFB-2016-01) and by the Animal Ethics Committee of the University of Melbourne (approval 1312902.1). Field research was conducted under the authority of permits 1007062 and 10008630 of the Department of Environment, Land, Water and Planning (Victoria).

Author contributions: P.T. conceived the idea; P.T., D.M.F., and M.F.-B. collected the data; P.T. analyzed the data and wrote the first draft; all authors contributed substantially to revisions.

Data availability: Analyses reported in this article can be reproduced using the data and R scripts provided by [Toni et al. 2020b](#).

Handling editor: Michael D. Jennions

REFERENCES

- Arak A. 1988. Sexual dimorphism in body size: a model and a test. *Evolution*. 42:820–825.
- Arnbom T, Fedak MA, Rothery P. 1994. Offspring sex ratio in relation to female size in southern elephant seals, *Mirounga leonina*. *Behav Ecol Sociobiol*. 35:373–378.
- Australian Bureau of Meteorology. 2019. Australian Government, Bureau of Meteorology, Climate data online. <http://www.bom.gov.au/>. Accessed 24 August 2019.
- Bateman AJ. 1948. Intra-sexual selection in *Drosophila*. *Heredity*. 2:349–368.
- Bates D, Mächler M, Bolker BM, Walker SC. 2015. Fitting linear mixed-effects models using lme4. *J Stat Softw*. 67:1–48.
- Bercovitch FB, Widdig A, Nürnberg P. 2000. Maternal investment in rhesus macaques (*Macaca mulatta*): reproductive costs and consequences of raising sons. *Behav Ecol Sociobiol*. 48:1–11.
- Bookmythe I, Mautz B, Davis J, Nakagawa S, Jennions MD. 2017. Facultative adjustment of the offspring sex ratio and male attractiveness: a systematic review and meta-analysis. *Biol Rev Camb Philos Soc*. 92:108–134.
- Bowen WD, Ellis SL, Iverson SJ, Boness DJ. 2001. Maternal effects on offspring growth rate and weaning mass in harbour seals. *Can J Zool*. 79:1088–1101.
- Bowers EK, Thompson CF, Sakaluk SK. 2015. Persistent sex-by-environment effects on offspring fitness and sex-ratio adjustment in a wild bird population. *J Anim Ecol*. 84:473–486.
- Burnham KP, Anderson D. 2002. Model selection and multimodel inference. New York (NY): Springer-Verlag.
- Cameron EZ. 2004. Facultative adjustment of mammalian sex ratios in support of the Trivers-Willard hypothesis: evidence for a mechanism. *Proc Biol Sci*. 271:1723–1728.
- Case TJ. 1978. On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. *Q Rev Biol*. 53:243–282.
- Clutton-Brock TH. 1983. Selection in relation to sex. In: Benda BJ, editor. *Evolution from molecules to men*. Cambridge: Cambridge University Press. p. 457–481.
- Clutton-Brock TH. 1988. Reproductive success: studies of individual variation in contrasting breeding systems. In: Clutton-Brock TH, editor. Chicago (IL): University of Chicago Press.
- Clutton-Brock TH. 1991. The evolution of parental care. Princeton (NJ): Princeton University Press.
- Clutton-Brock TH, Albon SD. 1982. Parental investment in male and female offspring in mammals. In: King's College Sociobiology Group, editor. *Current problems in sociobiology*. p. Cambridge (UK): Cambridge University Press. p. 223.
- Clutton-Brock TH, Albon SD, Guinness FE. 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature*. 313:131–133.
- Clutton-Brock TH, Albon SD, Guinness FE. 1988. Reproductive success in male and female deer. In: Clutton-Brock TH, editor. *Reproductive Success: Studies of individual variation contrasting breeding systems*. Chicago (IL): University of Chicago Press. p. 325–343.
- Clutton-Brock TH, Iason GR. 1986. Sex ratio variation in mammals. *Q Rev Biol*. 61:339–374.
- Cockburn A, Legge S, Double MC. 2002. Sex ratios in birds and mammals: can the hypotheses be disentangled? In: Hardy ICW, editor. *Sex ratios: concepts and research methods*. Cambridge (UK): Cambridge University Press. p. 266–286.
- Le Cren ED. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). *J Anim Ecol*. 20:201–219.
- Davis NE, Forsyth DM, Coulson G. 2010. Facilitative interactions between an exotic mammal and native and exotic plants: Hog deer (*Avis porcinus*) as seed dispersers in south-eastern Australia. *Biol Invasions*. 12:1079–1092.
- Delean S, De'ath G, Marsh H. 2009. Climate and maternal effects modify sex ratios in a weakly dimorphic marsupial. *Behav Ecol Sociobiol*. 64:265–277.
- Douhard M. 2017. Offspring sex ratio in mammals and the Trivers-Willard hypothesis: in pursuit of unambiguous evidence. *BioEssays*. 39:1–10.
- Douhard M. 2018. The role of fathers in mammalian sex allocation. *Mamm Rev*. 48:67–74.
- Douhard M, Festa-Bianchet M, Coltman DW, Pelletier F. 2016. Paternal reproductive success drives sex allocation in a wild mammal. *Evolution*. 70:358–368.
- Douhard M, Festa-Bianchet M, Pelletier F. 2016. Maternal condition and previous reproduction interact to affect offspring sex in a wild mammal. *Biol Lett*. 12:20160510.
- Douhard M, Festa-Bianchet M, Pelletier F. 2020. Sons accelerate maternal aging in a wild mammal. *Proc Natl Acad Sci USA*. 117:4850–4857.
- Edwards AM, Cameron EZ. 2014. Forgotten fathers: paternal influences on mammalian sex allocation. *Trends Ecol Evol*. 29:158–164.
- Edwards AM, Cameron EZ, Deakin JE, Ezaz T, Pereira JC, Ferguson-Smith MA, Robert KA. 2019. Sexual conflict in action: an antagonistic relationship between maternal and paternal sex allocation in the tammar wallaby, *Notamacropus eugenii*. *Ecol Evol*. 9:4340–4348.
- Edwards AM, Cameron EZ, Pereira JC, Ferguson-Smith MA. 2016. Paternal sex allocation: how variable is the sperm sex ratio? *J Zool*. 299:37–41.
- Festa-Bianchet M, Jorgenson JT. 1998. Selfish mothers: reproductive expenditure and resource availability in bighorn ewes. *Behav Ecol*. 9:144–150.
- Fisher RA. 1930. The genetical theory of natural selection. London (UK): Oxford University Press.
- Forchhammer MC. 2000. Timing of foetal growth spurts can explain sex ratio variation in polygynous mammals. *Ecol Lett*. 3:1–4.
- Foster WK, Taggart DA. 2008. Gender and parental influences on the growth of a sexually dimorphic carnivorous marsupial. *J Zool*. 275:221–228.
- Galante L, Milan AM, Reynolds CM, Cameron-Smith D, Vickers MH, Pundir S. 2018. Sex-specific human milk composition: the role of infant sex in determining early life nutrition. *Nutrients*. 10:1–11.
- Le Gall-Payne C, Coulson G, Festa-Bianchet M. 2015. Supersize me: heavy eastern grey kangaroo mothers have more sons. *Behav Ecol Sociobiol*. 69:795–804.
- Gélin U, Wilson ME, Coulson GM, Festa-Bianchet M. 2013. Offspring sex, current and previous reproduction affect feeding behaviour in wild eastern grey kangaroos. *Anim Behav*. 86:885–891.
- Gélin U, Wilson ME, Cripps J, Coulson G, Festa-Bianchet M. 2016. Individual heterogeneity and offspring sex affect the growth-reproduction trade-off in a mammal with indeterminate growth. *Oecologia*. 180:1127–1135.
- Gendreau Y, Côté SD, Festa-Bianchet M. 2005. Maternal effects on post-weaning physical and social development in juvenile mountain goats (*Oreamnos americanus*). *Behav Ecol Sociobiol*. 58:237–246.
- Georgiadis N. 1985. Growth patterns, sexual dimorphism and reproduction in African ruminants. *Afr J Ecol*. 23:75–87.
- Glass R, Forsyth DM, Coulson G, Festa-Bianchet M. 2015. Precision, accuracy and bias of walked line-transect distance sampling to estimate eastern grey kangaroo population size. *Wildl Res*. 42:633–641.
- Gomendio M, Clutton-Brock TH, Albon SD, Guinness FE, Simpson MJ. 1990. Mammalian sex ratios and variation in costs of rearing sons and daughters. *Nature*. 343:261–263.
- Graham MH. 2003. Confronting multicollinearity in ecological multiple regression. *Ecology*. 84:2809–2815.
- Hewison AJ, Gaillard JM. 1999. Successful sons or advantaged daughters? The Trivers-Willard model and sex-biased maternal investment in ungulates. *Trends Ecol Evol*. 14:229–234.
- Hudson RJ. 1985. Body size, energetics, and adaptive radiation. In: Hudson RJ, White RG, editors. *Bioenergetics of wild herbivores*. Boca Raton (FL): CRC Press. p. 1–24.
- Hurvich CM, Tsai CL. 1989. Regression and time series model selection in small samples. *Biometrika*. 76:297–307.
- Jarman PJ. 1989. Sexual dimorphism in Macropodoidea. In: Coulson GM, Eldridge MDB, editors. *Macropods: the biology of kangaroos, wallabies and rat-kangaroos*. Melbourne (Australia): CSIRO Publishing. p. 433–447.

- Kahn AT, Jennions MD, Kokko H. 2015. Sex allocation, juvenile mortality and the costs imposed by offspring on parents and siblings. *J Evol Biol.* 28:428–437.
- Karkach AS. 2006. Trajectories and models of individual growth. *Demogr Res.* 15:347–400.
- King WJ, Festa-Bianchet M, Coulson G, Goldizen AW. 2017. Long-term consequences of mother-offspring associations in eastern grey kangaroos. *Behav Ecol Sociobiol.* 71:77.
- King WJ, Garant D, Festa-Bianchet M. 2015. Mother-offspring distances reflect sex differences in fine-scale genetic structure of eastern grey kangaroos. *Ecol Evol.* 5:2084–2094.
- King WJ, Goldizen AW. 2016. Few sex effects in the ontogeny of mother-offspring relationships in eastern grey kangaroos. *Anim Behav.* 113:59–67.
- King WJ, Wilson ME, Allen T, Festa-Bianchet M, Coulson G. 2011. A capture technique for free-ranging eastern grey kangaroos (*Macropus giganteus*) habituated to humans. *Aust Mammal.* 33:47–51.
- Kirkpatrick TH. 1965. Studies on the Macropodidae in Queensland. 2. Age estimation in the grey kangaroo, the red kangaroo, the eastern wallaroo and the red-necked wallaby, with notes on dental abnormalities. *Queensl J Agric Anim Sci.* 22:301–317.
- Komdeur J. 1998. Long-term fitness benefits of egg sex modification by the Seychelles warbler. *Ecol Lett.* 1:56–62.
- Krackow S. 2002. Why parental sex ratio manipulation is rare in higher vertebrates. *Ethology.* 108:1041–1056.
- Kruuk LE, Clutton-Brock TH, Albon SD, Pemberton JM, Guinness FE. 1999. Population density affects sex ratio variation in red deer. *Nature.* 399:459–461.
- Landete-Castillejos T, Gortázar C, Vicente J, Fierro Y, Garcia A, Gallego L. 2004. Age-related foetal sex ratio bias in Iberian red deer (*Cervus elaphus hispanicus*): are male calves too expensive for growing mothers? *Behav Ecol Sociobiol.* 56:1–8.
- Liu Y, Tang D, Zhan X. 2019. Sex allocation and progress in the studies on offspring sex ratio of birds. *Sci Sin Vitae.* 49:392–402.
- MacKay A. 2019. Conséquences écologiques et évolutives de l'asynchronie de date de mise bas chez le kangourou gris de l'est (*Macropus giganteus*) dans un environnement imprévisible. [PhD thesis] Université de Sherbrooke.
- MacKay A, Forsyth DM, Coulson G, Festa-Bianchet M. 2018. Maternal resource allocation adjusts to timing of parturition in an asynchronous breeder. *Behav Ecol Sociobiol.* 72:7.
- Magrath MJ, van Lieshout E, Pen I, Visser GH, Komdeur J. 2007. Estimating expenditure on male and female offspring in a sexually size-dimorphic bird: a comparison of different methods. *J Anim Ecol.* 76:1169–1180.
- Mainguy J, Côté SD, Festa-Bianchet M, Coltman DW. 2009. Father-offspring phenotypic correlations suggest intralocus sexual conflict for a fitness-linked trait in a wild sexually dimorphic mammal. *Proc Biol Sci.* 276:4067–4075.
- Merkling T, Welcker J, Hewison AJM, Hatch SA, Kitaysky AS, Speakman JR, Danchin E, Blanchard P. 2015. Identifying the selective pressures underlying offspring sex-ratio adjustments: a case study in a wild seabird. *Behav Ecol.* 26:916–925.
- Montana L, Rousseu F, Garant D, Festa-Bianchet M. 2020. Siring success in kangaroos: size matters for those in the right place at the right time. *Behav Ecol.* 31:750–760.
- Moreno J, Møller AP. 2011. Extreme climatic events in relation to global change and their impact on life histories. *Curr Zool.* 57:375–389.
- Myers JH. 1978. Sex ratio adjustment under food stress: maximisation of quality or numbers of offspring? *Am Nat.* 112:381–388.
- Nager RG, Monaghan P, Houston DC, Genovart M. 2000. Parental condition, brood sex ratio and differential young survival: an experimental study in gulls (*Larus fuscus*). *Behav Ecol Sociobiol.* 48:452–457.
- Poole WE. 1973. A study of breeding in grey kangaroos, *Macropus giganteus* Shaw and *M. fuliginosus* (Desmarest), in central New South Wales. *Aust J Zool.* 21:183.
- Poole WE. 1975. Reproduction in two species of grey kangaroos, *Macropus giganteus* Shaw and *Macropus fuliginosus* (Desmarest). II. Gestation, parturition and pouch life. *Aust J Zool.* 23:333–353.
- Poole WE, Carpenter SM, Wood JT. 1982. Growth of grey kangaroos and the reliability of age determination from body measurements I. The eastern grey kangaroo, *Macropus giganteus*. *Aust Wildl Res.* 9: 9–20.
- Poole WE, Catling PC. 1974. Reproduction in the two species of grey kangaroos, *Macropus giganteus* Shaw and *M. fuliginosus* (Desmarest). I. Sexual maturity and oestrus. *Aust J Zool.* 22:277–302.
- Post E, Forchhammer MC, Stenseth NC, Langvatn R. 1999. Extrinsic modification of vertebrate sex ratios by climatic variation. *Am Nat.* 154:194–204.
- R Core Team. 2020. R: a language and environment for statistical computing. <https://www.r-project.org/>.
- Rickard JJ, Russell AF, Lummaa V. 2007. Producing sons reduces lifetime reproductive success of subsequent offspring in pre-industrial Finns. *Proc Biol Sci.* 274:2981–2988.
- Rioux-Paquette E, Garant D, Martin AM, Coulson G, Festa-Bianchet M. 2015. Paternity in eastern grey kangaroos: moderate skew despite strong sexual dimorphism. *Behav Ecol.* 26:1147–1155.
- Robert KA, Braun S. 2012. Milk composition during lactation suggests a mechanism for male biased allocation of maternal resources in the tammar wallaby (*Macropus eugenii*). *PLoS One.* 7:e51099.
- Rutkowska J, Cichoń M. 2002. Maternal investment during egg laying and offspring sex: an experimental study of zebra finches. *Anim Behav.* 64:817–822.
- Ryan CP, Anderson WG, Gardiner LE, Hare JF. 2012. Stress-induced sex ratios in ground squirrels: support for a mechanistic hypothesis. *Behav Ecol.* 23:160–167.
- San José C, Braza F, Aragon S. 1999. The effect of age and experience on the reproductive performance and prenatal expenditure of resources in female fallow deer (*Dama dama*). *Can J Zool.* 77:1717–1722.
- Schwanz LE, Robert KA. 2014. Proximate and ultimate explanations of mammalian sex allocation in a marsupial model. *Behav Ecol Sociobiol.* 68:1085–1096.
- Schwanz LE, Robert KA. 2016. Costs of rearing the wrong sex: cross-fostering to manipulate offspring sex in tammar wallabies. *PLoS One.* 11:e0146011.
- Shipley LA, Gross JE, Spalinger DE, Hobbs NT, Wunder BA. 1994. The scaling of intake rate in mammalian herbivores. *Am Nat.* 143:1055–1082.
- Sikes RS, Wolff JO, Sherman PW. 2007. Facultative sex ratio adjustment. In: Wolff JO, Sherman PW, editors. *Rodent Societies: an ecological and evolutionary perspective*. Chicago (IL): University of Chicago Press. p. 129–138.
- Stearns SC. 1992. *The evolution of life histories*. Oxford (UK): Oxford University Press.
- Székelly T, Líker A, Freckleton RP, Fichtel C, Kappeler PM. 2014. Sex-biased survival predicts adult sex ratio variation in wild birds. *Proc Biol Sci.* 281:20140342.
- Thomas L, Buckland ST, Rexstad EA, Laake JL, Strindberg S, Hedley SL, Bishop JR, Marques TA, Burnham KP. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. *J Appl Ecol.* 47:5–14.
- Toni P. 2018. Combat leads to intraspecific killing in eastern grey kangaroos. *Aust Mammal.* 40:109–111.
- Toni P, Forsyth DM, Festa-Bianchet M. 2020a. Forage availability and maternal characteristics affect costs of reproduction in a large marsupial. *Oecologia.* 193:97–107.
- Toni P, Forsyth DM, Festa-Bianchet M. 2020b. Determinants of offspring sex in kangaroos: a test of multiple hypotheses. *Behav Ecol.* doi:10.5061/dryad.fbbg79csr
- Trivers RL. 1972. Parental investment and sexual selection. In: *Sexual selection and the descent of man*. Chicago (IL): Aldine Publishing Company. p. 136–179.
- Trivers RL, Willard DE. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science.* 179:90–92.
- Tyndale-Biscoe CH, Janssens PA. 1988. *The Developing Marsupial*. In: Tyndale-Biscoe CH, Janssens PA, editors. Berlin (Germany): Springer-Verlag.
- Weladji R, Holand Ø. 2003. Sex ratio variation in reindeer *Rangifer tarandus*: a test of the extrinsic modification hypothesis. *Wildlife Biol.* 9:29–36.
- Wingfield JC, Kelley JP, Angelier F. 2011. What are extreme environmental conditions and how do organisms cope with them? *Curr Zool.* 57:363–374.
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009. *Mixed effects models and extensions in ecology with R*. In: Gail M, Krickeberg K, Samet JM, Tsiatis A, Wong W, editors. New-York (NY): Springer.