



Original Article

Paternity in eastern grey kangaroos: moderate skew despite strong sexual dimorphism

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Understanding sexual selection requires adequate measures of reproductive success. In wild mammals, reliable data on variation in male reproductive success are available for very few species. We assessed the distribution of paternities and quantified skew in male reproductive success in 2 populations of a marsupial with strong sexual dimorphism, the eastern grey kangaroos (*Macropus giganteus*) over 5 years. We assigned fathers to 356 juveniles, or 79% of those with known mother. We found a relatively weak mating skew and the most successful males did not monopolize a large fraction of paternities. Nearly half of the adult males we monitored fathered at least 1 young. The yearly opportunity for sexual selection (*I_s*) for males ranged from 1.80 to 3.98, and Nonacs' *B* index of mating skew was significant but low, ranging from 0.01 to 0.07. Considering the strong sexual dimorphism, long breeding season, and strong male dominance hierarchy, our results suggest an unexpectedly low reproductive skew. That is surprising given the wide range in male weights: the smallest fathers weighed 40% less than the heaviest ones. Skew in eastern grey kangaroos is weaker than that estimated for other species with lower sexual size dimorphism. We found substantial year-to-year variability in reproductive skew. Because male mating success varies according to the characteristics of competitors and the distribution of breeding opportunities, multiple years of monitoring are required to obtain reliable estimates. In the absence of data on paternity, strong sexual dimorphism cannot be assumed to imply high polygyny and strong sexual selection.

Key words: intrasexual competition, male reproductive success, mammals, Nonacs' *B* index, opportunity for sexual selection, sexual size dimorphism.

INTRODUCTION

Sexual selection plays a central role in evolutionary biology as it is a main driver of mating systems (Emlen and Oring 1977, Andersson 1994). At the core of sexual selection, mating competition leads to an individual variation in reproductive fitness, called reproductive inequality. Much research in evolutionary ecology seeks to understand the relationships between reproductive inequality, mating system, and ecological conditions. For instance, many authors have argued that precopulatory sexual selection should be stronger in polygynous than in monogamous species and should increase with the degree of polygyny (Clutton-Brock and Vincent 1991; Brø-Jørgensen 2011; Plard et al. 2011). That suggestion, however, is not universally accepted, especially given uncertainties about the ability of a few males to monopolize matings (Clutton-Brock 2007; Kokko et al. 2012). For wild mammals in particular, reliable data on male reproductive success are available for a very limited number of species (Lukas and Clutton-Brock 2014). Further empirical data and

comparative work are thus required to document the distribution of paternities in polygynous species, quantify reproductive inequality among males and examine how differences in ecology, demography, and their interaction affect the strength of sexual selection (Clutton-Brock 2007).

Previous studies of mammals described reproductive skew in males by providing percentages and mean number of young produced per reproductive individual. Those studies, however, often present very different interpretations of the strength of reproductive skew. For example, skew was considered low among reproducing Galápagos sea lions (*Zalophus wollebaeki*) as 71% sired 1 young, and only 1.5% sired 4 (Pörschmann et al. 2010). In that study, however, 81% of males were not known to sire any young over the 2 years of study. In the bridled nailtail wallaby (*Onychogalea fraenata*), a solitary marsupial, 76% of males did not sire any young and the most successful male fathered 13% of offspring, leading to the suggestion that reproductive skew was low (Fisher and Lara 1999). Yet, in the brown-throated 3-toed sloth (*Bradypus variegatus*), where 74% of males did not sire any young, reproductive skew was considered high (Pauli and Peery 2012).

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Reproductive inequality can be described by the opportunity for sexual selection I_s , the variance in reproductive success divided by the square of the average reproductive success (Wade 1979; Shuster and Wade 2003). Being a squared coefficient of variation of reproductive success, standardized by definition, I_s has been used to compare reproductive inequality among different reproductive episodes and/or different ecological systems. I_s also quantifies the maximum potential for sexual selection and thus provides a useful statistic to describe mating systems (Krakauer et al. 2011; Shuster and Wade 2003). The accuracy of I_s in predicting sexual selection, however, has been questioned because it can be biased by random processes influencing reproductive success (Sutherland 1985; Krakauer et al. 2011).

Multiple alternative metrics are available to quantify reproductive inequality: Kokko et al. (1999) listed 21 indices of inequality, including several used in fields other than biology. The variety of ecological and demographic conditions under which mating competition occurs, however, implies that no unique measure can adequately describe all aspects of sexual selection (Klug et al. 2010; Krakauer et al. 2011; Jennions et al. 2012). Different indices can provide different estimations of skew according to the number of competitors or the distribution of reproductive success, leading Kokko et al. (1999) to suggest that simply describing the data, as in the examples cited above, may be more informative than quantifying the skew with an index. An index, however, is necessary to contrast an observed with a random distribution or to compare inequalities. Comparative studies found that most indices ranked inequalities rather similarly, although some appeared more appropriate in specific situations (Tsuji and Kasuya 2001; Nonacs 2003). Nonacs (2003) suggested that the B index was the most appropriate to characterize reproductive skew. This index takes into account the observed variance corrected by that expected if all group members had an equal probability of mating, when the index would equal 0 (Nonacs 2000). Positive values represent a skew, whereas negative values indicate that matings are more evenly distributed than expected under random, equal mating probabilities.

Most studies on male reproductive success of wild mammals have been performed in eutherians, usually in species with short breeding seasons characterized by intense and overt competition among males for access to mates (Festa-Bianchet 2012). Very few studies have examined sexually dimorphic marsupials such as macropodids, whose extended breeding season may allow a few dominant males to monopolize matings (Delean 2007; Fisher and Lara 1999). Eastern grey kangaroos (*Macropus giganteus*) are sexually dimorphic (Jarman and Southwell 1986), as males can weigh up to 4 times as much as the smallest breeding females. This species may breed at any time of the year, but most matings occur in spring and summer (Poole 1983). Males establish a clear dominance hierarchy which is thought to determine access to oestrous females (Miller et al. 2010). Males court and defend oestrous females, and a copulatory sequence can last well over an hour (E. Rioux-Paquette, personal observation). Although solicitation of male–male competition by females has been reported in other macropods (Sigg and Goldizen 2006), we very rarely saw this behavior during our observations. Sexual selection appears to have led to male phenotypic traits favoring fighting ability, particularly large arms, size, and mass (Warburton et al. 2013). Given these characteristics, we hypothesized that reproductive skew among males would be high, as a few highly competitive males could monopolize oestrus females. However, with the exception of a small enclosed population (Miller et al. 2010), there has been no genetic assignments of paternity in this species. Here, we take

advantage of an unusually high success in paternity assignments and a large sample size in 2 wild populations to quantify the skew in male reproductive success. We then compare the reproductive skew observed in kangaroos with published B indices and opportunity for selection for male mammals, to determine if there are any clear patterns of variability in these indices.

METHODS

Study areas and study species

We studied kangaroos at 2 sites in Victoria, Australia: Wilsons Promontory National Park (38°57'S, 146°20'E) and Anglesea Golf Course (38°24'S, 144°11'E). Based on age estimates of captured pouch young (Poole et al. 1982), 62% of births at Wilsons Promontory and 54% at Anglesea occurred in December–January. Because gestation lasts 35–38 days (Poole 1975), most matings occurred in November and December. In both study sites, we recorded births in all months of the year, however, less than 10% of births occurred between May and October. For females that reproduced in consecutive years, the interbirth interval averaged about 380 days but varied as a function of reproductive success, offspring sex, and year (Gélin et al. 2015). The mating system of kangaroos has been described as female-defence, with dominant males serially defending oestrous females (Jarman and Southwell 1986) and data from a semicaptive population suggest that dominant males have higher reproductive success (Miller et al. 2010).

Research at Wilsons Promontory started in 2008. The warmest month is February with an average temperature of 20.7 °C and the coolest months are July and August with 8.6 °C. Mean annual rainfall is 1055 mm (<http://www.weatherzone.com.au/climate/station.jsp?It=site&Ic=85096>). The study area includes grassland habitats around an emergency landing strip. The density of kangaroos during the study was high, varying from 4.3 to 7.1/ha (Gélin et al. 2013). About 30–60% of adults were marked, depending on year and section of the study area.

At Anglesea, marked kangaroos have been monitored since 2007. Kangaroos use open grassy areas on the golf course and nearby patches of woodland and scrub. Density is lower than at Wilsons Promontory, but high compared with most populations, varying from 3.3 to 3.6 kangaroos/ha (Coulson et al. 2014). About 45–60% of adults were marked depending on the year. In both populations, kangaroos are habituated to humans, making it possible to capture and recapture individuals.

Kangaroos were captured by remote injection of Zoletil (King et al. 2011). Adults were marked with visual collars and Allflex ear tags. Females of less than 18 kg and males of less than 38 kg were marked with ear tags only. Pouch young of at least 1 kg were marked with Leader ear tags. In both study areas, the proportion of marked individuals increased over time, but we do not have exact estimates of either population, partly because they are not isolated and animals, especially males, move in and out of the study areas. By 2012, about half the adult females at the Wilsons Promontory and over half of those at Anglesea appeared to be marked. In 2010–2012, we attempted to capture and sample every adult male seen in both study areas. That included any male the size of an adult female (about 28–30 kg) and larger. Each year, new unmarked adult males arrived for the main breeding season (November–January). We do not know how many unmarked males we did not capture, but the high success in paternity assignment, especially in 2010–2012 at the Wilsons Promontory and all years at Anglesea (Table 1) suggests that we sampled the vast majority of breeding males.

All animal manipulations described here were approved by the Animal Care Committee of the Université de Sherbrooke, affiliated with the Canadian Council on Animal Care (protocol MFB-2012-2) and by the Faculty of Science Animal Ethics Committee of the University of Melbourne (Projects 486-004-0-92-1157, 654-125-0-94-1617 & 06146).

Paternity assignment

A tissue sample from the ear was collected at first capture of each kangaroo, either with a 2-mm biopsy punch or by collecting the tissue displaced by ear tags. Tissue was also collected from 5 unmarked kangaroos found dead at Wilsons Promontory. Tissue samples were preserved in 95% ethanol and refrigerated at 4 °C prior to DNA extraction. DNA was extracted with a modified salt-extraction protocol (Aljanabi and Martinez 1997). After the evaporation of ethanol, samples were placed in a saline extraction buffer (2-mM EDTA, 10-mM Tris-HCL, and 0.4-M NaCl). Sodium dodecyl sulfate 20% and proteinase K were added, and the sample was incubated overnight at 60 °C. The next morning, after the digestion was completed, a 6-M saline solution was added and the solution was then centrifuged at 10 300 rpm for 30 min. To precipitate DNA, 600 µL of the supernatant was transferred and an equal volume of isopropanol was added. Samples were incubated at -20 °C for between 40 and 50 min and pelleted by centrifugation at 13 000 rpm for 20 min. The DNA pellet was kept by removing the solution, washed with 200 µL of 70% ethanol, dried at 60 °C for 2 h and resuspended in 200 µL of distilled water.

DNA concentration was initially determined for each sample by gel electrophoresis migration and then diluted to a final concentration of 5 ng/µL. Polymerase chain reactions (PCR) were performed using 9 fluorescently labelled microsatellite loci already characterized for macropods (Supplementary Table S1): eastern grey kangaroo G12-6, G16-1, G16-2, G19-1, G26-4, G31-1, G31-3 and tammar wallaby T3-1T, T32-1 (Zenger and Cooper 2001a, 2001b). Two microliters of DNA were used for the PCR amplification, for a of 10-µL total reaction volume, which was amplified in a GeneAmp PCR System 9700 thermocycler (Applied Biosystems, Foster City, CA). Recipes for all loci are detailed in Supplementary Table S2. Conditions were set as follows: 5 min at 94 °C, cycles of 30 s at 94 °C, 45 s at the annealing temperature (54 °C or 56 °C depending on the locus, see Supplementary Table S1) and 45 s at 72 °C and a final extension of 10 min at 72 °C. The number of cycles was also dependent on the locus and was either 25 or 30 cycles (Supplementary Table S1). Samples were then prepared by adding 0.15 µL of Liz (Applied Biosystems) internal size standard and 8.35 µL of Formamide Hi-Di (Applied Biosystems) to 1.5 µL of multiplexes of PCR products. Details of the multiplex are in Supplementary Table S1. PCR products were visualized using an AB 3130xl capillary DNA sequencer (Applied Biosystems) and analysed using Genemapper version 4.1 (Applied Biosystems).

Allelic frequencies were first compared among years with an F_{ST} test in Arlequin 3.5 (Excoffier and Lischer 2010). There were no significant differences between years for either population (F_{ST} from -0.004 to -0.002, all $P > 0.96$); therefore, we pooled adults from all years. For each population and locus, Hardy-Weinberg equilibrium and potential linkage disequilibrium were tested using GENEPOP version 4.0.10 (Raymond and Rousset 1995) for all years combined. Table-wide significance levels for both tests were adjusted by the sequential Bonferroni method, correcting for multiple tests (Rice 1989). Finally, the presence of null alleles was assessed using Cervus 3.0 (Kalinowski et al. 2007).

Maternal links were established from field observations of mother/young associations and confirmed by genetic analyses. Paternal identities were determined using microsatellites. Individuals genotyped at more than 6 loci (Wilson's Promontory: 8.95 ± 0.34 ; Anglesea: 8.99 ± 0.11) were considered in the analyses and Cervus was used to assign paternity with a 95% statistical level of confidence. Assignments were performed separately for each year because our rough estimate of the proportion of adult males sampled differed among years, ranging from 0.50 to 0.80 at Wilsons Promontory and 0.55 to 0.80 at Anglesea. Candidate males included all those captured on the study area over the entire study. Because numbers of candidate males did not vary much for either site, we used the same number for all years. At Wilsons Promontory, the total number of males was set to 138 and at Anglesea, 70. We assumed the proportion of loci mistyped to be 0.02. Paternities inferred by Cervus were verified to ensure that assigned fathers were not known to be dead when mating occurred, or known to be younger than 36 months, the age of sexual maturity (Poole and Catling 1974). Colony version 2.0 (Jones and Wang 2010) was used to identify potential paternal half-siblings sired by the same uncaptured males.

Measuring reproductive skew

We defined reproductive success as the number of offspring genetically assigned to each male. To document reproductive inequality among males, we tested the null hypothesis of random mating and calculated skew indices.

For each study area, we compared the observed annual distribution of paternities with a simulated Poisson distribution of equal mating probabilities with variance equal to the mean (Kokko et al. (1999)). Significantly different Poisson distributions are expected to feature different variances. We thus generated a fictitious population of candidate sires equal in number to observed males. From that population, reproductive success was simulated by random sampling with replacement of a number of sires corresponding to the number of paternal assignments. We simulated 1000 mating episodes to generate the distribution of paternities.

We calculated the B index (Nonacs 2000, 2003) to assess reproductive skew and computed 95% confidence intervals (CIs) for this index by simulating a random distribution of matings. Finally, we calculated the opportunity for sexual selection (I_s), calculated by dividing the variance in genetic reproductive success by its squared mean (Jones 2009), and compared it with that expected from random mating, using the simulated distribution described above. We compared observed and simulated distributions with a Kolmogorov-Smirnov test and a Fisher's exact test, as they included low frequencies.

RESULTS

Microsatellite analyses

Of 558 individuals genotyped at Wilsons Promontory, 272 aged 3 years and older were included in analyses of alleles and genotypes disequilibrium. At Anglesea, 212 of 438 individuals genotyped were included in analyses. The mean number of alleles per locus was 9.89 (range 6-15) at Wilsons Promontory and 10.33 (range 7-18) at Anglesea, a nonsignificant difference ($P = 0.80$) (Supplementary Table S3). Expected heterozygosity for loci ranged from 0.690 to 0.865 (mean 0.780) at Wilsons Promontory and from 0.641 to 0.881 (mean 0.774) at Anglesea. No locus deviated from

Hardy–Weinberg equilibrium and there was no evidence of null alleles (Supplementary Table S3). At Wilsons Promontory, of 36 pairs of loci, only 2 (5.6%) showed evidence of linkage disequilibrium after Bonferroni correction: T3-1T and G26-4; and G19-1 and G31-1. Analyses conducted separately for each year, however, revealed no consistent linkage disequilibrium and thus all loci were kept for analyses. At Anglesea, 4 of 36 pairs (11.1%) showed linkage disequilibrium after Bonferroni correction, but again there was no consistent disequilibrium across years. We therefore kept all loci to conduct our analyses.

Parentage assignment

At Wilsons Promontory, 256 young were assigned to 139 mothers. At Anglesea, we sampled 195 young born to 120 mothers. There were mismatches at 1 locus for 6 mother–young pairs (1.3% of pairs, 0.15% of loci). We considered these assignments reliable. We defined a cohort as young born between August 1st of year X-1 and July 31st of year X. Paternity was assigned with a 95% level confidence for 196 young (76.6% of those sampled) at Wilsons Promontory and 160 (82.1%) at Anglesea (Table 1). Yearly paternity assignment success increased from 53.3% in 2008 to 90.2% in 2012 at Wilsons Promontory, in agreement with our increasing efforts to sample adult males, and varied between 66.7% and 92.3% at Anglesea (Table 1). We only allowed a maximum of 1 mismatch between assigned fathers and young. At Wilsons Promontory, 1 assigned father (0.5%) had 2 mismatching loci and was removed from subsequent analyses. At Anglesea, 16 fathers (10%) had 1 mismatch with the genotype of their putative offspring: these were kept as father–young pairs. The highest yearly mean number of young assigned per father was 2.17 in 2011 at Wilsons Promontory and 2.40 in 2008 at Anglesea (Table 1).

The mean number of young sired by fathers of at least 1 young at Wilsons Promontory was 1.80, with a variance of 2.16. At Anglesea, reproducing males sired on average 1.72 young with a variance of 1.32. The highest number of young assigned to 1 male within a year was 8 at Wilsons Promontory and 9 at Anglesea. Program Colony assigned an additional 43 young at Wilsons Promontory and 19 at Anglesea to unsampled males (Supplementary Table S4). Differences between mean and variance in number of young assigned using only Cervus or combining Cervus and Colony were not significant (Wilsons Promontory: $\bar{X}_1 = 1.80$, $\bar{X}_2 = 1.81$, $t = 0.02$, $DF = 7.97$, $P = 0.99$, $\text{var}_1 = 1.86$, $\text{var}_2 = 1.71$, $t = 0.29$, $DF = 8$, $P = 0.78$; Anglesea: $\bar{X}_1 = 1.72$, $\bar{X}_2 = 1.59$, $t = 0.51$, $DF = 9.67$, $P = 0.62$, $\text{var}_1 = 1.32$, $\text{var}_2 = 1.20$, $t = 0.14$, $DF = 9.90$, $P = 0.89$). These results suggest that young of unknown paternity were not sired by a few highly successful males. Therefore, subsequent analyses included only paternity assignments using Cervus, but excluded data for 2008 for Wilsons Promontory and 2007 and 2012 for Anglesea, due to low sample sizes (Table 1).

Test for random mating

Just over half of reproducing males sired only 1 young per year: 53.7% at Wilsons Promontory and 54.4% at Anglesea (Figure 1). About a quarter of fathers had more than 2 young per year (Figure 1). The most successful male each year sired 14.3–18.8% of young at Wilsons Promontory and 10.4–21.4% at Anglesea. Because we did not sample all males each year, we could not precisely determine the number of nonreproductive males. The distribution of reproductive success including males with 0 offspring sired was therefore only examined in years where more than

80% of young were assigned a father: 2011 and 2012 at Wilsons Promontory and 2010 and 2011 at Anglesea (Figure 1). At Wilsons Promontory, on average during these 2 years, 56.8% (63 of 111) of sampled male-years did not sire any offspring. At Anglesea, the corresponding proportion was 56.6% (47 of 83).

At Wilsons Promontory, simulated distributions of matings for both years were not different from Poisson distributions according to a Kolmogorov–Smirnov test (2011: $D = 0.002$, $P = 1.0$; 2012: $D = 0.004$, $P = 0.81$), as expected if males had equal probabilities of mating. The observed distribution of reproductive success was different from the simulated 1 for 2011 (Kolmogorov–Smirnov test: $D = 0.20$, $P = 0.03$; Fisher's exact test, $P = 0.03$). In 2012, the observed distribution was not clearly different from the simulated 1 (Kolmogorov–Smirnov test, $D = 0.17$, $P = 0.07$; Fisher's exact test, $P = 0.20$). For both years, observed variances were higher than expected (2011: $\text{var}_{\text{obs}} = 2.40$, $\text{var}_{\text{sim}} = 0.94$; 2012: $\text{var}_{\text{obs}} = 2.26$, $\text{var}_{\text{sim}} = 0.95$, both $P < 0.05$).

For Anglesea, both simulated distributions also fit a Poisson distribution (all $P > 0.05$). For 2010, the observed distribution was different from the simulated 1 (Kolmogorov–Smirnov test, $D = 0.24$, $P = 0.02$; Fisher's exact test, $P = 0.03$). For 2011, however, observed and expected distributions were similar (Kolmogorov–Smirnov test, $D = 0.06$, $P = 1.0$, Fisher's exact test, $P = 0.95$). Similarly to Wilsons Promontory, observed variances in paternity were 1.3 to 3.1 times higher than expected (2010: $\text{var}_{\text{obs}} = 3.24$, $\text{var}_{\text{sim}} = 0.90$; 2011: $\text{var}_{\text{obs}} = 1.18$, $\text{var}_{\text{sim}} = 0.81$, both $P < 0.05$).

Reproductive skew

For all sites and years, the B index was different from 0 (95% CIs did not include 0), suggesting a nonrandom distribution of male reproductive success (Table 2). For Anglesea in 2011, the B index was only marginally significant (CI 0.0001 to 0.06, Table 2).

The average opportunity for sexual selection (I_s) was similar for males in the 2 study sites (mean $I_{s\text{Wilsons Promontory}} = 2.61$, $I_{s\text{Anglesea}} = 2.89$, $t = -0.26$, $DF = 1.02$, $P = 0.84$). The observed I_s was higher than the simulated 1 (one-tailed test, $P < 0.05$, Table 3) for both sites in all years.

Sexual dimorphism

We contrasted our measured variability in mass with the general impression that eastern grey kangaroos are very sexually dimorphic (Jarman and Southwell 1986). Although the largest males, at 75 kg at Anglesea and 63 kg at the Wilsons Promontory, were much heavier than any breeding female (mean 27.7 kg + 2.8 SD, range 21–34 kg), males as light as 33 kg were assigned paternities. The average mass of fathers at the Wilsons Promontory was 49.1 + 7.6 SD, range 33–62 kg. We did not recapture individuals sufficiently often at Anglesea to provide comparable data for that population.

DISCUSSION

As expected, our analyses suggest an unequal distribution of reproductive success among male eastern grey kangaroos. Surprisingly, however, we found limited reproductive monopolization by the most successful males. Observed reproductive variances were higher than those expected under random mating, but observed and simulated mating distributions differed only in some years. The B index showed that males had unequal probabilities of mating. Overall, our analyses documented nonrandom mating in half of the population-year combinations, suggesting that sexual selection should exist in both populations.

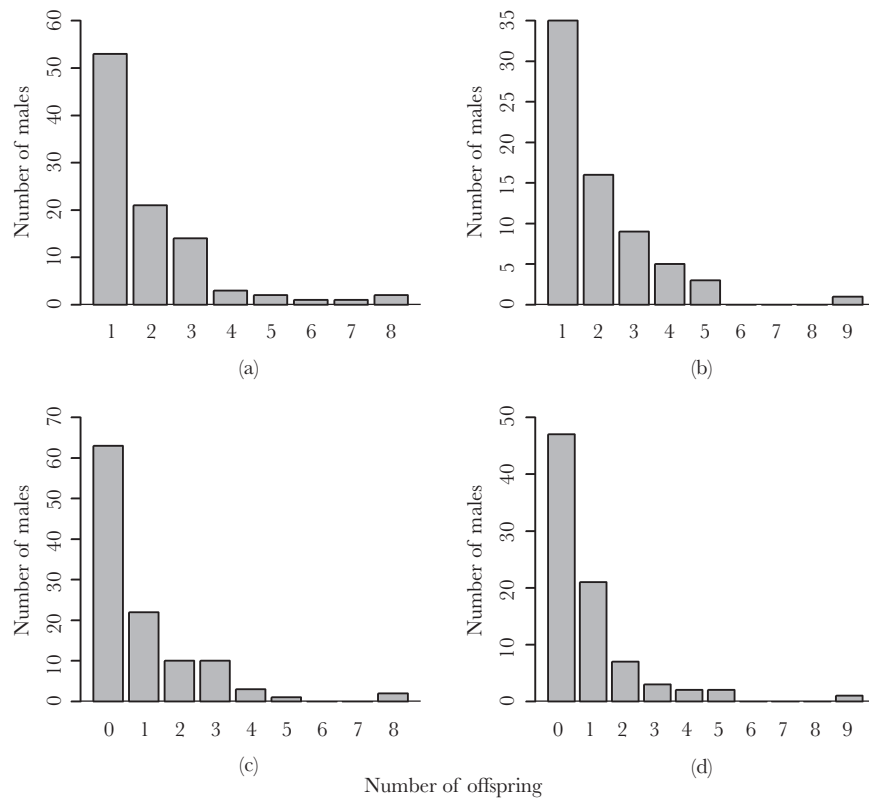


Figure 1

Number of offspring sired by eastern grey kangaroo males that reproduced at 2 study areas in Victoria, Australia, (a) Wilsons Promontory, 2009–2012 and (b) Anglesea, 2008–2012; and for all mature males at (c) Wilsons Promontory 2011–2012, and (d) Anglesea 2010–2011. Note that more years of data are included in (a)–(b) than (c)–(d) (see text).

We had expected to quantify a highly polygynous mating system in kangaroos, considering the strong sexual size dimorphism (Loison et al. 1999; Vanpé et al. 2008), long breeding season giving dominant males the opportunity to serially monopolize receptive females (Say et al. 2001) and a clear dominance hierarchy among males (Ellis 1995). Yet, reproductive skew was low in both study areas. In addition to the fact that quantification of skew in male reproductive success is challenging (Kokko et al. 1999), and that different methods to investigate reproductive skew might lead to different results (see below), alternative reasons may explain this result. In some species, the cost of searching for receptive females can be substantial (Lane et al. 2010). With a long breeding season, mate-searching behavior could compromise a male’s body condition, and possibly future reproduction, if it reduced feeding (Pörschmann et al. 2010). Given the small size of our study areas (about 1 km²) in relation to the size of a kangaroo, however, the energetic cost of mate searching may not be excessive. Sperm depletion can also lower reproductive success of dominant males (Preston et al. 2001), but there is no information on whether this affects kangaroos. Alternately, strong female choice may not be based on male social status.

The mating system of eastern grey kangaroo has been described as female defence by dominant males (Jarman and Southwell 1986). Our results, however, suggest that alternative tactics are likely present in our study populations, because reproductive success was not monopolized by a few dominant males. It is difficult to explain, for example, how a 33-kg male could defend an oestrous female against males that are twice as heavy. The wide variation in mass and size of potentially breeding males also makes the

estimation of the proportion of successful males rather difficult to compare among studies. Although many males were not assigned any paternities (Figure 1c and d), the number of “zero paternities” largely depends on the threshold used to define candidate fathers. In kangaroos, the smallest father weighed 33 kg, but very few paternities were assigned to males weighing less than 35 kg. Had we set a threshold at 30 kg to be conservative, the number of males with zero paternities would have increased.

Although the distribution of male reproductive success has interested biologists for a long time, very few reliable data for wild mammals are available (Tatarenkov et al. 2008; Festa-Bianchet 2012). Although determination of female reproductive success in mammals is usually straightforward, it is much more difficult to estimate male reproductive success, or to determine how many males do not sire any offspring (Wade and Shuster 2004): some males may mate outside the study area, or with unsampled females. Transient or peripheral males may be captured and sampled, but may not mate with sampled resident females. Because the ranging behavior of males may bias the calculation of the opportunity for selection (Wade and Shuster 2004), the estimation of how many males do not reproduce requires a very strong sampling effort. Consequently, some studies report only results for males that were assigned at least 1 paternity, which could substantially affect the calculation of skew (Rossiter et al. 2006; Ward et al. 2014). Absence of skew among reproducing males, however, does not imply that there is no skew in male reproductive success, because males that attempt unsuccessfully to reproduce should be included in estimations of reproductive skew. We contend that our estimates for kangaroos are reliable

Table 1

Paternity assignment in eastern grey kangaroos, for (a) cohorts 2008–2012 at Wilsons Promontory National Park and (b) cohorts 2007–2012 at Anglesea

Cohort	Young with known mother	Young assigned to a father	Assignment success rate	No. sires	Max. no. of young sired by 1 male	Mean no. of young assigned per male	Variance
Wilsons promontory							
2008	15	8	53.3	6	3	1.33	0.67
2009	53	32	60.4	21	6	1.52	1.36
2010	69	49	71.0	26	7	1.88	2.03
2011	58	52	89.7	24	8	2.17	2.67
2012	61	55	90.2	26	8	2.12	2.59
Anglesea							
2007	13	11	84.6	8	3	1.38	0.55
2008	60	48	80.0	20	5	2.40	1.62
2009	18	12	66.7	8	2	1.50	0.29
2010	48	42	87.5	19	9	2.21	4.29
2011	43	36	83.7	22	5	1.64	1.00
2012	13	12	92.3	10	5	1.20	0.18

Table 2

Mating skew index B (Nonacs, 2000) with 95% CIs for the reproductive success of male eastern grey kangaroos in 2 populations in Victoria, Australia: Wilsons Promontory National Park and Anglesea Golf Club

Cohort	B	95% CI
Wilsons Promontory		
2011	0.03	0.01, 0.07
2012	0.02	0.01, 0.07
Anglesea		
2010	0.07	0.04, 0.12
2011	0.01	0.00, 0.06

Only years for which more than 80% of young sampled were assigned to a father were considered.

Table 3

Observed and simulated opportunity for sexual selection (I_s) for eastern grey kangaroos of each sex at the Wilsons Promontory National Park (2011 and 2012) and for males at Anglesea Golf Club (2010 and 2011)

Cohort	I_{smales}	$I_{sfemales}$	$I_{smalesim}$	Critical value
Wilsons Promontory				
2011	2.70	1.41	1.06	1.44
2012	2.51	1.20	1.06	1.38
Anglesea				
2010	3.98	NA	1.11	1.52
2011	1.80	NA	1.24	1.78

I_{smales} : opportunity for sexual selection for males; $I_{sfemales}$: opportunity for sexual selection for females; $I_{smalesim}$: simulated opportunity for sexual selection for males.

The critical value for the difference between observed and simulated opportunity for sexual selection for males is also shown.

because we considered years with a minimum of 80% success in paternity assignments, and we found no evidence of highly successful unsampled males.

To compare skew between species, we considered only studies that genetically assigned paternities and included unsuccessful males in analyses, rather than limiting the calculation to successful breeders. However, we found several problems in these comparisons. First, similarly to our results, most studies (Tables 4 and 5)

reported substantial variation between breeding seasons or between populations, suggesting that reproductive skew cannot be reliably measured by a single value obtained over 1 mating season. Second, low statistical power may not allow the detection of differences between observed and random paternity distributions, a problem we faced with some year-specific analyses of mating distribution in kangaroos. The sample size in our study was unusually large for wild mammals, as we assigned paternity to 357 young (79.2% of those sampled), more than for most studies listed in Table 5. The yearly variability in reproductive distributions (Tables 2 and 4) strongly suggests that calculations of skew should be specific to a single breeding season for each population, because reproductive skew can be affected by many demographic parameters, such as sex ratio or the number and age structure of competing males that vary across years and populations (Cornwallis and Uller 2010; Krakauer et al. 2011). In addition, calculations of skew based on multiple years compare the success of some males that did not compete with each other because they were not present at the same time. Given that in mammals male mating success is mostly limited by competition with other males, that comparison appears problematic.

If we accept that interspecific comparisons are legitimate, skew in male reproductive success in kangaroos is surprisingly low, considering the strong sexual dimorphism, the long breeding season and the clear hierarchy among males. Among marsupials, reproductive skew is lower for semelparous antechinus species (*Antechinus stuartii* and *A. agilis*) than for eastern grey kangaroos, but it is higher for koalas (*Phascolarctos cinereus*), where male–male interactions are rare (Ellis and Bercovitch 2011) (Table 4). The value for the eastern grey kangaroo was lower than those reported for any ungulate except for white-tailed deer (*Odocoileus virginianus*), where males tend females for at least 24 h and appear incapable of monopolizing multiple receptive females (Sorin 2004). Eastern grey kangaroos also had lower reproductive skew than nearly all marine mammals (Table 2). Yearly B indices in both study populations were greater than those obtained for the northern muriqui (*Brachyteles hypoxanthus*) which was considered to have a low reproductive skew (Strier et al. 2011). The B index for kangaroos, however, was lower than for polygynous white-faced capuchins (*Cebus capucinus*) and Rhesus macaques (*Macaca mulatta*) (Table 5).

Our results suggest that, in the absence of data on paternity, the mere appearance of high polygyny and high potential for sexual selection based on morphology cannot be assumed to imply high polygyny and strong sexual selection. Importantly,

Table 4
Opportunity for sexual selection in male mammals based on genetic assignment of paternity

Species	Range of I_{season}	I_{mean}	I_{pooled}	N	Reference
Greater short-nosed fruit bat (<i>Cynopterus sphinx</i>) Harem defense	0.60–1.96 (3.28)	1.18		6	(Garg et al. 2012)
Greater short-nosed fruit bat (<i>Cynopterus sphinx</i>) Harem defense	4.04–11.73 (2.86)	7.88	4.76	2	(Storz et al. 2001)
Greater horseshoe bat (<i>Rhinolophus ferrumequinum</i>) Territory defense	1.56–4.35 (2.79)	2.83	3.7	10	(Rossiter et al. 2006)
Yellow-pine chipmunk (<i>Tamias amoenus</i>) Female defense	0.86–1.55 (1.80)	1.21	1.24	3	(Schulte-Hostedde et al. 2004)
Eastern chipmunk (<i>Tamias striatus</i>) Female defense			2.97	2	(Bergeron et al. 2012)
Galapagos sea lion (<i>Zalophus wollebaecki</i>) Harem defense	4.35–7.57 (1.74)	5.96		2	(Pörschmann et al. 2010)
Grey seal (<i>Halichoerus grypus</i>) Harem defense			3.46	4	(Amos et al. 1993)
Weddell seal (<i>Leptonychotes weddellii</i>) Territory defense	1.68–2.87 (1.71)	2.06	2.00	4	(Harcourt et al. 2007)
Bighorn sheep (<i>Ovis canadensis</i>) Female defense	2.45–8.32 (3.40)	4.52		6	(Coltman et al. 2002)
Soay sheep (<i>Ovis aries</i>) Female defense	2.56–5.26 (2.05)	3.59		3	(Coltman et al. 1999)
White-tailed deer (<i>Odocoileus virginianus</i>) Female defense	1.85	1.85		1	(Sorin 2004)
Yellow baboon (<i>Papio cynocephalus</i>) Female defense			2.37	14	(Alberts et al. 2006)
Agile antechinus (<i>Antechinus agilis</i>) Unknown, promiscuous	1.38–2.25 (1.63)	1.82		2	(Kraaijeveld-Smit et al. 2003)
Brown antechinus (<i>Antechinus stuartii</i>) Unknown, promiscuous	1.91	1.91		1	(Holleley et al. 2006)
Koala (<i>Phascolarctos cinereus</i>) Territory defense		3.85		4	(Ellis and Bercovitch, 2011)

The mating system is indicated after the scientific name of each species. The range in values for each breeding season (I_{season}) is followed in parentheses by the ratio of the season with the highest and lowest I_{season} values, the mean of all seasons (I_{mean}). The value I_{pooled} is reported when data were pooled over all seasons. N indicates the number of breeding seasons for each study.

Table 5
Nonacs' B index characterizing male reproductive skew based on genetic assignment of paternities, listed from lowest to highest

Species	B index	Significance	Reference
Northern muriqui (<i>Brachyteles hypoxanthus</i>) Multimale groups	0.012	0.16	(Strier et al. 2011)
Greater horseshoe bat (<i>Rhinolophus ferrumequinum</i>) Territory defense	−0.039–0.017	0 of 19 years ^a	(Ward et al. 2014)
Rhesus macaque (<i>Macaca mulatta</i>) Female defense	0.0485–0.1068	6* of 6 years	(Widdig et al. 2004)
White-faced capuchin (<i>Cebus capucinus</i>) ^b Female defense	0.083–0.401	5* of 8 groups	(Muniz et al. 2010)
Mountain gorilla (<i>Gorilla beringei</i>) Harem defense	0.107–0.432	5* of 5 years	(Bradley et al. 2005)

Mating system description after scientific names.

Significance column, asterisks refer to a significant difference from the result expected assuming equal probability of mating among males.

^aSignificant with all 19 years combined ($B = 0.0047$, $P < 0.001$).

^bValues were calculated combining all years where a given male had tenure and not year by year.

the opportunity for selection represents the upper limit of the strength of sexual selection and not the actual selection on a trait (Sutherland 1985; Klug et al. 2010; Jennions et al. 2012). Therefore, the lower opportunity for selection we calculated for eastern grey kangaroos, compared with other species with lower sexual size dimorphism, does not imply that the actual strength of selection on size is lower. Other studies have also reported a lack of relation between the opportunity for selection and sexual size dimorphism (Kappeler and Schaffler 2008; Ohsawa et al. 1993).

We suggest that metrics of reproductive inequality are useful to study how ecological and demographic conditions can influence the distribution of paternities, but cannot be used directly to infer selective processes (Klug et al. 2010). Our study clearly underlines the need to examine alternative evolutionary explanations for the relationships between reproductive inequality and sexual dimorphism (Krüger et al. 2014).

SUPPLEMENTARY MATERIAL

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

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REFERENCES

- Aljanabi SM, Martinez I. 1997. Universal and rapid salt-extraction of high quality genomic DNA for PCR-based techniques. *Nuc Acid Res.* 25:4692–4693.
- Alberts SC, Buchan JC, Altmann J. 2006. Sexual selection in wild baboons: from mating opportunities to paternity success. *Anim Behav.* 72:1177–1196.
- Amos W, Twiss S, Pomeroy PP, Anderson SS. 1993. Male mating success and paternity in the grey seal, *Halichoerus grypus*: a study using DNA fingerprinting. *Proc R Soc Lond Ser B Biol Sci.* 252:199–207.
- Andersson M. 1994. *Sexual selection*. Princeton: Princeton University Press.
- Bergeron P, Montiglio P-O, Réale D, Humphries MM, Garant D. 2012. Bateman gradients in a promiscuous mating system. *Behav Ecol Sociobiol.* 66:1125–1130.
- Bradley BJ, Robbins MM, Williamson EA, Steklis HD, Steklis NG, Eckhardt N, Boesch C, Vigilant L. 2005. Mountain gorilla tug-of-war: silverbacks have limited control over reproduction in multimale groups. *Proc Natl Acad Sci USA.* 102:9418–9423.

- Brø-Jørgensen J. 2011. Intra- and intersexual conflicts and cooperation in the evolution of mating strategies: lessons learnt from ungulates. *Evol Biol.* 38:28–41.
- Clutton-Brock T. 2007. Sexual selection in males and females. *Science.* 318:1882–1885.
- Clutton-Brock TH, Vincent ACJ. 1991. Sexual selection and the potential reproductive rates of males and females. *Nature.* 351:58–60.
- Coltman DW, Festa-Bianchet M, Jorgenson JT, Strobeck C. 2002. Age-dependent sexual selection in bighorn rams. *Proc R Soc Lond B.* 269:165–172.
- Coltman DW, Smith JA, Bancroft DR, Pilkington J, MacColl ADC, Clutton-Brock TH, Pemberton JM. 1999. Density-dependent variation in lifetime breeding success and natural and sexual selection in Soay rams. *Am Nat.* 154:730–746.
- Cornwallis CK, Uller T. 2010. Towards an evolutionary ecology of sexual traits. *Trends Ecol Evol.* 25:145–152.
- Coulson G, Cripps J, Wilson ME. 2014. Hopping down the main street: eastern grey kangaroos at home in an urban matrix. *Animals.* 4:272–291.
- Delean S. 2007. Longitudinal population demography of the allied rock-wallaby, *Petrogale assimilis*. [PhD thesis]. [Townsville]: James Cook University.
- Ellis L. 1995. Dominance and reproductive success among nonhuman animals: a cross-species comparison. *Ethol Sociobiol.* 16:257–333.
- Ellis WAH, Bercovitch FB. 2011. Body size and sexual selection in the koala. *Behav Ecol Sociobiol.* 65:1229–1235.
- Emlen ST, Oring LW. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science.* 197:215–223.
- Excoffier L, Lischer HE. 2010. Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. *Mol Ecol Res.* 10:564–567.
- Festa-Bianchet M. 2012. The cost of trying: weak interspecific correlations among life-history components in male ungulates. *Can J Zool.* 90:1072–1085.
- Fisher DO, Lara MC. 1999. Effects of body size and home range on access to mates and paternity in male bridled nailtail wallabies. *Anim Behav.* 58:121–130.
- Garg KM, Chattopadhyay B, Doss PS, Kumar VAK, Kandula S, Ramakrishnan U. 2012. Promiscuous mating in the harem-roosting fruit bat, *Cynopterus sphinx*. *Mol Ecol.* 21:4093–4105.
- Gélin U, Wilson ME, Coulson G, 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, Coulson G, Festa-Bianchet M. 2015. Experimental manipulation of female reproduction demonstrates its fitness costs in kangaroos. *J Anim Ecol.* 84:239–248.
- Harcourt RG, Kingston JJ, Cameron MF, Waas JR, Hindell MA. 2007. Paternity analysis shows experience, not age, enhances mating success in an aequally mating pinniped, the Weddell seal (*Leptonychotes weddellii*). *Behav Ecol Sociobiol.* 61:643–652.
- Holleley CE, Dickman CR, Crowther MS, Oldroyd BP. 2006. Size breeds success: multiple paternity, multivariate selection and male semelparity in a small marsupial, *Antechinus stuartii*. *Mol Ecol.* 15:3439–3448.
- Jarman PJ, Southwell CJ. 1986. Groupings, associations, and reproductive strategies in eastern grey kangaroos. In: Rubenstein DI, Wrangham RW, editors. *Ecological aspects of social evolution*. Princeton (NJ): Princeton University Press. p. 399–428.
- Jennions MD, Kokko H, Klug H. 2012. The opportunity to be misled in studies of sexual selection. *J Evol Biol.* 25:591–598.
- Jones AG. 2009. On the opportunity for sexual selection, the Bateman gradient and the maximum intensity of sexual selection. *Evolution.* 63:1673–1684.
- Jones OR, Wang J. 2010. COLONY: a program for parentage and sibship inference from multilocus genotype data. *Mol Ecol Res.* 10:551–555.
- Kalinowski ST, Taper ML, Marshall TC. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Mol Ecol.* 16:1099–1106.
- Kappeler PM, Schäffler L. 2008. The lemur syndrome unresolved: extreme male reproductive skew in sifakas (*Propithecus verreauxi*), a sexually monomorphic primate with female dominance. *Behav Ecol Sociobiol.* 62:1007–1015.
- 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.
- Klug H, Heuschele J, Jennions MD, Kokko H. 2010. The mismeasurement of sexual selection. *J Evol Biol.* 23:447–462.
- Kokko H, Klug H, Jennions MD. 2012. Unifying cornerstones of sexual selection: operational sex ratio, Bateman gradient and the scope for competitive investment. *Ecol Lett.* 15:1340–1351.
- Kokko H, Mackenzie A, Reynolds JD, Sutherland WJ. 1999. Measures of inequality are not equal. *Am Nat.* 72:358–382.
- Kraaijeveld-Smit FJL, Ward SJ, Temple-Smith PD. 2003. Paternity success and the direction of sexual selection in a field population of a semelparous marsupial, *Antechinus agilis*. *Mol Ecol.* 12:475–484.
- Krakauer AH, Webster MS, Duval EH, Jones AG, Shuster SM. 2011. The opportunity for sexual selection: not mismeasured, just misunderstood. *J Evol Biol.*
- Krüger O, Wolf JBW, Jonker RM, Hoffman JI, Trillmich F. 2014. Disentangling the contribution of sexual selection and ecology to the evolution of size dimorphism in pinnipeds. *Evolution.* 68:1485–1496.
- Lane JE, Boutin S, Speakman JR, Humphries MM. 2010. Energetic costs of male reproduction in a scramble competition mating system. *J Anim Ecol.* 79:27–34.
- Loison A, Gaillard J-M, Pélabon C, Yoccoz NG. 1999. What factors shape sexual size dimorphism in ungulates? *Evol Ecol Res.* 1:611–633.
- Lukas D, Clutton-Brock TH. 2014. Costs of mating competition limit male lifetime breeding success in polygynous mammals. *Proc R Soc Lond Ser B Biol Sci.* 281:20140418.
- Martin AM, Festa-Bianchet M, Coltman DW, Pelletier F. 2015. Comparing measures of breeding inequality and opportunity for selection with sexual selection on a quantitative character in bighorn rams. *J Evol Biol.* 28:223–230.
- Miller EJ, Eldridge MDB, Cooper DW, Herbert CA. 2010. Dominance, body size and internal relatedness influence male reproductive success in eastern grey kangaroos (*Macropus giganteus*). *Reprod Fert Devel.* 22:539–549.
- Muniz L, Perry S, Manson JH, Gilkenson H, Gros-Louis J, Vigilant L. 2010. Male dominance and reproductive success in wild white-faced capuchins (*Cebus capucinus*) at Lomas Barbudal, Costa Rica. *Am J Primatol.* 72:1118–1130.
- Nonacs P. 2000. Measuring and using skew in the study of social behavior and evolution. *Am Nat.* 156:577–589.
- Nonacs P. 2003. Measuring the reliability of skew indices: is there one best index? *Anim Behav.* 65:615–627.
- Ohsawa H, Inoue M, Takenaka O. 1993. Mating strategy and reproductive success of male patas monkeys (*Erythrocebus patas*). *Primates.* 34:533–544.
- Pauli JN, Peery MZ. 2012. Unexpected strong polygyny in the brown-throated three-toed sloth. *PLoS One.* 7:e51389.
- Plard F, Bonenfant C, Gaillard JM. 2011. Revisiting the allometry of antlers among deer species: male–male sexual competition as a driver. *Oikos.* 120:601–606.
- Poole WE. 1975. Reproduction in the two species of grey kangaroos, *Macropus giganteus* Shaw and *M. fuliginosus* (Desmarest) I Gestation, parturition and pouch life. *Aust J Zool.* 23:333–353.
- Poole WE. 1983. Breeding in the grey kangaroo, *Macropus giganteus*, from widespread locations in eastern Australia. *Aust Wildl Res.* 10:453–466.
- 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 kangaroo, *Macropus giganteus* Shaw and *M. fuliginosus* (Desmarest) I Sexual maturity and oestrus. *Aust J Zool.* 22:277–302.
- Pörschmann U, Trillmich F, Mueller B, Wolf JBW. 2010. Male reproductive success and its behavioural correlates in a polygynous mammal, the Gala'pagos sea lion (*Zalophus wollebaeki*). *Mol Ecol.* 19:2574–2586.
- Preston BT, Stevenson IR, Pemberton JM, Wilson K. 2001. Dominant rams lose out by sperm depletion—A waning success in siring counters a ram's high score in competition for ewes. *Nature.* 409:681–682.
- Raymond M, Rousset F. 1995. GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. *J Hered.* 86:248–249.
- Rice WR. 1989. Analyzing tables of statistical tests. *Evolution.* 42:223–225.
- Rossiter SJ, Ransome RD, Faulkes CG, Dawson DA, Jones G. 2006. Long-term paternity skew and the opportunity for selection in a mammal with reversed sexual size dimorphism. *Mol Ecol.* 15:3035–3043.
- Say L, Pontier D, Natoli E. 2001. Influence of oestrus synchronization on male reproductive success in the domestic cat. *Proc R Soc Lond Ser B Biol Sci.* 268:1049–1053.

- Schulte-Hostedde A, Millar JS, Gibbs HL. 2004. Sexual selection and mating patterns in a mammal with female-biased sexual size dimorphism. *Behav Ecol.* 15:351–356.
- Shuster SM, Wade MJ. 2003. *Mating systems and strategies*. Princeton: Princeton University Press.
- Sigg DP, Goldizen AW. 2006. Male reproductive tactics and female choice in the solitary, promiscuous bridled nailtail wallaby (*Onychogalea fraenata*). *J Mammal.* 87:461–469.
- Sorin AB. 2004. Paternity assignment for white-tailed deer (*Odocoileus virginianus*): mating across age classes and multiple paternity. *J Mammal.* 85:356–362.
- Storz JF, Bhat HR, Kunz T. 2001. Genetic consequences of polygyny and social structure in an Indian fruit bat, *Cynopterus sphinx* II Variance in male mating success and effective population size. *Evolution.* 55:1224–1232.
- Strier KB, Chaves PB, Mendes SL, Fagundes V, Di Fiore A. 2011. Low paternity skew and the influence of maternal kin in an egalitarian, patrilocal primate. *Proc Natl Acad Sci USA.* 108:18915–18919.
- Sutherland WJ. 1985. Chance can produce a sex difference in variance in mating success and explain Bateman's data. *Anim Behav.* 33:1349–1352.
- Tatarenkov A, Healey CIM, Grether GF, Avise JC. 2008. Pronounced reproductive skew in a natural population of green swordtails, *Xiphophorus helleri*. *Mol Ecol.* 17:4522–4534.
- Tsuji K, Kasuya E. 2001. What do the indices of reproductive skew measure? *Am Nat.* 158:155–165.
- Vanpé C, Kjellander P, Galan M, Cosson J-F, Aulagnier S, Liberg O, Hewison AJM. 2008. Mating system, sexual dimorphism, and the opportunity for sexual selection in a territorial ungulate. *Behav Ecol.* 19:309–316.
- Wade MJ. 1979. Sexual selection and variance in reproductive success. *Am Nat.* 114:742–747.
- Wade MJ, Shuster SM. 2004. Sexual selection: harem size and the variance in male reproductive success. *Am Nat.* 164:E83–E89.
- Warburton NM, Bateman PW, Fleming PA. 2013. Sexual selection on forelimb muscles of western grey kangaroos (Skippy was clearly a female). *Biol J Linn Soc.* 109:923–931.
- Ward HL, Ransome RD, Jones G, Rossiter SJ. 2014. Determinants and patterns of reproductive success in the greater horseshoe bat during a population recovery. *PLoS One.* 9:e87199.
- Widdig A, Bercovitch FB, Streich WJ, Sauermann U, Nürnberg P, Krawczak M. 2004. A longitudinal analysis of reproductive skew in male rhesus macaques. *Proc R Soc Lond Ser B Biol Sci.* 271:819–826.
- Zenger KR, Cooper DW. 2001a. Characterization of 14 macropod microsatellite genetic markers. *Anim Genet.* 32:166–167.