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ORIGINAL ARTICLE

Diana O. Fisher

Offspring sex ratio variation in the bridled nailtail wallaby, *Onychogalea fraenata*

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Abstract The bridled nailtail wallaby is a sexually size dimorphic, promiscuous, solitary macropod. Sex ratios of pouch young were studied at two sites over 3 years, beginning with 14 months of severe drought. Females that were in better condition were more likely to have sons, and condition was dependent on body size. Females at one site were heavier, were consequently in better condition, and produced more sons than females at the other site. Females that declined in condition had more daughters during the most severe part of the drought than females that maintained condition, but endoparasite infection did not affect the pouch young sex ratio. Age also appeared to affect sex ratio adjustment, because weight was strongly influenced by age. Sex ratio bias was not caused by early offspring mortality, but occurred at conception. Mothers did not appear to bias energy expenditure on sons or daughters; males and females did not differ in condition at the end of pouch life. Pouch young sex ratio variation was most consistent with the Trivers-Willard hypothesis, but could also have been influenced by local resource competition, since sons dispersed further than daughters. Offspring condition was related to survival, and was correlated with maternal condition.

Key words *Onychogalea fraenata* · Macropodidae · Offspring sex ratio · Bridled nailtail wallaby · Trivers-Willard hypothesis

Introduction

Fisher (1930) demonstrated that equal parental expenditure on offspring of each sex is evolutionarily stable, because if one sex predominates, the other will gain a frequency-dependent reproductive advantage. An equal sex ratio is predicted by Fisher's explanation unless one sex is more costly in terms of future reproductive success of the mother than the other, in which case the less costly sex should be over-produced so that parents receive the same reproductive benefits from each (Gomendio et al. 1990).

The Trivers-Willard hypothesis and the local resource competition hypothesis provide adaptive explanations of sex ratio bias when one assumption of Fisher's model is not met: when the form of the relationship between the costs and fitness benefits of producing each sex differs (Charnov 1982; Frank 1990). If one sex has greater variance in reproductive success than the other, the Trivers-Willard hypothesis states that mothers in better condition or of higher rank should produce more offspring of the sex that benefits more from their mothers' condition or rank (Trivers and Willard 1973). In polygynous and promiscuous mammals, this usually means that mothers in better condition should produce more sons, since sons of healthier mothers should be larger, and therefore gain more matings. Conversely, mothers in poor condition should produce daughters, since daughters are likely to breed regardless of their size. This hypothesis has been supported in studies of many, but not all sexually dimorphic, polygynous or promiscuous mammals (Austad and Sunquist 1986; Gosling 1986; DeGayner and Jordan 1987; Dickman 1988; Sunquist and Eisenberg 1993; Arnbom 1994; Moses et al. 1995; Hardy 1997a; Hewison et al. 1999). The Trivers-Willard hypothesis is consistent with all known cases of sex ratio variation within macropod marsupial populations, but has never been shown to be the exclusive explanation (Stuart-Dick 1987; Higginbottom 1991; Ashworth 1995; Sunnucks and Taylor 1997). The most common alternative model in macropods is local resource competition, which predicts that if sons disperse further than daughters, mothers and sisters compete more with daughters than with sons (Clark 1978; Hardy 1997b). Because sons are less costly to maternal reproductive success than daughters, a male-biased offspring sex ratio is expected.

D.O. Fisher (✉)
Department of Zoology, The University of Queensland
St Lucia, 4072 Queensland, Australia
e-mail: dfisher@zoology.uq.edu.au, Fax: +61-7-33651655

Adaptive explanations of sex ratio bias have been criticised in the past on the grounds that the mammalian mechanism of sex determination should restrict parental manipulation of offspring sex, and because sex-biasing mechanisms are poorly understood (Williams 1979; Clutton-Brock and Iason 1986). However, several sex-biasing mechanisms that operate at conception have now been identified in mammals (Pratt et al. 1987; Krackow 1995; James 1996; Flint et al. 1997).

The bridled nailtail wallaby (*Onychogalea fraenata*) is a small, solitary, sexually dimorphic macropod. Previous field studies of this species have investigated home range, habitat use, parasites and diet (Evans 1992, 1996; Turni 1996); this is the first published data on reproduction or behaviour in the wild. This study investigates the effects of female condition on the sex ratio of pouch young, and examines the effects of weight, drought and site on condition. I discuss factors influencing offspring sex ratio and investment in terms of the Trivers-Willard and the local resource competition models of sex allocation, consider other potential explanations, and interpret the results in terms of the life history of the bridled nailtail wallaby.

Methods

Study animals and area

Bridled nailtail wallabies were once widespread in eastern Australia, but now survive in the wild in only one population of around 300–500 individuals in central Queensland [Taunton National Park (scientific)]. They are locally abundant at two sites (sites 1 and 2 here) covering ~750 ha within the 11,000-ha conservation reserve. They occur at densities of 0.2/ha at site 1 and 0.1/ha at site 2 (D. Fisher, unpublished data).

Bridled nailtail wallabies have a promiscuous mating system in which ability to displace other males at oestrus females is the most important factor in male reproductive success, so that body weight reflects the probability of paternity. Adult males may reach 8 kg, twice the weight of females. Females give birth to a single offspring every 4.5 months after reaching sexual maturity at about 6 months old, when they are approximately 40% of maximum adult female weight (Johnson 1997). Young cease to be carried in the pouch the day before the birth of the next offspring, but continue to suckle by putting their head into the pouch for a further 4 or 5 weeks, while the neonate attaches to a different teat. Both sexes disperse at 7–8 months old; females disperse about one home range diameter from their mother's home range centre, while males disperse four times as far on average (M. Lara and D. Fisher, unpublished data).

The study area was near the town of Dingo in central Queensland (23°33′S, 149°13′E). Mean annual rainfall is 711 mm; half of this falls between December and February (Evans 1992). The region suffered a severe drought from 1992 to 1995. Total rainfall in 1994 was 265 mm, and there was no rain at all between May and October 1994. The drought was considered to have ended after December 1994.

The two study sites within the park differ markedly in vegetation and annual rainfall, although they are only ~4 km apart. Site 1 consisted of 25-year-old dense forest regrowth around 4 m tall (brigalow, *Acacia harpophylla* and yellowwood, *Terminalia oblongata*) adjacent to a cleared paddock. Site 2 consisted of a cleared paddock, riverine swamp with leichardt bean (*Cassia brewsteri*), stony ridges with rosewood forest (*A. rhodoxylon*) and open woodland with poplar box (*Eucalyptus populnea*). Mean annual rainfall at site 1 was ~80% of rainfall at site 2.

Field methods and analysis

Wallabies were trapped at night in wire cage traps (380 × 380 × 760 mm) with treadles (Mascot traps, Sydney, Australia) baited with hay. Traps were placed at intervals of approximately 200 m throughout the sites, closer together in areas of higher wallaby density. Trapping was carried out for a week at each site separately, during each of 13 quarterly field trips between November 1993 and December 1996.

Wallabies were sexed, weighed to the nearest 50 g using a 10-kg spring balance, and leg lengths were measured to the nearest millimetre using callipers each time that an individual was captured. To compare age with body weight, I measured the weight and leg length of 14 known-age captive females that were maintained elsewhere at captive breeding facilities, either in semi-free range enclosures or pens. Wild adults could not be aged because there were no captures of wallabies tagged during previous studies, and the molar progression ageing method for macropods involves radiography and anaesthesia (Delaney 1993), which is too invasive for this highly endangered species.

An index of general health was determined by scoring the tightness of the skin covering the vertebrae and ribs, severity of lice infestation (*Heterodoxus* sp.; Turni 1996), the presence of infected sores or scabs, amount of muscle or fat cover and fur glossiness. Each of these measures was scored from 1 (unhealthy) to 4 (healthy). I used the modal score of each wallaby as the health index, assuming that the most common rating reflects a typical score for that individual.

Wallabies were marked using two identical sheep ear-tags (Reflexite, Melbourne, Australia) which had reflective plastic welded to them on both sides in a unique combination of colours. During 1996, blood was collected from 24 reproductive female wallabies and tested serologically for antibodies to the exotic endoparasites *Toxoplasmosis gondii* and *Echinococcus granulosus* (Turni 1996).

The stage of female reproductive cycles was assessed by recording the presence of pouch young and the presence of a second lactating free teat, indicating that an older infant was suckling from outside the pouch. Lactation from free teats was scored as very heavy with the teat engorged, medium, or light with watery milk. Light lactation was assumed to indicate that the older infant was being weaned. To calculate ages and birth dates, foot length was measured to the nearest millimetre. Infants were weighed to the nearest 1 g using a 1.5-kg spring balance. Fifteen fully furred infants and their mothers were fitted with radio-transmitters (Holohil, Carp, Canada, or Sirtrack, Havelock North, New Zealand). Transmitters for infants were on expandable collars. I tracked mothers and dependent infants using a hand-held Yagi antenna (Telonics, Mesa, USA) every 1–2 days, and other females about twice a week during field trips.

Associations between individuals at site 1 were assessed by spotlighting at 10 km/h from a vehicle for 50–90 h per field trip. Identities could be determined from ~80 m away using × 8 binoculars. The date, time and location of each wallaby was recorded with respect to landmarks and numbered posts placed at 25-m intervals along tracks.

The ages and dates of birth [(±95% confidence limits (CL)] of pouch young were calculated from foot length versus age growth curves developed using captive bridled nailtail wallabies (Hendrikz and Johnson, in press). Four wild pouch young were captured as both neonates and furred young; their known birth dates fell within the 95% CL of their predicted birth dates from this growth curve.

For each female captured more than once, published data on timing and variability of events during the oestrus cycle and pouch life (Johnson 1997) were used to determine whether pouch young had survived to weaning and whether reproductive failures had occurred (Table 1). These data on captive wallabies indicate that females mate about 1 month before permanent pouch exit of the young and the resulting blastocyst in remains in embryonic diapause, enabling mothers to give birth again immediately after the

Table 1 Criteria for determining whether pouch young survived, died, or reproductive failure occurred when mothers were captured repeatedly (*PY1* pouch young carried by the female at the first capture date, *PY2* pouch young carried by the female at the second capture date). Females that lose a pouch young enter oestrus 8–21 days later, gestation is 24 days, pouch life is 119–126 days, birth is 0–2 days after pouch exit of the previous young (Johnson 1997)

Observation	Conclusion
PY2 birth date–PY1 birth date = 32–45 days	Oestrus cycle failure/failed attachment/death of neonate
Mother ≥3 kg, captured without pouch young, birth date of pouch young at capture 2 = 3–45 days after date of capture 1	Oestrus cycle failure/failed attachment/death of neonate
PY2 birth date–PY1 birth date = 46–117 days	PY1 died
PY1 birth date + 160 days < PY2 birth date, mothers teat regressed, mother with a pouch young	PY1 died
PY1 birth date + (119–128) days = PY2 birth date	PY1 survived
PY1 birth date + (140–160) days = mother's next capture date, mothers teat elongated and lactating	PY1 survived
PY1 birth date + (140–160) days = date when mother seen with a young out of the pouch	PY1 survived

young leaves the pouch permanently. Values (Johnson 1997) and criteria for determining whether or not reproductive failures occurred are given in Table 1.

Individual mothers were used as replicates to test the hypotheses that maternal condition, body weight and drought influence offspring sex ratio. Because the litter size was one and some mothers were captured once, while others were captured repeatedly with varying intervals between captures, only the first offspring of known sex captured for each female was used. I used residual values from a regression of body weight on leg length as an index of body condition for adult females and young. The residual value is the difference between the actual weight of each individual at the time of capture and the average weight of wallabies of that leg length. A Von Bertalanffy regression curve was fitted to the age versus body weight data for captive females (SAS 1989). Loss of condition for mothers captured at the beginning and end of the drought was determined by finding the difference between the residual values at each time, giving individual values for weight loss with leg growth taken into account. Wallabies that did not lose weight were given a score of zero.

Stepwise logistic regression (SAS 1989) was used to test for effects of maternal condition, weight, site and drought on offspring sex throughout the study period, and to test for effects of loss of condition and maternal weight on offspring sex for females captured more than once during the drought (Trexler and Travis 1993). A logistic curve was fitted to the condition versus sex ratio data to show how maternal condition affected the probability of having a son (SAS 1989). The relationships between condition, weight, site and drought, and the effect of maternal condition on the condition of furred young were examined using analysis of covariance. Analysis of variance was used to investigate the effect of sex on furred-young body weight and of endoparasite exposure on condition for those females that were tested for parasites. I first tested assumptions of normality and homoscedasticity using a Shapiro-Wilks test and a Barlett test, respectively, and transformed data where necessary (Sokal and Rohlf 1981; SAS 1989).

G-tests were used to compare survival to weaning of each sex, survival in relation to the sex of the previous pouch young, and effect of maternal parasite exposure on the sex ratio. Chi-squared tests were used to compare overall pouch young sex ratios with an expected ratio of 1:1, and the sex ratio of offspring of large females with the ratio predicted if reproductive failures in these females were followed only by male births.

Results

Eighty-five individuals were first captured as reproductive females, and 151 as pouch young. Fifteen females were only ever captured with either neonates that were too young to sex, or with no young. Young of 70 adult females could be sexed, and 41 of these females were captured more than once (2–15 times, mean = 4). Survival to weaning could be determined for 27 young of different mothers, while 18 infants were captured as furred pouch young, enabling body weight and condition near the time of permanent pouch exit (when the dependent infant is no longer carried) to be estimated. Six young-at-foot (dependent young with their mothers after permanent pouch exit) were captured.

Effects of maternal condition and age on pouch young sex ratio

Females in better condition were more likely to have sons (Fig. 1, the probability of having a son, $P = 1/1 + e^{(-0.3202-0.00186C)}$, where C is the condition index), and for bridled nailtail mothers, condition was the best predictor of offspring sex ratio (logistic regression $\chi^2 = 6.39$, $P = 0.01$). The effects of weight, drought and site were not significant after the effect of condition was removed, and these were omitted by the stepwise logistic

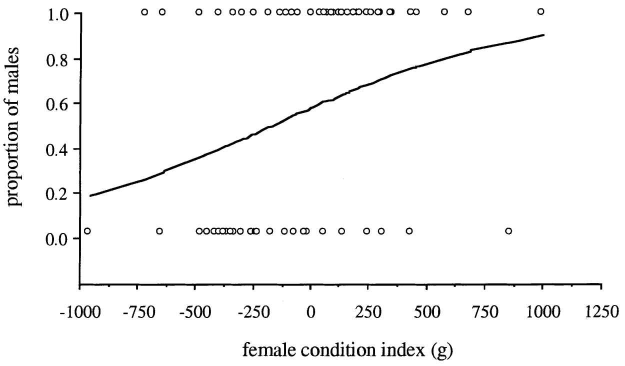

Fig. 1 Fitted logistic curve showing the relationship between female condition index and the number of sons per breeding event ($n = 40$ mothers with a son, 30 mothers with a daughter)

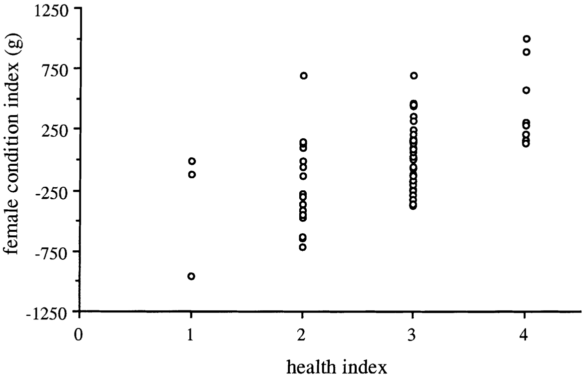

Fig. 2 Female condition index vs health index for 70 females [$n=3$ for health index = 1 (very unhealthy), 18 for index = 2, 41 for index = 3, and 8 for index = 4 (very healthy)]

regression model selection procedure. The pouch young sex ratio for the entire study was not significantly different from 1:1 (79 males:62 females, $\chi^2=2.1$, $P>0.1$).

The external appearance of female wallabies clearly reflected body condition. Weight relative to leg length (the condition index) was significantly correlated with the level of obvious ectoparasite infection and coat condition (the subjective health index) (Fig. 2; Spearman's rank correlation $\rho=0.52$, $P=0.0001$). In contrast, endoparasite exposure (a positive test to antibodies to *Toxoplasma* or *Echinococcus*) had no effect on condition ($F=0.54_{1,21}$, $P<0.47$, $n=23$) or offspring sex ratio (Table 2).

Larger females were in significantly better condition (Fig. 3), and condition was very strongly related to body weight ($F=249_{1,68}$, $P<0.0001$, $n=70$, $r^2=0.79$). The strength of this association was not due to a non-linear relationship between leg length and body weight; exponential and logarithmic models fitted the data no better than linear regression ($r^2=0.21$ in each case). Body weight also differed significantly between the two study sites; on average, females at site 2 were 15% heavier than those at site 1 (Fig. 3; ANOVA performed on log-transformed data, $F=22_{1,68}$, $P<0.0001$). Females at site 2 were therefore in better condition than those at site 1 (Fig. 3), but only because of their larger body size. Condition did not differ between the two study sites when body weight was taken into account (ANCOVA performed on log-transformed data, $F=0.11_{1,67}$, $P=0.75$).

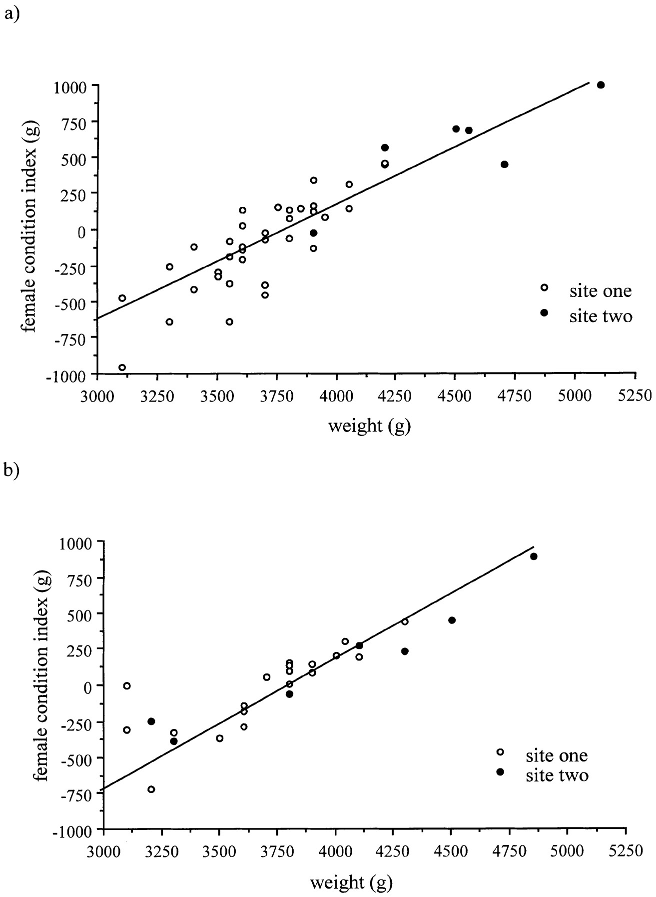

Fig. 3 Regression of female condition index on body weight: during the drought ($n=38$ at site 1, 6 at site 2) (**a**); after the drought ($n=19$ at site 1, 7 at site 2) (**b**)

Drought did not play a major role in the variation in offspring sex ratios observed during this study. Drought did not significantly affect female condition ($F=0.22_{1,68}$, $P=0.64$), and there was no difference in the relationship between weight and condition before and after the drought (Fig. 3; ANCOVA, $F=1.24_{1,67}$, $P=0.27$).

Although the overall condition of females was not influenced by drought, females that were captured both at the beginning and end of the drought year (1994) were more likely to have daughters during this period if they had lost more weight after leg growth was taken into account (logistic regression $\chi^2=8.2$, $P=0.004$; Fig. 4). Furthermore, females that had lost weight produced

Table 2 Survival of sons vs daughters, survival of young born after a son vs after a daughter, and effects of maternal parasite exposure on offspring sex ratio

	Son	Daughter	Significance	G^2
Young survived to weaning	3	7	n.s	1.7
Young died before weaning	9	7		
Young survived to weaning, young followed a ...	3	5	n.s.	2.1
Young died before weaning, young followed a ...	11	5		
Mother exposed to parasites	5	5	n.s.	1.6
Mother not exposed to parasites	8	6		

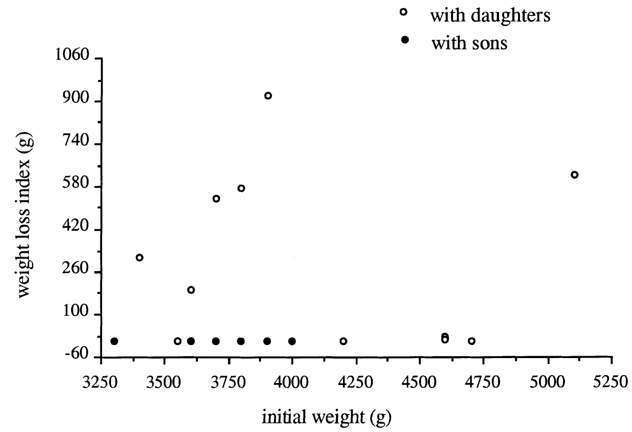

Fig. 4 Female weight loss index during the most severe 8 months of drought (March to October 1994) vs initial female weight ($n = 11$ mothers with daughters, 6 mothers with sons that were captured at the beginning and end of this period)

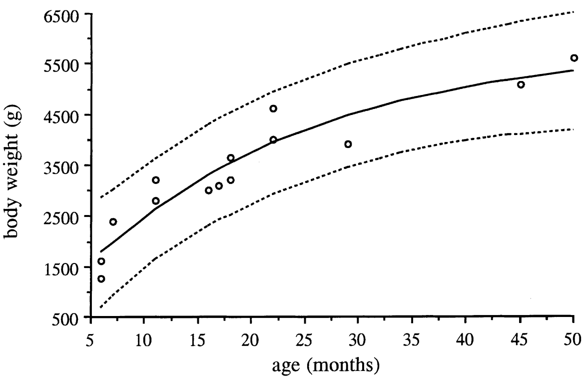

Fig. 5 Body weight vs age for 14 captive females. The regression line is fitted using a Von Bertalanffy model ± 95% confidence limits ($r^2 = 0.90$)

only daughters during this time ($n = 6$), while those that maintained weight had a roughly equal offspring sex ratio (6 males:5 females; Fig. 4).

The age of bridled nailtail wallaby mothers was also related to offspring sex ratio, because more males than females were born to old mothers, while the sex ratio born to young females was apparently unbiased. Twenty-two old females were identified by their very worn teeth, large size (4200–5100 g) and low growth rate during the study, and six primiparous females were captured, weighing 2200–2800 g. The body weight of known-age females was strongly related to age (Fig. 5, $r^2 = 0.90$). Seventy-three percent of the old females' last known pouch young were males (16 males:6 females, $\chi^2 = 4.5$, $P < 0.05$), while the primiparous females' pouch young were 3 males:3 females.

Maternal investment in pouch young

Pouch young captured at the furred stage were estimated to be 1–9 days younger than the minimum age of per-

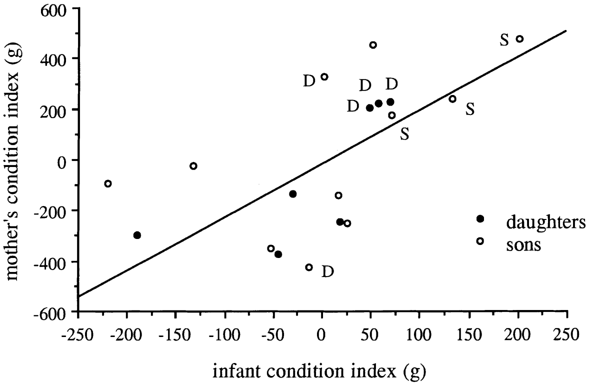

Fig. 6 Regression of condition index of mothers on condition index of pouch young at the furred stage ($n = 7$ daughters, 11 sons; *D* died before weaning, *S* survived to weaning, *unlabelled* fate unknown)

manent pouch exit (Johnson 1997). The three individuals known to have survived to weaning were in better condition than the five known to have died before weaning (Fig. 6). There was no difference between survival of male and female young, and young were equally likely to die before weaning if they followed a son or a daughter (Table 2).

The condition of furred pouch young was influenced by that of their mothers ($F = 9.16_{1,18}$, $P = 0.008$, $r^2 = 0.36$; Fig. 6), but offspring condition did not differ between males and females of the same body weight (ANCOVA, $F = 0.53_{1,15}$, $P = 0.48$). Male and female furred pouch young did not differ in body weight ($F = 0.6_{1,17}$, $P = 0.45$).

Reproductive failures

Failed reproductive cycles (implying that either no young was born following permanent pouch vacation by the previous infant, or a neonate failed to attach, or died immediately after attachment) were only observed in individuals >4100 g ($n = 8$) that showed signs of age. None of the 67 oestrus cycles analysed in smaller females were failures. Failures were not associated with poor body condition. In fact, large/old females were more likely to be in good condition (Fig. 3). The frequency of reproductive failures in large females (>4100 g) is insufficient to explain sex ratio variation. Of 64 cycles analysed in large females, 11 were failures. If large females achieved a male-biased offspring sex ratio by selectively aborting or killing daughters, then males would be born following failed cycles and the expected birth sex ratio following the 53 normal cycles would be 26.5 males:26.5 females. Even if a son were born following every failed cycle, the sex ratio would then be 38 males:26 females, which is still significantly lower than the observed ratio of 16 males:6 females amongst old females ($\chi^2 = 5.8$, $P = 0.002$). Therefore, the observed sex biases must have occurred at conception.

Discussion

Relationships between offspring sex and maternal condition

Female bridled nailtail wallabies in better condition, and those that maintained condition during the drought, were more likely to have sons than daughters (Fig. 1). Although drought was not related to loss of condition for females generally, it affected some females disproportionately (Fig. 4). Every female known to have lost weight during the drought produced a daughter at the end of the 1994 dry season, after 6 months without rain (Fig. 4). Sex ratio variation is thus consistent with the predictions of the Trivers-Willard hypothesis (Trivers and Willard 1973). Poor condition in mothers was related to small body size and not to endoparasite exposure (Table 2). Heavy louse infestation did reflect poor condition, however.

If the Trivers-Willard effect accounts for these results, then it is expected that reproductive success of male bridled nailtail wallabies should vary more than that of females, and maternal condition should influence the reproductive success of males more than females (Trivers and Willard 1973; Hewison et al. 1999).

Lifetime reproductive success is unknown, but available data strongly suggest that reproductive success is more variable for males than for females. This is because the relationship between breeding, size and age differs between the sexes, and because females breed continuously throughout adult life, while males breed little or not at all until they are in the heaviest 5% of the population (Johnson 1997). In order to reach breeding weight, males must survive at least 14 months after permanent pouch exit, although they are physically mature 9 months earlier (Johnson 1997). Even large males have unequal breeding success, since they compete for oestrus females, and some large males father a disproportionate number of offspring. Short-term estimates of reproductive success tend to overestimate variance in lifetime reproductive success, however, especially in males (Clutton-Brock 1987, 1988).

Too few marked infant bridled nailtail wallabies survived to adulthood during the study to determine whether maternal condition influences the reproductive success of sons and daughters differently. Maternal condition was, however, correlated with infant condition at permanent pouch exit (Fig. 6). If low infant weight translates into small size or decreased strength at adulthood, then sons of mothers in poor condition will be at a competitive disadvantage in contests for females. Information on the way in which maternal condition affects descendants' life history characteristics and lifetime reproductive success is scarce for wild mammals (Clutton-Brock 1988). Despite this, the Trivers-Willard hypothesis has been supported by many studies of marsupials and other mammals (Austad and Sunquist 1986; Clutton-Brock and Iason 1986; DeGayner and Jordan 1987; Dickman 1988; Hiraiwa-Hasegawa 1993; Arnbom 1994; Hardy 1997a; Kojola 1997).

As this hypothesis predicts, rainfall and body condition are positively correlated with male bias within populations of other sexually size dimorphic macropods such as euros (*Macropus robustus*), red-necked wallabies (*M. rufogriseus*), tammar wallabies (*M. eugenii*), parma wallabies (*M. parma*), and some populations of eastern grey kangaroos (*M. giganteus*) (Johnson 1986; Stuart-Dick 1987; Stuart-Dick and Higginbottom 1989; Higginbottom 1991; Ashworth 1995; Sunnucks and Taylor 1997).

In contrast with the results for sexually size dimorphic macropods, Delaney (1993) did not find variation in pouch young sex ratio between years in the allied rock wallaby (*Petrogale assimilis*), a small, facultatively socially monogamous species in which the sexes do not differ in body weight, despite drought during part of the study. Neither was there an effect of age or body size on pouch young sex ratio in this species.

Effects of maternal size, age and local resource competition on offspring sex ratio

Ages of wild adult bridled nailtail wallabies could not be determined, but age was strongly related to body weight in captive and semi-free range females (Fig. 5). Weight in turn was strongly associated with maternal condition, and mothers in better condition had significantly more sons (Fig. 1). The relationship between condition, weight and age in bridled nailtail wallaby females suggests that older females were more likely to have sons because they were usually in better condition. Indeed, very large, old females had 73% male offspring. Despite this, age is unlikely to be a better predictor of offspring sex ratio than condition, because body weight strongly reflects age (Fig. 5), and weight is less strongly related to offspring sex ratio than condition.

Most females at site 2 were very large, probably because they were relatively old, and because they tended to keep growing for longer (i.e. their asymptotic body weights were higher; D. Fisher, unpublished data). This resulted in a male-biased offspring sex ratio at that site, because condition was related to body weight (Fig. 3). Females at site 2 were in better condition than those at site 1 only because they were heavier; condition did not differ between sites when weight was taken into account.

Age influences offspring sex ratio in several species of large mammals. Older female red deer, sheep, grey kangaroos and euros have more male biased offspring sex ratios (Clutton-Brock et al. 1982, 1984; Stuart-Dick 1987; Kent 1992; Ashworth 1995). In red deer, age and weight are associated with the mother's position in the female dominance hierarchy, so that the relationship between weight and offspring sex ratio is still consistent with the predictions of the Trivers-Willard model (Clutton-Brock 1984). A female dominance hierarchy is unlikely to be a mechanism linking body size and condition to offspring sex ratio in bridled nailtail wallabies for two reasons. Firstly, the frequency of observed associations between females was very low (<0.01% of sightings) and interactions were never aggressive. Secondly, females at site 2 were more likely to have sons, but did not interact with females at site 1.

Condition appears to improve with age in female bridled nailtail wallabies. It may be that older, more experienced mothers are able to devote more resources to offspring, as in red deer and sheep (Clutton-Brock 1984; Kent 1992). If so, an excess of sons in older mothers would also be consistent with the Trivers-Willard model.

Age-related sex ratio variation occurs in grey kangaroos and red-necked wallabies but is not consistent with the Trivers-Willard hypothesis, because these species decline in condition with age. Instead, the local resource competition hypothesis has been invoked as one explanation. Daughters are philopatric in both species, but offspring sex ratio becomes more male biased with maternal age in grey kangaroos, and more female biased with age in red-necked wallabies. Grey kangaroo daughters apparently benefit from longer association with their mothers and tend to be born earlier in their mother's life, while red-necked wallaby daughters impose greater costs on their mothers than do sons, and are born later (Johnson 1986; Stuart-Dick 1987; Stuart-Dick and Higginbottom 1989). Ashworth (1995) could not identify any reproductive costs of sociality in euro mothers with philopatric daughters, which also decline in condition and have more male-biased offspring sex ratios as they age. She suggested that sex bias may be the consequence of an increase in the reproductive value of sons to older mothers; old females are predicted to take more risks by investing in sons, because they may not live to breed again (Clutton-Brock 1984).

The local resource competition hypothesis is a possible explanation for sex ratio variation in the bridled nailtail wallaby because sons disperse further than daughters. Consequently, there may be greater competition for resources between mothers and daughters or sisters than between male relatives (Cockburn 1994; Hardy 1997b). Previous studies have supported this hypothesis by identifying reproductive costs of sociality to mothers with philopatric daughters (e.g. Johnson 1986; Ashworth 1995). This test could not be carried out on bridled nailtail wallabies because both relatives and non-relatives are highly solitary; adult daughters are unlikely to impose a cost because they do not associate with their mothers or use the same feeding or resting areas. According to genetic data, the 19 pairs of females seen feeding within 25 m of each other during this study (0.01% of observations) could not have been pairs of closely related individuals (M. Lara, unpublished data).

Costs and viability of sons and daughters

The third alternative explanation for sex ratio variation in bridled nailtail wallabies is that offspring costs or viability differ between sons and daughters. This is unlikely to be the case, because neither sex was heavier at permanent pouch exit, and because as in euros, eastern grey kangaroos, red-necked wallabies and allied rock wallabies, there were no apparent sex differences in the survival to weaning of bridled nailtail wallaby pouch young (Johnson 1986; Stuart-Dick 1987; Higginbottom 1991; Delaney 1993; Ashworth 1995), and the duration of maternal investment is similar for both sexes.

Neither sex appeared to suffer poorer condition or higher mortality in relation to maternal condition, although small sample sizes make these results tentative (Fig. 6, Table 2). There was no effect of offspring sex on immediate reproduction; sons did not precede reduced or increased weaning success relative to daughters (Table 2).

Why and how do bridled nailtail wallabies bias offspring sex ratio?

In contrast to the other macropods that bias investment according to sex (Johnson 1986; Stuart-Dick 1987; Higginbottom 1991; Ashworth 1995), bridled nailtail wallaby mothers appear to achieve this bias solely by adjusting offspring sex ratio, and not by investing different resources in each sex, by associating with daughters or weaning one sex later than the other. Several polygynous, sexually dimorphic seals and ungulates also do not bias expenditure on offspring of either sex (LeBoef et al. 1989; Byers and Moodie 1990; Green and Rothstein 1991; Smiseth and Lorentsen 1995).

The Trivers-Willard effect is not the only explanation for female-biased offspring sex ratios for mothers in poor condition. Non-adaptive mortality of males may be the cause, if nutritional stress affects male foetuses disproportionately, due to sexual selection for faster growth in males (Clutton-Brock 1984; Clutton-Brock and Iason 1986). This explanation cannot apply to bridled nailtail wallabies; offspring of small mothers that had lost condition at the end of the drought were virtually all daughters, even though no small females experienced reproductive cycle failures (Fig. 4).

The mechanism of sex ratio bias in favour of sons is not selective abortion or infanticide. As in euros, allied rock wallabies and red-necked wallabies, birth/conception failures in bridled nailtail wallabies were probably associated with senescence (Higginbottom 1991; Delaney 1993; Ashworth 1995). Reproductive senescence is caused by deterioration in the ovarian environment with age rather than by general ill health or poor nutrition, so this explanation is not inconsistent with the finding that older mothers were generally in better condition (Packer et al. 1998). The extent of male bias in the offspring of large females was greater than that predicted from the rate of reproductive failures, even if every failure was followed by the birth of a son. The unknown mechanism of sex ratio bias in bridled nailtails must therefore occur at conception. Many proposed sex-biasing mechanisms in mammals have involved post-conception loss (Gosling 1986; Cockburn 1994), although several mechanisms at conception have been identified, such as varying timing of conception relative to ovulation, and physiological changes in X- and Y-bearing sperm and the female's reproductive tract (Pratt et al. 1987; Krackow 1995; James 1996; Flint et al. 1997).

Conclusion

Sex ratio variation in bridled nailtail wallabies is most consistent with the Trivers-Willard model. It may also be influenced by local resource competition, because sons disperse further than daughters, but is inconsistent with the other proposed adaptive or non-adaptive explanations. Mothers do not appear to bias expenditure on either sex, and the mechanism of sex ratio bias operates at conception rather than later during the period of maternal investment.

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