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Adjustment of offspring sex ratios in relation to the availability of resources for philopatric offspring in the common brushtail possum

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The local-resource-competition hypothesis predicts that where philopatric offspring compete for resources with their mothers, offspring sex ratios will be biased in favour of the dispersing sex. This should produce variation in sex ratios between populations in relation to differences in the availability of resources for philopatric offspring. However, previous tests of local resource competition in mammals have used indirect measures of resource availability and have focused on sex-ratio variation between species or individuals rather than between local populations. Here, we show that the availability of den sites predicts the offspring sex ratio in populations of the common brushtail possum. Female possums defend access to dens, and daughters, but not sons, occupy dens within their mother's range. However, the abundances of possums in our study areas were determined principally by food availability. Consequently, in food-rich areas with a high population density, the per-capita availability of dens was low, and the cost of having a daughter should have been high. This cost was positively correlated with male bias in the sex ratio at birth. Low *per capita* availability of dens was correlated with male bias in the sex ratio at birth.

Keywords: sex allocation; local resource competition; marsupials; philopatry; *Trichosurus vulpecula*

1. INTRODUCTION

The local-resource-competition hypothesis predicts that in species with sex differences in natal philopatry the sex ratio of offspring should vary in response to the availability of resources for philopatric offspring. When resource availability is low, offspring of the philopatric sex will use resources that would otherwise be available to their mother; no such cost is imposed by offspring that disperse. Therefore, under conditions of low resource availability sex ratios should be biased towards the dispersing sex. When resource availability is high the ecological cost of producing philopatric offspring is reduced and (other things being equal) the sex ratio should approach parity. In mammals, daughters usually show natal philopatry, while sons disperse. Mammalian sex ratios are often male-biased, consistent with local resource competition between mothers and daughters (Clutton-Brock *et al.* 1982; Clutton-Brock & Iason 1986; Cockburn 1990), and there is evidence that the degree of sex-ratio bias at the species level is related to typical levels of resource competition (Johnson 1988).

The power of local resource competition to produce sex-ratio variation within species is less clear. In some cases, sex ratios vary between individual mothers in relation to their competitive ability (Silk 1983; Aars *et al.* 1995), but in others, for reasons that are not clear, this prediction fails (Packer *et al.* 2000). The sex ratio is also expected to vary between groups or populations in relation to local variations in the intensity of resource competition. Tests of this prediction have usually relied on indirect measures of competition, such as local density, population growth rate, body size or reproductive performance (Van Schaick & Hrdy 1991; Aars *et al.* 1995; Hewison & Gaillard 1996; Dittus 1998). The interpretation of these measures as indicators of resource availability is unclear because they may be influenced by many factors, and their relationship to offspring sex ratios may be inconsistent (Hewison *et al.* 1999; Packer *et al.* 2000). The strongest evidence for an effect of the intensity of mother–daughter competition on variation in the offspring sex ratio between populations comes from *Antechinus* species, where variation in the duration of mother–daughter competition, produced by extraordinary differences in maternal life span, is correlated with the sex ratio in the direction predicted by local resource competition (Cockburn *et al.* 1985). However, interpretation of this case is complicated by the fact that in populations where females do not live long enough to compete with their adult daughters the sex ratio shows a strong female bias, which is not predicted under local resource competition.

In this study, we use direct measures of the availability of resources to philopatric daughters to account for variation between populations in the offspring sex ratio of the common brushtail possum, *Trichosurus vulpecula*. We show that, in a series of eight populations, male biases in the offspring sex ratio are correlated with relative shortages of potential den trees. We present evidence that daughters occupy den trees that would otherwise be solely used by their mothers, and we explain how differences between populations in the availability of den trees are produced. Our results provide strong evidence for the power of local

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resource competition to produce inter-population variation in offspring sex ratios in a mammal.

2. METHODS

We studied nine populations of *T. vulpecula* in northern Queensland (seven populations) and northeastern New South Wales (two populations), Australia. The Queensland sites were situated *ca.* 100 km northwest of Townsville in the Mount Fox–Hervey's Range area, and the New South Wales sites were in the eastern arm of Paddy's Land State Forest (30°06′00″ S, 152°10′20″ E). All sites were eucalyptus-dominated open forest or woodland. At each site we established a 100 m × 100 m trapping grid covering *ca.* 40 ha. Possum density and the density of trees large enough to contain hollows usable as dens (i.e. diameter at breast height, DBH > 30 cm) were recorded at all sites. Potential den trees were defined as those with a DBH of more than 30 cm because a radio-tagging study (see § 3 below) showed that virtually all (292 out of 293) identified den trees were in this size range and that DBH was the best predictor of whether a tree contained useable dens (M. Clinchy, unpublished data). The sex ratio of offspring was measured at eight sites (only one offspring was sexed at one of the Queensland sites because of a very low abundance). Offspring were sexed during the period between birth and weaning, when either they are carried in the mother's pouch or, later, they ride on her back.

M.C., A.C.T., C.J.K. and P.J.J. used a combination of intensive live-trapping, radio-tracking, spotlighting and capture with a tranquillizer dart-gun to enumerate completely all individuals on both of the Paddy's Land study grids. All adult females ($n = 74$) were radio-tagged, and each female's location was checked every week over a three-year period (producing 2803 records of den use). The most central females on both grids ($n = 19$ in total) were experimentally removed to study the rate at which they were replaced by immigrants. Genotypes for 181 individuals were identified using six highly polymorphic (14–24 alleles per locus) microsatellite loci (Tv16, Tv19, Tv27, Tv53, Tv58 and Tv64) (Taylor & Cooper 1998). Parentage analyses were performed using the programs CERVUS (Marshall *et al.* 1998) and KINSHIP (Goodnight & Queller 1999), and the results were calibrated against 28 known mother–offspring pairs. Sibship analyses were performed using the program KINSHIP. C.N.J., A.P. and E.G.R. measured the soil fertility and body condition of adult females at the seven Mount Fox–Hervey's Range sites, all of which were matched for climate and topography. Soil fertility was calculated as the first principal component from an ordination of standard measures of soil chemistry, and was significantly positively correlated with proportions of phosphorous, nitrogen and organic matter, as well as with pH and conductivity. A condition score was calculated for each female as the ratio of her observed mass to that predicted from the regression of body mass on head length. We used logistic regression, weighted by sample sizes, for analyses involving the sex ratio (expressed as the proportion of males), and least squares regression otherwise. All variables were log-transformed for analysis, and all the relationships reported here as significant by parametric analysis were also significant by rank correlation.

3. RESULTS

Males dispersed at about the age of sexual maturity (figure 1). Dispersal distances for at least some males were small (although because our measures of dispersal distance were based on trapping they are probably underestimates) but sufficient to preclude overlap with the maternal home range. In contrast, all females who continued to be trapped after weaning remained within their mother's range.

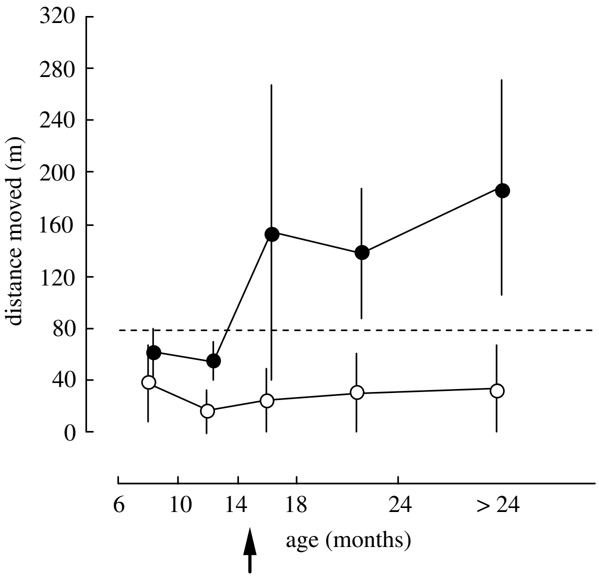

Figure 1. Relationship between age and distance moved (m, mean ± s.e.m.) by sons (filled circles, $n = 13$) and daughters (open circles, $n = 8$) from the centre of their mother's home range. The dashed line represents the mean radius of an adult female's home range. The arrow indicates the time of sexual maturity in males, as revealed by rapid enlargement of the testes to adult size; weaning is at approximately eight months. All estimates of movement are derived from trapping at the Queensland sites.

T. vulpecula are active at night, and spend the day in dens that provide protection from predators and extreme temperatures. In our study populations, hollows in large, old eucalyptuses were the most commonly used den sites. A detailed study of den use in the two Paddy's Land populations showed that 99.6% ($n = 2803$) of all dens recorded were in tree hollows. Females were selective in their use of dens. In 32 out of 40 females for which there were sufficient data (i.e. those that used five or more dens), there was a positive correlation (Spearman's r) between the number of times a den tree was used and its DBH (binomial $p < 0.001$). The mean correlation coefficient for all 40 females ($r = 0.26$) differed significantly from zero (95% confidence interval of the mean, 0.14–0.39; Shapiro–Wilk normality test, $W = 0.97$, $p = 0.341$). After the experimental removal of 19 females, neighbouring females that expanded their ranges into the vacancies thus created re-occupied dens formerly used by the removed females, preferring dens in larger trees (the median DBH of den trees that were re-occupied was 70.3 cm, compared with 59.9 cm for den trees that were not re-occupied; $U_{27,28} = 220.0$, $p = 0.008$). Other characteristics of dens that may have influenced selection, such as internal dimensions and size of opening, could not be measured.

Most den trees (76.1%) were used by only one female. In most cases (62 out of 88, binomial $p < 0.001$) where use of the same den ($n = 69$) by several (two, three or four) females was observed, the previous user had died ($n = 17$) or had been removed ($n = 19$) before the den was used by another female ($n = 30$). Only five pairs of females repeatedly (either one following the other on different days (19 observations) or both on the same day (58 observations)) used the same den while both were known to be still alive. Four of these five adult pairs were definitely mothers and daughters (based on tagging ($n = 1$) or unambiguous parentage analyses ($n = 3$, $p < 0.01$ in all cases)), and the fifth was either a mother and her daughter (parentage analyses inconclusive) or two full siblings (sibship analysis, $p < 0.01$).

Olfactory signals, rather than direct aggressive encounters, appeared to be key in maintaining exclusive access to dens. Each female had too many dens (up to 14) distributed over too large an area (1–2 ha) to be able physically to defend them all so successfully against interlopers (only 2.4% of dens were used by unrelated females while the original female was still alive). Moreover, females did not respond immediately to the physical absence of a neighbour, since more than six months (median, 31 weeks; range, 6–92 weeks) generally elapsed between the removal of a female and the re-occupation of one of her dens by a neighbour (50.9% of such dens being eventually re-occupied).

The number of potential den trees per adult female was strongly related to the offspring sex ratio (figure 2; $\chi^2_1 = 6.02$, $p = 0.014$ for the six Queensland populations; $\chi^2_1 = 5.21$, $p = 0.022$ for all eight populations). There was no relationship between the sex ratio and the age (between birth and weaning) at which offspring sex was determined ($\chi^2_1 = 0.69$, $p = 0.401$), showing that sex-ratio biases were not produced by sex-differential mortality during lactation or by sex differences in age at weaning.

The number of potential den trees per female varied between populations because population density was determined principally by factors other than the density of den trees. At our Queensland sites, population density was strongly related to soil fertility ($F_{1,5} = 19.25$, $p < 0.01$, $r^2 = 0.75$) and only weakly to the density of potential den trees ($F_{1,5} = 3.65$, $p = 0.13$, $r^2 = 0.35$). There was no significant relationship between soil fertility and the density of potential den trees ($F_{1,5} = 0.63$, $p = 0.46$, $r^2 = 0.11$). For all nine populations, the relationship between the density of den trees and the density of possums was marginally significant ($F_{1,7} = 5.928$, $p = 0.045$, $r^2 = 0.46$). Demographic evidence suggested that the New South Wales populations were also limited by food, rather than dens (Clinchy 1999).

There were no significant relationships between the sex ratio and the density of possums ($\chi^2_1 = 3.34$, $p = 0.068$ for all populations; $\chi^2_1 = 1.70$, $p = 0.192$ for the Queensland populations only), the absolute density of potential den trees ($\chi^2_1 = 0.03$, $p = 0.867$ for all populations; $\chi^2_1 = 0.20$, $p = 0.659$ for the Queensland populations only) or the mean body condition of possums ($\chi^2_1 = 2.88$, $p = 0.09$, data available for the Queensland populations only). Nor was there a correlation between the distance separating two populations and the similarity of their sex ratios (all populations, Spearman's $r = -0.005$, $p = 0.98$; Queensland populations only, Spearman's $r = 0.029$, $p = 0.911$). We did find a weakly significant relationship between the sex ratio and soil fertility ($\chi^2_1 = 4.38$, $p = 0.036$). This presumably arose indirectly through the close relationship between soil fertility and female density, which in turn produced the most variation between populations in the per-capita availability of den trees. Generalized linear modelling showed that the availability of den trees alone was a better predictor of the sex ratio (Akaike's information criterion, AIC = 4.57 (Akaike 1973)) than was soil fertility (AIC = 6.20) or both variables together (AIC = 5.84).

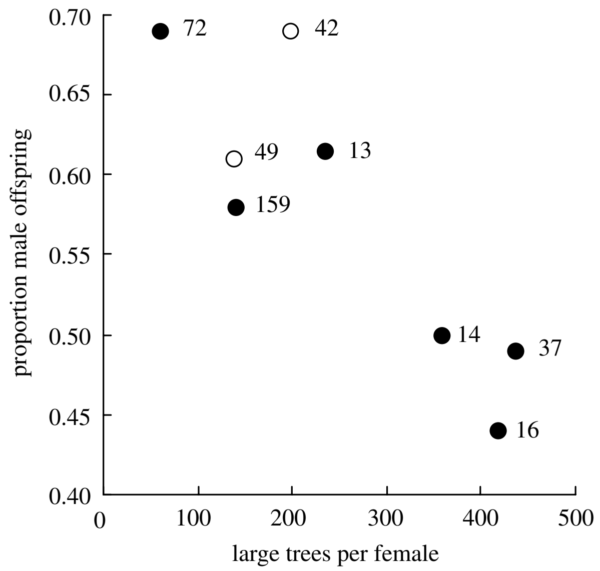

Figure 2. Relationship between the number of potential den trees and the sex ratio of offspring in common brushtail possums. Filled circles represent Queensland populations, open circles represent New South Wales populations. The numbers beside the points are numbers of offspring sexed in each population. Large trees are defined as those with diameters at breast height of more than 30 cm; trees in this size range were used for denning adult females.

4. DISCUSSION

Our data support several other studies demonstrating female philopatry and male dispersal in *T. vulpecula* (Winter 1976; Clout & Efford 1984; Ward 1985; Cowan *et al*. 1996, 1997; Efford 1998). Daughters settled within their mother's range, and therefore were potential competitors for resources, while males dispersed far enough to avoid direct competition with their mothers. Mothers and daughters might plausibly have competed for either dens or food; our data suggest that it was the intensity of mother–daughter competition for dens, rather than food, that varied between populations.

Females were selective in their use of dens, and the use of a den by one female clearly prevented access by others. Previous behavioural studies have suggested that females exclude one another from their dens (Winter 1976; Day *et al*. 2000) but until now unambiguous experimental evidence has been lacking. Overlap in den use between females, when it did occur, was restricted to mothers and daughters or full siblings. This is consistent with the natal philopatry of females, and demonstrates that the presence of a daughter may compromise the ability of a female to maintain the sole use of her preferred dens.

A mother who has a daughter in a population with low den availability will be obliged to restrict her own choice of dens in favour of her daughter, to share dens with her daughter, or to evict her. Each of these options represents a cost that is not incurred by producing a son. The number of potential den trees per female indicates the magnitude of this cost, and was the best predictor of the population sex ratio of offspring. This is strong evidence that variation in sex ratios was produced in response to local resource competition for dens. In some species, cooperative behaviour between mothers and philopatric offspring, leading to more effective acquisition and defence of resources, can select for sex ratios favouring the philopatric sex under conditions of resource shortage (the local-resource-enhancement hypothesis, Emlen *et al*. 1986). Such an effect is very unlikely in *T. vulpecula*, given that adults typically feed and den solitarily and that when interactions between adults do occur they are more likely to be antagonistic than affiliative (Winter 1976; Day *et al*. 2000).

The relationship between density and soil fertility in our Queensland populations suggests that possum abundance was determined principally by nutrient availability. Previous studies have demonstrated positive relationships between soil fertility, the concentrations of nutrients in eucalyptus foliage and the abundance of eucalyptus-feeding folivores, including *T. vulpecula* (Braithwaite *et al.* 1984; Cork & Catling 1996; A. P. McIlwee, unpublished data). The body condition and fecundity of females did not vary between populations in our study (C. N. Johnson and A. Payne, unpublished data). This is consistent with the idea that regulation of population density has resulted in the equalization of per-capita nutrient availability in all populations (Caughley *et al.* 1988). If so, the intensity of competition for nutrients would have been similar at all sites and this would explain why there was no effect of either soil fertility or population density on the offspring sex ratio. Food availability was important in that it produced variation in density between sites independently of the absolute density of den trees, so that the intensity of competition for den trees differed widely between locations.

Our results suggest that female *T. vulpecula* are able to adjust the sex ratio of their offspring in precise response to local conditions, producing heavily biased sex ratios of up to 2:1 sons to daughters in some populations. Adaptive variation in mammalian sex ratios is generally considered to be strongly constrained by the chromosomal determination of 50:50 sex ratios. Evidently, there is some mechanism that can overcome this constraint in *T. vulpecula*. Experiments involving rodents (Drickamer 1999) and lemurs (Perret 1996) have demonstrated that exposure to the urine of other females can affect offspring sex ratios. Consequently, the same olfactory signals used to maintain exclusive access to dens may also directly affect the offspring sex ratio in possums. Presumably, female possums in populations where dens are in short supply would more often encounter olfactory signals of other females at dens. If increased exposure to such signals results in male biases in the sex ratio in *T. vulpecula*, as it does in the mouse lemur, *Microcebus murinus* (Perret 1990, 1996), then this would produce male biases in populations where competition for dens is high.

As in other marsupials, the external genitalia of *T. vulpecula* are differentiated at birth, allowing sex to be determined in young only a few days old. We found no evidence of sex-differential mortality between the times of birth and weaning, so biases in the sex ratio must have been established at or before birth. The gestation period in this species is only 17 days, so it is clear that biases are established very early in development. There is evidence in another marsupial, *Antechinus agilis*, that biases in the sex ratio are established by conception (Davison & Ward 1998), but the mechanism responsible for this is not known. Marsupials, and, in particular, *T. vulpecula*, should continue to be excellent subjects for understanding the basis of sex-ratio variation in mammals.

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