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Manipulation of offspring sex ratio by second-mated female house wrens

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In 1973, Trivers and Willard proposed that offspring sex ratio should be associated with the quality of parental care likely to be provided to the offspring. We tested this hypothesis by comparing fledgling sex ratios in nests of first- and second-mated female house wrens (*Troglodytes aedon*). In our Wyoming population, second-mated females typically receive little or no male parental assistance and fledge fewer and lower-quality young compared with first-mated females. Assuming that being of lower quality has stronger negative effects on the future reproductive success of males than that of females in this polygynous population, we predicted that fledgling sex ratios in the nests of second-mated females would be female-biased compared with the fledgling sex ratios of first-mated females. Additionally, we asked whether any sex bias at fledging could have resulted from male-biased nestling mortality caused by sex-biased parental provisioning. As predicted, mean fledgling sex ratios in nests of second-mated females were more female-biased than fledgling sex ratios in nests of first-mated females. However, we found no evidence of either sex-biased nestling mortality or sex-biased parental provisioning. These findings suggest that females are responding to their status as second-mated females and to the associated low-quality parental care that their young are likely to receive by producing female-biased clutches rather than manipulating the offspring sex ratio through sex-biased nestling mortality.

Keywords: sex ratio manipulation; Trivers–Willard hypothesis; polygyny; *Troglodytes aedon*

1. INTRODUCTION

Trivers & Willard (1973) proposed that offspring sex ratio should be associated with the quality of parental care likely to be provided to the offspring. Because of sexual selection, offspring condition, which is determined largely by the quality and quantity of parental investment, will have different effects on fitness in males and females. According to Trivers (1985, p. 292), 'males in better than average condition as adults may enjoy larger [fitness] gains than females in better than average condition, while the reverse may be true when conditions are poor'. Competitive male offspring will be more likely to mate and will mate more often, especially in polygynous species. By contrast, a female in average or less than average condition will probably still have access to breeding opportunities. Parents should therefore adjust offspring sex ratios according to the quality of their breeding situation and their physical condition, producing more male offspring when resources and parental abilities are high and more female offspring when resources and parental abilities are low.

Associations between parental condition and offspring sex ratio have been observed in a number of vertebrates. Dominant female red deer (*Cervus elaphus*) are more likely to produce male offspring, while subordinate females are more likely to produce female offspring (Clutton-Brock *et al.* 1984). Associations between maternal condition and offspring sex ratio have been observed in woodrats (*Neotoma floridana*: McClure 1981) and humpback whales (*Megaptera novaeangliae*: Wiley & Clapham 1993). Recent studies on blue tits (*Parus caerulus*: Svensson & Nilsson 1996), zebra finches (*Taeniopygia guttata*: DeKogel 1997), and tawny owls (*Strix aluco*: Appleby *et al.* 1997) have also shown significant sex ratio biases associated with variation in parental care quality, as predicted by the Trivers–Willard hypothesis.

We tested this hypothesis by comparing sex ratios of broods produced by first- and second-mated females in a polygynous population of the house wren (*Troglodytes aedon*). In our Wyoming study population, second-mated females receive less male parental assistance, suffer greater nestling mortality and raise fewer and lower-quality young (i.e. underweight and undersized) than do first-mated females (Johnson *et al.* 1993). We predicted that the lower-quality broods of second-mated females will be female-biased compared with the broods of first-mated females. The Trivers–Willard hypothesis assumes that offspring condition carries over into adulthood (we present evidence for this elsewhere, Albrecht & Johnson (2002); also see Horak (1994) and Nowicki *et al.* (1998)) and that being in poor condition will eventually have stronger negative effects on male offspring due to male–male competition for breeding opportunities. Competition for breeding opportunities may be especially prevalent in species that nest in preformed tree cavities, such as house wrens, because such nest sites are usually a highly limited resource. In house wrens, there is often intense, interference-type competition among males for nest cavities (Johnson & Kermott 1990). Moreover, cavities are often clumped in space, allowing for monopolization of multiple cavities by individual males (Johnson & Kermott 1991). This creates a high environmental potential for polygyny (Emlen & Oring 1977; Martin 1993), further intensifying male–male competition.

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Biased sex ratios, if observed, may result from female manipulation of offspring sex at laying. Alternatively, or additionally, they may result from sex-biased nestling mortality that itself could result from the differential provisioning of male and female offspring (Stamps 1987; Droge *et al.* 1991; Clotfelter 1996). In this study, we also compared provisioning of male and female offspring in nests of first- and second-mated females. The ability for parents, especially female parents, to provision offspring of each sex differentially may have arisen in this species because of the consistent variation in the quality of breeding situations (e.g. breeding as a first- or second-mated female), and because of potential differences in fitness between male and female offspring in this polygynous species. Since sex ratios of young raised to independence should vary with the quality of the breeding situation, we asked whether broods produced by second-mated females are female-biased because of sex-biased parental provisioning causing male-biased nestling mortality.

2. METHODS

(a) *Study area and species*

We conducted this study during the breeding seasons of 1994 to 1997 on a population of house wrens breeding near Big Horn, Wyoming, USA (44° 40′ N, 106° 56′ W). Prior to wren arrival each spring, we erected two nest boxes, 25–45 m apart, on territories that had been occupied by males in previous years. All nest boxes were mounted on greased metal poles to exclude ground predators. We used leg bands to individually mark all adult wrens and nestlings for identification and monitoring purposes.

House wrens are small (10–12 g), insectivorous, migratory, cavity-nesting songbirds (their biology is summarized in Johnson (1998)). This species is nearly sexually monomorphic; males and females are identical in plumage and weight and males have only slightly longer ($< 5\%$) bills, wings and tails than females. Upon returning to the breeding grounds in spring, males establish a territory around one or more suitable nest cavities. Females lay clutches of 4 to 8 eggs. Only females incubate, but both parents may feed nestlings. Clutches begin hatching 11–13 days after the last egg is laid. Offspring fledge 16–18 days after hatching and are fed for 10–14 days thereafter. Males usually begin advertising for secondary mates at unoccupied nest sites on their territories when the first mate begins regular incubation with the laying of the penultimate egg. In the Wyoming population, the percentage of males mating polygynously varies yearly from 15 to 35%. As indicated above, second-mated females consistently produce fewer and lower-quality offspring than do first-mated females (Johnson *et al.* 1993). Polygynous males provide extensive parental assistance to the young of first mates, especially during the first third of the nestling stage while females remain in their nests brooding (i.e. warming) the altricial, heterothermic young (Czapka & Johnson 2000). By contrast, most second mates receive little or no male help rearing young and the need to brood the young prevents second-mated females from compensating for the lack of male feedings (Johnson & Kermott 1993). Whether second-mated females are, as a group, significantly younger and less experienced than first-mated females, and the extent to which this might contribute to the lower success of second-mated females, is not known. Females cannot be aged using external morphological characters and females of known age made up only a small proportion of the breeding females in our study each year. However, several lines of evidence indicate that, regardless of age effects, a lack of male parental assistance contributes substantially to the lowered success of second-mated females. In particular, the few second-mated females that do receive male help (e.g. after the first mate's nest fails) breed as successfully as do first-mated females (Johnson *et al.* 1992).

(b) *General field procedures*

To determine breeding progress and mating status of different females, we visited territories every 1 to 2 days, checked nest contents and identified the males that were associated with nests. For all nests on a territory, we used periodic nest checks to document the clutch size, date that eggs began hatching (referred to as Brood Day 1), number of young hatched, nestling mortality and number of young fledged. To obtain DNA for use in sexing nestlings (see § 2c, below), we collected blood samples from all nestlings in 39 nests of first-mated females and in 28 nests of second-mated females as soon as the young reached sufficient size, typically on Brood Day 8. Sample sizes of broods produced by first- and second-mated females are not equal because the frequency of nest failure was higher for second-mated females.

(c) *Identification of offspring sex*

We identified the sex of all offspring that fledged from focal nests using a PCR-based technique developed by Griffiths *et al.* (1996). We collected 100 µl blood samples from each nestling, stored them in lysis buffer at room temperature and then transported them to the University of New Mexico for laboratory analysis. We isolated DNA from blood samples using a Puregene DNA Isolation Kit (Gentra Systems, Inc.) and then subjected it to a PCR amplification. We verified this technique for house wrens by performing the procedure on blood samples taken from adults of known sex, 25 females and 25 males. In all 50 cases, sex was properly identified.

(d) *Comparison of offspring sex ratios*

We compared the sex ratio of broods of first- and second-mated females at the time of fledging. We report mean fledgling sex ratios (and all other means) ± 1 s.e. Analyses were performed using the Genmod procedure (logit link function, binomial distribution) of Sas (1990) with the number of male fledglings as the dependent variable and the number of fledglings in the brood as the binomial denominator. The discrepancy between the model and the data is reported by the deviance, which is distributed asymptotically as χ^2 (Crawley 1993). Our statistical comparisons of brood sex ratios of first- and second-mated females are one-tailed because we specifically predicted that broods of second-mated females would be more female-biased than those of first-mated females.

(e) *Parental provisioning rates of offspring of different sexes*

To assess whether parental provisioning was sex-biased, we asked whether offspring of one sex consistently gained more weight than offspring of the other sex. In 1996, we monitored provisioning indirectly by recording each nestling's weight gain over a 2–3 h period on the morning of Brood Day 5 in a sample of 27 nests (71 male nestlings and 73 female nestlings). We recorded the weights of individually marked nestlings at the beginning and end of the sampling period. We did not compare actual amounts of weight gained by male and female offspring among nests because the time elapsing between weighings varied among nests. Instead, we ranked nestlings within nests in terms of relative amount of weight gained and categorized them as being in the top or bottom half of their brood with respect to weight gain. In the 10 broods with an odd number of nestlings, the middle-weight nestling was excluded from this analysis. If provisioning is sex-biased, then male and female offspring should not be evenly distributed between the top half and bottom half of broods with respect to weight gain.

3. RESULTS

(a) *Sex ratios in nests of first- and second-mated females*

The mean fledgling sex ratio (proportion of males) in nests of second-mated females (0.444 ± 0.046) was significantly lower than the mean fledgling sex ratio in nests of first-mated females (0.501 ± 0.033) ($\chi^2 = 2.78$, d.f. = 1, $p = 0.047$). Lower fledgling sex ratios for second-mated females occurred in all four years of study.

In a number of bird and mammal species, offspring sex ratio varies with time of the breeding season (Howe 1977; Clutton-Brock & Jason 1986; Dijkstra *et al.* 1990; Daan *et al.* 1996). In the current study, clutches of second-mated females hatched, on average, later than those of first-mated females (30 June ± 1.14 days versus 14 June ± 0.60 days). This raises the possibility that the female-biased sex ratio in nests of second-mated females may be unrelated to the fitness drawbacks of producing male offspring in poor condition as we have proposed, but, instead, may reflect some fitness benefit of producing more female offspring later in the season. Although there appears to be a weak tendency for the fledgling sex ratio to decline during the season in nests of primary females ($r = -0.27$, $p = 0.10$), the opposite tendency occurs, i.e. fledgling sex ratio increases, in nests of both secondary females ($r = 0.12$, $p = 0.55$) and in 42 nests of monogamous females examined in conjunction with other studies ($r = 0.10$, $p = 0.53$). Note that any benefits of decreasing sex ratio as the season progressed should accrue to all adult females, regardless of mating status. If all females are included in a single analysis, there is no relationship between fledgling sex ratio and hatch date ($r = -0.05$, $p > 0.55$, $n = 109$). We therefore rule out seasonal effects as the cause of skewed sex ratios in nests of second-mated females.

(b) *Differential offspring mortality and provisioning*

Mean clutch sizes of first- and second-mated females included in this study were 7.0 ± 0.1 and 6.6 ± 0.1 eggs. Overall, 34 ± 7.1% of offspring died prior to fledging in nests of second-mated females compared with 10 ± 2.8% of offspring in nests of first-mated females (Wilcoxon–Mann–Whitney $Z = 2.97$, $p = 0.003$). If offspring mortality was male-biased, this could cause the observed female-biased fledgling sex ratio in nests of second-mated females. A small fraction of offspring that did die, died before Brood Day 8, which was the day we obtained DNA from offspring to determine their sex (on average, 10% and 7% of young that died, did so before Brood Day 8 in nests of second- and first-mated females, respectively). Thus, we could not determine directly whether mortality in nests of second-mated females was more male-biased than mortality in nests of first-mated females. Alternatively, we asked whether, within nests, the proportion of fledglings that were male decreased as nestling mortality increased. If so, this would suggest that male offspring die more frequently than female offspring. There was no relationship between fledgling sex ratio and proportion of the brood dying in nests of either first-mated females ($r = -0.05$, $p = 0.76$) or second-mated females ($r = 0.06$, $p = 0.74$). This strongly suggests that mortality does not have a major influence on sex ratios in either nests of first- or second-mated females.

(c) *Provisioning of young of different sexes*

Consistent with our observation that offspring mortality is not male-biased, we also found no evidence for sex-biased provisioning of offspring. When weights of young were taken from 27 nests approximately one third of the way through the nestling stage, i.e., on Brood Day 5, mean weights of male and female nestlings were found to be nearly identical (4.49 ± 0.13 g versus 4.45 ± 0.10 g, respectively; $F = 0.001$, d.f. = 1, $p > 0.95$). In addition, we detected no evidence that one sex was gaining more weight over a 2–3 h period on this same day, which is expected if provisioning was sex-biased. There was no difference in the distribution of male and female offspring into the top and bottom halves of their broods with respect to weight gain. Collectively, 32 males and 34 females appeared in the top half of their broods with respect to weight gain compared with 33 males and 35 females appearing in the bottom half of their broods with respect to weight gain ($\chi^2 = 0.03$, d.f. = 3, $p > 0.995$).

In this sample of 27 nests, 11 were nests of second-mated females. In these 11 nests alone, there was still no evidence for sex-biased parental provisioning. Male ($n = 23$) and female ($n = 25$) nestlings were distributed evenly into the top and bottom halves of their broods with respect to weight gain, with 12 males and 12 females in the top half, and 11 males and 13 females in the bottom half ($\chi^2 = 0.17$, d.f. = 3, $p > 0.975$).

4. DISCUSSION

As predicted, fledgling sex ratios in nests of second-mated females were significantly female-biased. We argue that this bias occurs because second-mated females typically produce offspring that are of lower quality (i.e. in poorer physical condition) than those of first-mated females (Johnson *et al.* 1993). In this species, as in other passerines, being in poor condition at fledging will often have stronger negative effects on male offspring than on female offspring (Hochachka & Smith 1991; Horak 1994; Kilner 1998; Albrecht & Johnson 2002). These are the circumstances for which the Trivers–Willard hypothesis was developed and for which female-biased offspring sex ratios are predicted. The cost to males of being in poor physical condition may be particularly high in house wrens because of the intense competition among the males for a limited supply of preformed tree cavities that are used as nest sites (Johnson & Kermott 1991; Johnson *et al.* 1992). In our study population, male house wrens are routinely challenged for their cavities. During such challenges, the resident male repeatedly pursues the intruder throughout the territory in tight, high-speed circular chases; on occasion, the two males will come together and fight physically (Kendeigh 1941, p. 27). Many contests for territories last for several hours and some last for longer than a day. Presumably, a male in poor physical condition will have difficulty obtaining or holding a territory.

Biased sex ratios may result from female manipulation of her offspring's sex during laying and/or from sex-biased nestling mortality, the latter of which can be caused by parents differentially provisioning male and female offspring (Stamps 1987; Droge *et al.* 1991; Clotfelter 1996). We found no evidence for preferential feeding of either sex in nests of first- or second-mated females, nor was there evidence that mortality was sex-biased. We were unable to obtain DNA from all offspring that died so we cannot definitively rule out an influence of sex-biased mortality on our results. However, we found no relationship between the degree of within-brood mortality and fledgling sex ratio. This strongly suggests that mortality occurred at random with respect to nestling sex and that the observed female bias at fledging in the nests of second-mated females reflects a bias that already existed at the time of hatching. In our dataset, sex ratio at laying could be determined for a subset of nests in which all eggs resulted in nestlings old enough to provide a sample of DNA for sexing. In this subsample, the mean sex ratio at laying in nests of second-mated females (0.455 ± 0.083, $n = 8$) was also less than the mean sex ratio at laying in nests of first-mated females (0.512 ± 0.049, $n = 19$). The sex ratio at laying in nests of second-mated females tends towards being less than 0.5, despite the small sample size (one-tailed Kruskal–Wallis 101.000, d.f. $= 1$, $p = 0.096$). This is consistent with the suggestion that nests with skewed fledgling sex ratios must have had skewed sex ratios at laying, a pattern that has been observed in a number of species (Ellegren *et al.* 1996; Komdeur 1996; Svensson & Nilsson 1996; Appleby *et al.* 1997; Bradbury *et al.* 1997).

(a) *An alternative ultimate explanation for sex ratio skewing*

The Local Resource Competition hypothesis (LRC) proposes that parents invest differentially in the production of male and female offspring because of sex-specific differences in natal philopatry and that by producing more individuals of the dispersing sex, parents benefit from reduced competition with their philopatric offspring (Gowaty 1993). In house wrens, the frequency of natal philopatry is low (2–7%), with males being at least twice as philopatric as females (Drilling & Thompson 1988; personal observation). Based on these sex differences in philopatry, one might expect that broods of all breeding females, independent of their mating status, should show a female-biased offspring sex ratio. Based on a sample of 109 broods of monogamous, first-mated and second-mated females, the overall fledgling sex ratio in the population is 0.472 ± 0.019, which is consistent with the LRC hypothesis. However, the mean fledgling sex ratio in nests of second-mated females, 0.444, is even more female-biased than in the population overall. If the evolutionary mechanism assumed in the LRC hypothesis was responsible for the greater female bias in nests of second-mated female house wrens, then it would also be expected that these females are biasing their offspring sex ratios because the male offspring fledging from their nests are especially likely to return to the natal area. This seems unlikely because, as stated above, young fledging from the nests of second-mated females fledge in relatively poor condition and are actually less likely to survive and be recruited into the population than are the males from nests of other females (Albrecht & Johnson 2002).

5. CONCLUSIONS

The skewed offspring sex ratios of second-mated females suggest that these females are responding to their mating status and to the low quality of parental care that their offspring are likely to receive, by manipulating the sex ratio of their broods at hatching to be female-biased. That there is no evidence of male-biased offspring mortality in our population, and, that in nests of second-mated, but not first-mated females, sex ratio at hatching tends to be female-biased, both suggest that the sex-ratio skew in nests of second-mated female house wrens is being produced at egg-laying (see Krackow (1995) and Sheldon (1998) for a discussion of cellular mechanisms for sex ratio adjustment in birds). Because our sample of nests of second-mated females for which the complete hatching sex ratio could be determined is small ($n = 8$), this hypothesis needs to be examined using larger samples of hatching sex ratios from nests of second-mated females.

House wrens provide a unique opportunity for further testing our assertion that production of low-quality offspring selects for female-biased offspring sex ratios among second-mated females. In several other populations of house wrens, polygyny occurs with regularity but the young in nests of second-mated females do not receive lower-quality parental care and do not fledge in poor condition relative to the young in nests of first-mated females (Drilling & Thompson 1991; Johnson 1998; S. S. Soukop, personal communication). Without diminished parental care quality and the associated decrease in offspring quality, there should be no selection favouring parental manipulation of offspring sex ratio, and we predict no differences in the fledgling sex ratios of second-mated and first-mated females in these other populations.

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