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## Experimental Evidence for Importance of Male Parental Care in Monogamous House Wrens

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One hypothesis for the predominance of monogamous pair bonds among birds is that biparental care is essential if individuals are to raise any young to independence (Wittenberger and Tilson 1980). To test this hypothesis and to assess the importance of male care in determining reproductive success, researchers have removed males from breeding pairs in a number of monogamous bird species (reviews in Wolf et al. 1988, Bart and Tornes 1989, Dunn and Hannon 1989). In one such study on an Ohio population of House Wrens (*Troglodytes aedon*), Bart and Tornes (1989) removed males from territories approximately one-third of the way through the nestling stage. Under normal breeding conditions, "widowed" females raised as many young as control females from intact pairs. Widowed females experienced reduced fledging success only during one unusually cold, wet spring.

Because Bart and Tornes (1989) did not remove males until several days after eggs hatched, they could not assess the importance of the male's presence during the earliest part of the nestling stage. However, male feeding assistance may be most critical at this time because females must provide the heterothermic young with heat during extended periods of brooding. Nestling House Wrens cannot thermoregulate as a brood until sometime between the fifth and tenth day of the nestling stage, depending on brood size (Dunn 1976). Until this time, the need to brood young may limit a female's ability to compensate fully for a lack of male parental effort (Wittenberger and Tilson 1980, Clark and Ricklefs 1988). Here we assess the importance of having male care during the early part of the nestling stage by examining the reproductive success of female House Wrens whose mates were removed two to four days before eggs hatched.

We conducted this study in 1990 on cattle ranches near Big Horn, Sheridan Co., Wyoming (44°40'N, 106°56'W). All wrens studied nested in wooden boxes mounted on greased poles to reduce nest predation.

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TABLE 1. Breeding success of 20 female House Wrens from intact pairs, and 10 females whose mates were removed during incubation stage of breeding cycle.

Measurement	Mean $\pm$ SE		Statistic <sup>a</sup>	P
	Control females (pair intact)	Widowed females (male removed)		
Clutch size	7.4 $\pm$ 0.1	7.5 $\pm$ 0.1	0.49	>0.60 <sup>b</sup>
Date of first egg	31 May $\pm$ 1 day	2 June $\pm$ 2 days	0.82	>0.40 <sup>b</sup>
Fledglings/egg (no. fledglings)	0.81 $\pm$ 0.04 (6.0 $\pm$ 0.3)	0.49 $\pm$ 0.10 (3.7 $\pm$ 0.8)	-2.75	<0.003
Proportion of clutch found unhatched on day 4	0.05 $\pm$ 0.02	0.06 $\pm$ 0.02	0.59	>0.25
Proportion of eggs resulting in live nestlings on day 6	0.90 $\pm$ 0.03	0.74 $\pm$ 0.06	-2.57	<0.006
Proportion of nestlings alive on day 6 that fledged	0.90 $\pm$ 0.04	0.68 $\pm$ 0.12	-1.61	<0.055
<b>Nestlings</b>				
Mass <sup>c</sup> (g)	9.9 $\pm$ 0.2	9.2 $\pm$ 0.4	1.90 <sup>d</sup>	<0.04
Tarsus length <sup>e</sup> (mm)	17.3 $\pm$ 0.1	17.0 $\pm$ 0.2	1.17 <sup>d</sup>	>0.10
Feather length <sup>e</sup> (mm)	20.3 $\pm$ 0.3	18.4 $\pm$ 1.0	2.06 <sup>d</sup>	<0.03

<sup>a</sup> Z-scores for Wilcoxon rank-sum tests unless otherwise indicated.

<sup>b</sup> Indicates two-tailed test; all other tests one-tailed.

<sup>c</sup> Comparison made for 20 control broods and 9 widow broods.

<sup>d</sup> *t*-test scores.

<sup>e</sup> Comparison made for 17 control broods and 8 widow broods.

We removed males from territories during the second half of the incubation stage to observe the response of "replacement" males to offspring of previous resident males (see Kermott et al. 1991). We report here the reproductive success of 10 females (hereafter "widows") on territories where we observed no replacement male. Widows began egg laying between 26 May and 13 June, and laid clutches of seven ( $n = 5$ ) or eight ( $n = 5$ ) eggs. Our "controls" consisted of all monogamous females who began laying clutches of seven ( $n = 12$ ) or eight ( $n = 8$ ) eggs within the same time period.

We checked widows' territories for the presence of replacement males, and counted eggs and young in their nests, each day following male removal until day 4 of the nestling stage (day 1 = the day that hatching begins). We checked widows' nests again on days 6, 9, 12, and 16. We counted eggs and young in nests of control females on days 1, 4, 6, 9, 12, and 16. We measured each nestling's mass, the length of its right tarsus, and the exposed length of its right ninth primary feather on days 12 and 16 at all nests. Nestlings usually fledge between days 16 and 18. Nestlings were absent from nests of 3 of 20 control females when we arrived to take measurements on day 16. Because each nest contained large, healthy young on day 12 and because we observed no evidence of nest predation (i.e. no disturbance to nest linings or grease on box poles), we assumed that each brood had fledged.

We used as measures of female breeding success the proportion of the clutch that resulted in fledged young and the mass and size of young produced. We compared measurements of tarsi and feathers record-

ed on day 16, and masses recorded on day 12. Masses on day 16 were uninformative because the most well-developed nestlings (i.e. those heaviest on day 12) often had lost mass by day 16. We compared means of proportions using Wilcoxon rank-sum tests, and mean mass and size measurements using *t*-tests. Brood means were used as our independent samples in the latter analyses to avoid pseudoreplication. One-tailed tests were used to compare measures of breeding success because we specifically asked whether widows raised fewer, lighter or smaller young.

Widows and control females did not differ in mean clutch size or mean date on which they began egg laying (Table 1). The proportions of widows (8/10) and control females (20/20) that fledged at least one nestling did not differ significantly (Fisher's exact test,  $P > 0.10$ ). However, widows produced 32% fewer fledglings per egg laid than control females (Table 1). Widows raised fewer young than control females through the first third of the nestling stage (i.e. through day 6). The fact that widows did not have more unhatched eggs in their nests than control females on day 4 (when all eggs should have hatched) suggests that lower success of widows resulted from a higher incidence of nestling death. All nestling death apparently resulted from starvation (we saw no evidence of nest predation at any nest). We also found a strong tendency for widows to have less success at raising nestlings during the last two-thirds of the nestling stage (i.e. after day 6) compared with control females. Nestlings raised by widows also developed more slowly than nestlings raised by control females as indicated by significantly lower masses on day 12, and significantly shorter primary feathers on day 16.

The fact that widows lost a disproportionate number of young during the first third of the nestling stage suggests that having male aid during this period increases female breeding success. Between days 1 and 6, males in monogamous pairs typically make 75 to 80% of all food deliveries, while females spend between 50 and 75% of their time during daylight hours in nests brooding young (Johnson 1992). Widows probably lost more young than control females during this period because they could not maintain normal levels of food delivery, brooding time, or both.

In contrast to Bart and Tornes (1989), we found that widows raised fewer young to fledging than control females during the latter two-thirds of the nestling stage, even though breeding conditions appeared favorable (no extended periods of cool or rainy weather occurred during our study). Variation between the Ohio and Wyoming study sites in factors such as food abundance and ambient temperature may account for some of the difference in our results. However, the lowered success of widows in our study also may reflect the added stress of having no male aid during the first third of the nestling stage.

Females that were either widowed or left undisturbed in this study were not chosen strictly at random, so our results must be viewed with some caution. Most control females had territories in areas where we had space to erect three boxes on the territory (each 30 to 50 m apart) to facilitate other aspects of our research. Most widows had territories in areas where this was not possible (e.g. near boundaries of areas on which we had permission to work). Although the physiognomy of territories held by widows and control females did not differ in any obvious way, an experiment with formal controls should be conducted to confirm our results. Our concern here is alleviated in part by corroborating data from a study on the breeding success of secondary females among polygynous trios in this population. Secondary females that received little or no aid from mates in feeding young during the first third of the nestling stage raised fewer and lighter offspring than secondary females with male aid (Johnson 1992).

Finally, to facilitate comparison with the results of Bart and Tornes (1989), we examined the success of only those widows on territories where we observed no replacement male (Bart and Tornes did not observe replacements). However, many widows' territories on our site were occupied by replacement males who removed offspring from nests in preparation for their own breeding attempts (Kermott and Johnson 1990, Kermott et al. 1991). Thus, in our population, a male's presence on the territory is more crucial in determining female reproductive success than the data here suggest.

In conclusion, our results suggest that male paren-

tal care in the period immediately after hatching may significantly affect female breeding success in species that hatch heterothermic young. In order to assess fully the importance of male care in these species by use of male removal experiments, we recommend that researchers remove males before eggs hatch.

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