Wilson Bull., 105(3), 1993, pp. 448–454

FLEDGING SUCCESS IN EXPERIMENTALLY MANIPULATED BROODS OF HOUSE WRENS

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ABSTRACT.—I manipulated brood size in a population of box-nesting House Wrens (*Troglodytes aedon*) to determine if fledging success was limited by the ability of parents to provision nestlings. Enlarged broods produced significantly more fledged young than did control or reduced broods, but fledglings from enlarged broods weighed 6–7% less than fledglings from other broods. Fledging success was unrelated to original clutch size, but parents that laid large clutches fledged heavier offspring. These results do not support the brood-provisioning hypothesis. Brood size in House Wrens may be limited by post-fledging survival or interseasonal costs of reproduction, but I was unable to assess these factors in this study. *Received 28 Sept. 1992, accepted 3 March 1993.*

Lack (1947) hypothesized that clutch size in altricial birds evolved in relation to the ability of parents to provide food for nestlings; however, most studies of fledging success in relation to brood size have shown that experimentally-enlarged broods fledge the most young (Lessells 1986). This has led to several important modifications of Lack's hypothesis. If fledglings from large broods leave the nest in poorer condition, then any apparent advantage of large brood size may disappear due to higher mortality of postfledglings (Magrath 1991). Likewise, parents that attempt to raise large broods may have lower future survival and/or reproductive success (Nur 1988). Finally, Lack (1947) suggested that the average clutch size for the population represented a single optimum for all individuals, but among-individual variation in clutch size might reflect differences in individual or territory quality (the individual-optimization hypothesis; Nur 1987).

In order to test these various hypotheses, it is essential to manipulate brood size to remove any potentially confounding relationships between individual quality and clutch size (Lessells 1986). In this study, I manipulated broods of House Wrens (*Troglodytes aedon*) to determine if nestling survival and fledgling mass were affected by brood size. I also examined nestling survival and fledgling mass of manipulated broods in relation to the original unmanipulated clutch size to determine whether females that laid large clutches were more capable of raising large broods.

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METHODS

The study was conducted on a 31-ha plot 22 km north of Saskatoon, Saskatchewan (52°07′N, 106°38′W). The study area consisted of similar portions of young aspen (*Populus tremuloides*) forest, native grassland, cultivated field, and farmyard. I placed 54 wren boxes in wooded areas on 15 May 1992 and an additional 28 bluebird boxes in open areas during early April. Nest boxes were 18 cm high with floor areas of 15 × 15 cm. Entrance holes in wren boxes were 2.9 cm in diameter and included two lateral slots to facilitate stick transport by wrens (Kennedy and White 1992). Entrance holes were 3.8 cm in diameter on bluebird boxes. Wrens initiated clutches in all 54 wren boxes and in five of the bluebird boxes.

Nest boxes were visited every five to seven days throughout nest-building, egg-laying, and incubation. Initiation dates of clutches found during egg-laying were estimated by backdating, assuming one egg was laid per day. Nests were paired according to hatching dates and were then randomly assigned to one of five brood-size treatments: +4 enlargements, +2 enlargements, ±0 controls, −2 reductions, and −4 reductions. Nestling transfers took place when nestlings were 0–4 days old and were accomplished in ≤10 min; transferred nestlings were of similar age and size. I did not replace unhatched eggs or nestlings that died. When nestlings were 10–14 days old, I banded them with Canadian Wildlife Service aluminum leg bands, weighed them with a Pesola spring balance (±0.1 g), and measured their unflattened wing chord using a steel wing rule (±0.5 mm). Five broods fledged before measurements were taken. Nestlings present in the nest box at banding were assumed to fledge unless they were found dead during a later visit (Robinson and Rotenberry 1991). Adult females were captured and banded at 21 nests.

There was no evidence of conspecific brood parasitism or double brooding: laying rates did not exceed one egg per day, and no new nests were initiated after previous nests had fledged. Most manipulated broods (36/41) were tended by two adults; the remaining five broods may also have been tended by two adults, but only one adult was observed.

I compared reproductive success among treatment groups using one-way ANOVAs. If an overall ANOVA was significant, I used least significant difference tests to identify treatment groups that differed significantly. For analyses of nestling mass and wing chord, I included nestling age as a possible covariate (i.e., ANCOVA). To test the individual-optimization hypothesis, I analyzed data on fledging success, fledgling mass, and wing chord in relation to manipulated brood size and original clutch size. Because reproductive success declines seasonally in House Wrens (Finke et al. 1987), I also replicated each analysis using nest initiation date as a potential covariate.

RESULTS

Broods were manipulated at 41 of 59 nests; 13 nests were abandoned or destroyed before hatching, and the remaining five nests hatched too late in the season to be included in the experiment (i.e., they could not be matched with a synchronously hatching brood for nestling transfers). There were no differences among treatment groups in timing of breeding, clutch size, or original brood size (Table 1). After nestling transfers were completed, manipulated brood size differed significantly among all groups except the −4 and −2 treatments (Table 1). These differences in brood size were maintained throughout the brood-rearing period, such that enlarged broods fledged more offspring and reduced broods fledged fewer offspring than did controls (Table 1). However, these differences in fledg-

TABLE 1
REPRODUCTIVE SUCCESS OF HOUSE WRENS IN RESPONSE TO BROOD-SIZE MANIPULATIONS

	Brood-size manipulation					ANOVA	
Trait	−4	−2	0	+2	+4	*F*	*P*
Pre-manipulation:							
Laying date (Julian)	158.6 ± 4.6[a]	160.1 ± 5.7	157.0 ± 4.2	158.9 ± 5.8	159.5 ± 5.0	0.53	0.71
Clutch size	7.86 ± 1.68	6.88 ± 0.83	7.09 ± 0.83	6.57 ± 0.98	7.38 ± 0.52	1.71	0.17
Initial brood size	7.14 ± 1.95	6.38 ± 0.74	6.73 ± 1.01	6.14 ± 0.69	6.75 ± 0.89	0.84	0.51
Post-manipulation:							
Manipulated brood size	3.14 ± 1.95	4.38 ± 0.74	6.73 ± 1.01	8.14 ± 0.69	10.75 ± 0.89	55.19	0.0001[b]
	A	A	B	C	D		
Number fledged	3.00 ± 2.16	4.25 ± 0.89	6.45 ± 1.13	7.86 ± 0.90	9.50 ± 1.60	27.22	0.0001
	A	A	B	C	D		
Number died	0.13 ± 0.35	0.14 ± 0.38	0.27 ± 0.47	0.29 ± 0.49	1.25 ± 2.05	1.84	0.14
Fledgling mass (g)	10.93 ± 0.64	10.80 ± 0.61	10.76 ± 0.33	10.21 ± 0.72	10.09 ± 0.60	2.97	0.035
	A	AB	AB	BC	C		
Fledgling wing chord (mm)	33.6 ± 6.6	32.6 ± 5.9	34.5 ± 3.0	33.7 ± 5.8	33.4 ± 5.3	0.13	0.97
Number of broods[c]	7 (6)	8 (6)	11 (10)	7 (7)	8 (7)		

[a] Data are $\bar{x} \pm 1$ SD.

[b] Groups sharing the same letter are not significantly different (least significant difference test).

[c] Smaller samples in parentheses are for mass and wing chord measurements.

ling numbers were partially offset by differences in fledgling mass: fledglings in +4 broods were 6–8% lighter than fledglings in reduced and control broods, and fledglings in +2 broods were 7% lighter than fledglings in −4 broods (Table 1). Wing chord was unaffected (Table 1).

Number of chicks fledging was strongly correlated with manipulated brood size (Fig. 1; $r = 0.93$, $F = 249.4$, $P = 0.0001$), but initial clutch size did not explain any additional variance in the data ($F = 0.08$, $P = 0.77$). Fledgling mass was negatively affected by manipulated brood size ($F = 6.68$, $P = 0.01$) and positively affected by initial clutch size ($F = 6.74$, $P = 0.01$); fledgling mass declined an average of 0.09 g for each additional chick in the brood (Fig. 1), but it increased by 0.23 g for each additional egg in the female's clutch. Nestling age had only a minor influence on body mass ($F = 3.30$, $P = 0.08$); thus, most nestlings had reached asymptotic body mass by age 10 days (see also Finke et al. 1987). Wing chord was not affected by manipulated brood size or original clutch size ($P \geq 0.20$), but did increase with nestling age ($F = 22.79$, $P = 0.0001$).

Although clutch size declined with laying date ($\mathrm{CS} = 8.2 - 0.10 \cdot \mathrm{DATE}$, $r^2 = 0.36$, $F = 29.50$, $P = 0.0001$, $N = 46$; DATE 1 = 1 June), no other measures of reproductive success were influenced by date ($P \geq 0.20$), nor were any of the preceding analyses altered by the inclusion of laying date as a potential covariate.

DISCUSSION

House Wrens were fully capable of raising enlarged broods to fledging age. Although there was some suggestion of higher nestling mortality in enlarged broods (especially in the +4 group), this trend was not significant. One enlarged brood of 12 (+4 manipulation) was severely infested by botfly larvae and fledged only six offspring; this single brood contributed half of the nestling mortalities in the +4 treatment group (all other mortalities involved 1 or 2 nestlings per brood). Even if the +4 broods did average one more nestling death than the control broods, they nevertheless raised three additional young. Similar results have been obtained in three other studies of fledging success in manipulated broods of House Wrens (Finke et al. 1987, Robinson and Rotenberry 1991, Harper et al. 1992).

Although enlarged broods fledged more young, they weighed about 6% less than control fledglings and about 7% less than fledglings from reduced broods. Robinson and Rotenberry (1991) also reported lighter fledgling masses in experimentally-enlarged broods of House Wrens, although Finke et al. (1987) did not. Harper et al. (1992) observed lower fledgling masses during one of four seasons. Postfledging survival has been positively correlated with fledgling mass in several species of birds (see Magrath 1991), which suggests that a lower proportion of fledglings from enlarged broods

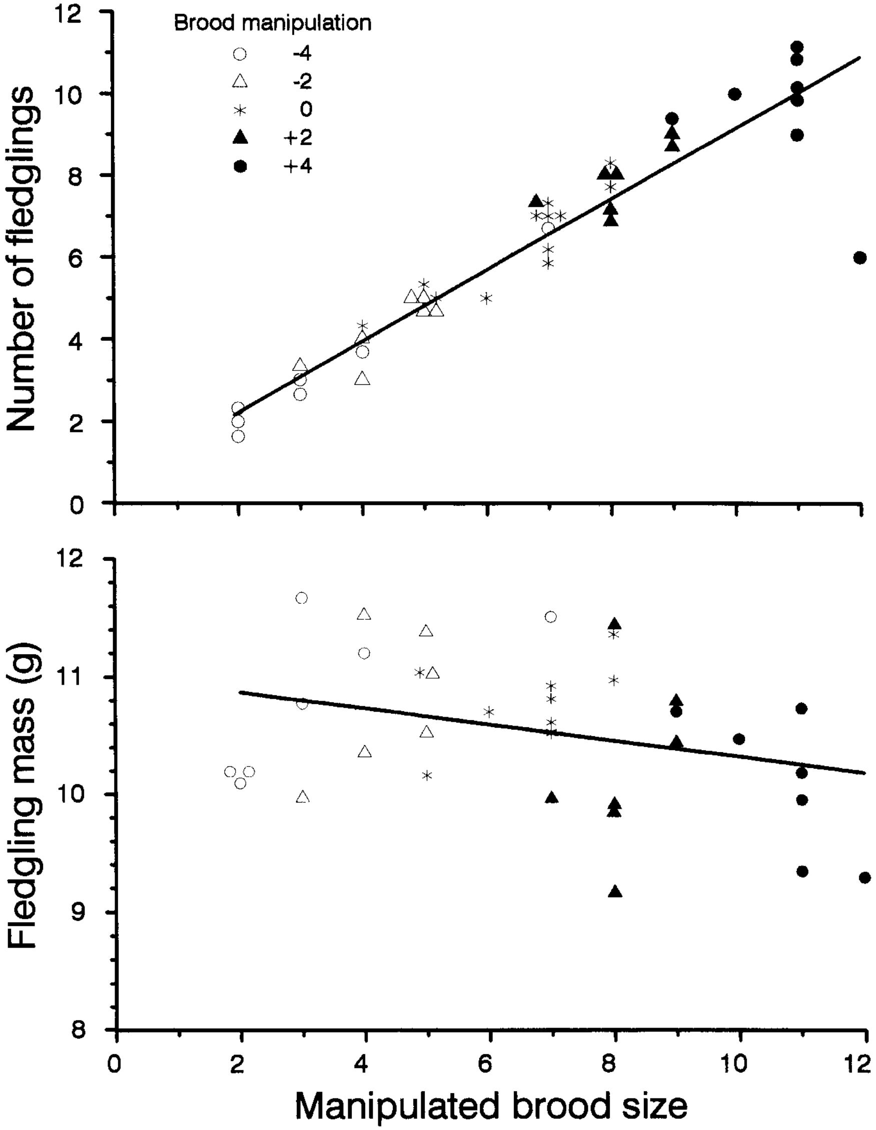

FIG. 1. Fledging success and fledgling mass in experimentally manipulated broods of House Wrens.

of House Wrens would survive to breed. However, Drilling and Thompson (1988) and Harper et al. (1992) observed no effects of brood-size manipulations on recruitment, although the power of their statistical tests was undoubtedly low. Given that +4 broods fledged 1.47 times as many offspring as control broods in this study, postfledging survival would have to be reduced by ≥32% among fledglings from +4 broods if overall recruitment rates were to favor control broods (assuming comparable adult survival, see below). Because the reduction in fledgling mass was only 6–7%, such a large disparity in postfledging survival seems unlikely. Natal philopatry is very low in House Wrens (averaging less than 3%; Drilling and Thompson 1988, Harper et al. 1992), so testing this possible trade-off between fledgling mass and recruitment will be difficult.

Fledging success was not related to territory or female quality, as implied by the individual-optimization hypothesis (Nur 1987). Although original clutch size ranged from 3 to 11 ($\bar{x} = 6.87$, SD = 1.29) and was equal to the range of brood-size manipulations (−4 to +4), manipulated brood size was the only factor correlated with number of fledglings. Thus, a female that laid four eggs was no less capable of fledging eight chicks than were females that had laid six, eight, or 10 eggs. However, females that laid large clutches fledged heavier young, regardless of what size brood they raised. Like the preceding analysis on the effect of brood-size manipulations, this analysis showed that nestling mass was much more sensitive to perturbation than were nestling survival or nestling structural growth (i.e., wing chord).

Other explanations for clutch-size limitation in House Wrens have received little support. Wrens are capable of laying supernormal clutches if eggs are removed from the nest during early laying (Kennedy and Power 1990), so the egg-formation hypothesis does not apply to wrens. Wrens are also capable of incubating experimentally-enlarged clutches (Baltz and Thompson 1988), thereby rejecting the incubation-limitation hypothesis. Wrens were not double brooded in this study, so there was little potential for intraseasonal costs of reproduction associated with raising enlarged first broods. Elsewhere, Finke et al. (1987) and Robinson and Rotenberry (1991) observed no effects of initial brood size on the propensity, timing, clutch size, or fledging success of second nesting attempts, although females that raised enlarged initial broods fledged lighter-weight nestlings in the second brood in Robinson and Rotenberry's (1991) study. Interseasonal costs of reproduction are difficult to evaluate in House Wrens due to low return rates, but Drilling and Thompson (1988) did not observe any differences in adult return rates as a function of brood-size manipulations in the preceding year.

Results obtained in this study, and those obtained by other researchers

(Finke et al. 1987, Baltz and Thompson 1988, Drilling and Thompson 1988, Robinson and Rotenberry 1991, Harper et al. 1992), do not support current hypotheses of clutch-size limitation for House Wrens. However, sample sizes have been inadequate to safely reject costs of reduced offspring recruitment or reduced adult survival that might be associated with larger broods (Graves 1991). Although House Wrens are an excellent species with which to study current and intraseasonal costs of raising enlarged broods, low return rates (Drilling and Thompson 1988) make them less suited for assessing interseasonal costs that might be associated with recruitment and survival.

ACKNOWLEDGMENTS

I was supported by an NSERC postdoctoral fellowship during field work and manuscript preparation. The Canadian Wildlife Service provided materials for nest box construction. C. R. Blem, R. G. Clark, E. D. Kennedy, and two anonymous reviewers provided helpful comments on the manuscript.

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