INTRAPOPULATION VARIATION IN HATCHING SYNCHRONY IN HOUSE WRENS: TEST OF THE INDIVIDUAL-OPTIMIZATION HYPOTHESIS

R. Given Harper,[1] Steven A. Juliano, and
Charles F. Thompson

Ecology Group, Department of Biological Sciences, Illinois State University,
Normal, Illinois 61761, USA

Abstract.—Intrapopulation variation in hatching synchrony has been documented in several avian species, although little attention has been paid to this phenomenon. We experimentally reversed some synchronously and asynchronously hatched broods to test an individual-optimization hypothesis to explain variation in hatching synchrony in a population of House Wrens (*Troglodytes aedon*) in central Illinois. Contrary to expectation, the number and quality (as measured by mass) of fledglings produced in reversed broods was the same as that for unmanipulated broods, as were recapture rates of juveniles and offspring recruitment to subsequent breeding populations. Thus, the results do not support the individual-optimization hypothesis as an explanation of intrapopulation variation in brood hatching intervals in this House Wren population. In this and other studies we have not been able to detect any advantage associated with producing either synchronous or asynchronous broods. Although other adaptive hypotheses to explain such variation remain to be tested, we suggest that variation in hatching intervals may indicate that female control of hatching pattern is imprecise and may be unrelated to fitness in this House Wren population. *Received 30 November 1992, accepted 14 March 1993.*

Variation in hatching synchrony has been reported among different species of passerines (see review by Clark and Wilson 1981; Slagsvold 1985, 1986a). In asynchronously hatched broods the youngest and oldest nestlings often differ by two to four days in age and, therefore, they also differ in size. This difference in age and size is thought to contribute to the higher mortality of the younger, smaller nestlings compared with that of their older, larger siblings (Lack 1954, 1968). Variation in hatching synchrony is presumably determined by varying the onset of full incubation (Clark and Wilson 1985, Magrath 1990, 1992), which raises the question of why parents begin incubating before the last egg is laid when doing so may lead to the death of one or more offspring.

Most of the tests of the numerous hypotheses (see Magrath 1990) that have been proposed to explain asynchronous hatching have relied either on interspecific comparisons or on experiments that created hatching synchrony in populations in which hatching is typically asynchronous (e.g. Slagsvold 1986b, Skagen 1987, Magrath 1989). Little attention has been paid to intrapopulation variation in hatching synchrony, although such variation has been documented in several species (e.g. Kendeigh 1952, Clark and Wilson 1981, Slagsvold and Lifjeld 1989a, Hebert and Sealy 1992, Harper et al. 1992, 1993).

Previous work on this population of House Wrens (*Troglodytes aedon*) in central Illinois (Harper et al. 1992, 1993) documented that there were approximately equal numbers of synchronous broods (one-day hatching spread) and asynchronous broods (two- to four-day hatching spread). The reproductive success of synchronous and asynchronous broods of the same size did not differ (Harper et al. 1992). This led us to consider the possibility that females vary the onset of incubation and, therefore, brood hatching intervals so as to maximize the number and quality of nestlings produced at each breeding attempt. We refer to this as the individual-optimization hypothesis of hatching synchrony.

An individual-optimization hypothesis proposes that an individual adjusts its behavior to match the environment in which it finds itself. Perrins and Moss (1975) first proposed an in-

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[1] Present address: Department of Biology, Illinois Wesleyan University, Bloomington, Illinois 61702, USA.

dividual-optimization hypothesis to explain variation in clutch size among individuals in the same population (see also Hogstedt 1980, Nur 1987, Pettifor et al. 1988). If female House Wrens adjust their incubation behavior and hatching synchrony to maximize reproductive success under different conditions (e.g. differences in territory or male quality), then individual females should vary hatching synchrony in their different broods, and, on average, asynchronous and synchronous broods of the same size should produce similar numbers of high-quality fledglings. Both expectations are met in the House Wren population that we studied (unpubl. data, Harper et al. 1992, respectively). The critical test, however, is to reverse hatching synchrony experimentally. If females adjust hatching synchrony to local conditions, reversed broods should have poorer reproductive success than unmanipulated broods. In this paper we present the results of an experiment comparing reproductive success (as measured by fledgling number and quality, juvenile survival, and offspring recruitment) of unmanipulated broods with that of broods in which hatching synchrony was reversed.

METHODS

The experiment was conducted from 1989–1991 on the Mackinaw (108 ha) and East Bay (20 ha) study areas in McLean County, Illinois (40°40′N, 88°53′W), where there were a total of 910 virtually identical nest boxes. The study areas consisted of a mixture of upland and floodplain deciduous forest surrounded by intensely cultivated land (see Finke et al. 1987, Drilling and Thompson 1988).

Definitions.—Broods were classified as synchronous or asynchronous based on estimated ages of nestlings as determined by mass at the time of the manipulation. Nestling mass for different age groups was: less than one day old, ≤1.4 g; one day old, 1.5–2.1 g (between dawn and 0800 Central Standard Time) and 1.5–2.2 g (0800–1100); two days old, 2.2–3.1 g (dawn–0900) and 2.3–3.1 g (0900–noon); three days old, 3.2–4.4 g; four days old, 4.5–5.8 g. These criteria were established from analyses of about 10,000 masses of known-age nestlings recorded in 1980–1982 (C. F. Thompson unpubl. data) and in 1988–1989. We are aware that misclassification of broods can occur based on methods that utilize some aspect of nestling size (see Harper et al. 1993), but even frequent visits to nests will not give exact measurements of hatching spread (Clark and Wilson 1981).

House wrens in this population are double brooded, with a modal clutch size of seven and six in the

first and second broods, respectively (Finke et al. 1987). We used only unreduced broods derived from modal clutches for experiments during both the first ("early-season") and second ("late-season") broods. Early-season nests had egg-1 dates (the date on which the first egg was laid) before the median egg-1 date of the year; late-season nests had egg-1 dates on or after the median egg-1 date of the year. Brood-day 0 is the day the first egg hatched and mass at fledging is nestling mass on brood-day 12. Fledging typically occurs between brood-days 14 and 17.

Experimental design.—Nestlings were exchanged among randomly chosen asynchronous and synchronous broods in 1989 and 1990. Those broods that originally hatched synchronously that became asynchronous after the manipulation are referred to as "reversed asynchronous" broods, and those that originally hatched asynchronously that were made synchronous are "reversed synchronous" broods. In addition to the reversed broods, we established two types of control broods to test for effects of exchanging nestlings among broods. The first was unmanipulated (referred to as "natural asynchronous" and "natural synchronous" controls). The second were broods between which nestlings were exchanged among broods, but the original brood size and degree of synchrony were maintained (referred to as "manipulated asynchronous" and "manipulated synchronous" controls).

General procedures.—All nest boxes were checked twice weekly from May to August to determine when clutches were started and their size. A clutch size was assigned when the same number of eggs was recorded on two consecutive visits to the nest. As hatching approached, nests were checked daily to determine brood-day 0. Because approximately one-half of all clutches hatched asynchronously, treatments were established on brood-day 4 after all eggs had hatched. On brood-day 4, we weighed nestlings on a portable Ohaus balance, recording their mass to the nearest 0.1 g. Nestlings were individually marked with small, expandable plastic bands (Harper and Neill 1990), and were exchanged among nests to establish the desired treatments. On brood-day 9 the plastic bands were removed and replaced with a numbered U.S. Fish and Wildlife Service aluminum band. Nestlings were last weighed on brood-day 12 (see Finke et al. 1987), and nests were visited daily after brood-day 13 to determine the date of fledging and the number of fledglings produced.

Juvenile recapture and recruitment.—We caught fledglings in mist nets in 1989 from early July to early September. The oldest juveniles that were recaptured had left the nest approximately two months prior to being mist netted. Fledgling wrens are dependent upon their parents for up to two weeks after leaving the nest (Kendeigh 1941), so we included in the analyses only those juveniles captured two or more weeks after leaving the nest. Mist nets were placed in open, old-field habitat on the periphery of the Mackinaw

TABLE 1. Linear contrasts (see text) between specific treatment combinations for the number of fledglings produced and mass at fledging.

| | | No. fledglings produced | | | | Mass at fledging | | | |
| | | Early season | | Late season | | Early season | | Late season | |
Contrast	Year	t	P	t	P	t	P	t	P
Reversed vs. control broods	1989	−0.65	0.52	−0.80	0.43	−0.29	0.77	4.59	0.0001
Reversed vs. control broods	1990	0.04	0.97	0.21	0.83	−0.06	0.95	0.66	0.51
Interaction[a]	1989	−1.22	0.23	−1.61	0.11	−1.04	0.30	4.07	0.0002
Interaction	1990	0.75	0.46	−0.60	0.56	−2.18	0.03	0.38	0.71
Manipulated vs. natural controls	1989	−0.11	0.91	0.08	0.94	−1.41	0.17	−4.15	0.0001
Manipulated vs. natural controls	1990	1.25	0.22	1.24	0.23	−0.95	0.35	0.30	0.77
Reversed asynchronous vs. reversed synchronous broods	1989	−0.30	0.77	1.05	0.30	0.59	0.56	0.15	0.88
Reversed asynchronous vs. reversed synchronous broods	1990	−1.36	0.18	0.30	0.77	0.43	0.67	−0.67	0.51

[a] Interaction is difference between reversed asynchronous and synchronous broods versus difference between control asynchronous and synchronous broods.

study area where juvenile wrens often congregated. Mist nets were opened in the mornings between 0500–1030 for a total of 1,753 net-h. Recruitment of offspring to subsequent breeding populations was determined by recapturing wrens that returned to breed on the study areas in 1990 and 1991.

Statistical analysis.—We used the Statistical Analysis System (SAS; SAS Institute 1987) for all analyses. Broods that were taken by predators were excluded from all analyses, and early- and late-season broods were analyzed separately because of significant seasonal differences in clutch size (Finke et al. 1987). One-tailed linear contrasts (Rosenthal and Rosnow 1985) were also performed on the following treatment combinations: (1) reversed versus control broods, testing the hypothesis that reversing the degree of hatching synchrony should produce fewer, lighter nestlings at the time of fledging; (2) interaction, testing the hypothesis that the difference between reversed asynchronous and synchronous broods in the number and mass of fledglings produced is less than the difference between control asynchronous and synchronous broods; (3) manipulated versus natural controls, testing the hypothesis that exchanging nestlings among broods should result in fewer, lighter fledglings in manipulated broods; (4) reversed asynchronous versus reversed synchronous broods, testing the hypothesis that fewer, lighter fledglings should be produced from reversed asynchronous and synchronous broods compared to nonreversed asynchronous and synchronous broods.

We employed the GLM procedure with the GT2 follow-up option to test for differences in the number of fledglings produced and in mass at fledging. Using the mean values for a brood eliminated problems caused by statistical nonindependence of nestlings within broods (James and McCulloch 1985). We used the TTEST procedure to compare the mass at fledging of foster (exchanged) and nonfoster (not exchanged) nestlings, and the FREQ procedure with the chi-square

option to compare survival to fledging for foster and nonfoster nestlings. Logistic regression (CATMOD procedure) was used to compare among treatments the likelihood of juvenile recapture and offspring recruitment to subsequent breeding populations. Sample sizes vary among some analyses because of observations with missing values for some variables.

RESULTS

Manipulation effects on nestlings.—Exchanging nestlings among broods did not affect their survival or mass at fledging. Foster and nonfoster nestlings survived equally well to fledging in 1989 (foster 97.7%, 86/88; nonfoster 97.0%, 518/534; $X^2 = 0.16$, df = 1, $P = 0.71$) and 1990 (foster 100%, 61/61; nonfoster 99.7%, 391/392; $X^2 = 0.29$, df = 1, $P = 0.69$). Similarly, the mean mass at fledging of foster and nonfoster nestlings also did not differ significantly in 1989 (foster $\bar{x} = 10.2$ g ± SE of 0.09 g, $n = 88$; nonfoster $\bar{x} = 10.1$ ± 0.05 g, $n = 539$; $t = -0.54$, df = 153.1, $P = 0.59$) or 1990 (foster $\bar{x} = 10.3$ ± 0.12 g, $n = 58$; nonfoster $\bar{x} = 10.4$ ± 0.04 g, $n = 388$; $t = 0.87$, df = 69.4, $P = 0.38$).

Contrasts revealed there were no significant differences in the number of fledglings in manipulated and control broods in 1989 or 1990, and in mean brood mass at fledging in the 1989 early season and in 1990 (Table 1). The mass at fledging for manipulated control broods in the late season of 1989 was significantly less than that for natural control broods, a difference that was likely due to the small sample size for manipulated synchronous broods (Fig. 1).

Number of fledglings produced.—The individual-optimization hypothesis predicts that fewer
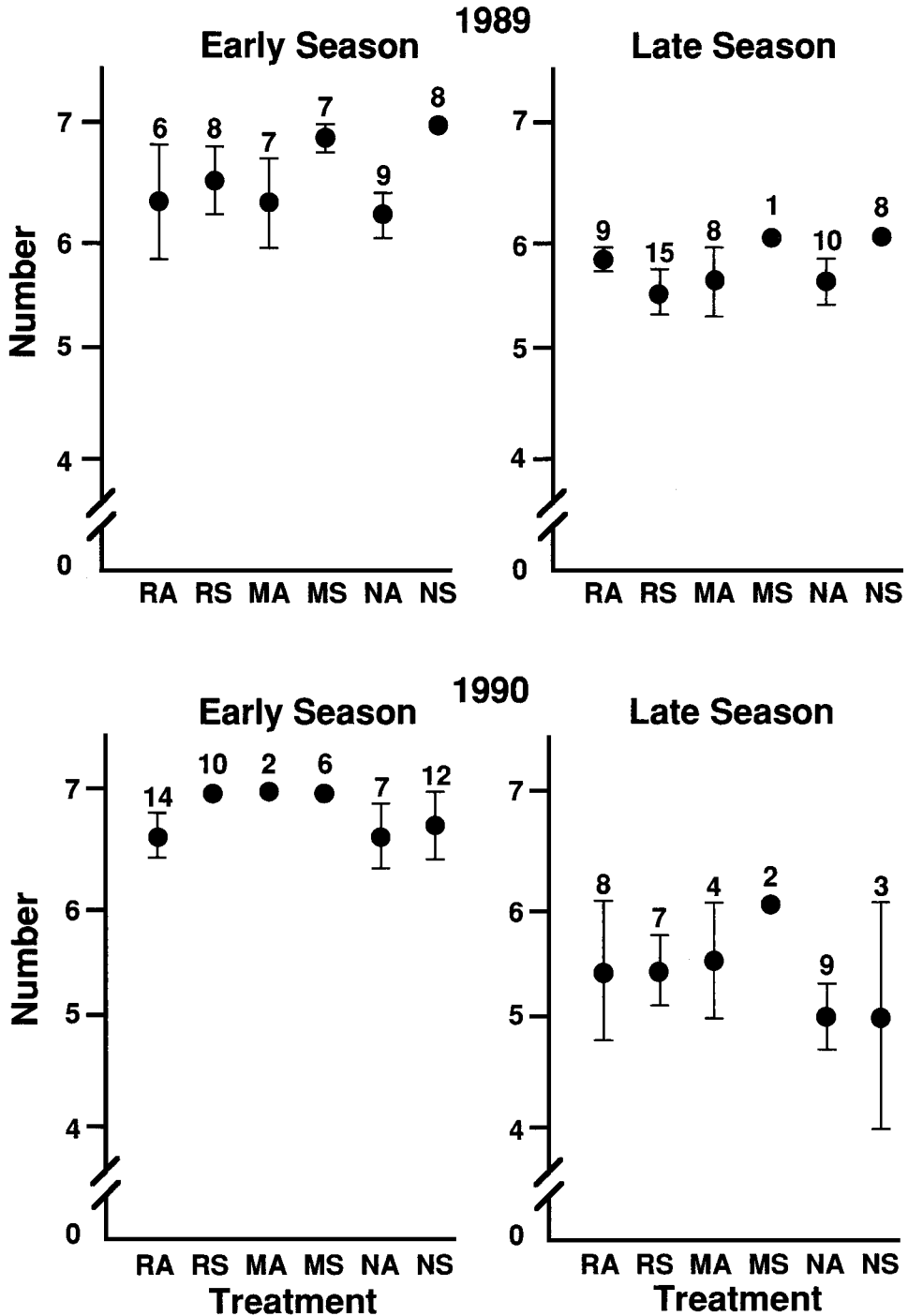
Fig. 1. Number of fledglings ($\bar{x} \pm$ SE) produced by House Wrens subjected to experimental treatments. Number of broods given above standard error bars. RA, reversed asynchronous broods; RS, reversed synchronous broods; MA, manipulated asynchronous controls; MS, manipulated synchronous controls; NA, natural asynchronous controls; NS, natural synchronous controls.

nestlings in reversed broods should survive than nestlings in nonreversed control broods. However, there were no significant differences in the number of fledglings produced among treatments in 1989 (early season $F_{5,39} = 1.60$, $P = 0.18$; late season $F_{5,45} = 0.97$, $P = 0.45$), or in 1990 (early season $F_{5,45} = 0.77$, $P = 0.57$; late season $F_{5,27} = 0.49$, $P = 0.78$; Fig. 1).

The number of fledglings produced in reversed broods and nonreversed control broods was not significantly different in either year (Table 1). Furthermore, in both years the differences between reversed asynchronous and synchronous broods were not significantly greater than the differences between control asynchronous and synchronous broods. There was also no significant difference in the number of fledglings produced between reversed asynchronous and reversed synchronous broods in either 1989 or 1990 (Table 1).

Mass at fledging.—Mass at fledging in reversed broods should be lower than that in nonreversed control broods if females adjust the degree of hatching synchrony to local conditions, but there were no significant differences in mean mass at fledging among treatments in the 1989 early season ($F_{5,40} = 1.0$, $P = 0.43$), or in both seasons of 1990 (early, $F_{5,46} = 1.51$, $P = 0.21$; late, $F_{5,27} = 0.54$, $P = 0.74$; Fig. 2). There was, however, a significant difference among treatments during the 1989 late season ($F_{5,46} = 6.27$, $P = 0.0002$). There were no significant differences in mean mass at fledging between reversed and nonreversed control broods in the early season of 1989 and 1990, but reversed broods were significantly heavier than nonreversed controls during the 1989 late season (Table 1, Fig. 2). The differences in mass between reversed asynchronous and synchronous broods were significantly less than the differences in mass between control asynchronous and synchronous broods. There was no significant difference in mean brood mass between reversed asynchronous and reversed synchronous broods in either year.

We also compared among treatments the mass of the heaviest nestlings and the difference in mass between the youngest and oldest nestlings in each brood to test for the effect that the mean mass at fledging of asynchronous and synchronous broods could be affected by the hatch spread of nestlings in asynchronous and synchronous broods. The results did not alter the conclusions based on mean brood mass. For ex-

ample, there were no significant differences in the mass of the heaviest nestlings among treatments in either 1989 (early season, $F_{5,37} = 0.75$, $P = 0.59$; late season, $F_{5,45} = 0.21$, $P = 0.96$) or in 1990 (early season, $F_{5,32} = 2.12$, $P = 0.09$; late season, $F_{5,18} = 1.45$, $P = 0.25$; other analyses not shown).

Juvenile recapture and offspring recruitment.— The individual-optimization hypothesis predicts that survival after fledging should be lower in reversed broods than in nonreversed control broods. Control broods were pooled within asynchronous and synchronous treatments to increase sample sizes for analyses of juvenile recapture and offspring recruitment. There was no significant effect of hatching synchrony and brood manipulation (i.e. reversed compared with control broods) on juvenile recapture rates, although there was a significant interaction between hatching synchrony and manipulation (Tables 2 and 3). Similarly, there were no significant differences in offspring recruited from treatments in either 1989 or 1990 (Tables 2 and 3).

DISCUSSION

The results of the experimental reversals of hatching synchrony were mostly inconsistent with the individual-optimization hypothesis. Broods in which hatching synchrony was reversed produced as many nestlings as did broods in which hatching synchrony was maintained. Similarly, in three of the four seasons, nestlings from reversed and nonreversed broods were also similar in quality at fledging, as measured by mass. The exception was in the 1989 late season, when nestlings in reversed broods, on average, were heavier than nonreversed broods. This is the opposite of that predicted by the individual-optimization hypothesis, and was likely caused by the small sample size and atypically low mass of that manipulated synchronous brood.

Fledging mass differed little among treatments and was positively correlated with post-fledging survival in this House Wren population (Thompson unpubl. data). Therefore, it is not surprising that the likelihood of recapturing juveniles from reversed broods was similar to that for juveniles from nonreversed broods. The significant interaction effect on juvenile recapture between the degree of synchrony and manipulation is probably attributable to the high proportion of juveniles recaptured from syn-
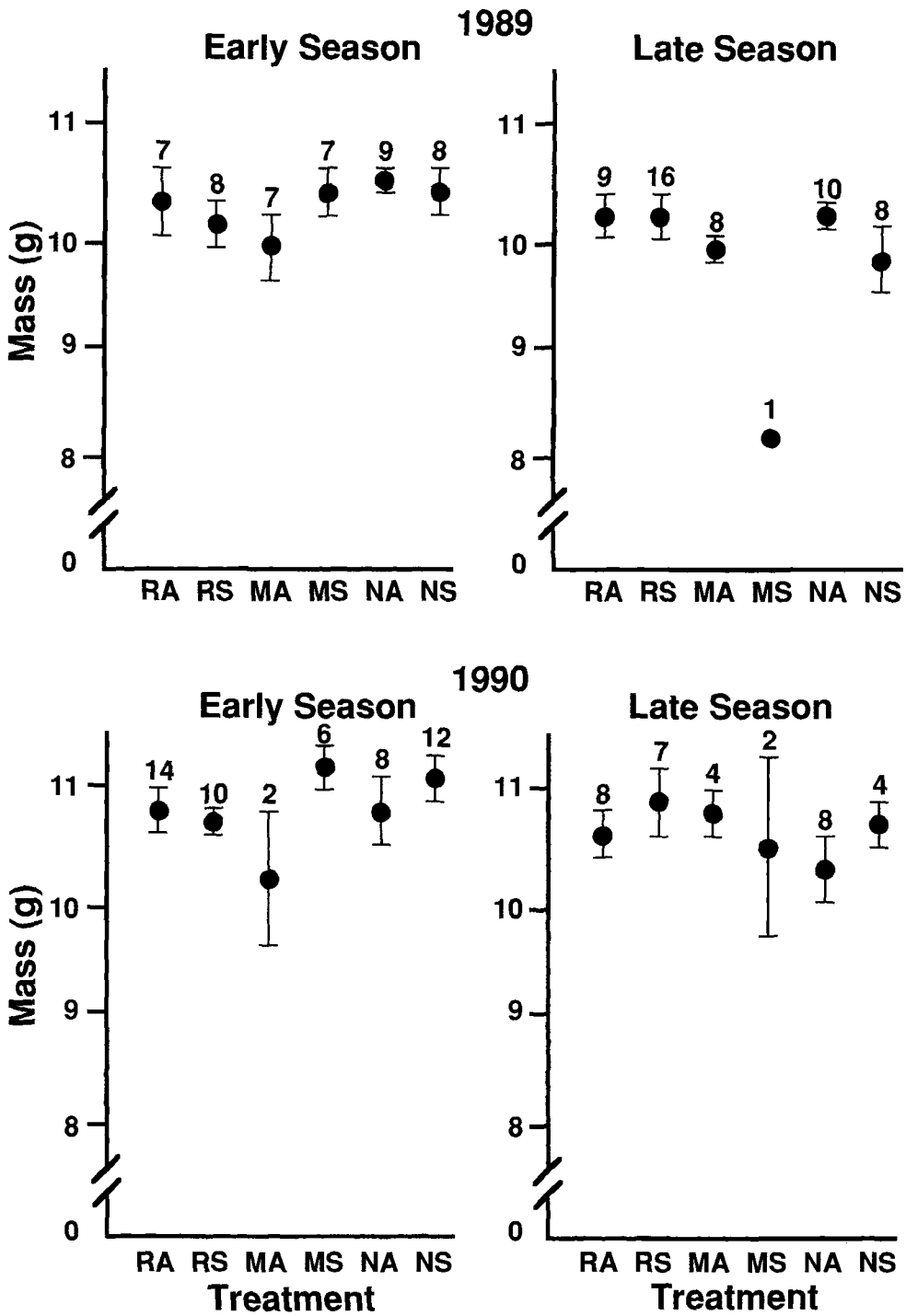
Fig. 2.   Mass at fledging ($\bar{x} \pm$ SE) of House Wren broods subjected to experimental treatments. Number of broods given above standard-error bars. Treatment abbreviations as in Figure 1.

TABLE 2. Percent ($\pm$ SE) of juveniles recaptured and offspring recruited.

Degree of synchrony[a]	Treatment[b]	Juveniles		Offspring	
		n^c	Recaptured	n^c	Recruited
			1989		
A	C	171	0.6 $\pm$ 0.58	201	2.5 $\pm$ 1.10
A	R	88	4.6 $\pm$ 2.22	90	2.2 $\pm$ 1.55
S	C	122	10.7 $\pm$ 2.79	158	4.4 $\pm$ 1.64
S	R	110	2.7 $\pm$ 1.55	135	0.7 $\pm$ 0.74
			1990		
A	C	—[d]	—	127	2.4 $\pm$ 1.35
A	R	—	—	136	3.7 $\pm$ 1.61
S	C	—	—	149	5.4 $\pm$ 1.85
S	R	—	—	108	2.8 $\pm$ 1.58

[a] A, asynchronous; S, synchronous broods.
[b] C, controls; R, reversed broods.
[c] Number of fledglings.
[d] Juveniles were recaptured only in 1989.

TABLE 3. Multiway contingency table (CATMOD) analysis of proportion of juveniles recaptured and offspring recruited.

Effect	Juvenile recapture		Offspring recruitment	
	X^2	P	X^2	P
Degree of synchrony	3.62	0.06	0.0	0.98
Brood manipulation[a]	0.24	0.62	1.63	0.20
Year	—[b]	—	1.40	0.24
Synchrony $\times$ manipulation	7.38	0.007	2.81	0.09
Synchrony $\times$ year	—	—	0.40	0.53
Manipulation $\times$ year	—	—	1.01	0.31
Manipulation $\times$ year $\times$ synchrony	—	—	0.11	0.74

[a] Brood manipulation = reversed vs. control broods.
[b] Juveniles recaptured only in 1989.

chronous control broods (see Table 2). Finally, similar proportions of offspring produced from reversed broods were recruited to subsequent breeding populations as those from nonreversed broods.

Although the individual-optimization hypothesis does not seem to explain the intrapopulation variation in hatching synchrony in this House Wren population, we think such hypotheses may have wide applicability as explanations for intrapopulation variation in life-history traits and, therefore, deserve serious attention (e.g. Perrins and Moss 1975, Slagsvold 1986b). For example, the results of some studies of clutch-size variation are consistent with an individual-optimization hypothesis because individuals, regardless of their clutch size, are not as successful at raising experimentally enlarged broods as they are at raising broods equal in size to that of the clutch they laid (e.g. Perrins and Moss 1975, Hogstedt 1980, Pettifor et al. 1988). Thus, individuals are doing the best they can under the conditions in which they find themselves. If conditions change, then clutch size will be adjusted accordingly. Studies of other demographic and behavioral traits that vary among individuals inhabiting heterogeneous environments are likely to reveal additional examples of individual optimization as a cause of interindividual variation.

Detection of individual adjustments to local conditions requires the use of experimental manipulations of the trait under study, even if correlations are established between the trait

and environmental conditions. Experiments are needed because the payoffs to unmanipulated individuals adopting the different values for the trait can be equal, as we have found for hatching synchrony in this House Wren population, or unequal, as is the case for clutch size where females that find themselves in poor habitat make the best of a bad situation (see Nur 1987). Thus, documentation of equal or unequal payoffs in and of itself does not provide a test of the hypothesis of individual optimization; only by manipulating the value of the trait can the costs associated with other possible values be detected.

Two different studies over a period of four years (Harper et al. 1992, this study) have failed to find evidence that there was differential success among individual House Wrens with different hatching synchronies within this population. There are, of course, many adaptive hypotheses (e.g. see Clark and Wilson 1981, Slagsvold and Lifjeld 1989b, Magrath 1990) that we have not as yet tested. However, if any of these explanations are valid, we would expect to find evidence, at least in some years or under some conditions, that there are detectable costs associated with producing synchronous or asynchronous broods; this has not been the case (Harper et al. 1992, this study). This leads us to suggest that variation in hatching synchrony may indeed have no fitness consequences in this population of House Wrens, and that this variation may be nonadaptive. Such an explanation has been proposed by Mead and Morton (1985) and by Stouffer and Power (1990) in their studies of White-crowned Sparrows (*Zonotrichia*

leucophrys oriantha) and European Starlings (*Sturnus vulgaris*), respectively.

An assumption underlying all adaptive hypotheses proposed to explain asynchronous hatching is that parents can control variation in hatching synchrony, primarily through incubation behavior (Magrath 1990). However, the presumption that the timing of the hatch is largely determined by the onset of fully effective and steady incubation has not been fully substantiated (e.g. Kendeigh 1952, Drent 1975, Hebert and Sealy 1992, Magrath 1992). Hebert and Sealy (1992) and Magrath (1992) have inferred some parental control of hatching spread in Yellow Warblers (*Dendroica petechia*) and Blackbirds (*Turdus merula*), respectively, but the precision of parental control of the degree of hatching synchrony in the House Wren has received no experimental scrutiny. Successive broods of female House Wrens do vary in hatching synchrony within the same year (Harper unpubl. data), but the incubation patterns associated with such variation are as yet unknown. If female House Wrens cannot control hatching synchrony of their broods through incubation behavior, then variation in hatching synchrony may be nonadaptive in this population. This assumption should be tested in the House Wren, as well as in other species.

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