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Source: *The American Naturalist*, Vol. 177, No. 5 (May 2011), pp. 617-629

Published by: [The University of Chicago Press](#) for [The American Society of Naturalists](#)

Stable URL: <http://www.jstor.org/stable/10.1086/659630>

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# Adaptive Sex Allocation in Relation to Hatching Synchrony and Offspring Quality in House Wrens

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Submitted September 10, 2010; Accepted January 31, 2011; Electronically published April 6, 2011

Dryad data: <http://dx.doi.org/10.5061/dryad.8484>.

**ABSTRACT:** Increased variance in the reproductive success of males relative to females favors mothers that optimally allocate sons and daughters to maximize their fitness return. In altricial songbirds, one influence on the fitness prospects of offspring arises through the order in which nestlings hatch from their eggs, which affects individual mass and size before nest leaving. In house wrens (*Troglodytes aedon*), the influence of hatching order depends on the degree of hatching synchrony, with greater variation in nestling mass and size within broods hatching asynchronously than in those hatching synchronously. Early-hatching nestlings in asynchronous broods were heavier and larger than their later-hatching siblings and nestlings in synchronous broods. The effect of hatching order was also sex specific, as the mass of males in asynchronous broods was more strongly influenced by hatching order than the mass of females, with increased variation in the mass of males relative to that of females. As predicted, mothers hatching their eggs asynchronously biased first-laid, first-hatching eggs toward sons and late-laid, late-hatching eggs toward daughters, whereas females hatching their eggs synchronously distributed the sexes randomly among the eggs of their clutch. We conclude that females allocate the sex of their offspring among the eggs of their clutch in a manner that maximizes their own fitness.

**Keywords:** sex allocation, sex ratio, hatching asynchrony, sibling competition, maternal effects, *Troglodytes aedon*, Trivers-Willard hypothesis.

Variation in individual quality generally affects the fitness of males and females differently, increasing variability in the reproductive success of males relative to that of females (Trivers and Willard 1973; Clutton-Brock et al. 1984; Møller and Ninni 1998; Rose et al. 1998). When high-quality males outreproduce low-quality males and when female reproductive success is less variable and falls between that of high- and low-quality males, maternal condition and capacity to invest in offspring should influence their relative investment in sons and daughters (Trivers and Willard 1973). When females are able to produce high-

quality offspring, they should preferentially invest in sons to produce males of high reproductive potential; when unable to produce high-quality offspring, however, females should produce daughters and avoid investing in low-quality sons of low reproductive potential. The later realization that factors aside from parental investment also generate sex-specific effects on offspring fitness has extended the original Trivers-Willard hypothesis to provide a more comprehensive framework by which to predict patterns of conditional sex allocation (Williams 1979; Leimar 1996; Carranza 2004; see also Cockburn et al. 2002 and West 2009 for review). A key insight has been the recognition that sex allocation will typically occur only in response to strong, predictable social and environmental stimuli that influence the fitness prospects of individual offspring (Clark 1978; Silk 1983; Komdeur 1996; Leimar 1996; Komdeur et al. 1997; West and Sheldon 2002).

Such a situation occurs in birds when predictable variation in the hatching span of the eggs within a clutch creates a size hierarchy among nestlings. For example, asynchronous hatching (>24 h between hatching of the first and last eggs of a clutch) is common among altricial birds (Clark and Wilson 1981; Ricklefs 1993; Stoleson and Beissinger 1995), causing nestlings to vary considerably in size shortly after hatching, with early-hatching nestlings nearly twice the mass and size of their youngest nestmates (Clotfelter et al. 2000; Lago et al. 2000). The initial hierarchy in mass and size among nestlings is often maintained throughout their development as a result of competitive asymmetry, with earlier-hatching, slightly older nestlings leaving the nest substantially heavier and larger than their later-hatching nestmates (Slagsvold 1986; Clotfelter et al. 2000; Lago et al. 2000; Badyaev et al. 2003a; Maddox and Weatherhead 2008). Because of the initial competitive advantage enjoyed by early-hatching nestlings in asynchronous broods, they also leave the nest heavier and larger than the mostly average-sized nestlings in broods with experimentally synchronized hatching, for which within-brood variation in mass and size has been

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minimized (Slagsvold 1986; Maddox and Weatherhead 2008).

In most species, nestling mass and size at the time of nest leaving have important fitness-related consequences because they correlate positively with survival and recruitment as a breeder (Alatalo and Lundberg 1986; Tinbergen and Boerlijst 1990; Hochachka and Smith 1991; Young 1996; Both et al. 1999). Thus, because the degree of hatching synchrony is largely determined by the time at which females begin incubating their eggs (Wiebe et al. 1998; Badyaev et al. 2003a; Ardia et al. 2006; Kontiainen et al. 2010), females that begin incubation before clutch completion can hatch their eggs asynchronously to bias investment toward a select portion of their offspring. For example, Jeon (2008) has shown that among offspring of different ages, parents should bias investment toward older offspring with higher fitness potential than their younger siblings, as is the case with asynchronous hatching. Alternatively, by delaying the onset of incubation until the end of egg laying, females can produce a synchronously hatching brood in which each offspring has similar prospects for survival and future reproduction, favoring a more equal distribution of investment among offspring (Jeon 2008).

In addition to affecting survival, natal environmental conditions often have a greater influence on the future reproductive success of males than females in species where males are larger than females (Kruuk et al. 1999; Wilkin and Sheldon 2009). In such cases, preferential investment will often benefit the fitness of sons to a greater extent than that of daughters, although sons may suffer greater costs than daughters under adverse conditions (Trivers and Willard 1973; fig. 1 in Sheldon 1998). Thus, the size hierarchy imposed by asynchronous hatching has often been associated with sex bias along the egg-laying sequence of the clutch in sexually size-dimorphic species, with the larger sex allocated to earlier-laid eggs of the clutch and the smaller sex allocated to later-laid eggs (Bortolotti 1986; Slagsvold 1990; Arnold and Griffiths 2003; Badyaev et al. 2003a; Ležalová et al. 2005). In fact, Carranza (2004) recently modeled how the predictable allocation of food resources among nestlings in relation to the size hierarchy imposed by the egg-laying and hatching order should direct the placement of the sexes within the clutch of a sexually dimorphic species. He predicted that a bias would occur toward the larger sex—typically males—among earlier-laid eggs and toward females among later-laid eggs but that such a pattern would be unlikely when males and females were similar in size.

There is evidence, however, of sex-biased allocation in clutches of size-monomorphic species (Ellegren et al. 1996; Albrecht 2000; Addison et al. 2008), suggesting that even when sons and daughters impose similar energetic costs

to produce, they may deliver different fitness returns depending on their environment. In house wrens (*Troglodytes aedon*), a sexually size-monomorphic species (Johnson 1998; Albrecht and Johnson 2002; Janota et al. 2002), differences in individual quality may profoundly affect the fitness of males because intrasexual competition for nest sites is intense (Kendeigh 1941; Belles-Isles and Picman 1987; Johnson and Kermott 1990) and larger or older high-quality males gain better breeding territories (DeMory et al. 2010). Such males may fertilize more of their mates' eggs (Dubois et al. 2006), attract secondary females (Johnson and Kermott 1991), and obtain extra-pair fertilizations (Soukup and Thompson 1998), all of which should substantially increase their reproductive success relative to that of smaller, lower-quality males. Thus, with a socially and genetically polygamous mating system, the fitness return from sons and daughters may vary unequally across an investment or environmental gradient, selecting for females that optimally allocate the sexes of their offspring among the eggs of their clutch. House wrens also exhibit natural variation in hatching span, with both synchronous and asynchronous hatching occurring naturally within the same population (Pennock 1990; Harper et al. 1992, 1994). Thus, females that hatch their eggs synchronously and those that hatch their eggs asynchronously might be expected to display different sex allocation strategies within their clutches.

Here we present the results of a study investigating (1) how the degree of hatching synchrony affects within-brood variation in mass and size among house wren progeny and (2) whether females that hatch their eggs synchronously and those that hatch them asynchronously allocate the sexes among the eggs of their clutches to maximize the fitness potential of their individual offspring. We predicted that early-hatching eggs would be more likely to contain males than females and that later-hatching eggs would be more likely to contain females than males within asynchronous broods (Carranza 2004), whereas we predicted that the sexes would be randomly distributed with respect to the egg-laying and hatching order within synchronous broods.

## Methods

### *Study Area and Species*

This study was conducted during the 2009 breeding season in the 130-ha Mackinaw study area, a tract of secondary deciduous forest bordering the Mackinaw River in McLean County, Illinois (40°40'N, 88°53'W). This site has 700 nest boxes spaced 30 m apart along north-south-oriented transects separated by 60 m (5.4 nest boxes/ha). The boxes are placed on 1.5-m poles and rest atop 48.3-cm-diameter

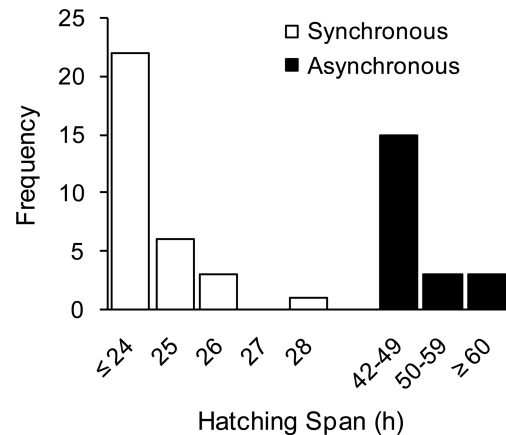
aluminum predator baffles (see Lambrechts et al. 2010 for details on the nest box design).

Male house wrens arrive from migration in late April, select and defend a nest box, and erect a stick base for their nest. Females return slightly later, select a mate, and line the nest with grasses before laying one egg per day until their clutch of four to eight eggs is completed. No female skipped a day during egg laying in this study. Females alone incubate the eggs and brood hatchlings, but both parents provision the young. Nest leaving typically occurs 15–17 days after the first egg hatches; the largest nestlings are the first to leave, and the rest of the brood follows within a few hours (Johnson et al. 2004). Johnson (1998) provides additional details on house wren biology.

We classified broods as synchronous if hatching was completed within ~24 h and asynchronous if hatching took two or more days to complete (Ellis et al. 2001*b*). We visited nests multiple times each day until hatching was complete; thus, we were able to estimate closely the span of time that elapsed between hatching of the first and last eggs, which showed a bimodal distribution (fig. 1) that confirmed the dichotomy used to classify broods as hatching synchronously or asynchronously. The proportion of synchronous and asynchronous broods varies among years (from 46% to 76% synchronous; Harper et al. 1992, 1993; Ellis et al. 2001*a*), with 60% hatching synchronously and 40% hatching asynchronously in this study. The environmental factors influencing variation in hatching span in house wrens are not fully understood, although the availability of food for provisioning nestlings is likely involved (see “Discussion”).

#### General Procedures

We checked nest boxes at least twice weekly for evidence of female settlement and then visited nests daily, numbering eggs as laid using nontoxic permanent markers. As hatching approached, we visited nests three to five times each day until hatching was complete to determine hatching order, uniquely marking each nestling’s tarsus with nontoxic colored markers. Four days after hatching began (brood day 4) and after all viable eggs had hatched, we weighed nestlings to the nearest 0.1 g using an electronic balance (Acculab Pocket Pro 250 or PP-201) and permanently marked them by clipping their toenails in a unique pattern. One week later (brood day 11), we weighed nestlings, measured their right tarsus to the nearest 0.1 mm using dial calipers, and took a blood sample (~50  $\mu$ L) from the brachial vein for sexing. Blood samples were collected in heparinized microhematocrit capillary tubes, kept on ice in the field, and, on return to the laboratory later the same day, transferred to Queen’s lysis buffer (Seutin et al. 1991) and stored at 4°C for later DNA



**Figure 1:** Distribution of broods in relation to hatching span (i.e., the number of hours elapsed between the hatching of the first and last eggs of a clutch). There was one synchronously hatching clutch of eight eggs that took ~28 h for hatching to complete.

extraction and sexing. Occasionally, nests would be abandoned or eggs did not hatch, so we collected dead nestlings and unhatched eggs and froze them at  $-20^{\circ}\text{C}$  until extracting DNA from their tissues. We extracted DNA using a high-salt method and sexed nestlings using polymerase chain reaction (PCR) and the sexing primers described by Kahn et al. (1998). PCR products were separated on 1.8% agarose gels and stained with ethidium bromide. We included control samples from known-sex adults in all PCR sets and electrophoresed them alongside nestling DNA.

#### Data Analysis

We obtained blood samples from 197 nestlings and tissue samples from 27 dead nestlings and two embryos from unhatched eggs, for a total of 226 offspring (table 1) from 47 broods (27 synchronous and 20 asynchronous); each brood was produced by a different female. Clutch sizes varied from four to eight eggs (11 clutches of four and five eggs each, 19 clutches of six eggs, four clutches of seven eggs, and two clutches of eight eggs); thus, to include clutches and broods of varying size in this analysis, we categorized egg-laying and hatching positions as “first,” “early,” “middle,” “late,” and “last” (Ellis et al. 2001*b*). Because an individual’s mass and size may be influenced, in part, by their older or younger siblings within the brood, we modeled the egg-laying and hatching order as a repeated measure. We used SAS statistical software (ver. 9.2; SAS Institute) for all analyses.

We first analyzed mass and size (i.e., tarsus length) variation among offspring within synchronous and asynchronous broods on brood day 11 using mixed-model

**Table 1:** Offspring sex in relation to egg-laying and hatching position in synchronous and asynchronous broods

Brood	Position				
	First	Early	Middle	Late	Last
Synchronous:					
Males (no.)	9	10	11	14	12
Females (no.)	16	17	12	12	13
Proportion male (LS mean $\pm$ SE)	.36 $\pm$ .09	.38 $\pm$ .09	.47 $\pm$ .10	.55 $\pm$ .10	.48 $\pm$ .10
Asynchronous:					
Males (no.)	13	11	16	6	6
Females (no.)	5	8	9	15	11
Proportion male (LS mean $\pm$ SE)	.72 $\pm$ .10	.58 $\pm$ .11	.63 $\pm$ .09	.28 $\pm$ .10	.35 $\pm$ .11

Note: LS = least squares.

ANOVA (PROC MIXED). The final model included the fixed effects of hatching order and degree of hatching synchrony, with brood identity as a random effect. We initially included hatching date (brood day 0) as a fixed effect along with all possible interactions. However, all interaction terms involving hatching date were not significant (all  $P > .2$ ) and were iteratively removed from the model. After stepwise removal of all nonsignificant interaction terms, the fixed effect of brood day 0 (indicating time of season) remained not significant ( $P > .4$ ) and was removed. As a follow-up test, we used the “slice” option in PROC MIXED (which uses ANOVA as opposed to pairwise  $t$ -tests) to compare nestlings within similar hatching positions in synchronous and asynchronous broods.

We then analyzed nestling mass shortly after hatching on brood day 4 using mixed-model ANOVA with sex, hatching order, and the degree of hatching synchrony (i.e., synchronous or asynchronous) as fixed effects and brood as a random effect. Our initial model included a three-way interaction between sex, hatching order, and hatching synchrony, but the effect was not significant ( $P > .5$ ) and was removed. We again used the slice option as a follow-up test, comparing the mass of male and female nestlings in similar hatching positions. We then analyzed nestling mass and tarsus length before nest leaving on brood day 11 and also tested for sex-specific growth (from brood day 4 to 11) within synchronous and asynchronous broods using a similar approach.

We analyzed nestling sex by means of a generalized linear mixed model (PROC GLIMMIX) with egg position and degree of hatching synchrony as fixed effects and brood identity as a random effect, using a binomial error structure and logit link function. This allowed us to analyze patterns along the egg-laying sequence among broods while accounting for nonindependence of offspring within broods and for the binomial error variance of the response variable (i.e., “female” or “male”; Krackow and Tkadlec 2001). For post hoc comparisons, we used the slice option in PROC GLIMMIX to compare sex ratios of nestlings in

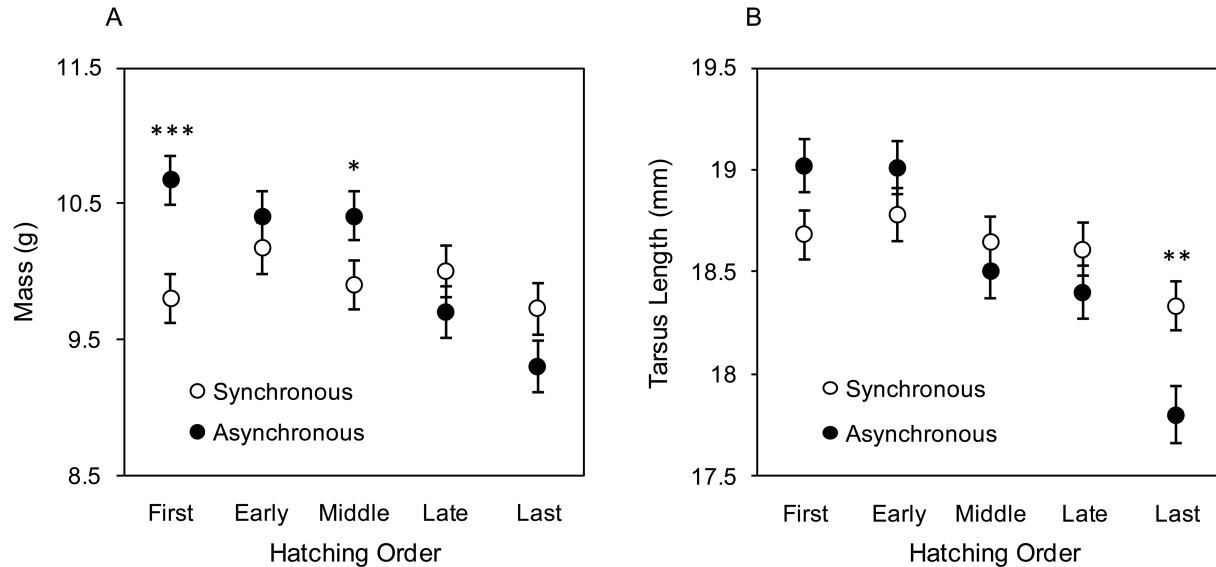
similar egg positions between synchronous and asynchronous broods. We also analyzed the probability that offspring sex along the egg-laying sequence differed from a 1 : 1 ratio using a binomial test (Wilson and Hardy 2002) with the FREQ procedure.

Although a previous study of this population found no difference in the condition of females that hatch their eggs synchronously and those that hatch them asynchronously (Ellis et al. 2001a), we reevaluated this with our data set using a two-sample  $t$ -test (PROC TTEST) to determine whether females that hatch their eggs synchronously and those that hatch them asynchronously differed in body condition (the residual of a mass  $\times$  tarsus linear regression). Finally, we used two-sample  $t$ -tests to determine whether the clutch size and the number of nestlings that survived to nest leaving differed between females that hatch their eggs synchronously and those that hatch them asynchronously and a generalized linear mixed model (as described above) to determine the probability that a hatchling would survive to leave the nest in synchronous and asynchronous broods. This analysis included only broods that were not depredated or abandoned by their parents, totaling 41 broods (22 synchronous and 19 asynchronous).

## Results

### *Nestling Mass and Size Variation within Synchronous and Asynchronous Broods*

There was an interaction between hatching synchrony and hatching order in their effect on nestling mass on brood day 11 ( $F_{4,152} = 6.95$ ,  $P < .0001$ ), as nestling mass declined with hatching order in asynchronous broods (post hoc slice,  $F_{4,152} = 13.38$ ,  $P < .0001$ ) but not in synchronous broods ( $F_{4,153} = 1.52$ ,  $P = .2$ ; fig. 2A). The initial hierarchy imposed by hatching asynchrony produced first-hatching asynchronous nestlings that not only weighed more than their younger nestmates on brood day 11 but also weighed more than first-hatching nestlings of the same



**Figure 2:** Nestling mass (A) and tarsus length (B) on brood day 11 (LS mean  $\pm$  SE) in relation to hatching order in synchronous and asynchronous broods. Asterisks above data points represent statistically significant differences between nestlings within synchronous and asynchronous broods (one asterisk indicates  $P \leq .05$ , two asterisks indicate  $P \leq .01$ , and three asterisks indicate  $P \leq .001$ ; see text).

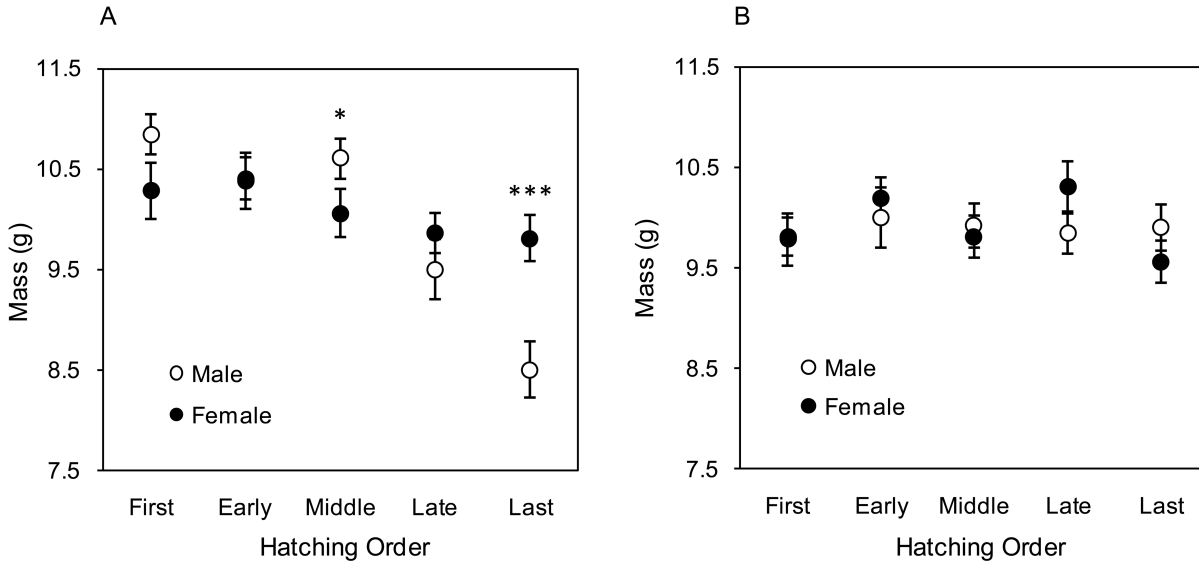
age in synchronous broods ( $F_{1,111} = 11.57$ ,  $P = .0009$ ; fig. 2A). Parallel to the effect on nestling mass, there was also an interaction between hatching synchrony and hatching order in their effect on tarsus length ( $F_{4,149} = 6.36$ ,  $P < .0001$ ; fig. 2B). First-hatching asynchronous nestlings tended to have slightly longer tarsi, on average, than similarly aged nestlings in synchronous broods ( $F_{1,88.4} = 3.18$ ,  $P = .0778$ ), whereas last-hatching asynchronous nestlings had shorter tarsi than those in synchronous broods ( $F_{1,97.6} = 7.10$ ,  $P = .009$ ). There was detectable variation among broods in nestling mass (Wald  $Z = 3.36$ ,  $P = .0008$ ) and tarsus length (Wald  $Z = 3.51$ ,  $P = .0004$ ).

#### *Sex-Specific Effects of Hatching Order on Nestling Mass, Size, and Growth*

A sex-specific effect of hatching order on nestling mass was apparent early in nestling development on brood day 4 (sex  $\times$  hatching order:  $F_{4,151} = 3.21$ ,  $P = .0145$ ). Although the mass of first-hatching males and females did not differ ( $F_{1,154} = 0.23$ ,  $P = .63$ ), last-hatching males were lighter than last-hatching females ( $F_{1,154} = 4.87$ ,  $P = .0288$ ). On brood day 11, there was a three-way interaction among sex, hatching order, and degree of hatching synchrony in their effect on nestling mass ( $F_{4,158} = 4.30$ ,  $P = .0025$ ). Post hoc tests revealed a strong interaction between sex and hatching order within broods

hatching asynchronously ( $F_{4,156} = 5.44$ ,  $P = .0004$ ) but not synchronously ( $F_{4,159} = 1.16$ ,  $P = .33$ ), showing that a sex-specific effect of hatching order had persisted within asynchronous broods (fig. 3). First-hatching males in asynchronous broods were heavier than similarly aged males in synchronous broods ( $F_{1,162} = 9.86$ ,  $P = .002$ ) and tended to be heavier than first-hatching asynchronous females ( $F_{1,161} = 2.88$ ,  $P = .0916$ ; fig. 3A), whereas last-hatching asynchronous males were lighter than similarly aged females ( $F_{1,160} = 14.32$ ,  $P = .0002$ ; fig. 3A). Female mass, however, was similar across hatching positions in both synchronous and asynchronous broods (all  $P \geq .15$ ). There was no sex-specific effect of hatching order on nestling tarsus length ( $F_{4,156} = 0.36$ ,  $P = .84$ ) and no difference in tarsus length between males and females ( $F_{1,145} = 1.05$ ,  $P = .31$ ).

We investigated growth rates by analyzing the mass gained from brood day 4 to 11. There was a three-way interaction among sex, hatching order, and hatching synchrony in their effect on nestling growth ( $F_{4,139} = 4.18$ ,  $P = .0031$ ). Despite being similar in mass on brood day 4, first-hatching males in asynchronous broods gained more mass than first-hatching females ( $F_{1,142} = 4.91$ ,  $P = .0282$ ; fig. 4A) and first-hatching males in synchronous broods ( $F_{1,119} = 6.86$ ,  $P = .010$ ). However, females hatching last in asynchronous broods gained more mass than similarly aged males ( $F_{1,142} = 5.59$ ,  $P = .0195$ ), allowing them to achieve a mass similar to that of their older



**Figure 3:** Nestling mass (LS mean  $\pm$  SE) on brood day 11 in relation to hatching order and sex in (A) asynchronous and (B) synchronous broods. There was a sex-specific effect of hatching order in asynchronous broods: mass declined along the hatching sequence, but to a greater extent for males than females. Asterisks above data points represent statistically significant differences between the sexes within broods (one asterisk indicates  $P \leq .05$ , and three asterisks indicate  $P \leq .001$ ; see text).

siblings. Within synchronous broods, growth rates tended to increase along the hatching sequence, but males hatching last gained more mass than similarly aged females ( $F_{1,140} = 5.75$ ,  $P = .019$ ; fig. 4B), overcoming their initial size disadvantage.

#### *Sex Allocation in Relation to Degree of Hatching Synchrony*

There was an interaction between position in the egg-laying sequence and degree of hatching synchrony on nestling sex ( $F_{4,216} = 2.86$ ,  $P = .0244$ ; fig. 5). Within asynchronous broods, first-laid eggs were more likely to be male than female (binomial test,  $Z = 1.89$ ,  $P = .0297$ ) and were more likely to be male than those in synchronous broods ( $F_{1,216} = 5.46$ ,  $P = .0203$ ); the production of sons declined among subsequent eggs ( $F_{4,216} = 2.65$ ,  $P = .0341$ ), as late-laid eggs were more likely to be female than male ( $Z = 1.96$ ,  $P = .0248$ ; table 1) and tended to be more likely female than those in synchronous broods ( $F_{1,216} = 3.45$ ,  $P = .064$ ). Within synchronous broods, however, there was no effect of egg position on offspring sex ( $F_{4,216} = 0.63$ ,  $P = .64$ ), and there were no deviations from a 1:1 sex ratio along the egg-laying sequence (all  $P \geq .16$ ). The mean sex ratio of synchronous and asynchronous broods did not differ (proportion males  $\pm$  SE:  $0.45 \pm 0.04$  for synchronous and  $0.51 \pm 0.05$  for asynchronous;  $F_{1,55.5} = 1.21$ ,  $P = .28$ ). The sex-biased egg-

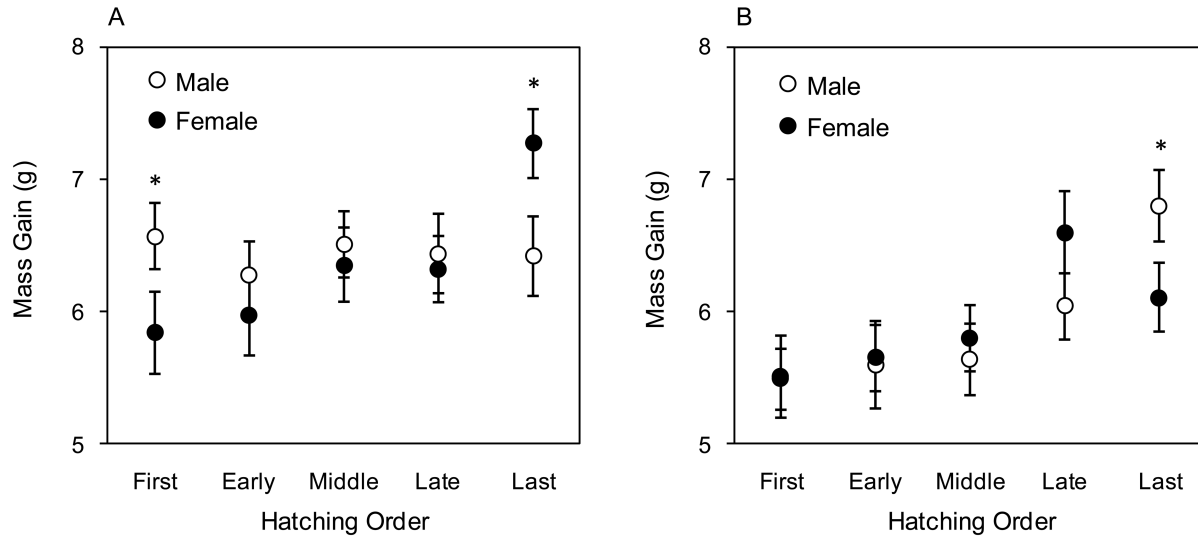
laying and hatching order within asynchronous broods was not attributable to sex-specific nestling mortality. There were 13 hatchlings that we could not sex because they disappeared from the nest before blood sampling, but there was no association between this mortality and degree of hatching synchrony or position in the hatching sequence (table 2).

#### *Female Condition and Brood-Level Productivity*

Females hatching their eggs synchronously and asynchronously did not differ in body condition ( $t_{37} = 0.04$ ,  $P = .97$ ) or clutch size ( $5.3 \pm 0.2$  vs.  $5.7 \pm 0.2$  eggs, respectively;  $t_{51} = 1.24$ ,  $P = .22$ ). Synchronous and asynchronous broods also did not differ in the number of fledglings produced ( $t_{39} = 0.62$ ,  $P = .54$ ) or in the probability that a hatchling would survive to leave the nest ( $F_{1,65.3} = 0.61$ ,  $P = .44$ ). Overall, nestling mortality was low ( $\sim 6\%$ ) and was unrelated to hatching pattern (table 2).

#### **Discussion**

Our results provide strong empirical support for the theoretical model described by Carranza (2004), which holds that it is the predictable allocation of resources within broods that determines the placement of the sexes in the egg-laying and hatching order. Within asynchronous

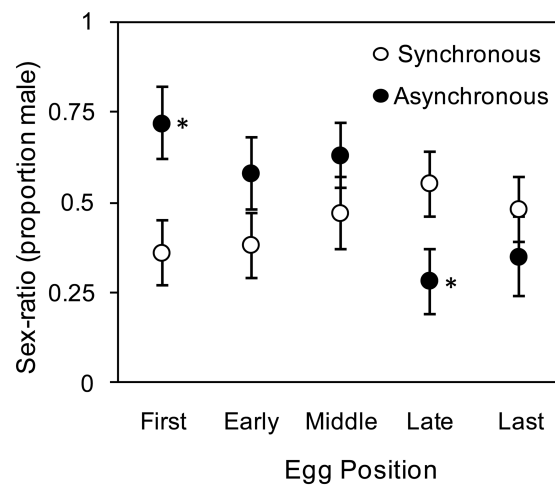


**Figure 4:** Mass gained (LS mean  $\pm$  SE) from brood day 4 to 11 in relation to sex and hatching order in (A) asynchronous and (B) synchronous broods. In asynchronous broods, male nestlings gained mass at a similar rate; however, last-hatching females grew faster than last-hatching males. Conversely, last-hatching males gained mass faster than last-hatching females in synchronous broods, despite being significantly lighter on brood day 4. Asterisks above data points represent statistically significant differences between the sexes within broods ( $P \leq .05$ ; see text).

broods, first-hatching nestlings—which are the heaviest and largest at the population level and, thus, most likely to survive and reproduce (Both et al. 1999)—are more likely to be male than female, whereas later-hatching nestlings are more likely to be female than male. Within synchronous broods, however, where nestlings are of similar, average mass and size, the sexes are distributed randomly with respect to egg-laying and hatching. Our finding of a sex-biased hatching order in asynchronous broods is also consistent with the results of previous studies of sexually dimorphic species (Badyaev et al. 2002, 2003a, 2003b; Arnold and Griffiths 2003; Ležalová et al. 2005). However, house wrens are sexually size monomorphic at the population level, but the mass of individual males is influenced by hatching order to a much greater extent than that of females, increasing the variability in the prospect for survival and future reproduction of male offspring relative to female offspring. A previous study of house wrens (Albrecht 2000) reported that last-laid, last-hatching nestlings were more likely to be female than male in a population in which all clutches hatch asynchronously, but a follow-up study of that same population found no such pattern (Johnson et al. 2005). We also found no sex bias among last-laid, last-hatching eggs in asynchronous clutches, consistent with the prediction of Carranza (2004) that sex bias should be negligible among last-hatching offspring because of their small size and low survival prospects.

Several lines of evidence suggest that the sex-biased in-

vestment by house wrens in sons and daughters that we report here comes about mainly through their placement in the egg-laying and hatching order rather than through biased provisioning of eggs or nestlings. First, the initial hierarchy in size imposed by hatching asynchrony is usually the strongest determinant of nestling mass and size



**Figure 5:** Nestling sex in relation to egg position (proportion of male offspring; LS mean  $\pm$  SE) in synchronous and asynchronous broods. Asterisks beside data points represent significant differences from a 1 : 1 (0.5) distribution ( $P \leq .05$ ; see text).



**Table 2:** Nestling deaths before brood day 11 in relation to hatching order in nondepredated, nonabandoned broods hatching synchronously and those hatching asynchronously

Brood	Hatching order					Total
	First	Early	Middle	Late	Last	
Synchronous	0	3	1	0	1	5
Asynchronous	0	2	2	1	3	8

before nest leaving (Clotfelter et al. 2000; Johnson et al. 2005; Maddox and Weatherhead 2008). Second, any variation in initial mass among nestlings that is attributable to differences in egg size disappears before nest leaving (Magrath 1992; Williams 1994; Styrsky et al. 1999; Christians 2002), and egg-mass variation along the laying sequence does not differ between synchronously and asynchronously hatching clutches (E. K. Bowers, unpublished data). In addition, androgens are not differentially allocated to eggs in relation to laying position or degree of hatching synchrony (Ellis et al. 2001*b*). Finally, while we did not test for sex-biased nestling provisioning, previous studies of house wrens (Albrecht and Johnson 2002) and other species (Lessells et al. 1998; Lessells 2002) have not found a sex bias in feeding, and the mean mass and structural size of male and female nestlings in our study did not differ, consistent with findings of previous work in our population (Janota et al. 2002).

It must be acknowledged that the patterns of sex allocation revealed in our study derive from a single breeding season; thus, we advise caution in generalizing our results to other populations and contexts, particularly given the extent to which plasticity in life-history traits are known to be influenced by environmental variation (Ricklefs and Wikelski 2002; Nussey et al. 2007). For example, previous studies of this population showed that house wren clutch sizes decline over the course of the breeding season, presumably in response to variation in food supply (Finke et al. 1987; Styrsky et al. 1999). This was also the case among the broods we studied (data not shown); however, within-brood patterns of variation did not change over the course of the breeding season, and patterns of brood-level productivity for synchronous and asynchronous broods were similar to those observed in other studies of this population over a span of 2 decades (Harper et al. 1992, 1994; Ellis et al. 2001*a*). Thus, the patterns of sex allocation we report are unlikely to be an anomalous response to unusual environmental conditions experienced during the breeding season.

When males were produced among later-laid eggs in asynchronous clutches, they became the lightest nestlings at the population level (fig. 3), indicating that there is a substantial cost to producing sons late in the egg-laying

and hatching order; conversely, sons hatching from first-laid eggs grew faster than daughters in the same position, becoming the heaviest and having the highest potential for survival and future reproduction. The mass of daughters, however, was unaffected by their placement within the egg-laying and hatching order (fig. 3), suggesting that the fitness prospects of sons is more variable than that of daughters across the environmental gradient that hatching position represents. The differential effect of hatching position on the sexes we report here indicates that the neonatal environment has a disproportionately greater influence on the fitness prospects of sons than daughters, which has rarely been demonstrated convincingly (Hewison and Gaillard 1999; Cockburn et al. 2002; Koskela et al. 2009). Although studies have documented sex-specific environmental sensitivity (reviewed in Sheldon et al. 1998 and Hewison and Gaillard 1999; see also Kruuk et al. 1999; Wilkin and Sheldon 2009), interpretation of this pattern has been confounded by sexual size dimorphism and the differing energetic and nutrient requirements of sons and daughters. Addressing this in a study of sexually size-monomorphic collared flycatchers (*Ficedula albicollis*), Sheldon et al. (1998) manipulated brood sizes to simulate an environmental gradient in resource availability and then determined whether there were sex-specific effects of the treatment on fitness-related traits among nestlings. There were no such effects, leading Sheldon et al. (1998) to conclude that, unlike sexually size dimorphic species, there were unlikely to be differential costs of producing sons and daughters in sexually monomorphic species. An earlier study of that same population found no evidence of sex-biased allocation in relation to environmental conditions (Ellegren et al. 1996), a not-unexpected result if environmental conditions do not influence the relative quality of sons and daughters (West and Sheldon 2002). However, unlike collared flycatchers, house wrens do manipulate offspring sex in relation to environmental conditions (Albrecht and Johnson 2002; Janota et al. 2002; Whittingham et al. 2002; this study), and we demonstrate that males and females are influenced differently by the natal environmental conditions created by variation in hatching synchrony. Thus, further investigation of the costs of producing sons and daughters apart from those arising through sexual dimorphism is needed (see also Rosivall et al. 2010).

The distinctive pattern of sex allocation in relation to the egg-laying and hatching order, as influenced by hatching synchrony, is strong evidence in support of the hypothesis that synchronous and asynchronous hatching represent different reproductive tactics by females to maximize fitness. Wiebe (1995) suggested that facultative adjustment of hatching synchrony in relation to food availability would be adaptive and that females should delay

incubation to hatch their eggs synchronously when resources are abundant but should hatch their eggs more asynchronously when resources are low (Wiebe and Bortolotti 1994; Wiebe 1995). Indeed, the variation of resources in time and space should favor individual plasticity in reproductive tactics (Kaplan and Cooper 1984). On the basis of Kaplan and Cooper's coin-flipping model, selection should favor individual plasticity in hatching span in temporally heterogeneous environments as opposed to canalization toward either synchronous or asynchronous hatching. Despite evidence of facultative adjustment of hatching span in two kestrel (*Falco*) species (Wiebe and Bortolotti 1994; Wiehn et al. 2000), little evidence has been presented from other taxa. Individual female house wrens in our multibrooded study population also switch between synchronous and asynchronous hatching of their clutches within breeding seasons (Harper et al. 1994; Ellis et al. 2001a). Thus, under favorable conditions females may hatch their eggs synchronously and produce average-quality offspring without imposing costs to late-hatching nestlings, whereas under less favorable conditions females may hatch their clutches asynchronously to produce heavy, large nestlings with high survival prospects, albeit at a potential cost to later-hatching offspring. This is indeed the case in house wrens, as the relative frequency of synchronous and asynchronous hatching not only varies from year to year but can also vary within breeding seasons in relation to the abundance of arthropod prey delivered to nests (Pennock 1990). Although environmental conditions during egg production, such as food availability (Wiebe and Bortolotti 1994) and temperature (Slagsvold and Lifjeld 1989; Ardia et al. 2006, 2009), may determine the degree of hatching synchrony, a balance between the quantity and quality of surviving offspring is likely a critical factor maintaining variation in hatching spans (Wiebe 1995).

Considerable progress has been made in recent years toward understanding the proximate mechanisms underlying offspring sex adjustment (reviewed in Pike and Petrie 2003 and Alonso-Alvarez 2006). Some mammals show evidence for selective abortion and resorption of embryos until the desired sex is conceived (reviewed in Cockburn et al. 2002 and Rosenfeld and Roberts 2004; but see Krüger et al. 2005), and this may occur for first-laid eggs of avian clutches (Emlen 1997). However, selective resorption within the clutch would lead to costly gaps in egg laying, thus increasing the susceptibility of prenatal offspring to predators and the elements (Emlen 1997); such gaps in the laying schedule are rarely seen in passerines, so selective resorption is generally thought to be unlikely (Pike and Petrie 2003; Goerlich et al. 2010). Because female birds are heterogametic and sex is determined before ovulation, preovulation control may be an efficient means of ad-

justing offspring sex without aborting embryos, thereby avoiding gaps in the egg-laying sequence (Oddie 1998; Petrie et al. 2001). Thus, studying sequence effects within clutches provides insight not only into whether sex adjustment has occurred (Rosivall 2008) but also into the potential mechanism. Because an egg typically requires 1 day to produce (Sturkie 1986), significant within-clutch sex bias without gaps in the laying sequence is generally taken as evidence for preovulatory sex adjustment (Komdeur et al. 2002; Pike 2005). That no female skipped a day during egg laying in this study or another showing within-clutch sex bias (Badyaev et al. 2003b) provides further support for a preovulatory mechanism of sex adjustment.

A proposed preovulatory mechanism that has recently received increasing support is that of hormone-mediated, non-Mendelian segregation of sex chromosomes during meiosis (Pike and Petrie 2003; Rutkowska and Badyaev 2008; Uller and Badyaev 2009). For example, an experimental increase in the level of circulating corticosterone (CORT), the major avian stress hormone, resulted in a female bias among offspring in Japanese quail (*Coturnix coturnix japonica*; Pike and Petrie 2006), and field studies of white-crowned sparrows (*Zonotrichia leucophrys*; Bonier et al. 2007) and European starlings (*Sturnus vulgaris*; Love et al. 2005) suggest that a strong causal link between increased maternal CORT level and a female bias among offspring exists. That baseline CORT level often varies with environmental conditions (Clinchy et al. 2004; Schoech et al. 2004, 2007; Kitaysky et al. 2007) and that such conditions also often influence incubation behavior suggest that CORT plays a role in determining incubation behavior, the degree of hatching synchrony, and sex allocation (see also Badyaev et al. 2005).

This study further illustrates the potential for confusion that is often created by generalizations about how the sexes should be allocated. For example, clutches hatching synchronously and those hatching asynchronously did not differ in the overall brood sex ratio, yet we found distinct patterns of within-brood sex allocation associated with the fitness potential of individual offspring. This clearly illustrates that studying sequence effects within broods is more informative than brood-level analyses (Rosivall 2008). Similarly, the Trivers-Willard hypothesis in the "narrow sense" (Cockburn et al. 2002) predicts that mothers in good condition should preferentially invest in sons but should bias investment toward daughters when they are in poor condition. Although this has been frequently supported in birds (Bradbury and Blakey 1998; Nager et al. 1999; Whittingham and Dunn 2000; Whittingham et al. 2002; Blanchard et al. 2007; Delmore et al. 2008) and polygynous mammals (reviewed in Cameron 2004 and Sheldon and West 2004; see also Holand et al. 2006), the pattern of investment is commonly reversed in other taxa

(Meikle et al. 1984; Hewison and Gaillard 1996, 1999; Hewison et al. 2005; Krüger et al. 2005; Koskela et al. 2009). Although female-biased investment may initially seem at odds with the Trivers-Willard model, such patterns are consistent with broader sex-allocation theory (Leimar 1996; West 2009) if preferential investment in daughters benefits maternal fitness to a greater extent than investment in sons, such as with varying population density and local resource competition (Meikle et al. 1984; Caley and Nudds 1987; Hewison and Gaillard 1996; Koskela et al. 2009; see Cockburn et al. 2002 and West 2009 for reviews). Thus, although narrow-sense interpretations of how pre- and postnatal conditions should influence sex allocation may lead to seemingly inconsistent results, the incorporation of life-history traits (Leimar 1996; West and Sheldon 2002; Sheldon and West 2004) is clearly necessary for a robust understanding of how parents should allocate offspring sex.

### Acknowledgments

We thank J. Hunt and two anonymous reviewers for helpful comments on early versions of the manuscript; S. A. Juliano for statistical advice; the 2009 Wren Crew, particularly K. Caron, for field assistance; and the ParkLands Foundation and the Sears and Butler families for use of their properties for this study. This research was supported, in part, by National Science Foundation grants IBN-0316580 and IOS-0718140; the School of Biological Sciences, Illinois State University; and an R. D. Weigel Research Grant from the Beta Lambda chapter of the Phi Sigma Society. This work was performed in accordance with (1) Illinois State University Institutional Animal Care and Use Committee number 10-2009, (2) U.S. Fish and Wildlife Service (USFWS) banding permit 09211, and (3) USFWS collecting permit MB692148-0.

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Associate Editor: Jean-Michel Gaillard  
 Editor: Judith L. Bronstein



Nestling house wrens shortly before leaving their nest. Photograph by E. Keith Bowers.