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ORIGINAL ARTICLE

Growth benefit to house wren nestlings of having an asynchronously late-hatching nestmate is greater for extra-pair offspring

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Abstract
Because nestling growth influences survival and future reproductive success, early-life conditions that impact growth have potentially large effects. One notable source of variation in early-life conditions for birds is the relative timing of egg hatching: hatching asynchrony leads to size hierarchies among nestlings and may affect competition for, or parental allocation of, resources. Paternity is another potentially important factor, as extra-pair offspring have been shown in some systems to be of higher quality and therefore might be better competitors. We tested whether the presence of an asynchronously late-hatched nestmate affected nestling growth in a population of house wrens (*Troglodytes aedon*) and whether paternity status (within-pair vs. extra-pair) affected growth either individually or in interaction with hatching synchrony. We measured mass and wing chord of nestlings repeatedly between the ages of 0 and 10 days and determined the paternity status of each nestling. Both mass and wing chord were significantly greater in nestlings who shared the nest with at least one late-hatched nestling. This effect was significantly greater for extra-pair chicks for wing chord, but not mass. We found no effect on nestling mass or wing chord of paternity status alone, hatch timing (early or late), hatch date, brood size, sex, or social father mass. Considered together, these results suggest that hatching synchrony affects nestling growth and that extra-pair nestlings may be more responsive to early-life conditions in some aspects of growth. We discuss possible mechanisms for these effects.

Significance statement
Bird eggs can hatch synchronously or asynchronously. In nests with asynchronous hatching, nestlings are different sizes, which may affect competition among them and therefore their growth rates. If hatching asynchrony does influence nestling growth, it may have far-reaching impacts on the fitness of the nestlings. We measured mass and wing length in house wren nestlings. Nestlings with an asynchronously late-hatching nestmate were larger in both measures, demonstrating an advantage to having a younger nestmate. This advantage was greater for extra-pair nestlings for wing length. This suggests a difference between extra-pair and within-pair nestlings in their responsiveness to early-life conditions, which might be due to the genetics of the extra-pair chicks or to differences in parental investment. This study documents a previously unknown potential benefit of hatching asynchrony, as well as a context-dependent difference between extra-pair and within-pair nestlings.

Keywords Competition · Hatching synchrony · Extra-pair paternity · Growth · *Troglodytes aedon*

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Introduction

Growth early in life can have far-reaching impacts on lifetime success (Tilgar et al. 2010). Factors affecting early growth therefore have the potential to exert strong selection pressure. In altricial birds, nestling growth affects the probability of survival to independence (Magrath 1991; Maddox and Weatherhead 2008; Maness and Anderson 2013; de Boer et al. 2016) and future reproductive success (Tilgar et al. 2010). One notable source of variation in early-life conditions for birds is the relative timing of egg hatching. Eggs within a clutch may hatch synchronously, over the course of a single day, or asynchronously over several days (Lago et al. 2000). This variation in hatching synchrony is produced by variation in the timing of the onset of incubation: if incubation begins after all eggs are laid, the eggs hatch synchronously, while earlier incubation onset generates hatching asynchrony because any eggs laid after the onset of incubation will hatch later than their clutchmates (Stenning 1996). The degree of hatching synchrony within a nest might influence nestling growth by affecting either the competition faced by each nestling from its nestmates for food or the allocation of food by the parents.

Hatching asynchrony could affect nestling growth either positively or negatively. Late-hatching nestlings might be expected to grow faster for their age than their earlier-hatching siblings or to allocate resources differently, in order to “catch up” in growth and development prior to fledging (Nilsson and Svensson 1996). If reduced survival of the late-hatched chick is disadvantageous to the parents, they may compensate for the size disadvantage of those chicks by preferentially feeding smaller chicks (Du et al. 2015). The mother may also aid late-hatching chicks in faster growth by giving them a developmental advantage (de Boer et al. 2016), e.g., by laying progressively larger eggs (Slagsvold et al. 1984) or by depositing different amounts of hormones or carotenoids (Newbrey et al. 2008) in the eggs. In these cases, earlier-hatching chicks may face greater competition from their late-hatched nestmates.

Alternatively, competition with older, larger nestmates and/or a developmental disadvantage may cause late-hatching chicks to grow less quickly for their age than their siblings (Smiseth et al. 2003; de Boer et al. 2016). Parents may also preferentially provision larger chicks (Smiseth et al. 2003; Avilés et al. 2011) or bring food items more appropriate to larger chicks (Slagsvold and Wiebe 2007), in some cases leading to brood reduction due to the mortality of the smaller chick (Ricklefs 1965; Mock 1987; Mock and Ploger 1987; Bryant and Tatner 1990). In this case, earlier-hatching chicks face reduced competition from their late-hatched nestmates and would be expected to experience a growth benefit of hatching asynchrony. Supporting this, an experimental manipulation of hatching synchrony in zebra finches (*Taeniopygia guttata*) found that the first-hatched nestling grew faster in asynchronously hatched broods due to reduced scramble competition from nestmates (Gilby et al. 2011).

The determinants of the degree of hatching synchrony remain poorly understood (Stoleson and Beissinger 1995). The energetic constraint hypothesis suggests that female condition determines the timing of onset of incubation and therefore hatching synchrony, but this was not supported in house wrens (*Troglodytes aedon*; Ellis et al. 2001). The peak load hypothesis suggests that greater hatching asynchrony spreads out the parental care demands of the chicks, reducing the peak care load; this hypothesis has received mixed support across species (Mainwaring et al. 2014). Environmental conditions have been shown to affect the benefits of hatching synchrony in the European roller (*Coracias garrulus*), with asynchronous broods performing better than synchronous broods under poor (low-food) conditions and the opposite occurring under good conditions (Parejo et al. 2015). However, it is not clear whether individual females actively adjust the degree of hatching synchrony in response to environmental conditions—as is suggested by the general pattern of increased hatching asynchrony in nests hatched late in the season (Stoleson and Beissinger 1995)—or whether these environment-dependent benefits simply maintain population-wide heterogeneity in hatching synchrony (Parejo et al. 2015).

One difficulty in determining the factors underlying variation in hatching synchrony is the fact that nests may also vary in traits other than hatching synchrony. One such important additional potential source of variation in nestling growth is nestling paternity. An explanation proposed for extra-pair paternity—the situation in which a chick is sired by a male other than its social father—is that females seek to improve the genetic quality of their offspring through copulating with extra-pair males either of superior absolute genetic quality (Hasselquist et al. 1996) or more optimally matched to the female’s own genotype (Masters et al. 2003; Freeman-Gallant et al. 2006). Extra-pair chicks should then be of higher genetic quality than their within-pair nestmates. This prediction has been supported in some systems by evidence that extra-pair offspring have higher mass, fledge earlier, and have higher post-fledging survival (Hasselquist et al. 1996; Freeman-Gallant et al. 2006; Johnson et al. 2009; Schlicht et al. 2012); however, other studies have found no such evidence that extra-pair offspring are of higher quality (e.g., Dunn et al. 2009; Schmoll et al. 2009; Sardell et al. 2011). One possible explanation for this uneven support is that extra-pair chicks perform differently from within-pair chicks only in specific circumstances (Sardell et al. 2011; Schlicht et al. 2012). In the tree swallow (*Tachycineta bicolor*), extra-pair offspring grew faster than within-pair offspring only in favorable conditions (O’Brien and Dawson 2007).

If hatching synchrony and nestling paternity interact with each other in their effects on nestling growth, this interaction may have obscured their effects when these variables were analyzed separately. We investigated whether hatching synchrony (presence or absence of an asynchronously late-hatching nestmate) and paternity status (within- vs. extra-pair) affected nestling growth in a population of house wrens and whether these two factors interacted: do extra-pair and within-pair nestlings differ in the impact of hatching asynchrony on growth? We focused on the siblings of asynchronously late-hatched nestlings rather than the late-hatched nestlings themselves because they constitute the majority of nestlings and because they therefore comprise the largest contribution to parental fitness.

Methods

Study system

During April–August 2009, we studied house wren nesting in artificial nest boxes in patches of mixed deciduous forest at Cornell University Experimental Ponds Unit 1, in Ithaca, NY, USA. The house wren is an insectivorous cavity-nesting songbird which lays clutches of 4–8 eggs, with clutch size declining over the course of the season (Young 1994). Nestlings are altricial and weigh ~1 g at hatching; they gain ~1 g per day up to a mass of 9–11 g, at which point mass gain levels off (Zach 1982). Broods vary in their degree of hatching synchrony (Lago et al. 2000), with nests usually containing either zero or one asynchronously late-hatching chicks, rarely two or more. Nestlings fledge within 48 h of each other, 14–19 days after the oldest nestling hatched, regardless of the age or size of the youngest nestling (Johnson et al. 2004).

Field methods

We visited nest boxes every 1–4 days throughout the breeding season to monitor nesting progress. Nests were visited ≥4 h after sunrise, which is well after laying occurs in this species and later than hatching usually occurs (Johnson 2014). Nestlings were individually marked, and mass and wing chord were measured opportunistically by KL from the date of hatching (day 0) to day 10. Nestlings were weighed with a Jennings Mack 20 digital precision jewelry scale to the nearest 0.01 g. Nestlings were not all measured at the same ages due to logistical constraints. Broods were considered asynchronous if they hatched over a period longer than 24 h. Nestlings were designated "late" if they hatched ≥24 h later than their earliest-hatching nestmate. It was not possible to record measurement data blind with respect to individual identity or presence of late-hatched nestmates because nestlings were measured at the nest box with their nestmates present; however, measurements were blind with respect to paternity status, as paternity analysis was performed after the completion of the field season.

Adults were captured, weighed using a Pesola scale to the nearest 0.1 g, and banded with unique combinations of leg bands (one numbered aluminum USGS band and three colored plastic bands). Blood (≤50 μl) was collected from the brachial vein and stored in Longmire buffer for later genetic analysis. Most females were caught in the nest box during incubation, with one female captured during egg laying. Males were captured in mist nets using playback. As part of a separate study, some males had the tips of their primary feathers trimmed; this had no effect on any variables tested—see supplementary material for details.

We measured 121 nestlings in 23 nests. Of these, 112 nestlings were measured at two or more ages; on average, each nestling was measured at 4.5 different ages (range 1–8). One nestling was excluded from further analysis due to obvious developmental abnormalities. Fourteen nestlings in 10 nests hatched late. Forty-four nestlings (nine extra-pair; eight late-hatching) had an asynchronously late-hatching nestmate, and 76 nestlings (12 extra-pair; six late-hatching) did not (Table 1).

Genetic analysis

Genomic DNA was extracted from whole blood using Qiagen DNeasy Blood and Tissue Kits (Qiagen, Valencia, CA) according to the manufacturer's instructions. Nestlings were sexed using the following 10 μl PCR reaction (adapted from Fridolfsson and Ellegren (1999)): 3.0 mM $MgCl_2$, 200 μM dNTPs, 2 pmol of primers 2550F and 2718R, 0.25 U of JumpStart Taq polymerase (Sigma-Aldrich), and 1 μl of genomic DNA, run according to the thermocycling parameters described by Dubois et al. (2006), then viewed on a 3% agarose gel. This reaction amplifies a sex-linked intron that has different lengths on the Z and W chromosomes, allowing sex determination by examining the length of the PCR products.

We performed paternity analysis using seven variable microsatellite loci. We reran analyses from the PCR step onward to confirm any mismatches with the social parents, and chicks with at least one confirmed non-null mismatch with the social parents were considered extra-pair (see LaBarbera et al. 2010 for details).

Paternity and sex were determined for 105 nestlings, of which 21 were extra-pair and 54 were female.

Statistical analysis

We ran two separate generalized additive mixed models (package *gamm4*; Wood and Scheipl 2014) to test which factors affected nestling mass or wing chord. We used additive rather than linear models to permit a non-linear relationship between age and size (mass or wing chord). Including the relationship between age and size in the models allows us to control for age when considering the effects of all other variables on size. Both models

Table 1 Sample sizes (no. of nestlings [no. of measurements]) in every combination of early- or late-hatched, possessing or not possessing a late-hatched (LH) nestmate, and within-pair or extra-pair paternity status

	LH nestmate	No LH nestmate	Total	Extra-pair	Within-pair	Total
Early-hatched	36 [207]	70 [273]	106 [480]	20 [97]	74 [368]	94 [465]
Late-hatched	8 [37]	6 [29]	14 [66]	1 [6]	10 [52]	11 [58]
Total	46 [244]	75 [302]	120 [546]	21 [103]	84 [420]	105 [523]
Extra-pair	9 [55]	12 [48]	21 [103]			
Within-pair	33 [183]	51 [237]	84 [420]			
Total	42 [238]	63 [285]	105 [523]			

included hatch date, brood size, sex, paternal mass, hatch timing (early or late), paternity status (within-pair or extra-pair), presence of an asynchronously late-hatching nestmate (presence or absence), and the interaction between paternity status and presence of an asynchronously late-hatching nestmate as fixed effects, with age as a smooth term and a random effects structure of nestling identity nested within nest identity. This random effects structure accounts for the fact that nestlings probably have individual variation as well as variation among nests; variation from these sources is controlled for in the random effects, allowing size to be compared among individuals and nests (Sofaer et al. 2013). Hatch date, brood size, and paternal mass were brood-level descriptors, while age, sex, hatch timing, paternity status, and presence of an asynchronously late-hatching nestmate were individual-level descriptors. Paternal mass was included as an index of the social male's quality, which could affect nestling provisioning. The term "age" was the true age since hatching of each nestling; that is, late-hatched nestlings were of younger ages than their siblings on any given date. Presence of a late-hatched nestmate did not include the focal individual, i.e., if a nest had only one late-hatched nestling, then all nestlings in the nest *except for* that late-hatched nestling would be classified as having a late-hatched nestmate. A late-hatched nestling could not count as its own late-hatched nestmate.

The small sample size of late-hatched nestlings (Table 1) prevented us from testing whether hatch timing interacted with other variables, such as paternity. Model results were visualized using R package *visreg* (Breheny and Burchett 2016).

Results

Sex, hatch order, paternity, and presence of a late-hatched nestmate

The proportion of females did not differ significantly by paternity status (9/21 female extra-pair vs. 45/84 female within-pair; $z = -0.879$, $P = 0.379$) or hatch timing (7/11 female late-hatching vs. 47/94 female early-hatching; $z = 0.856$, $P = 0.390$). The proportion of extra-pair nestlings did not differ by hatch timing (1/11 extra-pair late-hatched nestlings vs. 20/94 extra-pair earlier-hatched nestlings; $z = -0.956$, $P = 0.337$) nor did the proportion of nestlings with an asynchronously late-hatching nestmate differ by hatch timing (8/14 late-hatching nestlings with a late-hatched nestmate vs. 36/106 earlier-hatching nestlings with a late-hatched nestmate; $z = 1.69$, $P = 0.091$). However, the low sample sizes for extra-pair and late-hatching nestlings in all of these comparisons reduce our ability to detect such differences if they were present.

Nestling growth

Both mass and wing chord were significantly affected by nestling age and presence of a late-hatched nestmate, with nestlings sharing nests with late-hatched chicks having greater mass and longer wing chord for their age (Table 2, Fig. 1). Presence of a late-hatched nestmate also interacted significantly with paternity status in the model of wing chord: within-pair nestlings showed less benefit than extra-pair nestlings from having a late-hatched nestmate (Fig. 2a). This interaction term was not significant in the model of nestling mass, although visualization of the data suggests a trend in that direction (Fig. 2b). Hatch date, brood size, sex, paternal mass, hatch timing, and paternity status alone did not significantly affect nestling size (Table 2).

Discussion

We found support for an effect of competitive context within the nest on nestling growth and that this effect is greater for extra-pair than within-pair nestlings. Nestlings with at least one late-hatched nestmate had greater masses and longer wing chords, and in the case of wing chord, this pattern was driven primarily by extra-pair nestlings. Nestling mass has been positively linked to juvenile survival in several altricial species (Magrath 1991; Maddox and Weatherhead 2008; Maness and Anderson 2013), suggesting that in our system, individuals from asynchronous broods are expected to have higher survival. Wing chord is also likely to be a predictor of survival, as house wrens fledge synchronously regardless of the development of

Table 2 Results of models of nestling mass and wing chord

Nestling measure	Variable	Estimate ± SE	*t* [*F*]	*P*
Mass	Age[a]	n.a.	3146	<0.001*
	Hatch date	−0.008 ± 0.007	−1.150	0.251
	Brood size	−0.085 ± 0.155	−0.550	0.582
	Hatch timing (E)	0.125 ± 0.160	0.786	0.432
	LH nestmate (P)	0.573 ± 0.246	2.334	0.020*
	Paternity (WP)	0.214 ± 0.167	1.283	0.200
	Sex (M)	−0.015 ± 0.090	−0.167	0.867
	Male mass	−0.096 ± 0.263	−0.365	0.715
	LH nestmate (P)* paternity (WP)	−0.259 ± 0.223	−1.163	0.245
Wing chord	Age[a]	n.a.	4762	<0.001*
	Hatch date	−0.015 ± 0.014	−1.072	0.284
	Brood size	−0.127 ± 0.289	−0.440	0.660
	Hatch timing (E)	0.020 ± 0.264	0.077	0.939
	LH nestmate (P)	1.274 ± 0.407	3.132	0.002*
	Paternity (WP)	0.505 ± 0.268	1.881	0.061
	Sex (M)	0.186 ± 0.144	1.289	0.198
	Male mass	0.014 ± 0.504	0.029	0.977
	LH nestmate (P)* paternity (WP)	−0.761 ± 0.356	−2.137	0.033*

E early-hatched, *LH* late-hatched, *P* present, *WP* within-pair, *M* male

[a] Age was included in the models as a smooth, so has no estimated effect size and reports an *F*-value rather than a *t*-value

smaller nestlings in the brood (Johnson et al. 2004), and fledgling birds incapable of extended flight have been shown to suffer considerably greater mortality rates than those with a well-developed flight ability (Sullivan 1989).

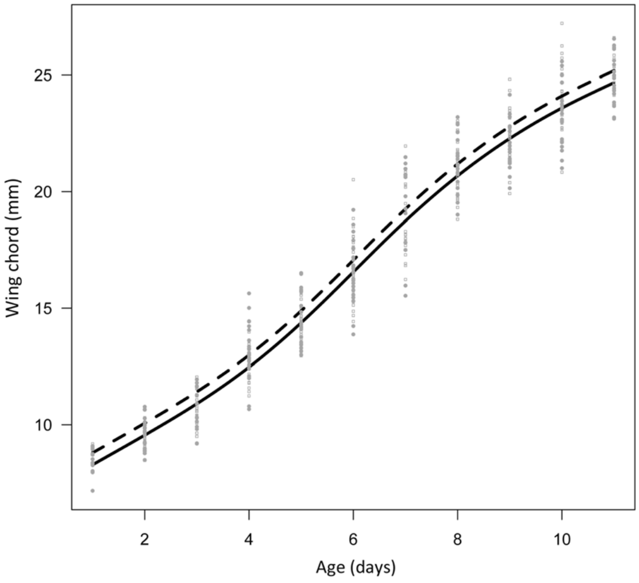

Fig. 1 Relationship between wing chord and nestling age, as fitted by a generalized additive mixed model (see "Methods"), with all other variables held constant. Nestlings with at least one asynchronously late-hatched nestmate (*dashed line*) have longer wings for their age than nestlings without any late-hatched nestmates (*solid line*). *Gray points* are partial residuals

The mechanism of the growth advantage experienced by nestlings with at least one late-hatched nestmate is unclear. Late-hatched nestlings are likely less able to physically compete for food due to smaller body size (Smiseth et al. 2003); however, this alone is insufficient to account for the effect observed here, since smaller brood sizes would similarly provide a context of reduced competition, and yet brood size did not affect nestling growth. It may be that late-hatching nestlings provide some benefit of a greater number of nestmates, perhaps through increased provisioning by the parents due to the additional stimulation of more begging nestlings (Biermann and Sealy 1982), or savings in the energetic costs of thermoregulation in a nest with more nestmates (Wegrzyn 2013). Consistent with this hypothesis, brood parasitic brown-headed cowbird (*Molothrus ater*) nestlings experience higher rates of mass gain and skeletal growth when raised with one or more host siblings than when raised alone (Kilner et al. 2004).

Several benefits of hatching asynchrony have been suggested, including reducing the maximum demand for parental care of the brood (Mainwaring et al. 2014) and facilitating brood reduction in unpredictable environments (Ricklefs 1965; Mock 1987; Mock and Ploger 1987; Bryant and Tatner 1990). This study provides evidence of an additional benefit to hatching asynchrony: that of increased growth of the early-hatched nestlings. It remains unclear whether this increased growth comes at the expense of the asynchronous nestlings. Even if it does, however, the growth benefit alone need not outweigh the cost of production of an additional

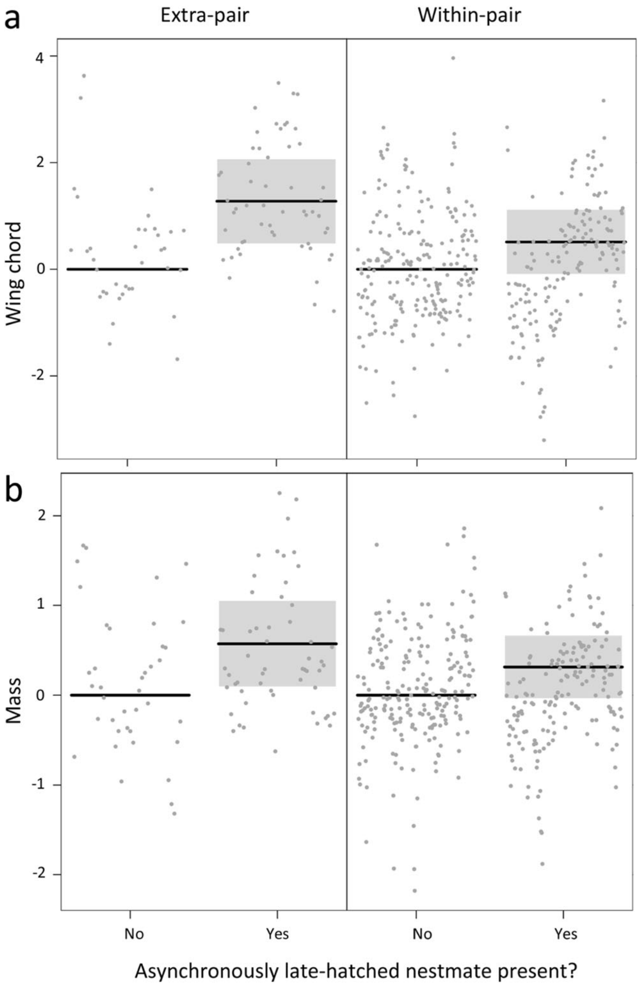

Fig. 2 Contrast plot of fitted data illustrating the predicted effect on **a** wing chord or **b** mass of changing the presence of an asynchronously late-hatched nestling. The presence of an asynchronously late-hatched nestmate appears to increase nestling size in extra-pair, but not within-pair nestlings, although this interaction is only significant in the model of wing chord. *Shaded area* is the confidence interval (not present in the first level in each plot because that is the reference level and therefore has no uncertainty); *gray points* are partial residuals

nestling; at the time of egg laying—when clutch size is determined—the potential benefit of the additional asynchronous chick includes not only the growth benefit to its nestmates but also the fitness benefit of that chick surviving to reproduce, weighted by the likelihood that it will do so. (This is the same calculation by which facultative brood reduction can be selected for [Ricklefs 1965].) The growth benefit to the early-hatched nestlings, being relatively small, is unlikely to be the sole explanation for hatching asynchrony; rather, in helping to balance the costs, it may make hatching asynchrony beneficial under a somewhat broader range of conditions than would otherwise be the case.

We find evidence that, in our system, extra-pair young are more responsive to competitive context than within-pair young. Context dependence of the effects of extra-pair paternity has been found in several other systems (Sardell et al. 2011; Schmoll 2011; Schlicht et al. 2012); for example, in tree swallows, extra-pair nestlings grow faster when in favorable conditions, while within-pair nestlings show no such benefit from favorable conditions (O'Brien and Dawson 2007). Context dependence of the effects of extra-pair paternity could help to explain both the mixed support for an advantage of being extra-pair (Schmoll 2011) and the variation among populations and species in the frequency of extra-pair paternity (Taff et al. 2013). However, while we found a difference between extra-pair and within-pair offspring in their response to hatching asynchrony, we did not find evidence that this difference constitutes a *benefit* of extra-pair paternity: extra-pair offspring did not outperform within-pair offspring overall. Possibly, extra-pair nestlings would have outperformed within-pair nestlings under more extreme conditions than those we observed. Additionally, the difference between extra-pair and within-pair offspring in their responsiveness to the environment may constitute a form of "bet-hedging" by the female, with greater variation in offspring phenotype increasing the likelihood that some offspring may be well suited to the current environment (Yasui and Garcia-Gonzalez 2016).

The simplest explanation for the significant interaction between paternity status and hatching asynchrony in the model of wing chord is that females seek extra-pair copulations with males whose genes predispose their offspring toward greater responsiveness to the early developmental environment (O'Brien and Dawson 2007). Although this responsiveness was not a benefit in itself in our system, it may be underlain by genes that are beneficial in other ways or other contexts. However, it is worth considering several alternative explanations for this interaction that do not rely on extra-pair offspring being innately different from their within-pair nestmates. One possibility is that extra-pair offspring are more likely to be early in the hatching sequence (Johnson et al. 2009). However, in this study, we saw no significant difference in the proportion of early- vs. late-hatching nestlings that were extra-pair. Additionally, hatch timing did not significantly affect nestling growth. Another possibility is a greater responsiveness of parental provisioning of extra-pair offspring to hatching asynchrony, but there is no evidence that birds provision extra- and within-pair offspring differently (Westneat 1995; Whittingham et al. 2003). Alternatively, the same factors that influence a female's likelihood of beginning incubation early, resulting in hatching asynchrony, may also influence female allocation of resources into eggs (O'Brien and Dawson 2007; Newbrey et al. 2008) and specifically have a greater influence on female allocation of resources into extra-pair eggs. There is no mechanistic obstacle to a female assessing the paternity of the egg currently in production: females could estimate the sire of their current egg with relatively high accuracy based on the timing of copulations alone and females may even be able to select sperm from specific sires to fertilize their eggs (Birkhead and Møller 1993).

Although we did not find support for an effect in our system, other studies have reported significant effects on nestling growth of hatch timing, hatch date, brood size, sex, and paternity status (Lago et al. 2000; Freeman-Gallant et al. 2006; Johnson et al. 2009; Tarof et al. 2011; Schlicht et al. 2012). It is possible that we might have observed an effect of hatch timing on growth if we had been able to classify nestlings by exact hatch order (i.e., first, second…) rather than by the broader categories of early vs. late. Within house wrens, late-hatched nestlings have been found both to be lighter (Lago et al. 2000) and to not differ in mass (Harper et al. 1992), suggesting variation among populations in this relationship.

Our results underscore the importance of early-life conditions in shaping the success of individuals. Both the degree of hatching asynchrony and the paternity status of nestlings are determined primarily by the female (Ellis et al. 2001; Masters et al. 2003; Johnson et al. 2009). As evidence suggests that nestlings with reduced growth experience reductions in both survival (Magrath 1991; Maddox and Weatherhead 2008; Maness and Anderson 2013) and reproductive success (Tilgar et al. 2010), the effects of hatching asynchrony and paternity on an individual may be profound. Females may therefore play a critical role in determining the early-life conditions, and therefore future reproductive success, of their offspring.

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Compliance with ethical standards

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed involving animals were in accordance with the ethical standards of the institution at which the studies were conducted.

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