CHICAGO JOURNALS

ASN American Society of Naturalists

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Sibling Cooperation Influences the Age of Nest Leaving in an Altricial Bird

E. Keith Bowers,* Scott K. Sakaluk, and Charles F. Thompson

Behavior, Ecology, Evolution, and Systematics Section, School of Biological Sciences, Illinois State University, Normal, Illinois 61790

ABSTRACT: In altricial birds, siblings raised within a nest usually leave the nest within hours of each other, despite often differing considerably in age. The youngest members of the brood are typically underdeveloped at this time and less likely than their older siblings to survive outside the nest, yet they risk abandonment if they do not fledge with their older siblings. Nest leaving is usually initiated by the older offspring, which may delay this process to provide more time for their younger siblings to mature, increasing the younger siblings' postfledging survival and their own inclusive fitness. We tested this hypothesis in a population of house wrens *Troglodytes aedon* and found that broods with broad age spans among siblings had longer nestling periods than broods with narrow age spans and that delayed fledging improves the survival and reproductive prospects of younger siblings, although at a potential cost to future siblings. We also manipulated age spans through cross-fostering and found that older foster nestlings postponed fledging when raised with younger broodmates, as predicted if the age of younger nestlings determines the time of fledging. Our results support kin-selection theory and demonstrate that the exact time of fledging is attributable, in part, to sib-sib interactions.

Keywords: evolution of cooperation, hatching asynchrony, house wren, kin selection, life-history evolution, nestling period, sibling interactions, *Troglodytes aedon*.

Leaving the nest of one's birth is one of the most consequential ontogenetic stages in the life of many animals, but very little is known about nest-leaving behavior. In birds, for example, difficulty in studying nest leaving, or fledging, arises because of difficulty in predicting when the event will occur (Johnson et al. 2004) and in determining how the timing of fledging influences fitness (Radersma et al. 2011). Although the risk of predation and parasitism selects for shortened nestling periods (i.e., the time from hatching until fledging; Martin 1995; Roff et al. 2005; Badyaev et al. 2006; Remeš 2006), if young, underdeveloped fledglings experience reduced survival, selection should fa-

vor longer nestling periods so that offspring can reach a developmental threshold that improves postfledging survival (Carrier and Auriemma 1992; Michaud and Leonard 2000; Green and Cockburn 2001; Day and Rowe 2002). Thus, the age at which offspring leave the nest is influenced by a trade-off between opposing selective forces, with predation and parasitism selecting for shorter nestling periods and improved postfledging survival selecting for longer nestling periods (see also Remeš and Martin 2002; Remeš 2007).

In multiparous, altricial species in which all offspring leave the nest over a short span of time (e.g., on the same day), the age or developmental stage at which nestlings fledge may affect their inclusive fitness if younger, underdeveloped siblings survive less well than their older, better-developed siblings (fig. 1). Sibling interactions, particularly among neonates, have probably been best studied from the perspective of avian hatching asynchrony (Mock and Parker 1997), which is common in altricial birds and occurs when a broad time span elapses between the hatching of the first and last eggs of a clutch. This creates a pronounced age-related hierarchy among siblings after hatching is complete, in which earlier-hatching, older offspring are larger and heavier than their later-hatching, younger siblings (Forbes and Glassey 2000; Johnson et al. 2009; Bowers et al. 2011). Although eggs hatch asynchronously over a span of several days, nestlings usually fledge within hours of each other (Nilsson and Svensson 1996; Nilsson and Gårdmark 2001; Johnson et al. 2004; Radersma et al. 2011), and younger, underdeveloped offspring are at risk of abandonment and starvation if they do not fledge with their older siblings (Johnson 1998). In a population of house wrens *Troglodytes aedon*, Freed (1988) documented that the older, better-developed nestlings in asynchronously hatched broods delayed fledging for several days beyond the age at which they are capable of doing so and hypothesized that kin selection accounts for the delayed fledging. Specifically, delayed fledging by older nestlings may allow their younger siblings to catch up develop-
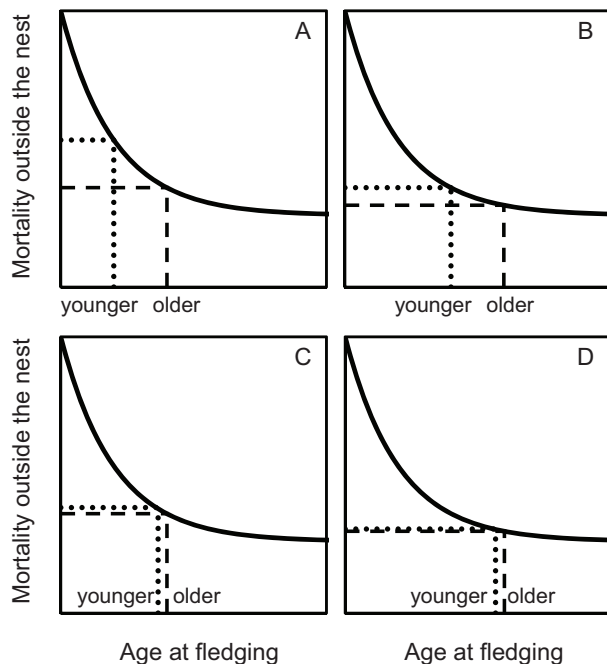
Figure 1: Schematic plot of the relationship between the age at fledging and postfledging mortality risk of siblings depicted as a negative exponential function (adapted from fig. 2 in Roff et al. 2005). *A* and *B* depict nests with broad age spans among siblings (asynchronous hatching), and *C* and *D* depict nests with narrower age spans (synchronous hatching). The difference in age between older and younger siblings is the same in *A* and *B* and is also the same in *C* and *D*. Increased predation risk within the nest should reduce the age at fledging, but as the risk of mortality within the nest decreases (moving from *A* and *C* to *B* and *D*), delayed fledging by older individuals has a more pronounced effect on the postfledging survival of their younger siblings than on their own survival. However, the marginal reduction in mortality of younger nestlings depends on the extent to which siblings differ in age; thus, the inclusive fitness of older siblings in asynchronous broods (e.g., *A* and *B*) benefits more from delayed fledging than those in synchronous broods (*C* and *D*).

nestlings should be associated with longer nestling periods than nests with narrower age spans; although they found a trend in the predicted direction, it was not statistically significant. However, clutches in their study population hatched entirely asynchronously (i.e., over a span of 40–76 h), as opposed to 1–76 h when synchronous and asynchronous hatching cooccur, which reduced the natural variation in sibling age spans and thus reduced the likelihood of detecting an effect statistically. Therefore, species or populations with greater variation in hatching spans and increased variation in age and developmental stages among nests may be better suited for testing the kin-selection hypothesis.

In this study, we tested the hypothesis that kin selection influences fledging age in a population of house wrens in which sibling age spans within a nest vary from 1 or 2 h up to 3 or, occasionally, 4 days (fig. 1 in Bowers et al. 2011; fig. A1 in the appendix, available online), predicting that age spans within a nest should determine the length of the nestling period because of the within-brood variation in developmental states among siblings. We also cross-fostered nestlings by transferring 4-day-old nestlings to recently hatched broods in place of 1-day-old nestlings and placing the 1-day-old nestlings in the 4-day-old nestlings' broods. If the kin-selection hypothesis is correct, broods that receive younger foster nestlings should have longer nestling periods than control broods; we also predicted that older foster nestlings would also delay fledging so that their younger siblings would fledge at a normal age (i.e., similar to those in control broods), because the time until fledging should be determined by the age and developmental state of the younger nestlings.

mentally, thus increasing their postfledging survival and the older siblings' inclusive fitness (fig. 1). Freed tested this hypothesis by inducing broods to fledge several days earlier than they usually do and demonstrated that earlier fledging had no adverse consequences for the older, more mature siblings but dramatically reduced the survival of their younger, underdeveloped siblings (Freed 1988).

Johnson and colleagues (2004) also studied fledging in house wrens and found that the age of fledging was unrelated to parental provisioning behavior. Moreover, the oldest, most well-developed nestling usually left the nest first, and these older siblings were followed by all of their younger siblings within 1.1 h, on average. Johnson and colleagues (2004) also noted that the kin-selection hypothesis predicts that nests with broad age spans among

Methods

Study Area and Species

We studied a population of house wrens during the 2009–2012 breeding seasons on the 130-ha Mackinaw study area, a tract of secondary deciduous forest surrounded by agricultural fields in McLean County, Illinois (40°40′N, 88°53′W). House wrens are 10–12-g, solitary-nesting songbirds whose breeding grounds are distributed widely across the middle latitudes of North America, and they winter in the southern United States and Mexico. House wrens are obligate cavity nesters and cannot excavate their own nest cavities, so they readily accept nest boxes, within which over 95% of the population's nests are built (Drilling and Thompson 1988). Nest boxes ($N = 700$) are spaced 30 m apart along north-south transects separated by 60 m (fig. 1 in DeMory et al. 2010) and are mounted on 1.5-m poles atop aluminum disks 48.3 cm in diameter

that deter predators; Lambrechts et al. (2010) provide details on nest box materials and dimensions.

Upon arriving in the study area from spring migration, females select a mate that is defending a nest site and, after completing nest construction, lay a clutch of 4–8 eggs. Approximately half of the females that successfully rear a brood early enough in the breeding season produce a second brood, and some females may occasionally attempt a third brood (Drilling and Thompson 1991; Bowers et al. 2012*a*, 2012*b*). Only females incubate eggs, which do not differ in average number or size between clutches that hatch synchronously or asynchronously; broods are classified as synchronous if hatching is completed within approximately 24 h and as asynchronous if hatching takes 2 or more days to complete (Ellis et al. 2001*a*; Bowers et al. 2011). Thus, the oldest and youngest siblings within asynchronously hatched broods typically differ in age by 42–76 h, although even 96-h hatching spans occur. Synchronous broods are comprised of nestlings that are essentially all of the same age and thus of the same body mass and size; not surprisingly, broods classified as asynchronous have nestlings that vary significantly in body mass and size (fig. 2 in Bowers et al. 2011). Synchronous and asynchronous broods also do not differ, on average, in the number or size of nestlings that survive to fledging (Bowers et al. 2011), but the proportion of broods that hatch synchronously and asynchronously differs among years (46%–76% synchronous; Harper et al. 1992, 1993; Ellis et al. 2001*b*). Only females brood hatchlings, which cannot thermoregulate until approximately 8 days of age, but both parents provision the young. The length of the nestling period is typically 14–17 days; the oldest, largest nestlings usually leave the nest first, with the rest of the brood following within a few hours (Johnson et al. 2004), although some nestlings (typically small, underdeveloped runts) occasionally remain in the nest and die of starvation (Johnson 1998). Parents do not appear to direct or play a role in the fledging process; for example, in a detailed study of fledging involving another house wren population, Johnson et al. (2004) noted that fledging age was unrelated to parental feeding rates. We also have evidence from our study population that fledglings are preferentially fed over nestlings, because it is not uncommon to find a single nestling in the nest after its siblings have fledged. This nestling is usually dead the next day and is clearly abandoned by the parents in favor of its fledged siblings.

Field Procedures

In 2009, we visited nests multiple times daily during hatching to document the span of time that elapsed between hatching of the first and last eggs of a clutch, which shows a strongly bimodal distribution (fig. 1 in Bowers et al. 2011). Eggs usually hatch during daylight hours (Johnson 1998), so hatching spans closely resemble a bimodal or multimodal distribution. Thus, in subsequent years, we visited nests once daily when hatching was expected to classify broods as synchronous or asynchronous on the basis of number of days required for all viable eggs in a nest to hatch, and the distribution of hatching spans in subsequent years matches the pattern observed in 2009 (fig. A1). In all years, we banded, weighed, and measured the tarsus length of all nestlings shortly before fledging on brood-day 11 (brood-day 0 is the day hatching begins). We subsequently visited nests daily thereafter to determine when fledging occurred.

In 2011, we conducted a cross-fostering experiment in which we exchanged randomly selected nestlings between brood dyads, placing a 4-day-old nestling into a 1-day-old brood and transferring a 1-day-old nestling from that brood into the 4-day-old's brood. Thus, we created broods with a foster nestling that was either 3 days older or 3 days younger than the rest of the brood, with the age of the brood defined by the age of the oldest nestling within the nest (including cross-fostered nestlings). We uniquely marked all nestlings by toenail clipping and visited nests daily to monitor nestling growth, weighing individual nestlings for the last time when they were 12 days old. This required visiting broods and handling younger foster nestlings when their older broodmates were 15 days old for the broods containing a younger foster nestling. Major disturbances near the time of nest leaving can cause premature fledging; thus, we took care to minimize disturbance and handled only the foster nestling, and these broods did not fledge earlier than usual (see "Results"). The range of fledging times (i.e., length of the nestling period) reported by Johnson et al. (2004) for unmanipulated house wren nests that experienced no disturbance to the nestbox for at least 4 days before fledging (14–19 days of age) is similar to the range that we report here for both our control and experimental broods (see "Results"). We did not handle nestlings older than 12 days of age but subsequently visited nests daily (or more frequently, time permitting) to determine when they fledged. We did not document any asynchrony in fledging, despite the experimental increase in within-brood age spans. Both synchronous and asynchronous hatching occurred in this manipulative experiment, and the proportion of nests hatched synchronously and asynchronously was the same for each treatment group (Fisher's exact test: $\chi^2 = 2.63$, $P = .273$). There was no evidence that our manipulations differentially affected the time of fledging for synchronously or asynchronously hatched broods, because there was no statistical interaction between our treatment and the degree of hatching synchrony in determining the age at fledging ($P = .45$). Thus, for clarity, we present data for syn-

Table 1: Summary of effects on the age at fledging from 2009 and 2010.

Variable	Estimate ± SE	Wald χ^2	df	P
Hatching synchrony	...	2.29	1	.130
Brood size	−.02 ± .07	.07	1	.791
Synchrony × brood size	−.25 ± .12	4.78	1	.029
Year	...	10.6	1	.001

chronous and asynchronous hatching from 2009–2010 and only the effects of our manipulations in the 2011 experiment; however, pooling data for hatching asynchrony in 2011 with data from 2009–2010 produces the same result (data not shown). Approximately 48% of the 1-day-old foster nestlings died (25 of 52 nondepredated broods) and were removed from the nest by their foster parents before fledging, typically within 4 days of age; because we visited nests daily, we were able to document the age at which any nestling died. Although the design of our 2011 experiment necessarily altered the relatedness of broodmates, unmanipulated nestlings often differ in relatedness because of differences in paternity (e.g., Soukup and Thompson 1997; Forsman et al. 2008). Thus, because offspring of mixed paternity commonly cooccur within a nest, it is unlikely that this had an influence on our results; if it did, the fledging ages in the experiment should be the opposite of what we found (see "Results") and also the opposite of our data on natural age spans of nonfostered siblings from 2009–2010.

Data and Analyses

We used SAS statistical software (SAS 9.3) for all analyses. In analyses of the time until fledging, we used Cox proportional hazards regression models (survival analysis; PROC PHREG) to analyze the length of the nestling period (interval from brood-day 0 to fledging) with nests that were abandoned by parents or destroyed by predators as censored values. Because many females in our study produced multiple broods, we used the robust sandwich covariance matrix estimation (SAS Institute 2011) to account for the nonindependence of broods produced by the same female, similar to a mixed-model ANOVA. However, unlike an ANOVA, survival analysis analyzes times to an event in ways that the comparison of means cannot (Fox 2001); most notably, survival analysis allows for the inclusion of censored values (e.g., broods that were depredated before fledging age). We first analyzed differences in the time until fledging between broods hatching synchronously ($N = 100$; 6 of which were censored because of nest predation) and asynchronously ($N = 86$; 2 of which were censored because of nest predation) from 2009 and 2010 using survival analysis. Clutches that hatched synchronously and

asynchronously were the same, on average, with respect to clutch size ($t = 0.06$, $P = .95$) and brood size at the time of fledging ($t = 1.57$, $P = .12$). Because brood size and time of season could influence when nestlings fledge, we initially included these covariates, in addition to year, as main effects along with all two-way interactions and obtained a parsimonious model from the full model via elimination of nonsignificant terms, beginning with removal of two-way interactions. Thus, the results in table 1 are from a reduced model. Forstmeier and Schielzeth (2011) recently cautioned that model simplification may influence Type I error rates; however, our results from the reduced model are the same as from the full model (see the full model in table A1, available online).

We analyzed the length of the nestling period for broods in 2011 in relation to our age-manipulation treatments: broods that received a 4-day-old foster nestling ($N = 53$; 6 of which were censored because of nest predation), broods that received a 1-day-old nestling ($N = 59$; 7 of which were censored because of predation and 25 of which were censored because of foster-nestling mortality before fledging), and unmanipulated control broods ($N = 54$; 5 of which were censored because of predation). We censored broods in which the 1-day-old foster nestling died between transfer and fledging because both the age span of nestlings present at the time of fledging and brood sizes were altered by their death (table 2; foster-nestling mortality did not occur for broods receiving an older nestling). Because nearly half of the 1-day-old foster nestlings died before fledging, we also tested whether broods that received a 1-day-old foster nestling differed in the length of the nestling period depending upon whether the foster nestling was still alive at that time.

The kin-selection hypothesis predicts that delayed fledging should improve the prospects for survival and reproduction of younger siblings within the nest but should have less of an effect on the survival of the oldest siblings (fig. 1). Thus, we tested whether delayed fledging influenced the recruitment of both the oldest nestling within the nest and their younger broodmates using a generalized

Table 2: Mean age of the oldest nestling at fledging and number of nestlings that survived to leave the nest by treatment group in the 2011 cross-fostering experiment (excluding depredated nests)

Treatment	Mean age ± SE (days)	Mean no. young ± SE	N
Older nestling	18.3 ± .2	5.2 ± .2	47
Younger nestling:			
Alive	16.4 ± .2	5.4 ± .3	27
Dead	15.3 ± .3	4.3 ± .3	25
Control	15.2 ± .1	5.2 ± .3	49

estimating equation (GEE; PROC GENMOD) assuming binomial errors and a logit link function with maternal identity as a random effect to account for nonindependence of broods produced by the same female; we also tested whether our manipulation of the within-brood age structure in 2011 influenced their subsequent recruitment as breeders to the local population in 2012 by capturing and identifying the adults breeding in our study population throughout the 2012 breeding season.

Delayed fledging may postpone future reproductive events by parents and create a conflict between parents and offspring over fledging age. Moreover, delayed fledging could create a cost to older siblings' inclusive fitness by reducing the number of future siblings that parents would have otherwise produced if they had not extended care for their first brood. Thus, we combined data from 2009–2011 to determine whether delayed fledging early within breeding seasons influenced whether a female would produce a second clutch of eggs after her first brood left the nest using a GEE, as above, with a binary response distribution (i.e., whether the female produced a second clutch) and logit link function; we included the date at which a female's first brood left the nest in this analysis, because this is known to have an effect on whether females produce two broods in a single breeding season (Bowers et al. 2012*a*). We also analyzed the recruitment of offspring produced over the course of the breeding season using a GEE, as above, to determine whether siblings reared together early within breeding seasons had a higher chance of survival than siblings produced later. For females that produced a second clutch of eggs, we analyzed whether the age at fledging for their first brood influenced the interbrood interval (i.e., the time elapsed from the fledging of her first brood until she initiated her second clutch of eggs; Bowers et al. 2012*a*) using survival analysis as above. We also tested whether the delayed fledging earlier within the breeding season had an influence on a female's clutch size in her second brood using a mixed-model ANOVA with maternal identity as a random effect to account for the nonindependence of females that bred in multiple years.

Results

Synchronous versus Asynchronous Hatching, 2009–2010

Fledging occurred most often between brood-days 15 and 16, with 50% of all broods fledging by the end of brood-day 15 (fig. 2). The mean length of the nestling period ($\pm$SE) was longer in 2009 (15.5 $\pm$ 0.2 days; $N = 41$) than in 2010 (15.2 $\pm$ 0.1 days; $N = 140$; table 1). Broods that hatched asynchronously, in which siblings varied in age by up to 4 days, tended to have longer nestling periods than synchronously hatched broods, but there was an in-
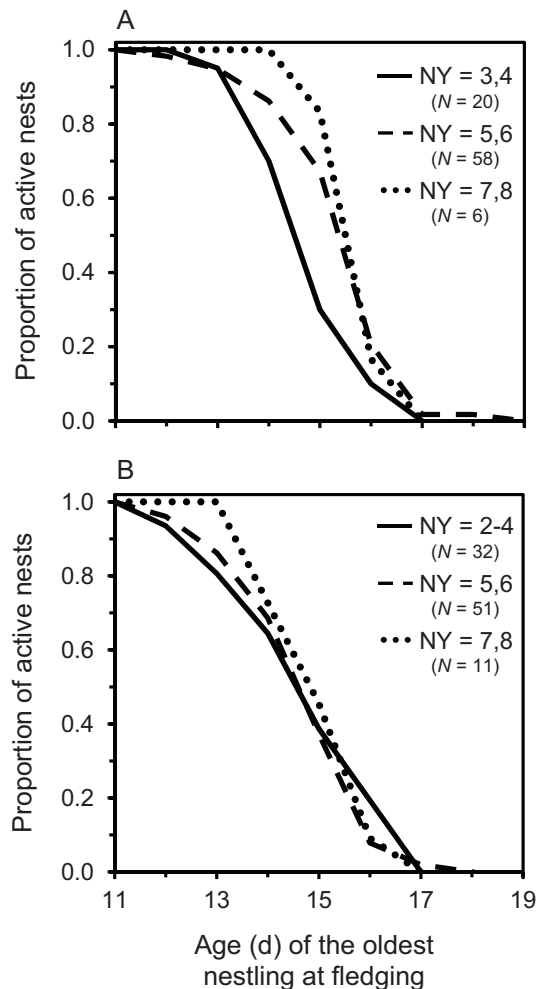

Figure 2: Proportion of active nests (not yet fledged) in relation to the number of young (NY) and the age of the oldest nestling in broods hatched (*A*) asynchronously and (*B*) synchronously. Small asynchronous broods tended to fledge at a similar age as synchronous broods, but asynchronously hatched young delayed fledging as brood size increased. For graphing purposes, we categorized brood sizes as three or four nestlings (solid line; including five synchronously hatched broods with two concurrent siblings at fledging), five or six nestlings (dashed line), and seven or eight nestlings (dotted line). d, days.

teraction between hatching synchrony and the number of siblings present in determining the age at fledging (fig. 2; table 1). Follow-up tests revealed that increasing brood size delayed the age at fledging for broods that hatched asynchronously (Wald $\chi_1^2 = 6.83$, $P = .009$; fig. 2*A*) but not for those that hatched synchronously (Wald $\chi_1^2 = 0.35$, $P = .554$; fig. 2*B*). Because hatching spans can vary from 1 to 4 days (fig. A1), we also analyzed the model depicted in table 1 using hatching spans instead of the synchronous versus asynchronous dichotomy, and using

hatching spans produced qualitatively the same result (tables A2, A3, available online).

Cross-Fostering Experiment, 2011

Experimental manipulation of within-brood age spans affected the length of the nestling period in association with the resulting age-related hierarchy (survival analysis Wald $\chi_2^2 = 63.15$, $P < .001$; fig. 3A, table 2). Post hoc comparisons revealed that broods receiving 1-day-old foster nestlings had longer nestling periods than control broods (Wald $\chi_1^2 = 33.10$, $P < .001$); broods with 4-day-old foster nestlings also delayed fledging for several days beyond the age at which they would normally do so (Wald $\chi_1^2 = 61.42$, $P < .001$), and they also fledged at an older age than broods containing a younger foster nestling (Wald $\chi_1^2 = 17.59$, $P < .001$). Thus, because older foster nestlings delayed fledging for several days, their younger broodmates were of a similar age as those in control broods at the time of fledging (fig. 3A).

Nearly half of the younger foster nestlings died before nest leaving (25 from 52 nondepredated broods), and we predicted that, when this occurred, it would shorten the length of the nestling period, because the age span among nestlings had been reduced. As predicted, broods with a younger foster nestling that was still alive near the time of fledging delayed this process compared with those in which the foster nestling had died shortly after cross-fostering (Wald $\chi_1^2 = 7.44$, $P = .006$) and also fledged at

an older age than similar-sized control broods (Wald $\chi_1^2 = 26.71$, $P < .001$; fig. 3B, table 2). Moreover, broods in which the younger foster nestling had died did not differ from control broods with respect to the age at fledging (Wald $\chi_1^2 = 2.79$, $P = .095$; fig. 3B).

Delayed Fledging and Recruitment to the Breeding Population

As predicted, the age at fledging in our 2011 cross-fostering experiment had a significantly positive effect on the likelihood that a younger sibling would survive to reproduce in the population (GEE parameter estimate $\pm$ SE $= 0.33 \pm 0.14$; $\chi_1^2 = 5.80$, $P = .016$; fig. 4). There was no effect of our treatment (i.e., whether the brood received an older or a younger nestling) on the likelihood that a younger sibling would recruit to the breeding population ($\chi_2^2 = 2.79$, $P = .246$), and the age at fledging did not influence the recruitment of the oldest offspring within a nest (GEE parameter estimate $\pm$ SE $= 0.20 \pm 0.17$; $\chi_1^2 = 1.39$, $P = .238$).

We also pooled data across years to analyze whether delayed fledging improves recruitment. The effect of fledging age from 2009–2011 on the recruitment of younger siblings remained significant (GEE parameter estimate $\pm$ SE $= 0.24 \pm 0.11$; $\chi_1^2 = 5.10$, $P = .024$), indicating that delaying fledging increases the likelihood that a younger sibling within a nest will recruit to the breeding population. Pooling data across years also revealed that delayed
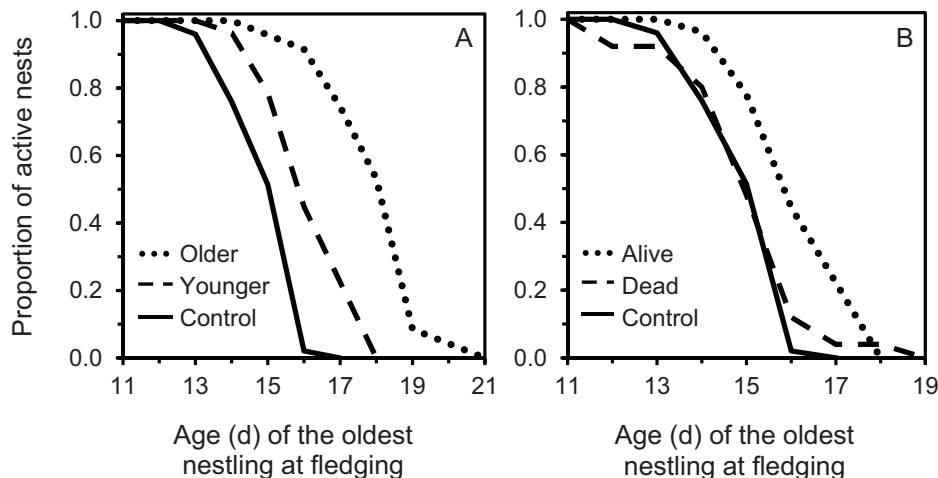

Figure 3: *A*, Proportion of active nests (not yet fledged) in relation to the age of the oldest nestling within the brood for the 2011 age-manipulation treatments, showing broods that received an older foster nestling (dotted curve), broods that received a younger foster nestling (dashed curve), and unmanipulated control broods (solid curve). *B*, Proportion of active nests in relation to the age of the oldest nestling for broods receiving a younger foster nestling and whether that nestling was still alive at the time of fledging (dotted curve) or died earlier in the nestling stage (dashed curve). When younger foster nestlings died before fledging, the remaining nestlings fledged at a similar age as nestlings in control broods. d, days.
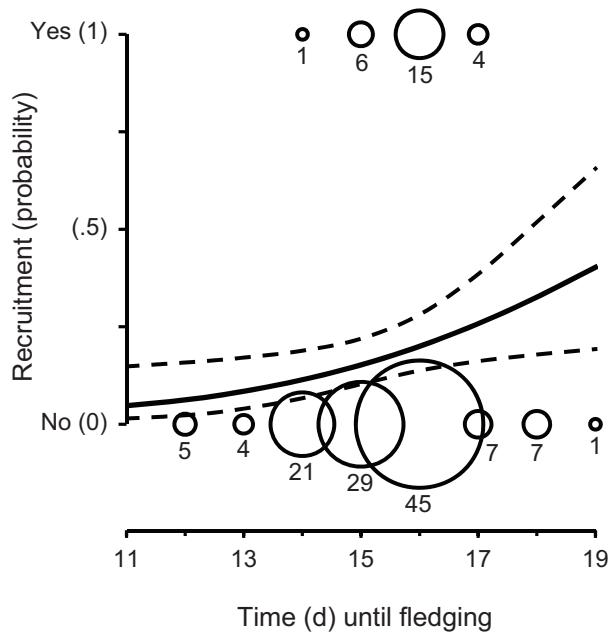
Figure 4: Recruitment of younger siblings within a nest in 2011, excluding the oldest nestlings, to the breeding population in 2012 in relation to the number of days (d) elapsed from hatching until fledging. Bubble sizes are proportional to the number of nests that produced recruits, which are given, and the solid curve depicts the predicted probability ± 95% confidence limits.

fledging marginally, but not significantly, increased the chances of recruitment for the oldest siblings within a nest (GEE parameter estimate ± SE = 0.31 ± 0.14; $\chi_1^2 = 3.63$, $P = .057$).

Parent-Offspring Conflict and the Costs of Delayed Fledging

Approximately 58% of females were double brooded during 2009–2011 (148 of 255 females that successfully fledged offspring from their first brood produced a second clutch). The likelihood that a female would produce a second clutch was not determined by the age of her first brood at the time they left the nest (GEE parameter estimate ± SE = 0.11 ± 0.10, $\chi_1^2 = 1.37$, $P = .242$); however, the day of the year on which a female's first brood fledged did influence whether she would produce a second clutch, because the likelihood of attempting a second brood decreased as the breeding season progressed (GEE parameter estimate ± SE = −0.062 ± 0.012; $\chi_1^2 = 20.9$, $P < .001$). For females that produced a second clutch, the age of their first brood at fledging did not affect the interbrood interval (survival analysis $\chi_2^2 = 0.252$, $P = .616$), and there was also no effect of the age of their first brood at fledging on the number of eggs that a female produced in their second

clutch (ANOVA $F_{1,136} = 0.07$, $P = .791$). However, females that initiated their second clutches later than others produced fewer eggs (ANOVA parameter estimate ± SE = −0.063 ± 0.008; $F_{1,138} = 61.6$, $P < .001$), and the offspring from later-season nests were less likely to be locally recruited as breeders than were offspring produced earlier within the breeding season (GEE parameter estimate ± SE = −0.042 ± 0.008; $\chi_1^2 = 27.0$, $P < .001$).

Discussion

Our results demonstrate that the length of the nestling period is strongly dependent on the magnitude of differences in age and developmental stages among nestmates. As predicted, broods with broad age spans and large differences in maturity among nestlings fledge at an older age than those with narrower age spans, and this delay improves the chances that younger siblings will recruit to the local breeding population (fig. 4). Indeed, older nestlings appear to wait for their younger broodmates to reach some developmental threshold before leaving the nest, because older foster nestlings delayed fledging until their younger broodmates were the same age as nestlings in unmanipulated control broods, and nestlings in broods that received younger foster nestlings also delayed fledging for several days (fig. 3*A*; see fig. 2 in Nilsson and Svensson 1993 for a similar result). Moreover, the delayed fledging of broods with a younger foster nestling was contingent upon whether that younger nestling was still alive near the time of fledging, because broods in which the younger nestling died early in life fledged at the same time as control broods (table 2; fig. 3*B*).

Inclusive fitness benefits for older siblings depend not only on the degree of genetic relatedness but also on the number of siblings with which to cooperate (see also Royle et al. 2012). In our study, inclusive fitness benefits also depend on the degree to which siblings differ in age, because younger nestlings in a brood will always be less well developed than their older siblings. Therefore, whether older nestlings fledge at any particular time is a function of diminishing returns; although older nestlings can gain indirect fitness benefits by remaining in the nest, their inclusive fitness would necessarily increase at a diminishing rate as their younger siblings grow and mature or as the difference in maturity between older and younger siblings is reduced (fig. 1). As predicted, older nestlings in asynchronous broods delayed fledging to a greater extent as the number of younger siblings increased (fig. 2*A*), but synchronously hatched broods did not vary fledging times with respect to brood size (fig. 2*B*). Although brood size did not interact with our experimental manipulations of age structure to determine fledging times, broods with older foster nestlings delayed fledging to a greater extent

than did broods that received a younger foster nestling (fig. 3*A*), which suggests that the number of younger, underdeveloped siblings within a nest also plays a role in determining the time of fledging, because broods with older foster nestlings contained more underdeveloped nestlings than did broods with younger foster nestlings.

An alternative explanation for delayed fledging, however, is that it is an entirely selfish behavior whereby older nestlings delay fledging to continue receiving food from their parents. However, if the hypothesis of a freeloading firstborn were true, synchronously hatched broods, in which earlier-hatched nestlings are the same age as those in asynchronous broods, should delay fledging just as nestlings in asynchronous broods do. Moreover, studies of several other species that directly compared parental provisioning rates to fledglings versus nestlings that remained in the nest after some had fledged found that parents preferentially feed fledglings over nestlings (Lemel 1989; Kopachena and Falls 1993; Nilsson and Svensson 1993). In such cases, fledging earlier than one's younger siblings are capable of doing would be expected if earlier-hatched nestlings selfishly exploit their parents and siblings (Nilsson and Svensson 1993). Finally, Freed (1988) noted that the survival of first-hatched nestlings from asynchronous broods in his study population did not improve by remaining in the nest, as would be expected if their delayed fledging were attributable to the selfish acquisition of food, and this was also the case in our study. Indeed, when the postfledging survival of earlier-hatched nestlings is unaffected by remaining in the nest (i.e., their probability of survival has approached an asymptote and yields diminishing returns; fig. 1), the only way for them to improve their fitness further is to improve the fitness of their younger siblings (Parker et al. 1989). Regardless of whether delayed fledging is caused by freeloading firstborns, their remaining in the nest still increases the time for younger siblings to advance developmentally, thereby increasing the brood's inclusive fitness. From this perspective, freeloading does not directly benefit oneself, but kin.

There is, however, potential for parent-offspring conflict over the age of fledging in seasonally breeding species. Although delayed fledging improves the chances that current offspring survive to reproduce, it might not result in a net fitness benefit for parents if it reduces a parent's ability to invest in future offspring; thus, the adaptive nature of offspring (or parental) behavior should be considered from the perspective of all family members (see also Marshall and Uller 2007; Smiseth et al. 2008; Boncoraglio et al. 2011; Thorogood et al. 2011; Meunier and Kölliker 2012). Many adult house wrens can produce a second brood, and occasionally even a third, if they raise their first brood to independence sufficiently early (Bowers et al. 2012*a*, 2012*b*). Thus, delayed fledging reduces the par-

ents' ability to invest either in future offspring or in self-maintenance (Trivers 1974; Verhulst and Hut 1996; Svensson and Nilsson 1997). Although the fledging age per se of a female's first brood in the current study did not influence her likelihood of producing a second clutch or her clutch size, females initiating their second clutches later than others produced fewer eggs, which suggests that a 2- or 3-day delay in fledging by nestlings may reduce the reproductive success of at least some parents. Thus, parents may have evolved subtle attempts to influence fledging ages that have, as yet, gone undetected. Females in our study population show a high degree of plasticity in the degree of hatching synchrony and frequently switch between the two patterns among broods within and between breeding seasons. Intriguingly, synchronous hatching, which is determined mainly by female incubation behavior, shortens the length of the nestling period relative to asynchronous hatching and is more likely to occur early within the breeding season, whereas asynchronous hatching is more likely to occur later (Pennock 1990; E. K. Bowers, unpublished data), which would be expected if females were attempting to maximize their ability to produce a second brood.

Although parents might be expected to hasten the onset of fledging so that they could produce another brood (by reducing food provisioning to nestlings), this does not seem to be the case in many altricial species (Ceballos and Donazar 1990; Nilsson and Svensson 1993; Bustamante 1994; Michaud and Leonard 2000; Johnson et al. 2004). In house wrens, for example, Johnson et al. (2004) reported that parental provisioning does not decrease before fledging, and there is no evidence that other aspects of parental behavior change before fledging. Examples of parental influence over fledging are generally restricted to nonpasserine species with a very different ecology from that of altricial songbirds (e.g., Corbel and Groscolas 2008; Corbel et al. 2009; Riou et al. 2012). For example, in many seabirds, nestling development can require several months, and the success of parents' future reproduction depends on the time that current offspring gain independence; thus, parents are highly constrained in the time available for nestling development (Corbel et al. 2009). For songbirds, however, the duration of nestling development is relatively short compared with the span of time over which resources needed for reproduction are abundant. At our study site, there is an abundance of arthropod prey beginning in April and lasting for several months (Johnson 1998), yet the nestling period only spans approximately 2 weeks; thus, with stable prey availability and short periods of nestling development, the cost to parents of prolonging care for a few extra days may be sufficiently small that it is outweighed by the positive effect that delayed fledging has on the survival of their current offspring (fig. 4), particularly

when potential future offspring are much less likely to survive. Therefore, although delayed fledging may reduce a parent's future fecundity to some degree, their fitness may be maximized by prolonging care for current offspring, because these offspring are a parent's best hope of maximizing their fitness. For example, in a recent cross-fostering experiment on zebra finches *Taeniopygia guttata*, broods of nestlings were swapped among nests so that nestlings differed in age relative to the amount of time parents had already invested in provisioning. Parents adjusted the duration of feeding according to the developmental state of their foster offspring so that the age at which nestlings fledged was the same across treatments, regardless of how much provisioning their foster parents had done before cross-fostering (Rehling et al. 2012). It must be acknowledged, however, that these caged birds were provided food ad lib., and so we advise caution in generalizing these findings to natural settings.

Because the parents of altricial songbirds do not appear to adjust their behavior to influence the time of fledging, signals transferred among siblings likely communicate when the process should begin. The question that arises, then, is what cues do offspring use to determine when they should leave the nest? Viñuela and Bustamante (1992) suggested that younger nestlings could signal their developmental state to their older siblings behaviorally, particularly through wing flapping and jumping vertically within the nest, which is done to train muscles used in flight. Thus, the time at which most or all nestlings in a brood begin exercising their flight muscles simultaneously or begin approaching the nest exit (Nilsson and Svensson 1993; Radersma et al. 2011) may cue earlier-hatched, older individuals that their younger siblings are ready to leave the nest. At a proximate level, the glucocorticoid corticosterone appears to play a causal role in this process, with circulating levels of this hormone gradually increasing during the ontogeny of altricial nestlings and peaking at fledging (Heath 1997; Schwabl 1999; Love et al. 2003a, 2003b). Moreover, an experimental increase in corticosterone in the eggs of the altricial European starling *Sturnus vulgaris* had a positive effect on juvenile flight-muscle development and flight performance (Chin et al. 2009). Therefore, this hormone, which functions to promote the mobilization of energetic reserves, may play an important role in the transition from sedentary to active nestlings in the time leading up to fledging and the energetic demands of flight.

Although sibling interactions are often characterized by intense competition over parental resources (Mock and Parker 1997; Boncoraglio et al. 2009a, 2009b; Mock et al. 2011), this may be mitigated by their genetic relatedness (Parker et al. 1989). For example, resource competition among nestling barn swallows *Hirundo rustica* is lower and survival is higher among full-sib nestlings than among more distantly related nestmates (Boncoraglio and Saino 2008; Boncoraglio et al. 2009a). Thus, cooperation among altricial siblings may be more prevalent than previously thought (Royle et al. 1999; Forbes 2007; Romano et al. 2012). Hamilton's rule suggests that even a behavior that is costly to one's personal fitness can evolve if the behavior increases the fitness of individuals genetically related to the one expressing it (i.e., the actor), but the resultant benefit to the actor's inclusive fitness must outweigh the cost, if any (Hamilton 1964; West et al. 2007; Gardner et al. 2010). Indeed, the costs of delayed fledging to older siblings' inclusive fitness can manifest themselves in a number of ways, including both a reduction in the number of future siblings that parents might produce and any potential reduction in the survival of future siblings that is attributable to their delayed fledging. However, several lines of evidence suggest that the benefit an individual's current siblings obtain from delayed fledging outweigh the costs of that delay for their future siblings. First, offspring produced early in the breeding season have no guarantee that their parents will produce siblings in the future. Second, of those parents that produce another brood, the majority switch mates between broods (Drilling and Thompson 1991; Poirier et al. 2003), which reduces the average genetic relatedness between a current nestling and any future siblings that its parents produce. Finally, offspring produced late in the breeding season are much less likely to survive and reproduce than those produced earlier in the season and are thus less valuable to an individual's inclusive fitness than its current siblings. Therefore, selection may promote a form of selfish cooperation to increase the fitness of an individual's current siblings despite the potential costs to possible future siblings.

In addition to the costs of delayed fledging for an individual's inclusive fitness that are incurred by reducing the potential number of future siblings, remaining in the nest for an extended period of time prolongs the duration that an individual and its siblings are exposed to predators and parasites, thus generating potential costs for an individual's personal fitness. Applying Hamilton's rule to earlier-hatched siblings, the costs of delayed fledging to their personal fitness likely vary with the daily nest-predation rate, for example, as determined by nest type (i.e., open- vs. cavity-nesting species; Martin and Li 1992). However, the benefit of delayed fledging to their inclusive fitness should be similar across a gradient in predation risk, because nestmates are always closely related, assuming no brood parasitism and moderate to low levels of extra-pair paternity, conditions that are met in our study population (Soukup and Thompson 1997; Forsman et al. 2008). Thus, if the benefit of delayed fledging to inclusive fitness is similar and invariant across habitats or contexts for any given species, varying risk of predation should

determine whether older nestlings delay fledging. Given the evolutionary flexibility of offspring developmental periods (Remeš 2006), kin selection may favor delays in fledging by the oldest members of a brood when the risk of nest predation is low (fig. 1*B*), but this force may be overcome as predation risk increases (fig. 1*A*). We therefore propose that a trade-off between the inclusive fitness benefits of cooperating with one's younger siblings and the risk of predation to one's personal fitness contributes to inter- and intra-specific variation in the duration of offspring development and the age at which offspring leave the nest.

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Associate Editor: Thomas N. Sherratt
Editor: Judith L. Bronstein

The inside of a nestbox with an inspiring message for its occupants. Photograph by Keith Bowers.