Parental benefits and offspring costs reflect parent–offspring conflict over the age of fledging among songbirds

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Parent–offspring conflict has explained a variety of ecological phenomena across animal taxa, but its role in mediating when songbirds fledge remains controversial. Specifically, ecologists have long debated the influence of songbird parents on the age of fledging: Do parents manipulate offspring into fledging to optimize their own fitness or do offspring choose when to leave? To provide greater insight into parent–offspring conflict over fledging age in songbirds, we compared nesting and postfledging survival rates across 18 species from eight studies in the continental United States. For 12 species (67%), we found that fledging transitions offspring from comparatively safe nesting environments to more dangerous postfledging ones, resulting in a postfledging bottleneck. This raises an important question: as past research shows that offspring would benefit—improve postfledging survival—by staying in the nest longer: Why then do they fledge so early? Our findings suggest that parents manipulate offspring into fledging early for their own benefit, but at the cost of survival for each individual offspring, reflecting parent–offspring conflict. Early fledging incurred, on average, a 13.6% postfledging survival cost for each individual offspring, but parents benefitted through a 14.0% increase in the likelihood of raising at least one offspring to independence. These parental benefits were uneven across species—driven by an interaction between nest mortality risk and brood size—and predicted the age of fledging among species. Collectively, our results suggest that parent–offspring conflict and associated parental benefits explain variation in fledging age among songbird species and why postfledging bottlenecks occur.

bottleneck | fledging | parent–offspring conflict | postfledging | songbirds

Conflict between parents and offspring can arise from disagreements over how long periods of parental care should last (sensu, ref. 1). This occurs as extending parental care can enhance offspring fitness, but for adults, the benefits of continuing care are eventually outweighed by costs to future reproduction and survival (2). Consequently, parent–offspring conflict theory proposes that the optimal length of parental care differs between parents and their offspring, with offspring preferring care to continue for a longer duration than that preferred by adults (1, 3). The length of parental care and optimal timing of independence in animals may therefore be reflective of complex behavioral interactions between parents and offspring as they resolve this evolutionary conflict (4). Though likely strongest over the optimal timing of offspring independence (1), parent–offspring conflict also mediates the timing of other juvenile transitions during the period of parental investment. The age at which animals leave their nests, for instance, can

be regarded as a result of interactions between parents and their offspring. Thus, even though offspring may still be dependent on their parents after leaving the nest, the age at which they leave can depend on the outcome of conflict between parent and offspring interests (5).

In birds, research has shown that the age of fledging (nest leaving) is primarily associated with nest mortality risk (6–10), but for many taxa, there is compelling evidence that this timing is also mediated by parent–offspring conflict (summarized in ref. 3). One exception to this pattern, however, is in songbirds, where the role of parent–offspring conflict remains understudied, unclear, and controversial (2). Studies on fledging in songbirds have centered around a debate over two hypotheses: 1) the parental manipulation hypothesis (PMH), in which parents and offspring are in conflict over the optimal age of fledging and parents initiate fledging by manipulating offspring (11); and 2) the nestling choice or threshold

Significance

Parent–offspring conflict has explained a variety of ecological phenomena across animal taxa, but its role in mediating when songbirds fledge remains controversial. Our analysis of nesting and postfledging survival rates within 18 songbird species found that offspring commonly leave safer nesting environments for riskier postfledging ones—known as postfledging bottlenecks. This timing of fledging incurs a cost for offspring survival, but benefits adults by increasing their likelihood of raising at least one offspring to independence. Parents therefore appear to manipulate offspring into fledging earlier than expected based on the offspring's ensuing survival prospects. Our results suggest that parent–offspring conflict and associated variation in parental benefits explain variation in fledging age among songbird species and why postfledging bottlenecks occur.

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size hypothesis (NCH), in which parents and offspring are not in conflict and fledging is initiated by other factors only after offspring pass a developmental threshold (11, 12). Perpetuating debate between these hypotheses are studies that focus on the proximate factors (parental and offspring behaviors) of fledging. For instance, past studies have provided evidence in support of the PMH by documenting manipulative behaviors of adults, such as luring offspring with food or reducing their provisioning rates (5, 13, 14), but other studies have dismissed such observations as anecdotal or misinterpretations of adult behavior (2, 15). Additionally, studies on these hypotheses have failed to acknowledge an apparent paradox with respect to fledging. Songbird offspring may be subject to postfledging bottlenecks, whereby survival rates immediately following fledging are significantly lower than those in the nest (16), with offspring transitioning from a safer nest environment to a more dangerous postfledging one. As experimental and comparative postfledging work shows that songbird offspring benefit in terms of development and survival by staying in the nest longer (e.g., refs. 17, 18), this raises an important question: If offspring are safer and benefit by staying in the nest, why then, do they fledge so early?

Consideration of the ultimate factors of fledging (fitness perspectives of parents and offspring) has the potential to provide novel insights into this paradox, the PMH, NCH, and the role of parent–offspring conflict in mediating fledging age. As shown in a recent paper by Martin et al. (17), offspring survival rates can be used as proxies for fitness and address the costs and benefits of fledging from the perspective of parents and their offspring. For individual offspring, fitness is largely dependent on their own survival, and selection should favor behaviors that optimize their chances of survival, such as fledging when nest mortality is roughly equivalent to postfledging mortality risk (11). Parental fitness, however, is expected to differ from their offspring as their fitness is influenced by the survival of any offspring within a brood (17). This is the case as nest predation usually claims an entire brood, while fledglings are dispersed in space and the brood is usually not entirely predated (reviewed in ref. 19). Parents could therefore benefit from manipulating offspring into fledging at earlier ages, optimally when the probability of losing the entire brood outside of the nest becomes lower than losing the entire brood in the nest (17). Benefits for parents in terms of relatively early fledging could come at survival costs to individual offspring, however, resulting in postfledging bottlenecks. If true, this would suggest that parents manipulate offspring to fledge earlier to increase their own fitness prospects, even at the cost of survival to each individual offspring. Furthermore, if such parental benefits are uneven with respect to nest mortality risk, then parental benefits may explain the association between nest mortality risk and age at fledging among species (6–10).

As such, comparing survival before and after fledging may provide important evidence for or against the PMH and NCH, explain the paradox of postfledging bottlenecks, and by proxy, empirically evaluate the importance of parent–offspring conflict in the fledging age of songbirds. Under such comparisons, we would predict that: 1) if nestlings choose when to leave the nest, for nestling and fledgling survival to be roughly equal and for nest mortality alone—not parental benefits of fledging—to explain age at fledging among species (NCH and no bottleneck); 2) if parents manipulate offspring, for nestling survival to be greater than fledgling survival, the probability of losing an entire brood to be lower outside of the nest than in it, and parental benefits—as a result of nest mortality—to predict the age at fledging across species (PMH and a bottleneck); fledging ages should benefit parents in terms of brood survival, but come at the cost of postfledging survival for each individual offspring.

Here we use the theory from Trivers' (1) classic work to provide greater insight into when and why juvenile songbirds leave the nest. To do so, we compared nestling and fledgling survival rates for 18 species across eight study locations in Florida, Illinois, Ohio,

Pennsylvania, and Texas. First, we estimated daily survival rates for juveniles across the nesting and postfledging period and compared rates immediately before and after fledging. Second, we used daily survival rates to derive probabilities of mortality for the entire brood and compared brood mortality rates before and after fledging. Third, we used daily survival rates to estimate cumulative survival for offspring across the postfledging period. Lastly, we used nesting and postfledging survival rates to derive estimates of parent–offspring costs and benefits (daily survival rates per individual and per brood) of earlier fledging under scenarios where a bottleneck does and does not occur. Overall, the goals of our study were to use these survival estimates and comparisons to 1) provide evidence to support or refute the NCH and PMH; 2) test for prevalence, severity, and length of postfledging bottlenecks; and 3) empirically evaluate the influence of parent–offspring conflict on variation in the age at fledging among species by 1) estimating costs and benefits of the age at fledging for parents and offspring and 2) examining associations between nest mortality risk, age at fledging, and costs and benefits associated with parents and offspring in this conflict.

Results

Comparisons of nesting and postfledging survival rates (per-offspring basis) showed that, although there were cases where stage-specific rates were roughly equal (33%), daily mortality rates of fledglings following fledging (1–5 d) exceeded those of nestlings for most species (67%). Furthermore, probabilities of brood survival for all species were better outside than within the nest, providing evidence in favor of the parental manipulation hypothesis. Evidence of postfledging bottlenecks was detected for 12 of 18 species (Figs. 1 and 2). The severity of bottlenecks ranged from a 5.7 to 25.3% reduction (mean = 16.2% 1.9 SE) in daily survival upon leaving the nest and lasted for 1 to 5 d (mean = 2.5 0.3 SE). Bottlenecks occurred across nest types, nest heights, brood sizes, nestling period lengths, nest mortality risk, and habitat type (Fig. 3B and *SI Appendix,* Table S1).

For offspring, earlier fledging decreased daily survival by an average 9.2% (1.4% SE), resulting in an average 13.6 (1.1% SE) decline in cumulative postfledging survival under a bottleneck scenario compared to if no bottleneck had occurred (see *Materials and Methods* for details on calculations). Under scenarios where postfledging bottlenecks occurred, earlier fledging improved the daily probability of at least one fledgling of a brood surviving the immediate days postfledging by an average 6.0% (1.0% SE) relative to if no bottleneck had occurred. Extending these benefits across the postfledging period resulted in an average 14.0% (1.8% SE) increase in the likelihood of parents having at least one offspring survive until independence. As nest mortality rates increased, parents derived more fitness benefits (increase in daily brood survival) from offspring fledging at earlier ages ($\beta = 1.165$, $t = 11.32$, $P < 0.001$; Fig. 3A). Variation in nest mortality risk therefore resulted in a gradient of parental benefits following fledging (Fig. 3A), which predicted age at fledging among species ($\beta = -50.812$, $t = -2.61$, $P = 0.020$; Fig. 3B). Our post hoc analysis on the effects of brood size, nest mortality risk, and their interaction on parental benefits revealed a significant interaction ($\beta = 0.317$, $t = 5.08$, $P < 0.001$). The benefits of early fledging to adults generally tracked risk of nest mortality, but gains were context dependent. Adults with large broods derived the most benefits by fledging early in risky environments (e.g., low nesting grassland and shrubland species; *Right* side of interaction, Fig. 4) and delaying fledging when the risk of nest mortality was low (e.g., cavity nesting species; *Left* side of the interaction, Fig. 4).

Discussion

Our results provide evidence for the parental manipulation hypothesis and suggest that parents manipulate their offspring into
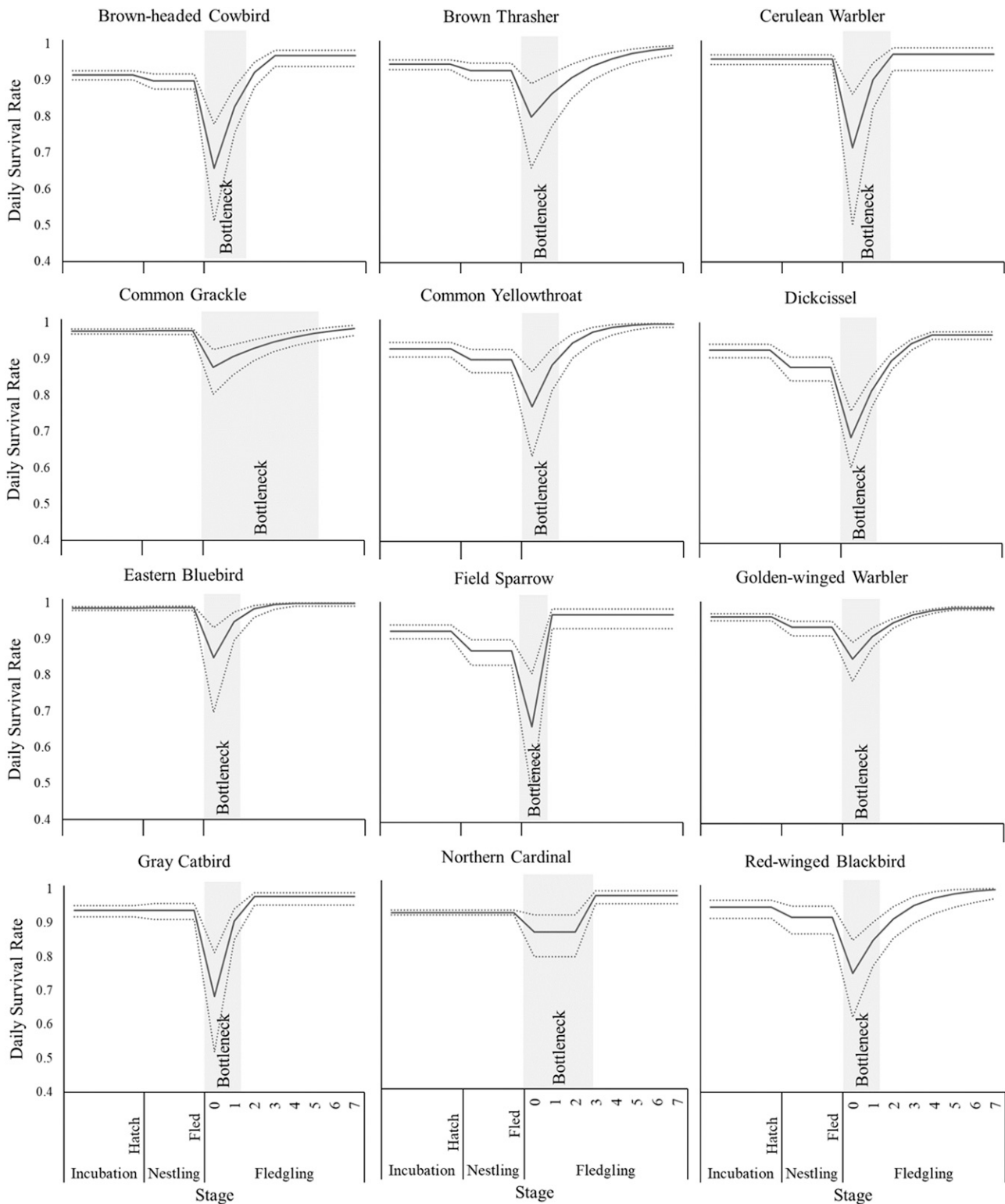
Fig. 1. Per-offspring daily survival rates of juvenile songbirds across the nesting and early postfledging period. Survival rates show clear bottlenecks (>5% drop in survival) during the immediate days after fledging ("postfledging bottleneck", gray boxes). Dashed lines represent 95% confidence intervals.

fledging at younger ages to improve their own fitness prospects, even at the cost of survival for each of their offspring, reflecting parent–offspring conflict. By spatially separating offspring and diluting mortality risk to the entire brood earlier, parents can benefit by greatly increasing the odds that at least one offspring survives until independence. Notably, parental benefits from earlier fledging varied among species depending on the interaction between risk of nest mortality and brood size (Fig. 4) and predicted fledging age across species (Fig. 3B). Collectively, our results are consistent with findings across other avian taxa that
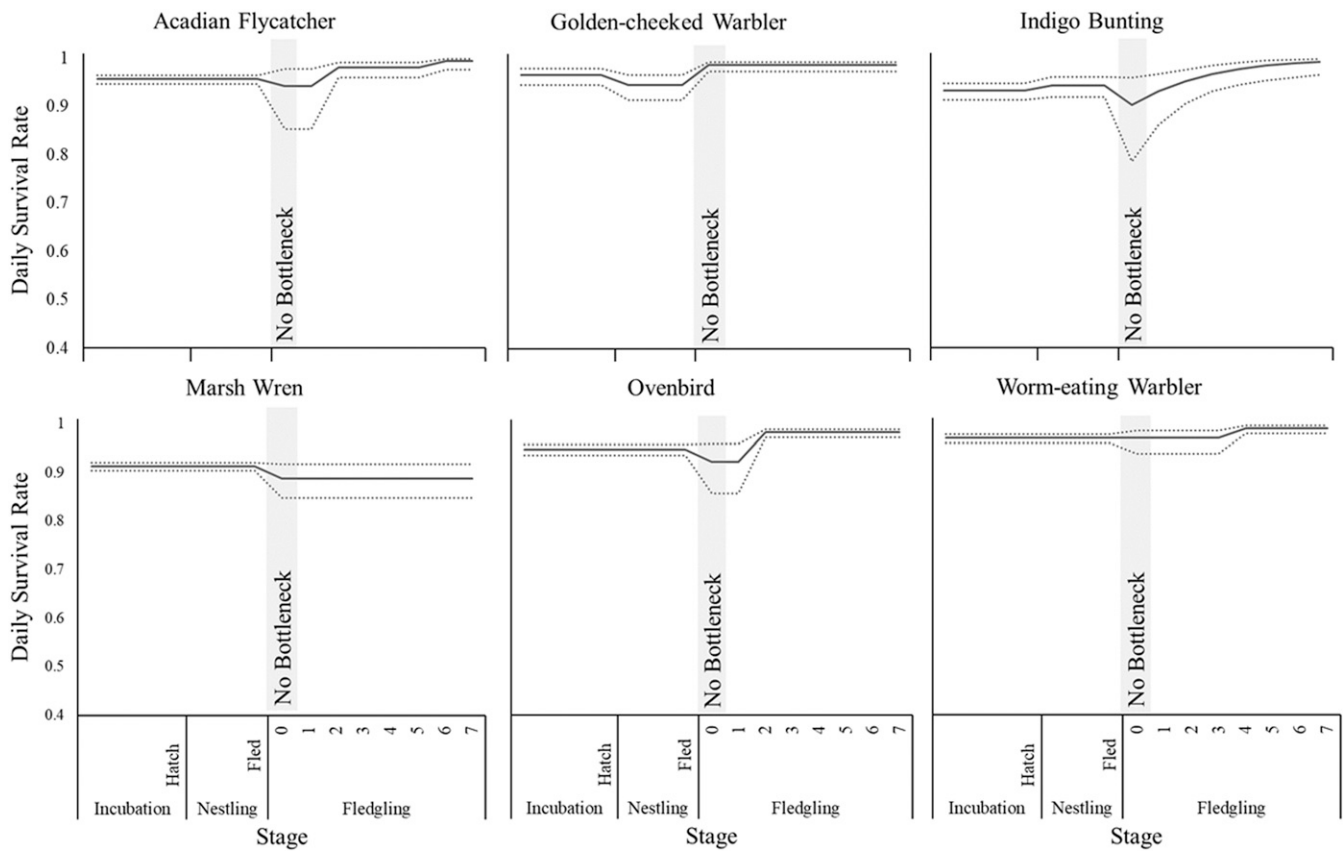
Fig. 2. Per-offspring daily survival rates of juvenile songbirds across the nesting and early postfledging period. Survival rates show little to no bottleneck (<5% drop) in survival during the immediate days after fledging. Dashed lines represent 95% confidence intervals.

parent–offspring conflict mediates fledging age among species (summarized in ref. 3) and explain why postfledging bottlenecks occur.

Our findings suggest that postfledging bottlenecks occur across many songbird species (Fig. 1), supporting findings of Naef-Daenzer and Grüebler (16). Furthermore, our findings show that bottlenecks vary markedly in their severity and length, can occur regardless of life history characteristics (e.g., nest types, nest heights, brood size, nestling period length, nest mortality risk, etc.) and habitat preferences, and further corroborate past research demonstrating the importance of the postfledging period for first year survival (20), the dynamics of avian populations (21), and life history evolution (17, 22). Our results are also consistent with past research documenting bottlenecks during juvenile life stages across a wide variety of taxa (e.g., refs. 23–25).

Past research has suggested that songbird offspring fledge earlier to escape high rates of nest mortality (7, 8); however, such behaviors would appear to be maladaptive, given postfledging bottlenecks found in our study, highlighting an apparent paradox. Furthermore, experimental evidence suggests that offspring would benefit from staying in the nest longer in terms of development and survival (17). As such, a key question remained unanswered: If offspring are safer and would benefit more by remaining in the nest, why then, do they fledge so early? Our analysis shows that earlier fledging of offspring accrues greater fitness benefits to parents under higher risk of nest mortality (Fig. 3A), whereas benefits for parents are negatively correlated with offspring fledging age (Fig. 3B). Parental benefits are not mediated in response to mortality risk alone, however, as spatially separating more offspring can further dilute mortality risk to the entire brood after fledging. Thus, if brood size and

mortality interact to better align fitness perspectives of parents and offspring, then parents may gain few to no benefits from manipulating offspring into fledging earlier (e.g., a brood size of 1). Like Martin et al. (17), our findings therefore suggest that the paradox between nest mortality risk and fledging age is explained by variation in parental benefits—and presumed manipulation—resulting from a key interaction between nest mortality risk and brood size. Notably, in some species parents may further dilute postfledging brood risk by dividing the brood between them (e.g., refs. 26–28). Though we were unable to assess this for all species and there may be other benefits to dividing offspring (e.g., parental foraging economics), brood division appears to be the last step that parents could take to ensure at least some reproductive success in a breeding season.

As mortality risk and clutch size can vary within species, this raises an important question: Do parents and their offspring alter their behaviors (i.e., fledging age, manipulative behaviors) in response to real-time changes in mortality risk and brood size? Predator playback experiments altering perceived predation risk (e.g., ref. 29) and experiments manipulating brood size (e.g., ref. 30) could be conducted to provide greater insights into this question. Or alternatively, observational studies could be conducted or compared to investigate differences in the magnitude and duration of bottlenecks within species. For instance, while we found no bottleneck in our ovenbird population, low postfledging survival rates found in King et al. (31) and Jenkins et al. (32) suggest that postfledging bottlenecks likely occur elsewhere, or vary annually, in the species. There might also be unique opportunities to understand the relationship between nest mortality risk and fledging age. For example, Bosque and Bosque (7) found that mainland species introduced to safer islands had
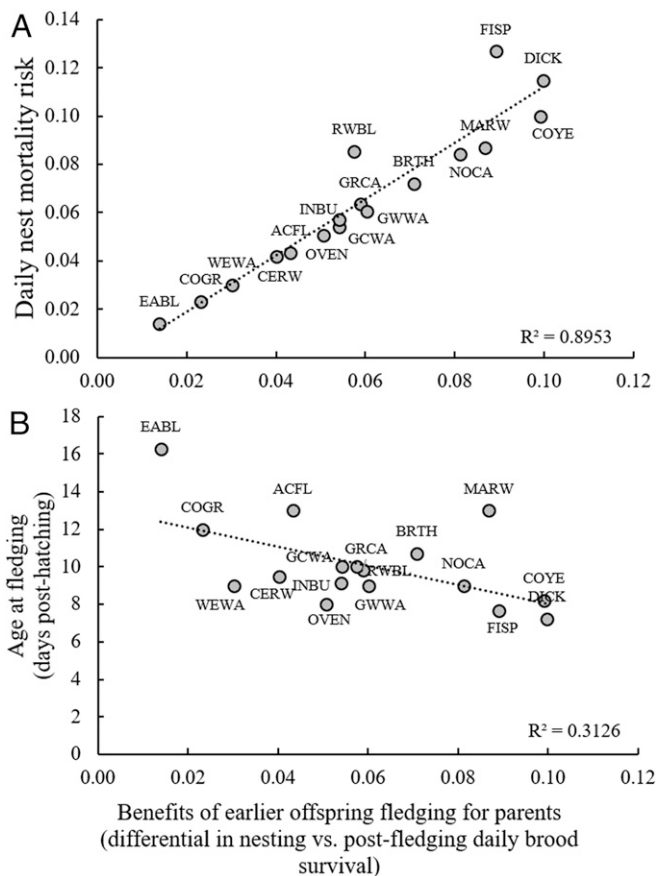
Fig. 3. Songbird offspring often fledge earlier than expected, when their risk of mortality is higher outside of the nest than in it. This earlier fledging can benefit parents, however, as spatially separating offspring can increase daily brood survival compared to a scenario where offspring remain in the nest. Therefore, differentials in nesting (i.e., broods stay in the nest) versus postfledging (i.e., broods leave the nest) daily brood survival reflects fitness benefits parents accrue as a result of earlier fledging by offspring. As earlier fledging benefits parents while incurring a cost to individual offspring—implying conflict between the generations—differentials in brood survival should also reflect parent–offspring conflict over fledging age. Across species (n = 17), differentials in daily brood survival show that (A) earlier fledging of offspring accrues greater fitness benefits to parents under higher risk of nest mortality, and (B) differences in parental benefits predict the age of fledging among species. Combined, these associations suggest that parent–offspring conflict mediates variation in the age of fledging among species. Postfledging daily brood survival was averaged for the length of each species' postfledging bottleneck period (range 1 to 5 d; 1 d for species that did not exhibit a bottleneck). Abbreviations (four letter codes) for study species are as follows: ACFL (Acadian Flycatcher), BRTH (Brown Thrasher), CERW (Cerulean Warbler), COGR (Common Grackle), COYE (Common Yellowthroat), DICK (Dickcissel), EABL (Eastern Bluebird), FISP (Field Sparrow), GCWA (Golden-Cheeked Warbler), GWWA (Golden-Winged Warbler), GRCA (Gray Catbird), INBU (Indigo Bunting), MARW (Marsh Wren), NOCA (Northern Cardinal), OVEN (Ovenbird), RWBL (Red-Winged Blackbird), and WEWA (Worm-Eating Warbler). Calculations of parental benefits can be found in Dataset S1.

similar incubation and nestling periods as their place of origin; this raises the question: How many generations might be needed for selection to act on various behaviors associated with age at fledging? Future research will be needed to determine the extent to which bottlenecks vary across space and time and the consequences of such variation on the behavioral ecology of songbirds.

While we did not examine parent–offspring behaviors and thus cannot confirm whether (or how) parents manipulate their offspring into fledging, our findings on the brown-headed cowbird

(*Molothrus ater*) provide evidence in favor of the parental manipulation hypothesis. Utilizing a rare breeding strategy known as brood parasitism (placing eggs into other species nests), cowbirds are known to parasitize over 200 host species (33), and as such, their offspring are not evolved for a specific host's nesting ecology. Thus, under the nestling choice hypothesis, we would expect cowbirds to leave their nest at the same age and stage of development regardless of the host species, yet cowbirds are known to fledge across a wide range of ages and stages of development (8 to 13 d) (34) *SI Appendix*, Fig. S1). Additionally, cowbirds left their nests earlier than expected based on evolutionary theory (Fig. 1), and results from a concurrent study suggest the age that cowbirds fledge is largely influenced by the age at which the host young fledge their nests (*SI Appendix*, Fig. S1). As such, the behavior of cowbird offspring suggests that, like their host siblings, their age of fledging may be mediated by parent–offspring conflict.

Parent–offspring conflict may indeed drive postfledging bottlenecks and fledging age among songbirds; however, there are several alternatives and caveats that may explain our findings. First, regardless of what age they leave their nest, there is likely an inherent cost in survival for offspring to fledge. All offspring of nesting animals are inexperienced upon leaving the nest, and such inexperience may manifest itself in terms of higher mortality while offspring learn to forage for food while avoiding predation. Inexperience appears unlikely to cause bottlenecks alone, however, based on our findings and those of Martin et al. (17). Experiments prolonging the nestling period have shown that offspring can benefit in terms of development and survival by staying longer in the nest (17). Furthermore, we found that roughly one in three species did not exhibit a bottleneck, providing examples of where inexperience alone was not enough to cause a significant decline in survival. Second, songbird offspring could be timing their fledging to benefit their siblings and improve their inclusive fitness (i.e., kin selection) (35, 36). Though more study is needed, altruistic acts by nestlings appear unlikely for species experiencing high nest mortality rates and given known rates of promiscuity and extra pair young among songbird species (37). Finally, a key assumption of our research is that nest survival remains constant if offspring would remain in the nest for the duration of the bottleneck period. While data from our research suggest this is likely the case (constant models best describe nestling survival for most species), this assumption remains poorly tested and warrants further inquiry.

Our results and findings from recent studies (17) provide greater insight into the ultimate factors driving fledging, but questions about the proximate factors remain: Are parents
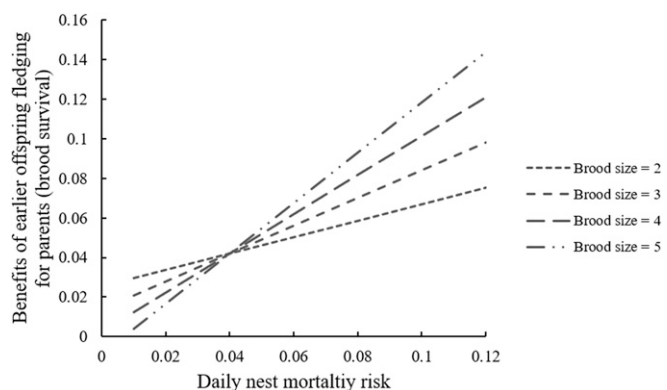
Fig. 4. An interaction between daily mortality risk and brood size predicts benefits to parents as a result of earlier fledging ages of offspring. Fitness benefits for parents reflect reduced probabilities of losing an entire brood due to earlier fledging by offspring.

manipulating their offspring into fledging, and if so, how? Have offspring evolved tactics to resist such manipulation (e.g., ref. 38)? Are fledging ages the result of resolved conflict or active manipulation by adults (e.g., ref. 39)? And if some offspring initiate fledging, what factors are associated with when they leave? To answer these questions, experimental research will be needed to disentangle behaviors of adults and their offspring. For example, cross-fostering different aged broods within species allows recording of parental behavior independent of offspring age and determination of fledging age independent of the amount of parental investment (5). Such experiments could therefore identify potential behaviors parents and offspring use to manipulate each other and the cues which trigger such behavior. This includes identifying more hidden aspects of adult behavior that may have been missed in past studies, such as parents deserting broods after a set period of parental care (14) or nest size/structure, where adults build their nests so that offspring are forced to fledge due to overcrowding or deterioration. Similarly, fostering broods of species with shorter nestling periods into those with much longer periods allows for observation of offspring behavior independent of parental manipulation. Thus, whether fostered broods stay or leave at the expected fledging age should provide important evidence as to whether fledging age is a result of voluntary behaviors of offspring or active manipulation by adults.

Conclusions

Our study provides greater insight into the factors driving when and why songbirds leave their nests as well as the prevalence of postfledging bottlenecks. While in a third of cases offspring may have initiated fledging, most species exhibited either improved parental benefits from offspring leaving the nest or a postfledging bottleneck, and therefore support the PMH. Studies have commonly identified mortality risk as a critical factor influencing the timing and age at which offspring transition from one life stage to the next (2, 10, 24, 40–44). While mortality risk still plays a critical role, our findings are in line with those found in other avian taxa (3), suggesting that for birds and other animals with parental care, the age of offspring during key transitions may also be mediated by conflicts between parents and their offspring (17). For many songbirds, parent–offspring conflict appears to mediate earlier fledging in response to higher risks of nest mortality, resulting in key tradeoffs between nest mortality risk and nestling period length observed across songbirds (7, 8, 40). These tradeoffs, in turn, appear to result in a series of events driving variation in trait development, pre- to postfledging carryover effects, postfledging bottlenecks, and differential postfledging survival which explain life history variation among species (17, 18, 22). Ultimately, our research highlights how incorporating estimates of fitness and theory on parent–offspring conflict can aid in improving our knowledge of the behavioral ecology of birds and other animals.

Materials and Methods

Though data for our study were derived from 18 species in eight different locations, methodologies were consistent across studies, with only a few minor differences in field techniques [see *SI Appendix*, Table S1 for full species list and associated studies (18, 27, 28, 45–50) for more details]. For each species, trained field assistants searched for and monitored nests across the breeding season by systematic searching and observing adult behaviors. For cavity nesting species, we either established or monitored previously established nest boxes throughout the field season. Nests were monitored every 1 to 6 d until they either failed or fledged young, with nests checked more frequently (every 1 or 2 d) as fledging approached. For each brood where at least one nestling fledged, nestlings were radio-tagged several days before fledging or on the actual day of fledging. In cases where nestlings fledged prior to our visit, we searched the surrounding vegetation to capture and tag individuals. For nestlings tagged on the day of fledging, we did our best to limit the potential effects of force fledging. In cases where nestlings

force fledged, we were able to recapture them and return them to the nest after processing. After returning them to the nest, we placed a bag over the nestlings for 5 to 10 min, which was enough to calm them down and for them to remain in the nest. As a result, we had occasions where nestlings were force fledged, captured, processed, and then returned to the nest and were resampled (in the nest) the next day (18). To estimate postfledging survival, we tracked individuals every 1 to 3 d after they fledged using a handheld receiver and antenna. We monitored each individual until they either died, dispersed, or their radio's battery failed (20 to 60 d depending on the species and whether an individual survived). We determined fledglings to have died if we tracked a signal back to a dead fledgling, a predator, or when we were unable to find a signal (after multiple days and attempts) for fledglings that were too young to have dispersed (18).

Statistical Analyses. To ensure all variables of interest were comparable among species, we reanalyzed all raw data under a standardized statistical approach. First, we estimated daily survival rates (DSRs) for nests of each species using the logistic exposure method in program MARK or SAS (51–53). For 1 of our 18 species, the brown-headed cowbird—a brood parasite that lays its eggs in other species nests to avoid the energetic demands of raising young (33)—we only used host nest records for which a cowbird egg or nestling was present and included host species as a random effect in our logistic exposure model. We note that we included the brown-headed cowbird in our study as cowbird offspring are genetically unrelated to their hosts, providing a unique perspective on parent–offspring conflict and the age of fledging among songbirds. For most species (12 of 18), we also calculated DSRs for the incubation and nestling period. Because nest survival may decline as nestlings age due to increased begging and provisioning by adults [reviewed in Martin and Briskie (54)], where possible, we explicitly tested for this possibility but only found evidence of decline in two species. As these declines did not qualitatively alter our findings, we deferred to our standardized approach.

We estimated age-specific DSRs of fledglings using multistate models in the program MARK. For each species, we reanalyzed postfledging data following methods in Jones et al. (47). We first assigned fledgling observations to either an alive or dead state, then fixed absorbing states (dead to dead, dead to alive) to zero and survival probabilities to 1, and estimated DSRs using transition probabilities (Ψ) where birds remained in the alive state. Past postfledging research has demonstrated fledging age as the main predictor of fledgling survival in songbirds (reviewed in refs. 16, 21). Thus, we incorporated age structures before deriving DSR estimates. For each species, we examined a total of 10 models with a priori hypotheses of age structure predicting DSRs of fledglings. More specifically, we used seven hypotheses derived from past postfledging studies (same among species), two models based on the timing of fledgling mortality for each species (unique for each species), and a null model (constant survival rate). We selected our top age models based on Akaike's information criteria adjusting for small samples size (AIC$_c$) (55), from which we derived our postfledging DSRs for each species. If the null model was within 2 delta AIC$_c$ of our top model, we presumed the null model was competitive and best reflected the age structure of the species. If the null was greater than 2 AIC$_c$ from the top model, then we selected the top model based on AIC$_c$ rank. We also took the product of these daily survival rates to calculate cumulative rates of survival across the postfledging period (up until 28 d postfledging, a point past which most fledglings survived and have acquired independence from their parents) (18). Age-mortality structures for species can be found in *SI Appendix*, Table S2. DSRs by nest stage and fledgling age for all species are listed in Dataset S1 in the supplementary materials.

To test for the presence of postfledging bottlenecks, we compared DSRs immediately before (our constant nestling DSRs) and after fledging (the first 1 to 5 d postfledging, which varied by species). We considered a bottleneck to be present if we observed a 5% or more reduction in daily survival following fledging, and if the lower 95% confidence interval for nest survival did not overlap the upper 95% confidence interval of postfledging survival by more than 5%.

We calculated costs and benefits of fledging age for parents and offspring using daily probabilities of a whole brood being lost and daily rates of offspring survival (per-offspring basis) across the postfledging period, respectively. Specifically, we tested for how mortality would differ if offspring would have stayed in the nest (nest mortality rates) versus leaving the nest (postfledging mortality rates). As such, benefits for adults were calculated as the difference in daily brood survival in and out of the nest (Fig. 3; nesting versus postfledging brood survival), while costs to offspring were calculated as the difference in per-offspring nestling and fledgling survival (Figs. 1 and 2). To compare brood survival in and out of the nest, we used daily nest

survival rates as estimates of brood survival in the nest, as when a nest is predated the entire brood is usually lost (19). In contrast, broods are spatially separated upon leaving the nest, making brood survival dependent on survival probabilities of individual offspring. Thus, to calculate brood survival out of the nest we first determined the average DSR during the bottleneck period via the product of bottleneck DSRs raised to the power of 1 over the bottleneck length: e.g., 2-d bottleneck, $X = (DSRday0 \times DSRday1)^{\wedge}(1/2)$. Brood survival was calculated as the probability that at least one offspring survives, which is 1 minus the probability that all offspring die; daily mortality rate during the bottleneck $(1-DSRbottleneck)$ raised the power of the brood size (^broodsize). Thus, we calculated brood survival out of the nest via the following formula: $X = 1-((1-DSRbottleneck)^{\wedge}broodsize)$. We then subtracted brood survival in the nest from survival out of the nest to calculate parental benefits of earlier fledging (for the full set of calculations see Dataset S1). Adult benefits for offspring fledging for species without bottlenecks were also calculated in the same way; by taking the difference between survival of the brood in and out (day 0 of the postfledging period) of the nest. As cowbird parents do not directly care for their offspring during this period, we did not include the species in our analyses regarding brood survival.

Because we found a large difference in the benefits for parents across species, we used general linear models (Proc Glm) (51) to examine interspecific associations between nest mortality risk, age at fledging, and parental benefits to try to determine why differences occur. As more offspring result in increased dilution of mortality risk to the entire brood outside of the nest, species with larger broods should gain a greater benefit from earlier fledging as mortality risk to nests increases. Thus, we conducted a post hoc analysis in which we examine the effects of brood size, nest mortality risk, and an interaction between the two parameters on the parental benefits (improvement in brood survival) of earlier fledging (Proc Glm) (51). To account for a potential confound of species size, we included species mass as a covariate in all our models. The effect of mass was insignificant and did not qualitatively change the results for any of our models and was subsequently dropped from our analyses (SI Appendix, Table S3).

For our comparative models, we attempted to correct for phylogenetic effects using phylogenetic generalized least squares (PGLS) analyses. For each model, we obtained a phylogenetic (consensus) tree via methods in Burleigh et al. (56) and used our estimates in a PGLS analysis with the Caper (57) package in R v3.5.2 (R Development Core Team) to test for a phylogenetic signal (λ). For both models, our dataset did not provide enough information to derive a reliable estimate of λ. Thus, we specified PGLS models with λ fixed at 1 (maximum signal) and compared results with our original models to see if phylogenetic corrections altered our results. Results from phylogenetically corrected models were qualitatively identical to our original results (SI Appendix, Table S4). Given that our findings did not change and applying phylogenetic corrections without adequate evaluation of phylogenetic signal can be inappropriate or misleading (58), we deferred to our original analyses when presenting results.

Data Availability. Data for this research are available through previously published manuscripts, dissertations, and theses (18, 27, 28, 45–50), and the *Supporting Information*.

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