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Behavior of adult and young grassland songbirds at fledging

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ABSTRACT. The behavior of adults and young at the time of fledging is one of the least understood aspects of the breeding ecology of birds. Current hypotheses propose that fledging occurs either as a result of parent-offspring conflict or nestling choice. We used video recordings to monitor the behavior of nestling and adult grassland songbirds at the time of fledging. We observed 525 nestlings from 166 nests of 15 bird species nesting in grasslands of Alberta, Canada, and Wisconsin, USA. Overall, 78% of nestlings used terrestrial locomotion for fledging and 22% used wing-assisted locomotion. Species varied in propensity for using wing-assisted locomotion when fledging, with nestling Grasshopper Sparrows (*Ammodramus savannarum*) and Henslow's Sparrows (*Centronyx henslowii*) often doing so (47% of fledgings) and nestling Song Sparrows (*Melospiza melodia*), Common Yellowthroats (*Geothlypis trichas*), and Chestnut-collared Longspurs (*Calcarius ornatus*) rarely doing so (3.5% of fledgings). For 390 fledging events at 127 nests, camera placement allowed adults near nests to be observed. Of these, most young fledged (81.5%) when no adult was present at nests. Of 72 fledging events that occurred when an adult was either at or approaching a nest, 49 (68.1%) involved feeding. Of those 49 fledgings, 30 (62.1%) occurred when one or more nestlings jumped or ran from nests to be fed as an adult approached nests. The low probability of nestlings fledging while an adult was at nests, and the tendency of young to jump or run from nests when adults did approach nests with food minimize opportunities for parents to withhold food to motivate nestlings to fledge. These results suggest that the nestling choice hypothesis best explains fledging by nestlings of ground-nesting grassland songbirds, and fledging results in families shifting from being place-based to being mobile and spatially dispersed.

RESUMEN. **Comportamiento de pájaros de pastizal adultos y juveniles al emanciparse**
El comportamiento de adultos y jóvenes al momento de la emancipación es uno de los aspectos menos comprendidos de la ecología reproductiva de las aves. Las hipótesis vigentes proponen que la emancipación ocurre por conflicto padres-progenie o por la propia elección del polluelo. Usamos videograbaciones para monitorear el comportamiento de polluelos y adultos de aves de pradera al momento de abandonar el nido. Observamos 525 polluelos de 166 nidos de 15 especies de aves anidando en las praderas de Alberta, Canadá y Wisconsin, Estados Unidos. En total, 78% de los polluelos usaron la locomoción terrestre para dejar el nido y el 22% usaron locomoción asistida por sus propias alas. Las especies variaron en cuán propensas eran a usar la locomoción asistida por sus alas al emanciparse, con dos especies de gorriones *Ammodramus savannarum* y *Centronyx henslowii* haciéndolo frecuentemente (47% de los polluelos) y los polluelos del gorrión *Melospiza melodia*, la mascarita *Geothlypis trichas* y el escribano *Calcarius ornatus* haciéndolo raramente (3.5% de los polluelos). De 390 eventos de emancipación en 127 nidos, la localización de las cámaras permitió la observación de adultos cerca del nido. De éstos, la mayoría de los polluelos (81.5%) se emanciparon cuando no había adultos presentes en el nido. De 72 eventos de emancipación que ocurrieron cuando un adulto se encontraba en el nido o acerándose a éste, en 49 (68.1%) mediaba la alimentación. De esos 49 polluelos, 30 (62.1%) ocurrieron cuando uno o más polluelos saltaron o corrieron de sus nidos para ser alimentados cuando algún adulto se acercaba al nido. La baja probabilidad de abandonar el nido cuando un adulto estaba en el nido, y la tendencia de los juveniles por saltar o correr de los nidos cuando los adultos se aproximaban con comida para reducir las oportunidades de los adultos de retener la comida y motivar a los polluelos a emanciparse, sugieren que los patrones de emancipación de pájaros de pradera que anidan en el suelo apoyan la hipótesis de la elección del polluelo en la que la emancipación resulta en familias dejando de estar basadas en un sitio a ser más móviles y espacialmente dispersas.

Key words: behavior, fledging, grassland birds, nesting ecology, parent-offspring conflict

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The behavior of nestlings and adults at the time of fledging is one of the least-studied aspects of the breeding ecology of birds, and most studies conducted to date have focused on cavity- or tree-nesting birds (Nilsson and Svensson 1993, Michaud and Leonard 2000, Johnson et al. 2004, 2013). There have been few comparable studies of the fledging behavior of grassland songbirds, likely because they hide their nests on the ground where vegetation makes direct observation difficult (e.g., Potter 1974, Smith and Merkt 1980). With the development of video-surveillance systems for ground-nesting grassland passerines, some understudied aspects of the nesting ecology of grassland songbirds have been examined, but not fledging behavior (Ribic et al. 2012a).

Hypotheses to explain what motivates nestlings to fledge were summarized by Johnson et al. (2004) and are generally derived from two concepts: (1) parent-offspring conflict, which predicts that parents should take an active role in getting nestlings to leave nests (parental manipulation hypothesis; Johnson et al. 2004) and (2) nestling choice, which predicts that nestlings achieve a threshold body size or level of development and then choose to leave nests (threshold size hypothesis; Johnson et al. 2004, also see Martin et al. 2018). Parent-offspring conflict is based on the idea that parental interests favor nestlings leaving nests sooner than would be optimal for nestlings (Trivers 1974). Nestlings have an interest in extending the period of care in nests, whereas parents, for a variety of possible reasons, prefer to direct resources to other activities, e.g., maximizing the possibility of successfully raising additional broods and having more time to prepare for migration (Johnson et al. 2004). A more recent argument is that survival of each individual offspring increases with its duration in the nest, whereas survival of at least one offspring from the nest increases with earlier fledging (Martin et al. 2018). Most studies have focused on the parent-offspring conflict hypothesis, specifically the potential adult manipulation of feeding rates prior to fledging to induce nestlings to leave nests (Nilsson and Svensson 1993, Michaud and Leonard 2000, Johnson et al. 2004, 2013). However, these studies have revealed no evidence of either reduced provisioning rates or food withholding prior to fledging. Some authors have reported anecdotal observations suggesting that adults may entice nestlings to leave nests by standing or flying nearby with or without food on the day of fledging (Meinertzhagen 1954, Rowan 1955, Bustamante and Hiraldo 1990, Michaud and Leonard 2000). Johnson et al. (2013) called for more study of this potential parental behavior, noting that video-surveillance systems would be necessary for data collection.

Ribic et al. (2018) presented video-based information on the time of fledging in grassland passerines. Here, we focus on the behavior related to fledging. Specifically, our objectives were to describe how nestlings leave their nests at fledging, describe behaviors of adults and nestlings at and just prior to fledging, and place those behaviors within the context of existing hypotheses.

Regarding the first objective, the authors of several Birds of North America species accounts have noted that nestlings of grassland birds cannot fly at fledging, including Grasshopper Sparrows (*Ammodramus savannarum*, Vickery 1996), Savannah Sparrows (*Passerculus sandwichensis*, Wheelwright and Rising 2008), Eastern Meadowlarks (*Sturnella magna*, Jaster et al. 2012), and Bobolinks (*Dolichonyx oryzivorus*, Renfrew et al. 2015). Recent work on the development of flight in birds has provided a more nuanced view of locomotion than the can-or-cannot fly dichotomy (e.g., Dial et al. 2015, Heers 2016, 2018). The new gradient is anchored at one end by terrestrial locomotion, including walking, running, and hopping, and at the other end by flight-capable locomotion, i.e., sustained flight as exhibited by adults. Between those modes of locomotion are modes characterized as "cooperative use of wings and legs" (Heers 2018) that become available to young birds as they develop; these modes include wing-assisted hops, wing-assisted jumps, wing-assisted incline running, and short, but not sustained, flights, all of which differ from terrestrial locomotion because the wings provide lift (Heers 2016). Although young grassland birds are not flight-capable at fledging, the extent to which they use wing-leg cooperation modes of locomotion when fledging is not well understood.

For the second objective, we focused on the last behavior of adults before young

fledged as the potential precipitating behavior that induces fledging. Applying the parent-offspring conflict perspective, a precipitating behavior would be one that does not include feeding (i.e., feeding would reward the nestling to stay in the nest and failure to feed would aggravate conflict), and nestlings would fledge sooner after last adult visits that did not include feeding than after last adult visits that did include feeding. In terms of luring, for ground-nesting grassland birds, flying near the nest would likely not be a productive behavior; instead, adults might stand near nests with food in their bills as a lure, then leave nests without feeding. In addition, if parental manipulation methods like luring young are occurring, adults need to be at or near nests (i.e., not obscured by the vegetation) to successfully induce fledging. If nestling choice is driving the fledging event, adults should continue to feed nestlings until the nestlings recognize that they have reached a desired energetic or developmental threshold and leave their nests. Under nestling choice, the presence of adults at nests when nestlings leave is irrelevant.

METHODS

We used video records from published studies of grassland birds. Study areas were located in Alberta, Canada, near Brooks (50.5642°N 111.8989°W) and in Wisconsin, USA, near Mount Horeb (43.0167°N, 89.7500°W). Videos of Alberta nests were contributed by Ng et al. (2019) ($N = 11$; 2013–2014), and those of Wisconsin nests were contributed by Renfrew et al. (2005), Ribic et al. (2012b), Ellison et al. (2013), and Byers et al. (2017) ($N = 155$; 1999–2011). Behavior of adults and nestlings at the time of fledging was recorded in grassy habitats composed of native mixed-grass prairie, continuous and rotationally grazed pastures, remnant tall-grass prairie, or warm-season and cool-season fields enrolled in the U.S. Department of Agriculture's Conservation Reserve Program.

Field methods. The general data collection design was similar across studies. Systematic nest searches were conducted from early or mid-May to late July. Nests were typically found either by rope-dragging or systematic walking by 2–8 technicians. Cameras were set up during incubation and nestling stages and remained in place for the duration of the nesting period. Commercially available cameras were chosen for their small size, weatherproof housing, and infrared light-emitting diodes to permit recording under low-light conditions. Cameras were placed 10–50 cm from nests, depending on visibility, and sometimes placed up to 40 cm above the ground on dowels when vegetation was relatively tall. Cameras were connected by 25- or 50-m cables to a battery and either a videocassette recorder (VCR) or digital video recorder (DVR). VCR systems captured ~ 4 images/s and required a daily videotape and battery change. DVR systems captured ~ 30 images/s and required a battery and SD card change every 3–4 days. Nests were checked via remote monitors to minimize disturbance; no instances of fledging were influenced by observers checking nests.

Video review. We watched, date-, and time-stamped videos of fledging by 525 nestlings from 166 nests of 15 species of birds (Table 1) to determine mode of departure of nestlings at fledging; fields of view ranged from 414 to 1320 cm² (Slay et al. 2012). We used a subset of 127 nests to determine the behavior of adults at the last nest visit before nestlings fledged; this subset was selected based on being able to see adults standing in vegetation near nests.

Digital video was watched using either VideoLAN VLC Media Player or DivX Player. Fledging events were determined by examining videos systematically. Because nestlings often briefly left nests before fledging permanently, we worked backward from the final fledging event and iteratively "rewound" the video until all nestlings were present in nests. In this way, the times of fledging (to the nearest second) could be determined by counting the increasing number of remaining nestlings. Mode of locomotion of the nestlings at fledging was recorded as either terrestrial or wing-assisted. Terrestrial was defined as a nestling using only its legs to leave the nest (includes walking, running, hopping, climbing, and pushing through the grass; wings could be used for balance, but no lift was provided). Wing-assisted was defined as the cooperative use of legs and wings to leave a nest with wings providing lift (i.e., wings are flapping and legs are off the ground; Heers 2018). Wing-assisted modes included wing-assisted jumping and apparent short

Table 1. Mode of departure of young grassland songbirds at fledging for species breeding in Wisconsin and Alberta, Canada.

Species[a]	Number of nests	Number of nestlings	Terrestrial	Wing-assisted	Proportion wing-assisted[b]
Obligate grassland birds					
Eastern Meadowlark	46	149	115	34	0.23
Bobolink	38	121	98	23	0.19
Grasshopper Sparrow	15	57	32	25	0.44
Savannah Sparrow	12	32	23	9	0.28
Chestnut-collared Longspur	10	33	33	0	0
Henslow's Sparrow	8	30	15	15	0.50
Dickcissel	1	3	2	1	–
Horned Lark	1	2	2	0	–
Sedge Wren	1	4	4	0	–
Western Meadowlark	1	3	3	0	–
Sprague's Pipit	1	4	4	0	–
Facultative grassland birds					
Clay-colored Sparrow	2	3	2	1	–
Field Sparrow	6	13	10	3	–
Generalists					
Song Sparrow	15	44	41	3	0.07
Common Yellowthroat	9	27	26	1	0.04
Total	166	525	410	115	0.22

[a]Categorization of species by habitat specialization is based on Vickery et al. (1999).
[b]Proportion wing-assisted was calculated for species with 20 or more young fledging.

flight. When it was unclear whether wing activity was used for lift or balance, the behavior was assigned to terrestrial mode (see Appendix S1 for further details). We also noted if nestlings were begging (mouth open) or not begging (mouth closed) as they left a nest. Video examples of nestlings leaving nests are provided in Ribic et al. (2019).

Adult behaviors during their last nest visit prior to a fledging event were categorized as feeding, maintenance, on nest, standing, luring, flying, or unknown. A visit was defined as feeding if food was observed in an adult's bill or an adult placed its bill within the gape of at least one nestling, regardless of whether the adult exhibited other behaviors. A visit was defined as maintenance if an adult removed a fecal sac, probed at a nest, dug in a nest, or removed vegetation from a nest and no feeding occurred. A visit was defined as being on a nest if an adult brooded nestlings or was sleeping (i.e., bill tucked under a wing; Slay et al. 2012). A visit was defined as standing if an adult with no food in its bill just stood over nestlings, stood at the rim of a nest, or stood in vegetation near a nest. A visit was defined as luring if an adult with food visible in its bill stood at the rim of a nest or in vegetation near a nest and did not feed nestlings before leaving. Visits were defined as unknown if an adult was at a nest, but its back was to the camera. Adult visits ended when they either flew or walked from a nest into the vegetation and out of view. Video examples of adult behavior at nests are provided in Ribic et al. (2019).

Data analysis. Unless stated otherwise, we focused all statistical analyses on species where we recorded ≥ 5 nests, including Chestnut-collared Longspurs (*Calcarius ornatus*), Eastern Meadowlarks, Bobolinks, Grasshopper Sparrows, Henslow's Sparrows (*Centronyx henslowii*), Common Yellowthroats (*Geothlypis trichas*), Song Sparrows (*Melospiza melodia*), and Savannah Sparrows. Species effects were included in each analysis to determine the degree to which observed behavior patterns were common among different species of grassland songbirds.

We attempted to analyze the data using general linear mixed models, but the models did not converge. Therefore, we used the analysis techniques described below that were

appropriate for the data structures, but were somewhat less flexible in the range of models that could be evaluated.

We calculated proportions of fledgings that used each mode of departure, fledging events that occurred when an adult was at a nest, and adult visit categories (except for unknown). All proportions were determined for each species and overall. We also determined the elapsed time between the last adult visit and time of fledging of a nestling; if an adult was at or standing near a nest when a nestling fledged, elapsed time was recorded as zero. Times were recorded to the nearest second. We calculated parametric and non-parametric summary statistics for elapsed time by the different visit categories; non-parametric summary statistics were used in some cases due to skewed distributions.

To determine if different species had similar patterns for mode of departure and adult behavior at fledging, we used a contingency table approach that accounted for the multiple observations made at nests. In standard contingency tables, only one observation is made of each independent sampling unit, in our case, nests. However, we had multiple observations at nests and simply pooling results across nests to assess species differences could yield a misleading result (i.e., greater than nominal risk of Type 1 or Type 2 errors, depending on the specific data configuration). Therefore, we used the Koehler and Wilson (1986) (K-W) method as implemented in TableSim (Rugg 2003). We present a brief explanation of the analysis technique here as applied to our data; see Garson and Moser (1995) for details on the aggregation problem in ecology and Rugg (2003) for program implementation details. The analysis is based on the idea that there is more variability across nests in a population of interest (e.g., species) than is accounted for in the multinomial model used to derive the standard chi-square test. Data from individual nests are used to estimate the parameters of a Dirichlet distribution with mean vector π_j (the true mean vector of category probabilities for population j) and scale parameter γ_j (a measure of variability). Estimates of the scale parameter are used to compute weights, α_j, which are used to properly pool the population response distributions into an overall average distribution, π. The scale parameter is estimated from the statistic C_j that indicates how variable fledging behavior is among nests in a species. If the statistic falls between 1.0 and 1.5, there is minimal extra between-nest variability and standard distributional assumptions are met well enough to obtain satisfactory results from standard tests; larger C_j values indicate variability among nests in a species and an adjustment to the species Dirichlet distribution is necessary. To generate the null distribution of the test statistic, the program sets π, rather than π_j, as the center of the Dirichlet distribution, while the scale parameters remain population-specific. Random nests consistent with the null distribution are generated for each species population, and a standard χ^2 test statistic computed. We used 20,000 Monte Carlo simulations for each test to determine significance. Because this method may not converge with sufficiently small sample sizes, we also used the Manly (1997) randomization method (as implemented in Rugg 2003) to reliably provide a test of species differences, although the Manly method provides little additional information about the structure of the data.

We used a permutation test to determine if elapsed time between an adult's last visit to a nest and fledging varied with adult visit categories. Summary statistics and the permutation test from package *coin* were conducted using R version 3.4.3 (The R Foundation 2018). In all cases, we used a P value of 0.05 for significance.

RESULTS

Mode of departure at fledging. Overall, 78% of 525 nestlings used terrestrial locomotion for fledging, and 22% used wing-assisted locomotion (Table 1). There were species differences in how nestlings departed (K–W model: $\chi^2 = 43.6$, $P < 0.0001$). C_j values were below 1.5 except for Eastern Meadowlarks ($C_j = 2.2$) and Savannah Sparrows ($C_j = 2.2$), indicating some nest-based differences for those two species. Species clustered into three groups, i.e., frequent, occasional, and infrequent users of wing-assisted locomotion, where wings were used when leaving nests in 47% (average for Henslow's Sparrows and Grasshopper Sparrows), 23% (Savannah Sparrows, Eastern Meadowlarks, and Bobolinks), and 3.5% (Song Sparrows, Common Yellowthroats, and Chestnut-collared Longspurs) of fledging events, respectively (Table 1).

Table 2. Presence of adult at fledging for species of grassland birds breeding in Wisconsin and Alberta, Canada.

Species[a]	Number of nests	Total fledging events	Adult at nest when nestling fledged	Adult not at nest when nestling fledged	Proportion of fledging events with adult at nest
Obligate grassland birds					
Eastern Meadowlark	31	93	21	72	0.23
Bobolink	30	91	14	77	0.15
Grasshopper Sparrow	14	53	7	46	0.13
Savannah Sparrow	9	22	0	22	0
Chestnut-collared Longspur	10	33	12	21	0.36
Henslow's Sparrow	5	20	5	15	0.25
Sprague's Pipit	1	4	0	4	0
Horned Lark	1	2	2	0	1.0
Facultative grassland birds					
Clay-colored Sparrow	2	3	1	2	0.33
Field Sparrow	3	9	0	9	0
Generalists					
Song Sparrow	13	37	8	29	0.22
Common Yellowthroat	8	23	2	21	0.09
Total	127	390	72	318	

[a]Categorization of species by habitat specialization is based on Vickery et al. (1999).

Adult behavior. There were 390 fledging events at the 127 nests where camera placement allowed adults near nests to be observed. Of these events, most (81.5% of 390) occurred when an adult was not at or near nests (Table 2). Species differed in how often adults were at nests when fledging occurred (K–W model: $\chi^2 = 15.1$, $P = 0.033$). Only Eastern Meadowlarks had a large C_j (2.77), indicating that adults varied more than expected in their attendance patterns at nests when fledging occurred. Species clustered into two groups: those where adults were rarely at nests at fledging (9.3% of the time; average for Savannah Sparrows, Common Yellowthroats, Grasshopper Sparrows, and Bobolinks) and those where adults were occasionally at nests at fledging (26.4% of the time; average for Chestnut-collared Longspurs, Henslow's Sparrows, Eastern Meadowlarks, and Song Sparrows; Table 2).

Adults not at nests when fledging occurs. Of 318 fledging events when an adult was not present, we were able to determine adult behavior during the last visit to the nest during 296 (93.1%) events. Most of those events (67.6% of 296 events at 96 nests) occurred after a feeding (Table 3). There were no species differences for this behavior (Manly test: $\chi^2 = 205.7$, $P = 0.36$). Of the 96 events that occurred after adults were at nests, but did not feed nestlings, 47 (48.9%, 27 nests) occurred after an adult performed maintenance at nests and 42 (43.8%, 25 nests) occurred after an adult stood at or near a nest, but did not interact with nestlings before leaving (Table 4). We never observed food in an adult's bill when they were standing at or near nests, i.e., no luring behavior.

The time between an adult's last visit to a nest and fledging of young did not differ among different adult behaviors (maxT = 1.2, $P = 0.46$). For the three most common adult behaviors, mean time of fledging was 4.1 $\pm$ 7.6 min (median = 0.78 min, interquartile range = 0.22, 4.3 min) after feeding nestlings, 2.9 $\pm$ 5.4 min (median = 0.85 min, interquartile range = 0.23, 2.7 min) after performing nest maintenance, and 5.9 $\pm$ 21.0 min (median = 0.9 min; interquartile range = 0.30, 3.8 min) after standing at or near nests.

Adult at nests when young fledged. Of 72 fledging events that occurred when an adult was either at or approaching a nest, 49 (68.1%,

Table 3. Behavior of adult grassland songbirds before fledging occurred when adults were not present at nests when fledging occurred.

Species[a]	Adult feeding nestlings	Adult did not feed nestlings	Unknown (adult back to camera; adult in nest)	Total fledge events
Obligate grassland birds				
Bobolink	52	22	3	77
Eastern Meadowlark	41	24	7	72
Grasshopper Sparrow	28	15	3	46
Savannah Sparrow	12	6	4	22
Chestnut-collared Longspur	19	1	1	21
Henslow's Sparrow	7	7	1	15
Sprague's Pipit	4	0	0	4
Facultative grassland birds				
Clay-colored Sparrow	2	0	0	2
Field Sparrow	7	2	0	9
Generalists				
Song Sparrow	15	11	3	29
Common Yellowthroat	13	8	0	21
Total	200	96	22	318

[a]Categorization of species by habitat specialization is based on Vickery et al. (1999).

Table 4. Behavior of adult grassland birds when they visited nests without feeding young and young fledged after the adult left the nest.

Species[a]	Maintenance	Standing	On nest	Total fledge events where adult did not feed nestlings
Obligate grassland birds				
Bobolink	14	5	3	22
Eastern Meadowlark	16	8	0	24
Grasshopper Sparrow	7	7	1	15
Savannah Sparrow	3	2	1	6
Chestnut-collared Longspur	1	0	0	1
Henslow's Sparrow	1	4	2	7
Sprague's Pipit	0	0	0	0
Facultative grassland birds				
Clay-colored Sparrow	0	0	0	0
Field Sparrow	0	2	0	2
Generalists				
Song Sparrow	4	7	0	11
Common Yellowthroat	1	7	0	8
Total	47	42	7	96

[a]Categorization of species by habitat specialization is based on Vickery et al. (1999).

31 nests) involved feeding (Table 5). When feeding was involved, one or more nestlings jumped or ran from nests (usually begging vigorously) in 61.2% of fledging events (30 events, 14 nests) and were either fed or begged adults for food outside the nest, and then did not return. The average proportion of nestlings in these nests that fledged by running or jumping to meet an adult was 0.62 ± 0.31 ($N = 14$ nests). In other cases where feeding

was involved, nestlings remained in nests to be fed, but then either fledged while an adult was still present (15 events, 14 nests) or left nests at the same time as the adult (four events, four nests). Further details about the behavior of adults and nestlings at fledging are provided in Appendix S1 and Table S1.

DISCUSSION

Although fledging by terrestrial locomotion was the most common behavior exhibited by all eight species in our study, young of most of our focal species sometimes fledged via various wing-assisted modes. This variation in mode of departure may be due to differences in stage of development (e.g., Martin et al. 2018). However, because our study was observational, we do not know if nestlings that used terrestrial locomotion for fledging were developmentally capable of wing-assisted locomotion, but instead chose the less energetically demanding mode (Heers 2018). We found differences among species in the propensity of young to use wing-assisted locomotion, with nestlings of some species doing so more often (Grasshopper and Henslow's sparrows) than those of other species (Song Sparrows, Common Yellowthroats, and Chestnut-collared Longspurs). For species that sometimes nest off the ground in shrubs like Song Sparrows and Common Yellowthroats (Guzy and Ritchison 1999, Arcese et al. 2002), first moving into the foliage around a nest to assess the surrounding environment before exercising wing-assisted capabilities may be safer for nestlings.

A special type of fledging occurred when all nestlings rushed from nests to be fed by an adult and then did not return to nests, e.g., primarily young Eastern Meadowlarks and Chestnut-collared Longspurs. The tendency of nestling Eastern Meadowlarks to behave this way may explain the extra variability we found among Eastern Meadowlark nests for adult presence at fledging. This behavior by young Eastern Meadowlarks was previously noted by Jaster et al. (2012) who stated that "Departure from nest, normally at 10–12 d, is usually associated with developing capability of reaching out for food from parent and then walking a few steps to meet approaching parent." Such behavior has not been reported previously for Chestnut-collared Longspurs or the other species in our study where it occurred.

We found no evidence that adults induce fledging by luring young from nests. Even with significant species differences in the probability of an adult being at nests when fledging occurred, the probability of an adult not being at a nest was > 60% for each species, limiting the opportunity for adults to manipulate the nestlings into fledging via luring. Indeed, the demonstrated ability of nestlings of grassland birds to leave and re-enter nests means that luring would not necessarily result in fledging. Unlike cavity- or shrub-nesting species, nestlings of grassland birds that might be lured from a nest can easily return. This constraint on the effectiveness of luring is most pronounced in species where nestlings run toward adults because nestlings act before an adult can attempt luring behavior. We also found no evidence that adults withheld food to induce fledging. Most (> 60%) nestlings of every species in our study fledged after a feeding bout, regardless

Table 5. Behavior of adult grassland songbirds when present at nests when young fledged.

Species[a]	Adult fed nestlings	Adult did not feed nestlings	Total fledge events
Obligate grassland birds			
Bobolink	11	3	14
Eastern Meadowlark	18	3	21
Grasshopper Sparrow	3	4	7
Chestnut-collared Longspur	12	0	12
Henslow's Sparrow	1	4	5
Horned Lark	2	0	2
Facultative grassland birds			
Clay-colored Sparrow	0	1	1
Generalists			
Song Sparrow	1	7	8
Common Yellowthroat	1	1	2
Total	49	23	72

[a]Categorization of species by habitat specialization is based on Vickery et al. (1999).

of whether an adult was at or near a nest. In addition, we found that nestlings fledged at the same time after the last visit by an adult regardless of the adult's behavior (i.e., feeding or not), which is counter to the prediction under the parent-offspring conflict hypothesis. Overall, our results agree with those reported for cavity-nesting birds (Johnson et al. 2004, 2013) and suggest that the time of fledging for grassland birds is determined by nestlings.

Parent-offspring conflict could manifest itself via mechanisms not proposed in the literature or may not manifest at all (analogous to the maintenance of sexual selection in polygynous species like Red-winged Blackbirds [*Agelaius phoeniceus*]; Searcy and Yasukawa 1995). However, if there is parent-offspring conflict in grassland birds, then that conflict is more likely to manifest when adults actually stop providing care for the young, which is 2–3 weeks post-fledging for grassland birds (Wheelwright et al. 2003, Yackel Adams et al. 2006), rather than at fledging. The young would certainly continue to benefit from food provided by parents, but the balance of interests would have shifted for the adults to favor retaining the benefits of the food for their own use. This re-framing of parent-offspring conflict away from the time of fledging was originally proposed for Black Kites (*Milvus migrans*, Bustamante and Hiraldo 1990). Additional evidence favoring the nestling choice hypothesis for grassland birds is the expectation that, absent countervailing pressures, nestlings should choose to stay in the nest until they have developed enough that leaving nests does not increase mortality risk (Roff et al. 2005). Naef-Daenzer and Grüebler (2016) found that this was the case for ground-nesting birds, but not for those that nest above ground. Therefore, we suggest that fledging by nestlings of ground-nesting grassland birds is simply a nestling choice-driven transition of families from being place-based (i.e., nest-based) to being mobile and spatially dispersed.

In addition, because nestlings of grassland birds often leave and return to nests multiple times in the hours prior to finally leaving nests, de-emphasizing the focus on fledging as an instantaneous, binary event may be useful. At least for grassland birds, fledging can be usefully framed as a relatively short phase in the development of young birds that precedes the final main phase of development, i.e., gaining the skills for independent living, further growth and development, and, ultimately, successful migration as a flight-enabled adult.

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REFERENCES

Arcese, P., M. K. Sogge, A. B. Marr, and M. A. Patten. 2002. Song Sparrow (*Melospiza melodia*), version 2.0. In: The Birds of North America (P. G. Rodewald, ed.). Cornell Lab of Ornithology, Ithaca, NY.

Bustamante, J., and F. Hiraldo. 1990. Factors influencing family rupture and parent-offspring conflict in the Black Kite *Milgrus migrans*. Ibis 132: 58–67.

Byers, C. M., C. A. Ribic, D. W. Sample, J. D. Dadisman, and M. R. Guttery. 2017. Grassland bird productivity in warm season grass fields in southwest Wisconsin. American Midland Naturalist 178: 47–63.

Dial, K. P., A. M. Heers, and T. R. Dial. 2015. Ontogenetic and evolutionary transformations: ecological significance of rudimentary structures. In: Great transformations in vertebrate evolution (K. P. Dial, N. Shubin, and E. L. Brainerd, eds.), pp. 283–301. University of Chicago Press, Chicago, IL.

Ellison, K., C. A. Ribic, D. W. Sample, M. J. Fawcett, and J. D. Dadisman. 2013. Impacts of tree rows on grassland birds and potential nest predators: a removal experiment. PLoS ONE 8: e59151.

Garson, G. I., and E. B. Moser. 1995. Aggregation and the Pearson chi-square statistic for homogeneous proportions and distributions in ecology. Ecology 76: 2258–2269.

Guzy, M. J., and G. Ritchison. 1999. Common Yellowthroat (*Geothlypis trichas*), version 2.0. In: The Birds of North America (P. G. Rodewald, ed.). Cornell Lab of Ornithology, Ithaca, NY.

Heers, A. M. 2016. New perspectives on the ontogeny and evolution of avian locomotion. Integrative and Comparative Biology 56: 428–441.

——— 2018. Flight and locomotion. In: Ornithology: foundation, analysis, and application (M. L. Morrison, A. D. Rodewald, G. Voelker, M. R. Colón, and J. F. Prather, eds.), pp. 273–308. Johns Hopkins University Press, Baltimore, MD.

Jaster, L. A., W. E. Jensen, and W. E. Lanyon. 2012. Eastern Meadowlark (*Sturnella magna*), version 2.0. In: The Birds of North America (P. G. Rodewald, ed.). Cornell Lab of Ornithology, Ithaca, NY.

Johnson, L. S., R. M. Hebert, F. M. Napolillo, and A. Allen. 2013. The process of fledging in the Mountain Bluebird. Journal of Field Ornithology 84: 367–376.

———, R. L. Rauch, and S. N. Dellone. 2004. The process and causes of fledging in a cavity-nesting passerine bird, the House Wren (*Troglodytes aedon*). Ethology 110: 693–705.

Koehler, J., and J. R. Wilson. 1986. Chi-square tests for comparing vectors of proportions for several cluster samples. Communications in Statistics A: Theory and Methods 15: 2977–2990.

Manly, B. F. J. 1997. Randomization, bootstrap and Monte Carlo methods in biology, 2nd ed. Chapman and Hall, New York, NY.

Martin, T. E., B. Tobalske, M. M. Riordan, S. B. Case, and K. P. Dial. 2018. Age and performance at fledging are a cause and consequence of juvenile mortality between life stages. Science Advances 4: eaar1988.

Meinertzhagen, R. 1954. The education of young Ospreys. Ibis 96: 153–155.

Michaud, T., and M. Leonard. 2000. The role of development, parental behavior, and nestmate competition in fledging of nestling Tree Swallows. Auk 117: 996–1002.

Naef-Daenzer, B., and M. U. Grüebler. 2016. Post-fledging survival of altricial birds: ecological determinants and adaptation. Journal of Field Ornithology 87: 227–250.

Ng, C. S., P. G. Des Brisay, and N. Koper. 2019. Chestnut-collared Longspurs reduce parental care in the presence of conventional oil and gas development and roads. Animal Behaviour 148: 71–80.

Nilsson, J. Å., and M. Svensson. 1993. Fledging in altricial birds: parental manipulation or sibling competition? Animal Behaviour 46: 379–386.

Potter, P. E. 1974. Breeding behavior of Savannah Sparrows in southeastern Michigan. Jack-Pine Warbler 52: 50–63.

Renfrew, R. B., C. A. Ribic, and J. L. Nack. 2005. Edge avoidance by nesting grassland birds: a futile strategy in a fragmented landscape. Auk 122: 618–636.

Renfrew, R., A. M. Strong, N. G. Perlut, and T. A. Gavin. 2015. Bobolink (*Dolichonyx oryzivorus*), version 2.0. In: The Birds of North America (P. G. Rodewald, ed.). Cornell Lab of Ornithology, Ithaca, NY.

Ribic, C. A., M. J. Guzy, T. A. Anderson, D. W. Sample, and J. L. Nack. 2012b. Bird productivity and nest predation in agricultural grasslands. In: Video surveillance of nesting birds (C. A. Ribic, F. R. Thompson III, and P. J. Pietz, eds.), pp. 119–134. Studies in Avian Biology 43, University of California Press, Berkeley, CA.

———, N. Koper, C. S. Ng, and K. Ellison [online]. 2019. Grassland bird nesting ecology: video samples of behavior, 2nd ed. Forest Service Research Data Archive, Fort Collins, CO. https://doi.org/10.2737/rds-2018-0034-2 (Accessed 31 January 2019).

———, C. Ng, N. Koper, K. Ellison, P. J. Pietz, and D. J. Rugg. 2018. Diel fledging patterns in grassland passerines: relative impacts of energetics and predation risk. Auk 135: 1100–1112.

———, F. R. Thompson III, and P. J. Pietz (eds.). 2012a. Video surveillance of nesting birds. Studies in Avian Biology 43, University of California Press, Berkeley, CA.

Roff, D. A., V. Remeš, and T. E. Martin. 2005. The evolution of fledging age in songbirds. Journal of Evolutionary Biology 18: 1425–1433.

Rowan, M. K. 1955. The breeding biology and behavior of the Redwinged Starling *Onychognathus morio*. Ibis 97: 663–705.

Rugg, D. J. 2003. TableSim—A program for analysis of small-sample categorical data. General Technical Report NC-232, U.S. Department of Agriculture, Forest Service, North Central Research Station, St. Paul, MN.

Searcy, W. A., and K. Yasukawa. 1995. Polygyny and sexual selection in Red-winged Blackbirds. Princeton University Press, Princeton, NJ.

Slay, C. M., K. S. Ellison, C. A. Ribic, K. G. Smith, and C. M. Schmitz. 2012. Nocturnal activity of nesting shrubland and grassland passerines. In: Video surveillance of nesting birds (C. A. Ribic, F. R. Thompson III, and P. J. Pietz, eds.), pp. 105–116. Studies in Avian Biology 43, University of California Press, Berkeley, CA.

Smith, J. N. M., and J. R. Merkt. 1980. Development and stability of single-parent family units in the Song Sparrow. Canadian Journal of Zoology 58: 1869–1875.

The R Foundation [online]. 2018. The R project for statistical computing. <https://www.r-project.org/> (Accessed 16 July 2018).

Trivers, R. L. 1974. Parent offspring conflict. American Zoologist 14: 249–264.

Vickery, P. D. 1996. Grasshopper Sparrow (*Ammodramus savannarum*), version 2.0. In: The Birds of North America (P. G. Rodewald, ed.). Cornell Lab of Ornithology, Ithaca, NY.

———, P. L. Tubaro, J. M. Cardosa da Silva, B. G. Peterjohn, J. R. Herkert, and R. B. Cavalcanti. 1999. Conservation of grassland birds in the Western Hemisphere. In: Ecology and conservation of grassland birds of the Western Hemisphere (P. D. Vickery and J. R. Herkert,

eds.), pp. 2–26. Studies in Avian Biology 19, Allen Press, Lawrence, KS.

WHEELWRIGHT, N. T., AND J. D. RISING. 2008. Savannah Sparrow (*Passerculus sandwichensis*), version 2.0. In: The Birds of North America (P. G. Rodewald, ed.). Cornell Lab of Ornithology, Ithaca, NY.

———, K. A. TICE, AND C. R. FREEMAN-GALLANT. 2003. Postfledging parental care in Savannah Sparrows: sex, size and survival. Animal Behaviour 65: 435–443.

YACKEL ADAMS, A. A., S. K. SKAGEN, AND J. A. SAVIDGE. 2006. Modeling post-fledging survival of Lark Buntings in response to ecological and biological factors. Ecology 87: 178–188.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website.

Appendix S1. Additional detail about the behavior of adults and young at fledging.

Table S1. Details about adult and nestling behavior when a parent was at nests when fledging occurred.