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PROVISIONING OF NESTLING DICKCISSELS IN NATIVE WARM-SEASON GRASS FIELD BUFFERS

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ABSTRACT.—We used video cameras in 2008–2009 to record provisioning activities at Dickcissel (*Spiza americana*) nests in and around Conservation Reserve Program field buffers in north-central Mississippi, USA. We simultaneously observed foraging flight distances of parents. Provisioning rate ($P = 0.412$), biomass ($P = 0.161$), and foraging distance ($P = 0.159$) did not increase with nestling age. Parents delivered larger items to meet demand associated with older nestlings ($P = 0.010$–0.001). This suggests energetic costs of changes in prey selection were less than costs of increasing the number or distance of provisioning trips. Presence of male helpers increased provisioning rate ($P < 0.001$) but not biomass ($P = 0.992$) because males brought smaller prey items ($P = 0.001$–0.021). Presence of observers 30 m from the nest reduced provisioning rates ($P = 0.005$) and biomass delivered ($P = 0.066$). Lack of habitat effects for any aspect of provisioning suggests grass field buffers provided nestling food resources similar to surrounding habitats. Use of continuous video monitoring of nest activity allows well-concealed activities including provisioning and male helping to be directly observed and better quantified. *Received 7 September 2011. Accepted 26 January 2012.*

Nestling provisioning by birds can affect reproductive success. Short periods of decreased provisioning (either in rate or biomass) may cause slower growth, reduced body condition, decreased survivorship, and reduced fledging success of nestlings (Bryant and Westerterp 1983, Martin 1987, Saino et al. 1997). Decreased provisioning can compromise future dominance ranks and lower probabilities of acquiring breeding territories (Metcalfe and Monaghan 2001). Provisioning rates may also index available food and, consequently, habitat quality (e.g., Brickle et al. 2000).

Adults of most passerines feed 60–100% arthropods to nestlings to provide the protein-rich diet necessary for rapid development. Parents can optimize net energetic gain per nest visit (foraging trip) by altering provisioning rates, load size (biomass), foraging distances, and prey taxa and sizes (Orians and Pearson 1979, Wright et al. 1998). Provisioning nestlings is energetically costly for parents and impacts parent survival (e.g., Dijkstra et al. 1990), size of future clutches, and intervals between broods and, ultimately, future reproductive potential (e.g., Dijkstra et al. 1990, Deerenberg and Overkamp 1999). Thus, parents should prefer larger prey (especially for large clutches or older nestlings with greater demand and wider gapes) that reduce searching time and provide more energy per provisioning trip (Wright et al. 1998, Britschgi et al. 2006). Parents should minimize search time by foraging close to the nest, and only forage at greater distances from the nest when food near the nest becomes difficult to find (Andersson 1981, Brickle et al. 2000, Britschgi et al. 2006) or when higher quality food sources are available at greater distances.

Studying provisioning rates in grassland birds is important because they are experiencing large declines in the United States (1966–2009) compared to other bird guilds (Brennan and Kuvlesky 2005, Sauer et al. 2011). Agricultural intensification, grassland habitat loss and fragmentation, and increased woody growth in remaining grasslands favoring forest-edge fauna have likely led to these declines of many grassland birds, especially in the Midwest and Great Plains (e.g., Samson and Knopf 1994, Brennan and Kuvlesky 2005). The U.S. Department of Agriculture's Conservation Reserve Program (CRP) since initiation in 1985 has added millions of hectares of grassland habitat to agricultural landscapes in the United States in the form of whole field plantings and a variety of buffer strip practices. Ostensibly, this program has benefited grassland bird populations (e.g., Ryan et al. 1998, Herkert 2009). However, little is known about provisioning rates, food availability (McIntyre and Thompson 2003), and habitat quality (reviewed by Haufler 2005) of CRP grasslands, especially in the southeastern USA (e.g., Smith et al. 2005) where grassland practices are less common choices for CRP than in other regions.

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Our objective was to quantify provisioning activities of Dickcissels (*Spiza americana*) using a combination of continuous video recording and direct observation. We hypothesized that: (1) provisioning rates and biomass delivered by Dickcissels would increase with nestling age and differ between nests in CRP buffers compared to nests in non-buffer habitats (potentially primary habitat); (2) prey size would increase with nestling age and nestling number, and differ between buffer and non-buffer nests; and (3) longer foraging trips would be associated with older nestlings, larger clutches, and larger prey sizes.

METHODS

*Focal Species.—*The Dickcissel has declined in the United States (trend = −0.7% since 1966; Sauer et al. 2011) and is listed by Partners in Flight (PIF) as a species of concern in the Southeastern Coastal Plain region because of anthropogenic threats to breeding habitat (Rich et al. 2004). Dickcissels are polygynous and nest in fallow fields, unmowed hayfields, and old fields with abundant forbs (Temple 2002). Nest building to hatching takes 15–21 days, and nestlings fledge after 8–10 days (Temple 2002). Dickcissels are mostly granivorous, but feed primarily on arthropods during the breeding season (Temple 2002).

*Study Area.—*We conducted our research at B. Bryan Farms Inc., a 2,104-ha privately-owned farm in Clay County, Mississippi within the Black Prairie physiographic region. Seventy-nine hectares of row crops had been enrolled in CP33–Habitat Buffers for Upland Birds in 2005. CP33 is not restricted to highly erodible farmland, allowing for wider implementation in intensive agricultural landscapes where grassland habitat is often scarce. Buffers are composed of 10 to 40-m strips of native warm-season grasses planted around agricultural field margins to provide habitat for Northern Bobwhite (*Colinus virginianus*) and other continentally declining birds such as Dickcissel, Indigo Bunting (*Passerina cyanea*), and Field Sparrow (*Spizella pusilla*) (Sauer et al. 2011) that may use CP33 buffers (e.g., Smith et al. 2005).

CP33 buffers were planted with big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), indiangrass (*Sorghastrum nutans*), partridge pea (*Chamaecrista fasciculata*), black-eyed susan (*Rudbeckia hirta*), and Maximilian sunflower (*Helianthus maximiliani*) in May 2004. These buffers were 4 and 5 years post-establishment at the time of our study. Producers are required to periodically disturb buffers (e.g., light disking or prescribed burning), and a subset of buffers was burned (in spring) or disked (in fall) each year as part of a broader experiment (Adams 2011, Dollar 2011, Hale et al. 2011). Dickcissels largely avoided nesting in disturbed buffers (Adams 2011), and we do not address disturbance effects. We located Dickcissel nests in areas along the periphery or near (<10 m) CP33 buffers. These 'non-buffer' habitats were structurally similar to old field habitats because of the greater forb, shrub, and sapling components compared to CP33 buffers (K. L. Baker, unpubl. data).

*Video Monitoring.—*We systematically searched buffers and surrounding habitats during May, June, and July 2008–2009 to locate nests. We video-recorded nestling provisioning activity during acceptable weather conditions (no rain or sustained winds ≥16 km/hr) on one to four mornings between days 4 and 7 post hatching. We did not film before day 4 to avoid nest abandonment by parents (Schadd and Ritchison 1998) or after day 7 to avoid premature fledging.

We placed tripods with mounted aluminum cans (to mimic video recorders) near nests to familiarize birds with the recording equipment 1 to 2 days prior to filming. We positioned hand-held camcorders (Sony Handycam DCR–SR42®) at nests on each recording day on tripods 0.5 to 1.0 m from nests (Dearborn et al. 1998). Camcorders were programmed to begin recording 20 min after the technician had departed (0545 to 0730 hrs CST) to allow birds to return to normal behavior. Each individual recording session lasted 4 hrs.

*Measuring Provisioning.—*Video footage was processed using Adobe Premiere Pro software©. We tabulated nestling provisioning rates (adult visits to nest/hr/nestling) and prey taxa for each 1-hr period of video footage. We identified nestling diet composition for taxonomical groupings of arthropods to Order. We measured length of each arthropod from the frons to the end of the abdomen, not including wings, antennae, or ovipositors (Sejberg et al. 2000), to estimate biomass (energy) delivered per nestling/hr. We assigned each prey item to one of three size categories (Schadd and Ritchison 1998): small (≤ adult bird beak length, ~16.1 mm, Temple 2002), medium (> adult beak length and up to 2 ×'s beak length), and large (>2 ×'s beak length).

We collected arthropods in 2009 from 0930 to 1130 hrs CST during mid-morning from mid-June through early July coinciding with peak breeding of Dickcissels. We visited three separate locations in each habitat type where Dickcissels were primarily foraging (burned buffers, disked buffers, control buffers, pasture fields, hay, milo, corn, soybean, riparian, roads). We took 50 sweep net samples per site (38.1 cm diameter net). We dried all arthropods at 60 °C for 24 hrs (Southwood 1978). Arthropods from each size category were weighed to the nearest ±0.0001 mg. We assigned a mean weight to apply to arthropods of the same taxa (Order) and size categories observed on video (Rogers et al. 1977). Less than 1.2% of the total items brought to nestlings were <5 mm, and we only identified arthropods >5 mm and placed them into one of the three size classes. Certain species of ground-dwelling arthropods may have been under-represented in sweep net samples (Doxon et al. 2011), but these were more likely to be small or fast moving insects not typically collected by Dickcissels (e.g., orthopterans, lepidopterans). We estimated availability of arthropod species and mass of each arthropod size class used in biomass calculations.

Foraging Observations.—We recorded foraging trips of Dickcissels from a 2.5-m ladder positioned ≥30 m from the nest during 2-hr monitoring periods concurrent with 4-hr videotaping sessions. We recorded straight-line distance traveled from the nest to where food was collected on georeferenced maps for each foraging trip. We grouped foraging distances into bands of 10–25, 26–50, 51–75, 76–100, 100–200, and 200+ m for analysis. We recorded cloud cover as: 0 (clear), 25 (1–25% cloudy), 50 (26–50% cloudy), 75 (50–75% or mostly cloudy), and 100% (complete overcast). We recorded wind speed using a modification of the Beaufort wind scale: 0–1.6 (calm), 1.6–8.0 (light breeze, grass and leaves slightly moving), 8.0–14.5 (grass, leaves, and small twigs constantly moving), and 16.1+ km/hr (small tree branches moving, ground debris blowing around).

Statistical Analysis.—We calculated provisioning rate as number of visits per nest per hour divided by the number of nestlings (Sejberg et al. 2000, Britschgi et al. 2006). Total biomass (g) was the sum of biomass brought to the nest by adults (both males and females) per hour divided by number of nestlings (Sejberg et al. 2000). We identified nestling diet composition from video observations. Foraging distance was the distance (m) from the nest to the location where parents collected food for their nestlings.

We used general linear mixed models to account for multiple nests in the same field (random effect) and repeated observation periods on individual nests to test hypotheses about continuous response variables (provisioning rate, biomass, foraging distances) (Littell et al. 2006, SAS Institute Inc. 2007). Predictor variables included nestling age, nest locations (buffer vs. non-buffer habitat), nestling number (foraging distance only), and male helping (male vs. no male). We included weather variables to test for effects of day-to-day variation in weather conditions on provisioning behavior before testing for effects of predictor variables. We dropped any weather variables that were not significant at $\alpha = 0.10$. We calculated provisioning rates and foraging distance in both 2008 and 2009 (biomass was calculated for 2009 only), and included year as a covariate in all analyses. We included observer presence (observers making foraging observations) as a covariate in nestling provisioning and biomass analyses to account for the possibility that technicians observing foraging trips could have affected provisioning activities.

We used selection ratios (Manly et al. 2002) for eight Orders delivered to nests to measure selection of prey types. Orthoptera, Lepidoptera, and Araneae comprised 99% of prey items and we restricted subsequent analyses of prey taxa to those three groups. We tested hypotheses about factors influencing prey type and prey size using multinomial generalized linear mixed models (PROC GLIMMIX; SAS Institute Inc. 2007) to account for multiple observations (i.e., each prey item provisioned) from the same nest. We used prey taxa and prey size (small, medium, and large) as response variables and buffer, observer presence, nestling age, and nestling number as predictor variables. We used a separate multinomial model to test if foraging distance was related to prey size, because foraging distance data only existed for a subset of the video observations when an observer was present. We used generalized linear mixed models to test effects of nestling age and nestling number on probability of male helping. We used $\alpha = 0.10$ for all tests.

RESULTS

We filmed 18 nests in 2008 and 25 nests in 2009 for 282, 1-hr observation periods (125 in

TABLE 1. Variables examined with general linear models for Dickcissel foraging in native grass field buffers in north-central Mississippi (USA), May to August 2008–2009.

Variable	*F*	df	*P*
Provisioning rate (visits/nestling/hr)			
Nestling age	0.98	3, 40.4	0.412
Buffer	0.01	1, 63.0	0.925
Observer present	7.97	1, 237	0.005
Male helping	15.60	1, 97.9	<0.001
Year	2.45	1, 38.9	0.126
Biomass (g/nestling/hr), 2009 only			
Nestling age	1.89	3, 21.9	0.161
Buffer	0.54	1, 15.3	0.475
Observer present	3.43	1, 130	0.066
Male helping	0.00	1, 82.4	0.922
Foraging distance from nest (m/nest/hr)			
Cloud cover	3.67	4, 87.8	0.008
Wind speed	3.09	3, 92.8	0.031
Nestling age	1.78	3, 68.4	0.159
Buffer	2.52	1, 34.8	0.121
Nestling number	0.32	4, 33.4	0.861
Male helping	1.05	1, 68.6	0.310
Year	0.56	1, 51.8	0.456

2008; 157 in 2009). We observed 2,384 individual provisioning events and recorded 2,417 prey items delivered to nestlings. Total filming hours for provisioning rates were 264.02 (124.35 in 2008; 139.67 in 2009). We observed 822 foraging trips over 118.30 observer hours (56.93 in 2008; 61.37 in 2009).

Nestling Provisioning Rate.—Cloud cover, wind speed, and temperature were not related to provisioning rates and were not included in subsequent analyses. Provisioning rates (mean ± SE) were higher when a male helped (3.63 ± 0.28 with male; 2.64 ± 0.18 without; $F_{1,97.9} = 15.60$, $P < 0.001$; Table 1, Fig. 1) and lower when observers were present (2.97 ± 0.21 with observer; 3.30 ± 0.20 without; $F_{1,237} = 7.97$, $P = 0.005$). Provisioning rate of nestlings did not increase from 4 to 7 days ($F_{3,40.4} = 0.98$, $P = 0.412$), did not differ between buffer and non-buffer habitats ($F_{1,63.0} = 0.01$, $P = 0.925$), and did not differ between 2008 (2.88 ± 0.28) and 2009 (3.39 ± 0.23; $F_{1,38.9} = 1.89$, $P = 0.126$).

Biomass Delivered.—Cloud cover, wind speed, and temperature were not related to biomass and were dropped from subsequent analyses. Biomass provided to nestlings in 2009 was 0.124 ± 0.005 g/nestling/hr. Biomass provided to nestlings was less when an observer was present (0.120 ± 0.012 g/nestling/hr) compared to periods with no observer present (0.138 ± 0.012; $F_{1,130} = 3.43$, $P = 0.066$; Table 1, Fig. 2). Nestlings received >50% more biomass on day 7 compared to day 4, but this difference was not significant ($F_{3,21.9} = 1.89$, $P = 0.161$). Biomass delivered did not differ between nests in buffer versus non-buffer habitats ($F_{1,15.3} = 0.54$, $P = 0.475$) and did not differ when males helped ($F_{1,82.4} = 0.00$, $P = 0.992$).

Prey Taxa.—Orthoptera comprised nearly all of nestling diets in 2008 (91% of items) and 2009 (86%). Less common prey (both years combined) included Lepidoptera (7%) and spiders (Araneae, 4%). Prey (Orthoptera, Lepidoptera, Araneae) provisioned by Dickcissels were not the most available taxa in surrounding habitats in 2009 (Fig. 3). Dickcissels preferentially selected Orthoptera ($w = 3.71$, $P < 0.001$) and avoided Araneae ($w = 0.22$, $P < 0.001$), Coleoptera ($w = 0.02$, $P < 0.001$), Diptera ($w = 0.06$, $P < 0.001$), Hemiptera ($w = 0.00$, $P < 0.001$), and Hymenoptera ($w = 0.02$, $P < 0.001$) based on selection ratios. Selection of Lepidoptera ($w = 1.33$, $P = 0.436$) and Mantidae ($w = 4.37$, $P = 0.491$) was not different from availability. We restricted subsequent analyses of prey taxa to Orthoptera, Lepidoptera, and Araneae because they comprised >99% of the prey items.

Dickcissels in 2008 were more likely to bring Orthoptera as nestling age increased (94% of total items on day 7 vs. 91% on day 4; $F_{4,600} = 2.73$, $P = 0.028$; Table 2), when nests were positioned in buffers versus adjacent habitats (94 vs. 91%; $F_{2,600} = 4.91$, $P = 0.008$), when observers were absent (95 vs. 90%; $F_{2,600} = 7.65$, $P < 0.001$), and when nests contained <5 nestlings (94–100% when ≤ 4 nestlings vs. 88% with 5; $F_{6,600} = 2.41$, $P = 0.026$); the size of these actual differences was small. Males were substantially more likely to bring Lepidoptera (21% for males vs. 4% for females) and less likely to bring Orthoptera (77 vs. 94%; $F_{2,600} = 7.59$, $P < 0.001$). None of these factors influenced prey taxa brought to nestlings in 2009 ($F = 0.04$–1.53, $P = 0.166$–0.992).

Prey Size.—Adults were more likely to bring medium versus small prey items as nestling age increased in 2008 (med. items = 73% of prey items on day 4 vs. 80 and 79% on days 5 and 6; $F_{4,640} = 3.36$, $P = 0.010$; Table 2). Adults were more likely to bring large items as nestling age increased in 2009 (e.g., 30% on day 7 vs. 11% on day 4; $F_{6,1026} = 6.26$, $P < 0.001$; Table 2, Fig. 4). Males in 2008 were more likely to bring medium prey compared

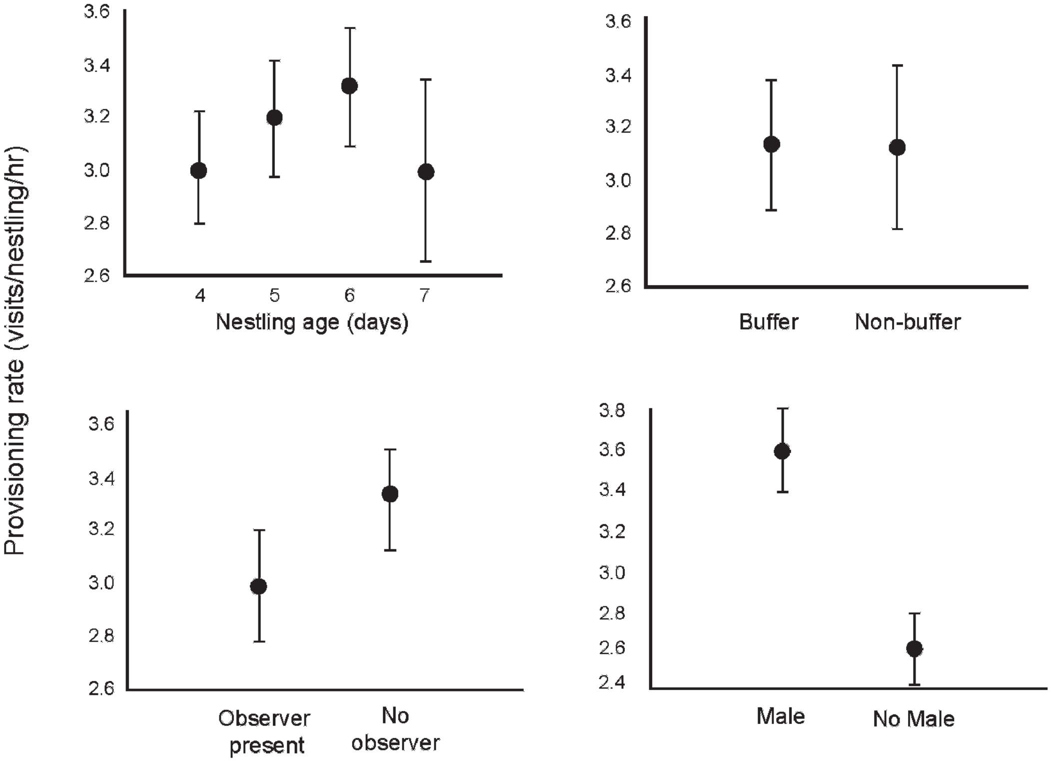

FIG. 1. Mean provisioning (least-squared means ± SE) rates at Dickcissel nests with young of various ages, buffer locations, and with/without observers present in north-central Mississippi (USA), May to August 2008–2009.

to both small and large items (16% small, 60% medium, and 23% large vs. 12, 79, and 9% for females; $F_{2,640} = 3.89$, $P = 0.021$; Table 2); males in 2009 were more likely to bring small items (27 vs. 20% for females; $F_{2,1026} = 7.28$, $P < 0.001$). Adults were slightly more likely to bring medium items versus small items when observers were present in 2008 (81% medium with observers vs. 76% without; $F_{2,640} = 2.35$, $P = 0.096$), but this effect was small and did not appear in 2009 ($F_{2,1026} = 0.11$, $P = 0.898$). Neither placement of nest in a buffer nor number of nestlings affected prey size delivered ($F = 0.01$–1.92, $P = 0.148$–0.994).

Foraging Distances.—Foraging distance decreased with increased cloud cover ($F_{4,87.8} = 3.67$, $P = 0.008$) and increased wind speeds ($F_{3,92.8} = 3.09$, $P = 0.031$; Table 1, Fig. 5). Foraging distance increased as nestlings became older, but this increase was not significant ($F_{3,68.4} = 1.78$, $P = 0.159$). Foraging distance was not different between nests in buffers and nests peripheral to buffers ($F_{1,34.8} = 2.52$, $P = 0.121$), was not related to nestling number ($F_{4,33.4} = 0.32$, $P = 0.861$), was not different when males helped ($F_{1,68.6} = 1.05$, $P = 0.310$), and did not differ between years ($F_{1,51.8} = 0.56$, $P = 0.456$). Size of prey items did not differ across foraging distances ($F_{10,491} = 0.94$, $P = 0.500$).

Probability of Male Helping.—We observed male helpers at four nests (22%) in 2008. We filmed 46 visits by males (13%) and 309 by females (87%) at these nests. We observed male helpers at five nests (20%) in 2009 when we filmed 83 nest visits by males (23%) and 278 by females (77%). We filmed a single case of a male brooding for 92 sec in 2008. Probability of male helping was not related to nestling age ($F_{3,239} = 1.96$, $P = 0.121$) or nestling number ($F_{4,239} = 0.06$, $P = 0.993$).

DISCUSSION

Nestling Provisioning.—Neither provisioning rate nor biomass delivered per nestling significantly increased with nestling age. However, parents chose larger items for older nestlings. This suggests energetic costs of changes in prey selection were less than costs of increasing number of trips.

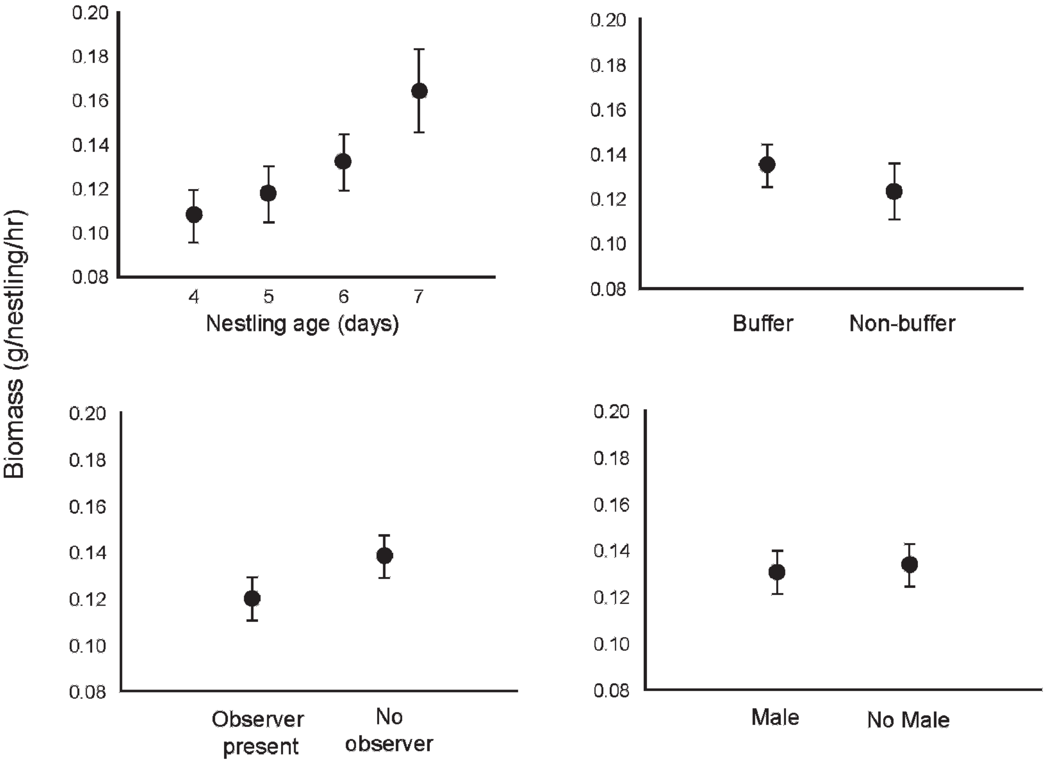

FIG. 2. Mean biomass (least-squared means ± SE) delivered to Dickcissel nestlings of various ages, buffer locations, and with/without observers in north-central Mississippi (USA), May to August 2008–2009.

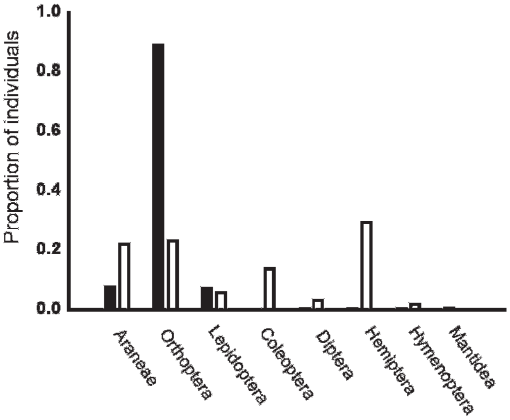

FIG. 3. Proportion of total number of arthropods observed on videos (dark bar) and collected in sweep nets (open bar) from different habitats available to nesting Dickcissels in north-central Mississippi (USA), May to August 2009.

However, adults may have made some other, more subtle changes to meet increased demand. Biomass delivered and foraging distance may have increased with increasing nestling age ($P = 0.161$ and 0.159, respectively), but these differences were not significant. Possibly, these were small, but biologically important responses that may have been significant with a larger sample. A likely explanation is that parents attempted to meet increased demand by searching farther for larger prey items. Increasing prey size may have allowed adult Dickcissels to avoid energetic costs that more frequent trips would have entailed. We did not observe feeding behaviors past nestling age of 7 days, and it is possible that biomass delivered continued to increase via changes in prey size and taxa.

Dickcissel prey selection favored Orthoptera, similar to other diet studies of grassland birds (e.g., Kaspari and Joern 1993, Kobal et al. 1998). However, selection of Lepidoptera and Coleoptera prey was comparatively less in our study. Orthoptera may have greater protein (e.g., Robel

TABLE 2. Variables examined with multinomial regression models for prey type and prey sizes brought to Dickcissel nests in native grass field buffers in north-central Mississippi (USA), May to August 2008–2009.

	2008			2009		
Variable	*F*	df	*P*	*F*	df	*P*
Prey type						
Nestling age	2.73	4, 600	0.028	1.53	6, 901	0.166
Buffer	4.91	2, 600	0.008	1.15	2, 901	0.318
Observer present	7.65	2, 600	<0.001	0.04	2, 901	0.965
Nestling number	2.41	6, 600	0.026	0.14	6, 901	0.992
Male helping	7.59	2, 600	<0.001	1.39	2, 901	0.250
Prey size						
Nestling age	3.36	4, 640	0.010	6.26	6, 1026	<0.001
Buffer	1.92	2, 640	0.148	0.01	2, 1026	0.994
Observer present	2.35	2, 640	0.096	0.11	2, 1026	0.898
Nestling number	0.51	8, 640	0.847	0.22	6, 1026	0.971
Male helping	3.89	2, 640	0.021	7.28	2, 1026	<0.001

et al. 1995) compared to other available arthropods (e.g., Lepidoptera and Araneae), and provide proportionally more biomass per prey item, while Lepidoptera are high in calcium and arachnids are high in phosphorus (Robel et al. 1995). Hemiptera were more abundant than Orthoptera at our study site, and they have greater energy content and fat than Orthoptera (Robel et al. 1995). Dickcissels may have avoided Hemiptera because they are small and fast-moving compared to Orthoptera, which could increase searching and handling time.

We excluded prey items <5 mm from analysis because observing adults provisioning nestlings can potentially miss small (<5 mm) items (E. D. Doxon, pers. comm.), and we may have biased our results against smaller arthropods. However, substantial bias is unlikely because we identified 82% of the prey brought to nests (at least to Order), and small (<5 mm) arthropods comprised a small amount of nestling diets. Grassland birds are also known to actively avoid small prey items (e.g., Kaspari and Joern 1993).

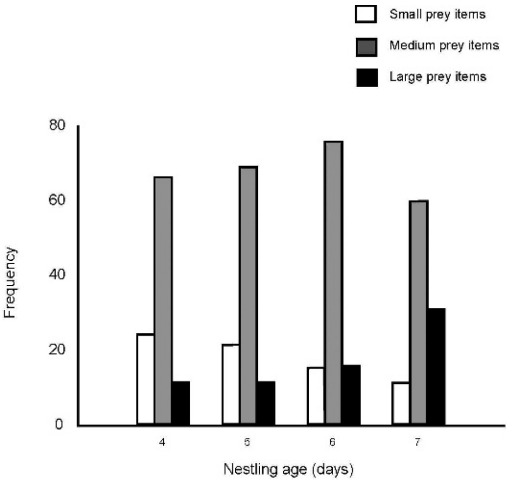

FIG. 4. Size of prey items brought to Dickcissel nestlings in north-central Mississippi (USA), May to August 2008–2009.

Foraging distance was not related to either prey size or nestling number as we hypothesized based on central place foraging theory (Orians and Pearson 1979, Kacelnik 1984), although Dickcissels may have made longer foraging trips in response to nestling age. Longer travel distances can have negative effects on survival of broods (e.g., Frey-Roos et al. 1995, Brickle et al. 2000) and future reproductive success of parents (e.g., Deerenberg and Overkamp 1999). Prey load and quality brought to young may compensate for longer foraging distances (Krebs and Avery 1985, Kacelnik and Cuthill 1990, Kaspari 1991), but we did not observe this in our study, suggesting Dickcissels foraged at distances (i.e., up to ~200 m from nest) that did not impose undue energetic costs.

Foraging trips were shorter when cloud cover or wind speeds were higher. This behavior may reflect an adjustment to increased stress levels and greater energy expenditure with increasing wind speeds (Wingfield et al. 1983). High winds and cloud cover (i.e., >75%) often occurred simultaneously and preceded rain at our site. Thus, females may have spent more time brooding and watching

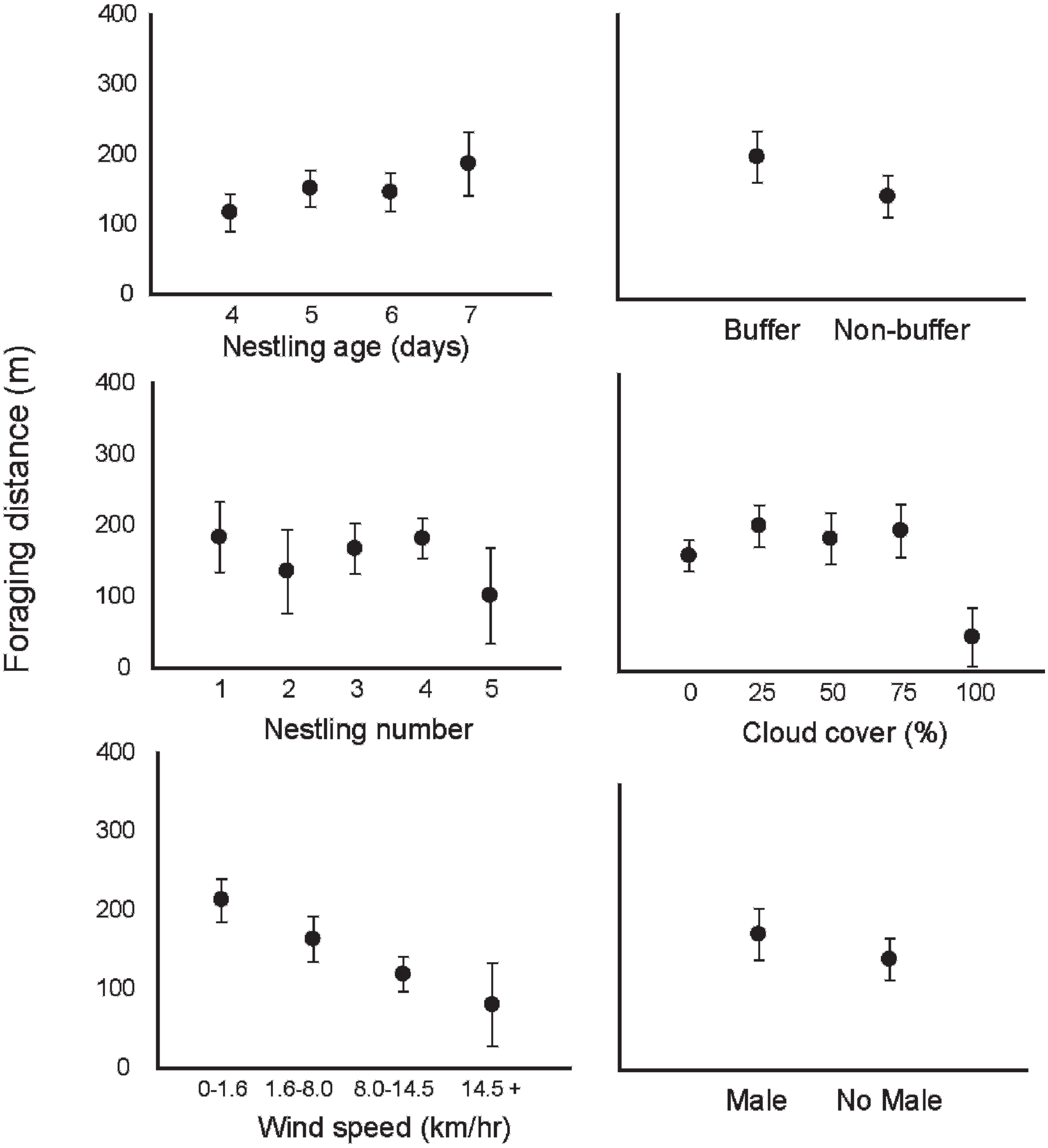

FIG. 5. Mean foraging distances (least-squared means ± SE) of adult Dickcissels from nests in north-central Mississippi (USA), May to August 2008–2009.

over nestlings, or foraged closer to the nest (*sensu* Johnson and Best 1982, Wittenberger 1982, Rosa and Murphy 1994) to provide physical protection to nestlings from convective cooling as a result of inclement weather and dissipative effects of high wind (Johnson and Best 1982).

Habitat Type Effects.—Old field habitats have often been considered primary habitats (compared to prairies) for Dickcissels (Zimmerman 1966, 1971; Temple 2002) because they may contain higher amounts of food, more forbs, and a more heterogeneous structure than prairies (Finck 1984). Adjacent non-buffer habitats in our study closely resembled old field vegetation and structure, and could potentially be considered primary habitat over planted buffers. Females that nested in non-buffer habitat (potentially primary habitat) should have provisioned in predictable ways (higher rates, more biomass, prey items of different size and taxa) compared to nests in buffers. The only difference we observed was that birds nesting in buffer habitat brought slightly more Orthoptera (2008) than those nesting in non-buffer habitats. Foraging distances did not differ between buffer and non-buffer sites, suggesting birds had relatively equivalent foraging resources and opportunities around the nest. Thus, in terms of nestling provisioning, any difference in habitat quality was not large, and native grass conservation buffers in the CRP may represent additional primary habitat.

Observer Effects on Provisioning.—Dickcissels made ~10% fewer feeding visits, brought proportionately fewer orthopterans (2008), and nestlings received ~14% less biomass when observers were present. Our results are of concern because human presence was low (1 observer) and was not near the nest (~30 m distant). Observers were careful to minimize disturbance (i.e., no loud noises or sudden behaviors), and human presence was not novel because technicians conducting nest searching and monitoring were present prior to filming. In contrast, using a ladder for observations may have potentially increased threats perceived by Dickcissels because it mimicked vertical perches used by visual predators (Andersson et al. 2009). Our observer presence would be qualitatively similar to or less intrusive than many farming activities occurring in agricultural landscapes (e.g., herbicide application, mowing, harvesting, checking fields) that would put humans and/or machinery in or near buffer habitats. Our levels of presence are qualitatively similar to many recreational activities (e.g., wildlife-watching, hiking, etc.) that occur in both crop and non-crop habitats (e.g., more natural areas) in agricultural landscapes. Human disturbance has become more frequent in recent years as the exurban footprint expands into agricultural landscapes and more natural areas such as parks and refuges allow access to increasing numbers of recreationists and ecotourists (Cordell et al. 2008).

Birds modify choices in foraging behavior and limit activity around the nest if threatened by predators, and humans may be perceived as predators (Dunn et al. 2010). Birds may thus choose to forage in habitats that are suboptimal (e.g., Fernández-Juricic and Telleria 2000) or reduce provisioning rates. Reduced nestling growth rate can be a direct result of chronic predator presence (Clinchy et al. 2004, Dunn et al. 2010), which indirectly may increase time to fledging and prolong nestling exposure to predation (Bize et al. 2003). Birds may also have chronic stress (elevated glucocorticosteroid levels) when food availability and predation risk act together (Clinchy et al. 2004, Eggers et al. 2008, Dunn et al. 2010) which may impact reproductive capacities (Zanette et al. 2003). Stressed females may pass elevated hormone levels to eggs with subsequent effects on offspring phenotype (Saino et al. 2005). Nestlings with poor body condition and slow growth rate may have lower social rankings as adults and continue to experience reduced body size and lifespan (Metcalfe and Monaghan 2001).

Human presence may reduce foraging rates of adults (e.g., Fernández-Juricic and Tellería 2000), influence seasonal timing of song (Gutzwiller et al. 1997), and decrease survival rates of nestlings and fledglings (e.g., Safina and Burger 1983). We know of no documentation of decreased provisioning as a direct result of human presence for grassland birds other than our study. Seemingly benign human activities may have more substantial effects on breeding success than currently assumed if reduced provisioning is a common response to low levels of human intrusion. Remote monitoring of birds with video technology also may decrease potential for research-related effects on nesting birds compared to direct observation.

Male Helping.—Male helping increased provisioning rates but biomass delivered was not different because males brought fewer Orthoptera (2008) and smaller prey items (2009) than females. The major benefit of male helping appears to be decreased effort by the female rather than increased provisioning of the young (and hence greater survivorship).

Several hypotheses may explain male helping. First, males may be more likely to help when food abundance is low (e.g., Wittenberger 1982). Rainfall during the breeding season increased almost two-fold in 2009 versus 2008 (May–Aug 2008 rainfall = 222 mm; May–Aug 2009 rainfall = 420 mm; Mississippi State Department of GeoSciences). Vegetation density and subsequent invertebrate abundance are typically greater in wetter years, but males helped in both years. Second, males may have more incentive to help at late-season nests (Igl and Best 2001) as predation risk increases (daily survival rate of nests decreased as the breeding season progressed in our study; Adams 2011). However, we observed male helping in the early (2009) and middle (2008 and 2009) parts of the nesting season. Third, helping may be more advantageous to the male at later nest ages because the nest's reproductive value increases close to fledging (Igl and Best 2001 and references therein). We observed male helping on days 4 through 7 but, because we only filmed during those days, we cannot say whether male helping increased at >7 days of the nestling period or was absent prior to day 4. Fourth, male provisioning could be favored in lower quality habitats (Igl and Best 2001), but there is no evidence that old field habitats and field buffers in which male helping has been observed (Igl and Best 2001, this study) are low quality for Dickcissels. Fifth, male helping may be unique to specific individual Dickcissels or local populations (Maddox and Bollinger 2000, Igl and Best 2001). However, 14 of 21 locations where this behavior has been observed (including our study) are in the core breeding range of Dickcissels (Igl and Best 2001). Males may be more likely to help when there are few females (Sejberg et al. 2000, Igl and Best 2001) because, in polygynous systems, monogamous males (or those with fewer females) have more time available to help compared to males with multiple females (Sejberg et al. 2000). We did not mark birds and cannot address this hypothesis.

CONSERVATION IMPLICATIONS

Accessible and nutritional arthropod prey for grassland birds is a key factor for conservation of grassland species that use conservation set-aside lands (Whittingham and Evans 2004). Native grass field buffers in our study provided nestling food resources similar to or better in quality (e.g., biomass and prey taxa) compared to surrounding habitats. Native grass habitats (like CP33 buffers) may typically provide habitat for more farmland birds compared to clean-farming practices (e.g., Deschenes et al. 2003); greater structural complexity on a landscape level may attract more birds overall (Rodenhouse and Best 1994, Jones et al. 2005). Agri-environmental practices which support arthropod populations and decrease perceived and actual predation risk may improve foraging rates and survival (Whittingham and Evans 2004). More research on nestling provisioning by grassland birds should be conducted in intensively managed agricultural landscapes and native prairies, particularly prey selection and foraging success of adults away from the nest. Continuous video documentation of nest activity allows well-concealed activities to be directly observed and better quantified. More intensive video documentation of Dickcissel nesting behavior should be conducted with other populations to understand the true frequency of male helping and identify its causes.

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LITERATURE CITED

ADAMS, H. L. 2011. Agricultural conservation buffers for breeding grassland birds in eastern Mississippi. Dissertation. Mississippi State University, Mississippi State, USA.

ANDERSSON, M. 1981. Central place foraging in the Whinchat, *Saxicola rubetra*. Ecology 62:538–544.

ANDERSSON, M., J. WALLANDER, AND D. ISAKSSON. 2009. Predator perches: a visual search perspective. Functional Ecology 23:373–379.

BIZE, P., A. ROULIN, L. F. BERSIER, D. PFLUGER, AND H. RICHNER. 2003. Parasitism and developmental plasticity in Alpine Swift nestlings. Journal of Animal Ecology 72:633–639.

BRENNAN, L. A. AND W. P. KUVLESKY JR. 2005. North American grassland birds: an unfolding conservation crisis? Journal of Wildlife Management 69:1–13.

BRICKLE, N. W., D. G. C. HARPER, N. J. AEBISCHER, AND S. H. COCKAYNE. 2000. Effects of agricultural intensification on the breeding success of Corn Buntings *Miliaria calandra*. Journal of Applied Ecology 37:742–755.

BRITSCHGI, A., R. SPAAR, AND R. ARLETTAZ. 2006. Impact of grassland farming intensification on the breeding ecology of an indicator insectivorous passerine, the Whinchat *Saxicola rubetra*: lessons for overall alpine meadowland management. Biological Conservation 130:193–205.

BRYANT, D. M. AND K. R. WESTERTERP. 1983. Time and energy limits to brood size in House Martins (*Delichon urbica*). Journal of Animal Ecology 52: 905–925.

CLINCHY, M., L. ZANETTE, R. BOONSTRA, J. C. WINGFIELD, AND J. N. M. SMITH. 2004. Balancing food and predator pressure induces chronic stress in songbirds. Proceedings of the Royal Society of London, Series B 271:2473–2479.

Cordell, H. K., C. J. Betz, and G. T. Green. 2008. Nature-based outdoor recreation trends and wilderness. International Journal of Wilderness 14:7–9, 13.

Dearborn, D. C., A. D. Angers, F. R. Thompson III, and J. Faaborg. 1998. Effects of cowbird parasitism on parental provisioning and nestling food acquisition and growth. Condor 100:326–334.

Deerenberg, C. and C. J. F. Overkamp. 1999. Hard work impinges on fitness: an experimental study with Zebra Finches. Animal Behaviour 58:173–179.

Dêschenes, M., L. Bêlanger, and J. F. Giroux. 2003. Use of farmland riparian strips by declining and crop damaging birds. Agriculture, Ecosystems, and Environment 95:567–577.

Dijkstra, C., A. Bult, S. Bijlsma, S. Daan, T. Meijer, and M. Zijlstra. 1990. Brood size manipulations in the Kestrel (*Falco tinnunculus*): effects on offspring and parent survival. Journal of Animal Ecology 59:269–285.

Dollar, J. G. 2011. Responses of butterfly and forb communities to management of semi-natural grassland buffers. Dissertation. Mississippi State University, Mississippi State, USA.

Doxon, E. D., C. A. Davis, and S. D. Fuhlendorf. 2011. Comparison of two methods for sampling invertebrates: vacuum and sweep-net sampling. Journal of Field Ornithology 82:60–67.

Dunn, J. C., K. C. Hamer, and T. G. Benton. 2010. Fear for the family has negative consequences: indirect effects of nest predators on chick growth in a farmland bird. Journal of Applied Ecology 47:994–1002.

Eggers, S., M. Griesser, and J. Ekman. 2008. Predator-induced reductions in nest visitation rates are modified by forest cover and food availability. Behavioral Ecology 19:1056–1062.

Fernández-Juricic, E. and J. L. Telleria. 2000. Effects of human disturbance on spatial and temporal feeding patterns of Blackbird *Turdus merula* in urban parks in Madrid, Spain. Bird Study 47:13–21.

Finck, E. J. 1984. Male Dickcissel behavior in primary and secondary habitats. Wilson Bulletin 96:672–680.

Frey-Roos, F., P. A. Brodmann, and H. Reyer. 1995. Relationships between food resources, foraging patterns, and reproductive success in the Water Pipit *Anthus* sp. *spinoletta*. Behavioral Ecology 6:287–295.

Gutzwiller, K. J., E. A. Kroese, S. H. Anderson, and C. A. Wilkins. 1997. Does human intrusion alter the seasonal timing of avian song during breeding periods? Auk 114:55–65.

Hale, S., S. Riffell, L. W. Burger Jr., H. L. Adams, and J. G. Dollar. 2011. Fire ant response to management of native grass conservation buffers. American Midland Naturalist 166:283–191.

Haufler, J. B. (Editor). 2005. Fish and wildlife benefits of Farm Bill conservation programs: 2000–2005 update. Technical Review 05-02. The Wildlife Society, Bethesda, Maryland, USA.

Herkert, J. R. 2009. Response of bird populations to farmland set-aside programs. Conservation Biology 23:1036–1040.

Igl, L. D. and L. B. Best. 2001. On the rarity of observations of food provisioning by male Dickcissels. Prairie Naturalist 33:111–118.

Johnson, E. J. and L. B. Best. 1982. Factors affecting feeding and brooding of Gray Catbird nestlings. Auk 99:148–156.

Jones, G. A., K. E. Sieving, and S. K. Jacobson. 2005. Avian diversity and functional insectivory on north-central Florida farmlands. Conservation Biology 19:1234–1245.

Kacelnik, A. 1984. Central place foraging in Starlings (*Sturnus vulgaris*). I. Patch residence time. Journal of Animal Ecology 53:283–299.

Kacelnik, A. and I. Cuthill. 1990. Central place foraging in Starlings (*Sturnus vulgaris*). II. Food allocation to chicks. Journal of Animal Ecology 59:655–674.

Kaspari, M. 1991. Central place foraging in the Grasshopper Sparrow: opportunism or optimal foraging in a variable environment? Oikos 60:307–312.

Kaspari, M. and A. Joern. 1993. Prey choice by three insectivorous grassland birds: reevaluating opportunism. Oikos 68:414–430.

Kobal, S. N., N. F. Payne, and D. R. Ludwig. 1998. Nestling food habits of seven grassland bird species and insect abundance in grassland habitats in northern Illinois. Transactions of the Illinois State Academy of Science 91:69–75.

Krebs, J. R. and M. I. Avery. 1985. Central place foraging in the European Bee-eater, *Merops apiaster*. Journal of Animal Ecology 54:459–472.

Littell, R. C., G. A. Milliken, W. W. Stroup, R. D. Wolfinger, and O. Schabenberger. 2006. SAS for mixed models. Second Edition. SAS Institute Inc., Cary, North Carolina, USA.

Maddox, J. D. and E. K. Bollinger. 2000. Male Dickcissels feed nestlings in east-central Illinois. Wilson Bulletin 112:153–155.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Kluwer Academic Publishers, Norwell, Massachusetts, USA.

Martin, T. E. 1987. Food as a limit on breeding birds: a life history perspective. Annual Review of Ecology and Systematics 18:453–487.

McIntyre, N. E. and T. R. Thompson. 2003. A comparison of Conservation Reserve Program habitat plantings with respect to arthropod prey for grassland birds. American Midland Naturalist 150:291–301.

Metcalfe, N. B. and P. Monaghan. 2001. Compensation for a bad start: grow now, pay later? Trends in Ecology and Evolution 16:254–260.

Orians, G. H. and N. E. Pearson. 1979. On the theory of central place foraging. Pages 155–177 *in* Analysis of ecological systems (D. J. Horn, G. R. Stairs, and R. D. Mitchell, Editors). Ohio State University Press, Columbus, USA.

Rich, T. D., C. J. Beardmore, H. Berlanga, P. J. Blancher, M. S. W. Bradstreet, G. S. Butcher, D. W. Demarest, E. H. Dunn, W. C. Hunter, E. E. Iñigo-Elias, J. A. Kennedy, A. M. Martell, A. O.

PANJABI, D. N. PASHLEY, K. V. ROSENBERG, C. M. RUSTAY, J. S. WENDT, AND T. C. WILL. 2004. Partners in Flight North American Landbird Conservation Plan. Version March 2005. Cornell Laboratory of Ornithology, Ithaca, New York, USA. www.partnersinflight.org/cont_plan/

ROBEL, R. J., B. M. PRESS, B. L. HENNING, K. W. JOHNSON, H. D. BLOCKER, AND K. E. KEMP. 1995. Nutrient and energetic characteristics of sweepnet-collected invertebrates. Journal of Field Ornithology 66:44–53.

RODENHOUSE, N. L. AND L. B. BEST. 1994. Foraging patterns of Vesper Sparrows (*Pooecetes gramineus*) breeding in cropland. American Midland Naturalist 131:196–206.

ROGERS, L. E., R. L. BUSCHBOM, AND C. R. WATSON. 1977. Length-weight relationships of shrub-steppe invertebrates. Annals of the Entomological Society of America 70:51–53.

ROSA, S. M. AND M. T. MURPHY. 1994. Trade-offs and constraints on Eastern Kingbird parental care. Wilson Bulletin 106:668–678.

RYAN, M. R., L. W. BURGER JR., AND E. W. KURZEJESKI. 1998. The impact of CRP on avian wildlife: a review. Journal of Production Agriculture 11:61–66.

SAFINA, C. AND J. BURGER. 1983. Effects of human disturbance on reproductive success in the Black Skimmer. Condor 85:164–171.

SAINO, N., S. CALZA, AND A. P. MØLLER. 1997. Immunocompetence of nestling Barn Swallows in relation to brood size and parental effort. Journal of Animal Ecology 66:827–836.

SAINO, N., M. ROMANO, R. P. FERRARI, R. MARTINELLI, AND A. P. MØLLER. 2005. Stressed mothers lay eggs with high corticosterone levels which produce low-quality offspring. Journal of Experimental Zoology 303A:998–1006.

SAMSON, F. AND F. KNOPF. 1994. Prairie conservation in North America. Bioscience 44:418–421.

SAS INSTITUTE INC. 2007. SAS/STAT® 9.2 user's guide. SAS Institute Inc., Cary, North Carolina, USA.

SAUER, J. R., J. E. HINES, J. E. FALLON, K. L. PARDIECK, D. J. ZIOLKOWSKI JR., AND W. A. LINK. 2011. The North American Breeding Bird Survey, results and analysis 1966–2009. Version 3.23.2011. USDI, Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland, USA. www.mbr-pwrc.usgs.gov/bbs/html

SCHADD, C. A. AND G. RITCHISON. 1998. Provisioning of nestlings by male and female Yellow-breasted Chats. Wilson Bulletin 110:398–402.

SEJBERG, D., S. BENSCH, AND D. HASSELQUIST. 2000. Nestling provisioning in polygynous Great Reed Warbers (*Acrocephalus arundinaceus*): do males bring larger prey to compensate for fewer nest visits? Behavioral Ecology and Sociobiology 47:213–219.

SMITH, M. D., P. J. BARBOUR, L. W. BURGER JR., AND S. J. DINSMORE. 2005. Breeding bird abundance and diversity in agricultural field borders in the Black Belt Prairie of Mississippi. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 59:43–56.

SOUTHWOOD, T. R. E. 1978. Ecological methods: with particular reference to the study of insect populations, Second Edition. Chapman and Hall, London, United Kingdom.

TEMPLE, S. A. 2002. Dickcissel (*Spiza americana*). The birds of North America. Number 703.

WHITTINGHAM, M. J. AND K. L. EVANS. 2004. The effects of habitat structure on predation risk of birds in agricultural landscapes. Ibis 146:210–220.

WINGFIELD, J. C., M. C. MOORE, AND D. S. FARNER. 1983. Endocrine responses to inclement weather in naturally breeding populations of White-crowned Sparrows (*Zonotrichia leucophrys pugetensis*). Auk 100:56–62.

WITTENBERGER, J. F. 1982. Factors affecting how male and female Bobolinks apportion parental investments. Condor 84:22–39.

WRIGHT, J., C. BOTH, P. A. COTTON, AND D. BRYANT. 1998. Quality vs. quantity: energetic and nutritional trade-offs in parental provisioning strategies. Journal of Animal Ecology 67:620–634.

ZANETTE, L., J. N. M. SMITH, H. VAN OORT, AND M. CLINCHY. 2003. Synergistic effects of food and predators on annual reproductive success in Song Sparrows. Proceedings of the Royal Society of London, Series B 270:799–803.

ZIMMERMAN, J. L. 1966. Polygyny in the Dickcissel. Auk 83:534–546.

ZIMMERMAN, J. L. 1971. The territory and its density dependent effect in *Spiza americana*. Auk 88:591–612.