



4-30-2013

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Recommended Citation

Skipper, Ben R. and Kim, Daniel H. (2013) "Provisioning rate, dietary composition, and prey selection of breeding Bobolinks and Grasshopper Sparrows," *Western North American Naturalist*: Vol. 73: No. 1, Article 3.

Available at: <http://scholarsarchive.byu.edu/wnan/vol73/iss1/3>

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PROVISIONING RATE, DIETARY COMPOSITION, AND PREY SELECTION OF BREEDING BOBOLINKS AND GRASSHOPPER SPARROWS

Ben R. Skipper^{1,3} and Daniel H. Kim^{2,4}

ABSTRACT.—We examined parental provisioning behavior of 2 grassland obligate birds, Bobolink (*Dolichonyx oryzivorus*) and Grasshopper Sparrow (*Ammodramus savannarum*) in south central Nebraska. We assessed rates of food delivery (provisions · nestling⁻¹h⁻¹) and prey composition by using video recordings. We estimated arthropod availability from sweep net samples collected during 2 breeding seasons. We evaluated the effects of provisioning rate and prey composition on nestling quality inferred through nestling mass. We focused our efforts on lepidopteran larvae and orthopterans, as these orders comprised the bulk of identified prey deliveries. Total provisioning rates at 53 Bobolink nests and 32 Grasshopper Sparrow nests did not predict nestling mass for either species in either year. In one of 2 years, we observed a positive relationship between unidentified prey items and Bobolink nestling mass and a negative relationship between percentage of lepidopteran larvae and Bobolink nestling mass. These observed relationships are likely spurious, however. Parents of both species provided lepidopteran larvae at higher rates than were expected based on availability, and this particular result highlights the potential importance of dietary content to developing nestlings.

RESUMEN.—Examinamos el comportamiento de aprovisionamiento parental de dos aves obligadas de pastizal, *Dolichonyx oryzivorus* y *Ammodramus savannarum* en el centro-sur de Nebraska. Evaluamos las tasas de entrega de alimento (elementos · cría⁻¹hora⁻¹) y la composición de las presas, utilizando grabaciones de videos, y la disponibilidad de artrópodos a partir de muestras tomadas con redes durante dos temporadas de apareamiento. Evaluamos los efectos de la tasa de aprovisionamiento y la composición de las presas sobre la calidad de las crías, inferida a través de la masa de las crías. Nos enfocamos en las larvas Lepidópteras y en los Ortópteros ya que estos órdenes abarcaron la mayor parte de las presas entregadas que fueron identificadas. Las tasas totales de aprovisionamiento en 53 nidos de *Dolichonyx oryzivorus* y en 32 nidos de *Ammodramus savannarum* no predijeron la masa de las crías para ninguna de las especies en ninguno de los años. En uno de los dos años, observamos una relación positiva entre los elementos de presas no identificadas y la masa de las crías de *Dolichonyx oryzivorus*, y una relación negativa entre el porcentaje de larvas Lepidópteras y la masa de las crías de *Dolichonyx oryzivorus*, aunque esto es probablemente espurio. Los padres de ambas especies proporcionaron larvas Lepidópteras en mayores tasas que las esperadas según la disponibilidad, resaltando la posible importancia del contenido dietario para las crías en desarrollo.

Productivity of altricial birds is often limited by high energetic demands placed on provisioning parents (Lack 1947, Robel et al. 1995). Parental prey selection and provisioning efforts have short- and long-term fitness consequences for both parents and nestlings (Newton 1998). Parental provisioning rates do not represent a direct measure of environmentally available food; rather these rates are a measure of resources available for nestlings (Schwagmeyer and Mock 2008).

Grassland systems provide an array of invertebrate prey, yet merely measuring caloric intake fails to account for differences in digestibility among prey items. Robel et al. (1995), for example, reported that lepidopteran larvae and orthopterans have similar caloric values.

More recently, Finke (2007) found that nutritionally similar items often differ in digestibility (i.e., chitin content) and, therefore, differ in energetic provision. Because lepidopteran larvae are low in chitin (Finke 2007), they leave a larger portion of calories available for nestling survival, quality, and ultimately recruitment into the breeding population (Lack 1947, Ricklefs 2000).

Bobolink (*Dolichonyx oryzivorus*) and Grasshopper Sparrow (*Ammodramus savannarum*) are obligate grassland-nesting species in which both parents provision their altricial young with arthropods, mainly insects (Martin and Gavin 1995, Vickery 1996). Although prior studies document nestling diets (Wittenberger 1982, Kaspari and Joern 1993) and provisioning

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rates for these species (Martin 1974, Kaspari 1991, Adler and Ritchison 2011), we know of no study for either species that relates delivery rates and dietary content to nestling quality. Our goals were to (1) determine the impact of provisioning rate on nestling mass; (2) investigate the relationship between dietary composition and nestling mass; and (3) investigate whether prey selected by provisioning parents reflected prey availability, which was estimated through sweep net sampling.

We predicted that (1) mean nestling mass would correlate positively with parental effort (provisions \cdot nestling⁻¹h⁻¹) for both species. Such a positive correlation would be in line with studies that demonstrate the importance of parental contributions to nestling mass, for example through mate removal experiments (see table 8.3 in Clutton-Brock 1991). Additionally, we predicted that (2) parents of both species would provision their young with lepidopteran larvae in excess of the larvae's environmental availability and that (3) nestling mass would increase with the proportion of lepidopteran larvae brought to the nest. Both predictions 2 and 3 follow from the previously demonstrated importance of lepidopteran larvae to developing nestlings (e.g., Nagy and Smith 1997).

STUDY AREA

We conducted our study during the summers of 2005 and 2006 at Mormon Island and Wild Rose Ranch (40°48' N, 98°26' W), owned and managed by the Platte River Whooping Crane Maintenance Trust (hereafter "trust"), in Hall County, Nebraska. The trust manages grasslands to promote structural vegetative heterogeneity for the benefit of migratory and resident birds. Management regimes use a combination of grazing and prescribed burning to mimic historical disturbance patterns.

METHODS

We concentrated nest searching on 16-ha study plots (12 in 2005, 11 in 2006). Plots were part of an ongoing study evaluating the impact of grassland management on the breeding ecology of grassland birds. Plot locations allowed us to sample all seral stages of a 4-year burn-graze and 6-year burn-hay rotation from early (spring burn with and without grazing) to late (2–3 years post disturbance) successional grasslands. We located nests by systematically

searching appropriate habitat and either flushing laying/incubating females from nests or observing parental behavior (Martin and Geupel 1993). We marked all nests and visited them at approximately 3-day intervals to monitor nest fate.

We used tripod-mounted video cameras to record adult provisioning rates and prey identity on day 6 for Grasshopper Sparrows and day 7 for Bobolinks (day of hatch = 0) within 1 h post-sunrise. Both species fledge as late as day 10, but we selected late-stage broods to maximize observable provisions (Norlund and Barber 2005) and to minimize female brooding time (Sanz and Tinbergen 1999). Additionally, day 6 and 7 represent the last day to safely manipulate nests of both species while minimizing the chance of premature fledging (D. Kim personal observation, Martin and Gavin 1995, Vickery 1996). We exposed nests by pinning back vegetation to provide an unobstructed view for a video camera placed 1.5 m from the nest and recorded nest activity for 1 h. We transcribed data, noting the number and type of prey items delivered. We considered each item brought to the brood as a single provision (i.e., a parent with 3 items during one trip brought 3 provisions). We recorded mass for all nestlings on day 6 by using Pesola spring scales accurate to 0.5 g, and we banded each nestling with appropriately sized USGS bands.

We assessed arthropod prey availability using sweep nets. While sweep nets do not provide an absolute measure of prey abundance, they do provide an index of arthropod availability (Cooper and Whitmore 1990). We collected samples from 27 regularly spaced points (100 sweeps per point) within each study plot. We sampled at 10-day intervals in 2005 (8 collections) beginning on 23 May and biweekly in 2006 (6 collections) beginning on 29 May. We sorted arthropods to order, focusing on lepidopteran larvae and orthopterans. Further, we excluded very small insects, such as leaf- and planthoppers (Homoptera), small Diptera, and small Hymenoptera, from our sweep net sample because these items are generally avoided (Kaspari and Joern 1993).

Due to our limited sample size of nests from some management units, we pooled all nests for each species by year into a single category (e.g., Bobolink 2005). We also pooled sampled insects across different management units by year to represent total insect availability. Although management may affect insect

TABLE 1. Summary of provisioning efforts.

Species	Year	Total provisions	Per capita rate*	No. (%)** Orthop ^a	No. (%)** Lep ^b	No. (%)** Unk ^c
Bobolink	2005	376	4.08 (0.40)	56 (16)	59 (15)	261 (69)
	2006	294	4.21 (0.38)	92 (31)	58 (20)	144 (49)
Grasshopper Sparrow	2005	80	2.40 (0.36)	20 (26)	9 (12)	49 (63)
	2006	223	3.09 (0.36)	126 (57)	40 (18)	57 (25)

*Number of provisions delivered per nestling per hour. Mean is given with the standard error in parentheses.

**Number of delivered items identified. Percent of total is given in parentheses.

^aOrthoptera

^bLepidoptera larvae

^cUnidentified items

TABLE 2. Mean (SE) of arthropods collected by sweep net in June of 2005 and 2006.

Year	Orthoptera	Lepidoptera ^a	Other
2005	227 (38.66)	57 (6.12)	943 (159.47)
2006	122 (37.69)	66 (13.47)	358 (112.98)

^aLarvae only

production and thereby provisioning behaviors (Zalik and Strong 2008), fencerows, dirt roads, and other soft edges separating management units did not prevent individuals from crossing into other management units. Although some individuals may not have foraged outside the management unit of their nest site, we frequently observed other individuals of both species traveling over 200 m into neighboring pastures of different management types to forage for prey, justifying the pooling of insects into a single category.

We analyzed data with SigmaStat for Windows 3.11 (Systat Software, Inc. 2004). When data met assumptions of normality, we used linear regression to examine the effects of provisioning rate and dietary composition on nestling mass. We excluded nests parasitized by Brown-headed Cowbirds (*Molothrus ater*) to minimize confounding variables associated with brood parasitism. We used chi-square analysis with Yates' correction for continuity to compare the composition of parental provisions with the composition of arthropods sampled using sweep nets. We compared mean nestling mass between years with *t* tests. We present brood size, nestling mass (mean nestling mass of brood), provisioning rate, and dietary composition as means with standard errors.

RESULTS

We documented provisioning rate and dietary composition for 53 (30 in 2005; 23 in

2006) Bobolink nests and 32 (11 in 2005; 21 in 2006) Grasshopper Sparrow nests. Mean Bobolink brood size (day 7) was 3.4 (SE = 0.21) nestlings in 2005 and 3.2 (SE = 0.32) in 2006. Grasshopper Sparrow day-6 brood sizes averaged 3.1 (SE = 0.34) nestlings in 2005 and 3.6 (SE = 0.20) in 2006. Mean Bobolink nestling mass averaged 17.66 g (SE = 0.50) in 2005 and 16.79 g (SE = 0.64) in 2006, with no observed variation between years ($t_{51} = 1.08$, $P = 0.29$). Mean nestling mass for Grasshopper Sparrows increased in 2006 (11.02 g, SE = 0.22) compared to 2005 (9.52 g, SE = 0.53; $t_{33} = 3.15$, $P = 0.004$).

Bobolink adults averaged 4.08 (SE = 0.40) and 4.21 (SE = 0.38) provisions · nestling⁻¹h⁻¹ for 2005 and 2006, respectively (Table 1). Grasshopper Sparrow adults provisioned at slightly lower rates, with 2.40 (SE = 0.36) and 3.09 (SE = 0.36) provisions · nestling⁻¹h⁻¹ in 2005 and 2006, respectively (Table 1). We detected no influence of provisioning rate on offspring mass for either species in either year (Bobolink 2005: $F_{1,28} = 0.51$, $P = 0.48$; Bobolink 2006: $F_{1,21} = 0.38$, $P = 0.54$; Grasshopper Sparrow 2005: $F_{1,7} = 1.59$, $P = 0.25$; Grasshopper Sparrow 2006: $F_{1,18} = 1.01$, $P = 0.33$).

In both 2005 and 2006, the majority of nestlings hatched and fledged within the month of June. Therefore, we considered insects collected in the month of June as representative of total insect availability, and we used these data in all analyses (Table 2).

A summary of delivered items is presented in Table 1. We identified the majority of visible items as either orthopterans or lepidopteran larvae. In some years, however, the majority of items delivered were unidentifiable due to the posture assumed by feeding birds or the position of items held inconspicuously in the bill. Dietary composition predicted

nestling mass in only 2 cases: Bobolink nestling mass and percent lepidopteran larvae fed ($F_{1,21} = 6.03$, $P = 0.023$ —negative interaction) and Bobolink nestling mass and percent unknown items fed ($F_{1,21} = 8.77$, $P = 0.007$ —positive interaction). These significant interactions both occurred in 2006. Both species provisioned nestlings with lepidopteran larvae at greater rates than the larvae were encountered in the environment (Bobolink 2005: $\chi^2 = 58.84$, $df = 2$, $P < 0.001$; Bobolink 2006: $\chi^2 = 22.36$, $df = 2$, $P < 0.001$; Grasshopper Sparrow 2005: $\chi^2 = 9.38$, $df = 2$, $P = 0.009$; Grasshopper Sparrow 2006: $\chi^2 = 108.17$, $df = 2$, $P < 0.001$).

DISCUSSION

Provisioning adults of both species selectively fed lepidopteran larvae to their offspring, as we had predicted. However, we found no support for the suggestion that such provisioning contributes to greater nestling mass. We note that mean nestling masses for both species were within previously reported values (Martin and Gavin 1995, Vickery 1996); however, provisions were fewer than previously reported for grassland passerines (Martin 1974, Zalik and Strong 2008, Adler and Ritchison 2011). Several factors may explain the lower provisioning rates observed in our study. First, parental feeding rates may have been affected by our decision to pin back vegetation for unobstructed camera angles, as some adults only approached the nest from the rear, where vegetative structure was unmanipulated. Second, it is possible that adults were not given enough time to acclimate to cameras before recording began, resulting in fewer provisions on an hourly basis. Although some provisioning adults returned to nests quickly (e.g., within 1 min), others took longer to resume provisioning behaviors. Third, lower provisioning rates could have resulted from our decision to film late-stage nestlings. Altricial nestlings develop asymptotically, with nestling mass plateauing near the time of fledging. Increased parental provisions to nestlings near fledging may only result in marginal gains to parents in terms of offspring survival. Fourth, Nur (1984) speculated that the negative relationship between provisioning rates and nestling mass he observed in Blue Tits (*Parus caeruleus*) could be the result of parents

increasing late nestling stage provisioning rates to compensate for broods with low average nestling quality. Fifth, parents may reduce provisioning rates late in the nesting period in an attempt to induce fledging, as suggested by Adler and Ritchison (2011).

Lepidopteran larvae and orthopterans composed the majority of identified prey delivered by parents, similar to results from other studies of Bobolink and Grasshopper Sparrow nestling diets (Wittenberger 1982, Kaspari and Joern 1993). However, contrary to our predictions, we found no positive relationship between the percentage of lepidopteran larvae and nestling mass in either species. In fact, Bobolink nestling mass decreased with an increase in percentage of lepidopteran larvae delivered in 2006. Previous studies identified the importance of soft-bodied larval insects to nestlings of altricial birds (Biermann and Sealy 1982, Goodbred and Holmes 1996, Pechacek and Kristin 2004), and our observation of a negative association is likely spurious. Despite our efforts to position cameras in a manner that would yield an unobstructed view of prey brought to the nest, a large number of items were unidentifiable due to parental posture, items held inconspicuously in the bill, or occlusion by vegetation (Table 1). We suspect that the items obstructed by parental posture are similar to those that were unobstructed by parental posture.

Although the objectives of this study did not include an assessment of prey size delivered, Kaspari (1991) found that prey size was an important variable affecting selection decisions, especially for central place foragers such as provisioning adult Grasshopper Sparrows. From the perspective of the provisioning adults, large prey items should be more economical in terms of energy and nutrients delivered to nestlings. However, excessively large items may impose handling constraints on nestlings, which are unable to efficiently process and digest large, hard-bodied insects (Bañbura et al. 1999). Prey size contributed to the large number of unidentified items we observed. Small and inconspicuously held items within the parents' bills may have represented mainly Homoptera or Acari. Our inability to identify a greater percentage of delivered prey items may have masked relationships between diet and nestling mass.

Provisioning parents selected lepidopteran larvae disproportionately to their availability

in the environment, suggesting that these prey items confer nutritional advantages over orthopterans. Robel et al. (1995) found little difference in nutritional composition (i.e., fat, crude protein, ash, crude fiber) between lepidopterans and orthopterans, however their nutritional testing did not measure digestibility. When examining dietary quality of insects for captive zoo animals, Finke (2007) found that measures of protein do not differentiate between nutritionally available protein from soft body parts and protein bound within chitin in sclerotized cuticle. Much of the sclerotized cuticle remains undigested by avian consumers and therefore nutritionally unavailable to them (Karasov 1990). Given that young birds are less efficient at digestion than adults (Karasov 1990), both species should preferentially select lepidopteran larvae for prey delivery if these larvae provide maximum net energy gain. Alternatively, the selection for lepidopteran larvae could reflect some other prey selection decision, such as ease of capture. Orthopterans may actively attempt to evade capture by jumping away from an approaching predator. In contrast, lepidopteran larvae are slow moving, rely on crypsis, and drop from vegetation to avoid capture.

While our results confirmed our prediction of parental prey selection for both Bobolink and Grasshopper Sparrows, the results contradict previous work by Kaspari and Joern (1993), who found a preference for orthopterans by Grasshopper Sparrows. However, Kaspari and Joern did not quantify food availability at their study site. We suspect that the limited soil moisture at their Nebraska Sandhills study area may restrict lepidopteran larvae availability; our study site along the Platte River maintained moisture throughout most of the breeding season, even in drought years.

ACKNOWLEDGMENTS

We appreciate the work ethic of 20 technicians who sorted and counted arthropod samples, especially D.K. Konkoly. Funding was provided by The Platte River Whooping Crane Trust and a Nebraska State wildlife grant awarded to DHK. All banding was done under federal banding permit 23224 and Nebraska State Scientific Permit 789. Comments by L. Ramirez, W. Wehtje, and 2 anonymous reviewers improved the content and clarity of this manuscript.

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Received 18 August 2011

Accepted 4 June 2012