Seasonal abundance and nutritional concentration of grassland arthropods.

3 authors, including:

Ben Skipper
Angelo State University
13 PUBLICATIONS **9** CITATIONS

Daniel H. Kim
U.S. Fish and Wildlife Service
20 PUBLICATIONS **276** CITATIONS

Some of the authors of this publication are also working on these related projects:

Project   Extra-pair paternity in Bewick's Wren View project

Project   Song dialects of mountain chickadees in Texas and New Mexico. View project

Seasonal abundance and nutritional concentration of grassland arthropods

BEN R. SKIPPER[1,4,*], DANIEL KIM[2], AND CHERYL MORRIS[3]

[1]*Department of Biology, University of Nebraska–Kearney, Kearney, NE 68849*
[2]*Platte River Whooping Crane Maintenance Trust, Inc., Wood River, NE 68883*
[3]*Omaha's Henry Doorly Zoo & Aquarium, Omaha, NE 68107*
[4]*Present address: Department of Biology, Angelo State University, San Angelo, TX 76909*

ABSTRACT.—A comprehensive understanding of foraging choices within an optimal framework requires a basic understanding of the differential nutritive concentrations and availability of prey items. Herein we present both nutritional data (e.g., the macronutrient, gross energy, and mineral concentrations) and temporal abundance of wild-caught arthropods from Nebraska prairies. Additionally, we report the size-mediated nutritional concentrations of 2 Orthoptera families: Acrididae and Tettigoniidae. Crude fat concentrations were 56%, 63%, and 53% higher in small, medium, and large Tettigoniidae than in Acrididae, respectively. Crude protein concentration varied minimally among arthropod groups (range 60.32%–76.00%), while caloric densities (gross energy) were similar among the majority of arthropod groups that were analyzed (range 16.54–23.36 kJ/g). In addition, small (early instar) orthropterans peaked synchronous to the mean first clutch hatch date for 2 species of grassland birds at the study site. Our results suggest that size and insect taxonomy influence crude fat and protein concentrations but do not appear to influence gross energy concentrations. Peak fat and protein concentration occurred during the early nestling phase for both avian species, implying synchrony between food availability and the nestling provisioning period for grassland nesting birds.

RESUMEN.—La comprensión integral de las opciones de alimentación dentro de un marco óptimo requiere un entendimiento básico de las diferencias en concentraciones nutritivas y de la disponibilidad de presas. En este trabajo presentamos datos nutricionales (por ej., macronutrientes, energía total y concentraciones minerales), así como la cantidad temporal de artrópodos salvajes capturados en las praderas de Nebraska. Adicionalmente, registramos las concentraciones nutricionales (controlando por el tamaño) de dos familias de ortópteros: Acrididae y Tettigoniidae. La concentración de grasa cruda fue mayor en los Tettigoniidae pequeños, medianos y grandes que en los Acrididae (56%, 63% y 53% respectivamente). La concentración de proteína cruda varió mínimamente entre los grupos de artrópodos (60.32%–76.00%), mientras que la densidad calórica (energía total) fue similar en la mayoría de los grupos de artrópodos analizados (16.54–23.36 kJ/g). Además, en el sitio de estudio, los ortópteros pequeños (en sus primeros instares) alcanzaron su punto máximo sincrónico durante la etapa de apareamiento e incubación de dos especies de aves de pastizales. Nuestros resultados indican que el tamaño y la taxonomía de los insectos, influyen en las concentraciones de grasa cruda y proteínas, pero no parecen influir en las concentraciones de energía total. La concentración máxima de grasas y proteínas se produjo durante la fase inicial de anidación de ambas especies de aves, indicando una sincronía entre la disponibilidad de alimentos y el período de anidación de las aves de pastizales.

Foundational ecological research examining life history for avian species centered on the availability of food items, which ultimately drives both clutch size and timing of the avian breeding season (Lack 1968). For many passerines, the onset of the breeding season entails a shift away from the plant-based diets of the nonbreeding season to diets composed of arthropods (Rotenberry 1980, Vickery 1996, Renfrew et al. 2015). This dietary switch exploits the flush of arthropod biomass as arthropods hatch or emerge from their overwintering diapause,

providing the necessary energetic and nutritional pulse for breeding birds and their rapidly developing offspring. Over time, natural selection favored synchronicity between the emergence of profitable food items and the breeding activities of many birds, especially as this synchronicity relates to the feeding of nestlings (e.g., Visser and Both 2005).

Following the hatch of eggs, parents must meet the nutritional and energetic demands of nestling passerines through the frequent delivery of foods capable of sustaining the nestlings'

rapid growth rate. At this time, the nestlings' ability to handle, swallow, and digest provisioned prey items (Slagsvold and Wiebe 2007, and references therein) constrains prey selection by adults to small, soft-bodied arthropods (Wiebe and Slagsvold 2014). As the young grow and their capacity to handle and digest larger prey items increases, prey delivered by parents may become progressively larger (Royama 1966). It follows then, that natural selection should favor synchronicity between breeding activities and not only the overall abundance of arthropods, but also the abundance of items that are usable by nestlings, the very individuals with the greatest energetic and nutritional demands.

Both the energetic and nutrient composition of prey items may further constrain the selection of arthropod prey delivered to nestlings. If nutritive values of prey items are size dependent, optimal prey selection early in the nestling period may differ from choices later in the nestling period when nestlings can process a greater variety of foods. Size-dependent nutritive value is known from some captive-reared and wild insect groups, including crude protein and crude fat content of captive-reared roaches (Oonincx and Dierenfeld 2012), mineral concentration of orthopterans and hemipterans (Studier and Sevick 1992), lipid concentration of arthropods (Lease and Wolf 2011), and mineral and dry matter concentration of orthopterans (Oonincx and van der Poel 2011). Orthopterans constitute a large portion of many avian diets, especially in grasslands where birds are abundant (Kaspari and Joern 1993, Nocera et al. 2007). In our study area, orthopterans constitute >50% of all identifiable items that are fed to the nestlings of 2 abundant, grassland-obligate songbirds, Grasshopper Sparrow (*Ammodramus savannarum*) and Bobolink (*Dolichonyx oryzivorus*; Skipper and Kim 2013), with other invertebrate groups composing the remainder. As such, our goal in this study was twofold. First, we sought to determine if peak arthropod abundance, and peaks for specific arthropod groups, overlapped the hatch date for 2 abundant grassland-obligate passerines, Bobolink and Grasshopper Sparrow. Second, we sought to compare the nutrient composition for arthropod groups thought to be important for grassland-obligate passerines and to compare size-mediated differences in nutrient composition for orthopterans.

METHODS

Arthropod Collection

We used sweep nets to collect arthropods every 2 weeks on managed prairie pastures ($n = 8$) in Hall County, Nebraska, from 29 May to 4 August 2006. Throughout this text, we define and refer to each sampling event as a period. Pastures used in this study were part of a 4-year burn/graze rotational management system. Pastures in year 1 were burned in early spring and grazed in late spring, while pastures in year 2 were rested in early spring and grazed in summer. Year-3 and year-4 pastures were rested to allow sufficient standing dead material for late-successional grassland species. We considered each year of this management system to be a treatment, and each treatment was replicated; therefore, we sampled from 2 pastures in each stage of the management rotation. Study plots within pastures were 16 ha, and we collected arthropods by sweeping nets at each of 27 regularly spaced points within plots. Beginning at each of the 27 survey points, we made 25 sweeps of the net while walking 10 paces in each of the cardinal directions for a total of 27,000 sweeps per pasture per sampling interval. Historically the surveyed fields included sedge meadows or mesic grasslands (Henszey et al. 2004), and vegetation content was verified using the vegetation sampling that was performed during the same breeding season as insect collection. Sedges (*Carex* spp.), rushes (*Eleocharis palustris* [L.] Roem. & Schult., *Scirpus* spp., and *Juncus* spp.), and prairie cordgrass (*Spartina pectinata* Bosc ex Link) were dominant species in sedge meadows. Big bluestem (*Andropogon gerardii* Vitman), little bluestem (*Schizachyrium scoparium* [Michx.] Nash), Indiangrass (*Sorghastrum nutans* [L.] Nash), switchgrass (*Panicum virgatum* L.), and prairie cordgrass historically dominated mesic grasslands, but Kentucky bluegrass (*Poa pratensis* L.), smooth brome (*Bromus inermis* Leyss), and reed canary grass (*Phalaris arundinacea* L.) were abundant species during insect collection, especially early in the season (Henszey et al. 2004). Sweep net contents, both animal and vegetal, were transferred to individually labeled 1-gallon (3.78-L) plastic bags and then frozen at −20 °C, <4 h after sample collection. After freezing the net contents, we sorted the arthropods to appropriate taxonomic order and stored the sorted arthropods

at −20 °C until we needed them for nutritional analysis. For abundance, we sorted and report on the following groups: Lepidoptera larvae, Lepidoptera adults, Orthoptera, Coleoptera, Diptera, Araneae, Hemiptera, and other arthropods (Hymenoptera, Odonata, Phasmatodea) that constituted <1% of the sample. We further subdivided lepidopteran larvae and adults, orthopterans, and dipterans into 3 size classes, small (<10 mm), medium (10–20 mm), and large (>20 mm), by using a ruler to measure each insect. We had insufficient samples of arthropod groups to analyze nutritional concentration by pasture treatment; therefore, we pooled arthropods across all sampling units and periods. Additionally, for nutritional concentration, we divided the orthopterans into their appropriate families (Acrididae, Gryllidae, and Tettigoniidae) and subdivided Acrididae and Tettigoniidae into 3 size classes (<10 mm, 10–20 mm, and >20 mm). Our decision to sort the orthopterans to family and not to lower taxonomic classifications reflected our goal of assessing the nutritive content of functional groups likely selected by grassland birds. Although nutritive content may vary among individual genera or species, grassland birds preying on arthropods are unlikely to be so discriminating. Instead, they likely use a morphospecies approach when selecting prey. Acrididae included, at least, individuals of *Melanoplus bivittatus*, *M. confusus*, and *M. flavidus*, all common species within the broader study area (Brust et al. 2008). Tettigoniidae included, at a minimum, individuals from *Neoconocephalus* spp. and *Orchelimum* spp.

Sample Preparation and Chemical Analysis

Prior to analyses, samples were dried at 55.0 °C in a forced-air drying oven for 5 d. Initial wet-weight samples of arthropod groups varied from 27.87 g (Gryllidae) to 115.93 g (medium Acrididae), with an average of 50.14 g (SD = 28.36 g) After drying the samples, we ground them to a consistent homogenous size (particle size < 1 mm^3) in a Wiley mill (model 4, Thomas Scientific, Sweesboro, NJ) to accommodate further analyses. All subsequent analyses used the manufacturer or the Association of Official Analytical Chemists (AOAC) recommended aliquot of ground, homogenized sample. Samples were analyzed for dry matter (DM) (Method 934.01, AOAC 2000) and organic matter (OM) (Method 942.05, AOAC 2000).

Crude protein (CP) was determined using a LECO Nitrogen Analyzer (Method 992.15, AOAC 2000) (model FP-528, LECO Corporation, St. Joseph, MI). Crude fat was determined via hexane extraction (Method 960.39, AOAC 2000) using a Soxtec 2045 extraction system (Foss, Eden Prairie, MN). Gross energy (GE) was determined via bomb calorimetry (model AC-500, LECO Corporation, St. Joseph, MI). Total dietary fiber (TDF) was determined in samples as a more accurate assessment of fiber than crude fiber, using the Prosky method (Prosky et al. 1994, AOAC 2003). With the exception of the mineral analysis, all analyses were conducted in the Comparative Nutrition Laboratory at Omaha's Henry Doorly Zoo and Aquarium. Minerals were analyzed via inductively coupled plasma spectrometry (Midwest Laboratories, Omaha, NE).

Avian Hatch Dates

We found and monitored nests of Bobolink and Grasshopper Sparrow, following the methods of Martin and Geupel (1993). Once nests were located, we performed nest checks every 3–4 d until the nest fledged young or failed. When we did not directly observe hatch day or when we found nests after hatching, we backdated the hatch based upon the developmental stage of the nestlings. Age determination was aided by comparing nestlings of unknown age to nestlings in known-age nests and using cues such as feather emergence and the opening of eyelids (Vickery 1996, Renfrew et. al. 2015).

Statistical Analyses

We conducted all statistical analyses in JMP (v. 14, SAS Institute, Cary, NC) and compared arthropod abundance across sampling periods with ANOVA models. Due to considerable variation in arthropod abundance from different treatments (e.g., year-1 vs. year-3 pastures), we blocked treatments before comparing seasonal arthropod abundance. For all analyses of abundance, we set alpha at 0.05 and used Tukey's HSD test to control for type I errors.

Nutrient analyses required pooling of samples across treatments to obtain an adequate mass appropriate for the conducted assays; therefore, we only present descriptive statistics (means and standard deviations). However, to preserve quality control, we ran all analyses in duplicate (TDF in triplicate). If the error
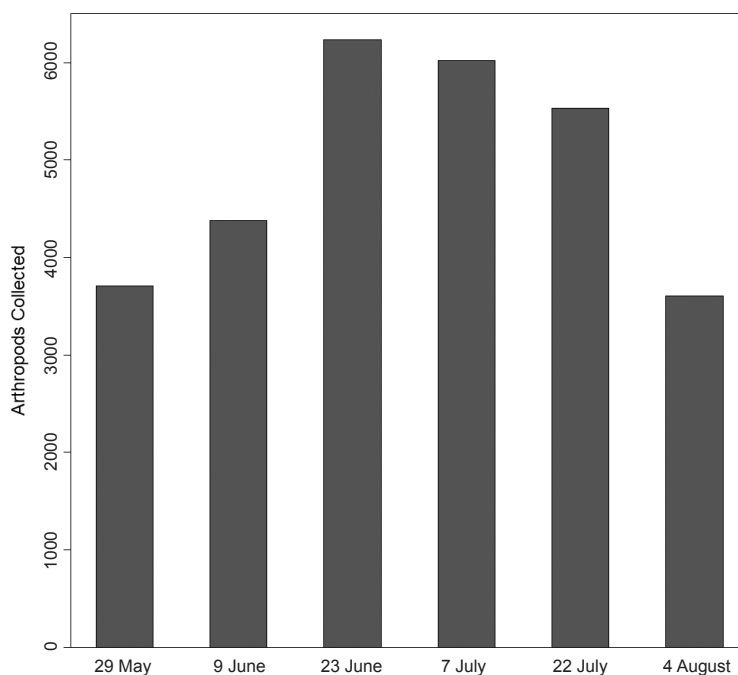
Fig. 1. Number of arthropods collected on managed prairie pastures in Hall County, Nebraska, in 2006. Collections were made across 8 pastures and included 27 sample points with 100 sweeps of the net at each point.

between samples was >5%, all samples were rerun. We report data as the mean of all analyzed runs with accompanying standard deviation.

Results

We collected over 29,000 individuals of 10 arthropod orders. Orthopterans were the most common arthropod group (44%), followed by arachnids (18%), dipterans (12%), coleopteran adults (7%), and lepidopteran larvae and hemipterans (6% each). Lepidopteran adults and coleopteran larvae each contributed 1% to our sample, while arthropods in our "other" category (5%) each constituted <1% of all arthropods sampled. Arthropod abundance, as a whole, was not uniform across the study period (χ^2 = 705.22, df = 2, P < 0.001). Instead, arthropod abundance increased from the first to the second sampling period, peaked in the third sampling period, and declined monotonically thereafter (Fig. 1). Controlling for pasture treatment, we found that several arthropod groups and size classes varied seasonally in their abundance. These groups and size classes included small, medium, and large lepidopteran larvae; small, medium, and large orthopterans; large dipter-

ans; and coleopteran adults (ANOVA results are presented in Table 1). We detected no change in abundance of the other arthropod groups throughout our sampling season.

Seasonal trends in peak abundance were inconsistent across arthropod groups. Small-bodied lepidopteran larvae had 2 peaks of abundance in periods 1 and 4, but they declined in abundance with later periods. Medium and large lepidopteran larvae peaked in period 2. Peak abundance of orthopterans shifted later in the season for each successively larger group. Small-bodied orthopterans peaked during sample period 3, while medium and large orthopterans peaked in periods 5 and 6, respectively (Fig. 2). Large dipterans were most abundant during period 2, while coleopteran adult abundance peaked in period 3. Abundance trends for all other arthropod groups were nonsignificant.

In 2006, the mean hatch date for 47 Bobolink nests was 13 June (SD 2.71 d), and for 27 grasshopper sparrow nests, the mean hatch date was 12 June (SD 3.13 d). For both species, the mean hatch dates occurred between our second and third arthropod sampling periods, 9 June and 23 June, respectively.
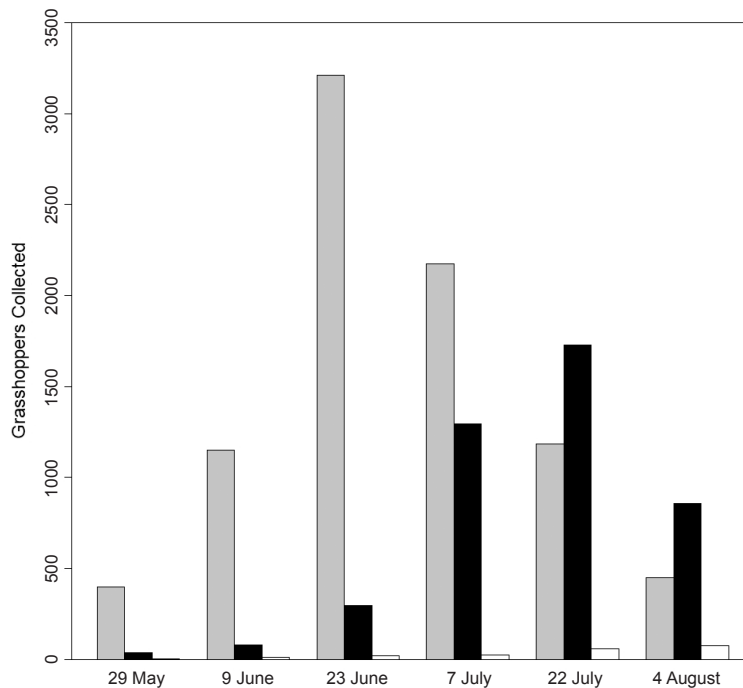
Fig. 2. Seasonal abundance of small (<10 mm, gray bars), medium (10–20 mm, black bars), and large (>20 mm, white bars) grasshoppers collected on managed prairie pastures in Hall County, Nebraska, in 2006.

Proximate nutrient concentrations of arthropods are presented in Table 2. The moisture concentration of arthropods was similar among the sampled taxonomic groups (range 68%–74%). Both Acrididae and Tettigoniidae displayed an incremental increase between moisture concentration and size (small, medium, and large). Ash concentration was generally low (4.5%–8.3% dry matter [DM]), with little variability among arthropod groups excepting Lepidoptera larvae (Table 2), which contained 41%–60% more ash compared to other groups. Within the Acrididae, ash concentration declined with increasing body size; however, the converse was true of the Tettigoniidae (Table 2).

Crude protein concentration varied among arthropod groups (Table 2), though some differences were small (e.g., Lepidoptera larvae and Chrysomelidae). Large Acrididae contained the highest crude protein (76.0% DM) and Lepidoptera larvae contained the least (60.7% DM). Acrididae had approximately 9% more protein than similarly sized Tettigoniidae. Within both the Acrididae and Tettigoniidae, crude protein concentrations increased with body size; however, the magnitude of this increase was greater in the Acrididae than in the Tettigoniidae. Crude fat concentration varied among arthropod groups and by size within Orthoptera families (Table 2). Acrididae contained the lowest crude fat concentration for all arthropod groups measured (below 8% DM for all size categories), while Tettigoniidae contained the greatest crude fat concentration (15%–19% DM). Crude fat concentration averaged 81% higher in Tettigoniidae than in Acrididae for each size class. Crude fat concentration decreased on average 16% between small and large Tettigonids and 12% in Acrididae. Although there appeared to be a trend of decreasing fat concentrations by size, the highest fat concentrations of all samples were measured in medium Tettigonidae (19.7% DM) (Table 2).

Total dietary fiber (TDF) varied little among arthropod groups except for Lepidoptera larvae, which contained at least twice as much TDF compared to the other arthropod groups (Table 2). Excluding Lepidoptera larvae, all other arthropod groups contained <13% TDF. There were no clear trends in TDF

TABLE 1. Mean (SD in parentheses) number of individuals collected with sweep nets on managed prairie pastures in Hall County, Nebraska, from May to August 2006. Analysis of variance (ANOVA) results represent the omnibus test. Within rows, means labeled by the same letters are not significantly different at the $\alpha = 0.05$ level (Tukey's HSD test).

Arthropod group	ANOVA results	29 May	9 June	23 June	7 July	22 July	4 Aug
Lepidoptera larvae (<10 mm)	$F_{5,39} = 4.70, P = 0.002$	35.5 (26.3)A	25.3 (15.3)ABC	6.3 (6.6)BC	33.3 (40.0)AB	9.8 (14.5)ABC	3.8 (6.3)C
Lepidoptera larvae (10–20 mm)	$F_{5,39} = 6.16, P = 0.003$	25.6 (31.4)AB	42.0 (29.1)A	8.3 (8.0)B	16.0 (20.8)B	6.9 (9.0)B	2.6 (1.9)B
Lepidoptera larvae (>20 mm)	$F_{5,39} = 7.17, P < 0.001$	2.5 (2.8)B	9.4 (7.7)A	3.4 (4.1)B	1.4 (1.2)B	1.0 (1.2)B	1.3 (1.0)B
Orthoptera (<10 mm)	$F_{5,39} = 3.65, P = 0.008$	49.8 (56.4)B	143.6 (163.0)AB	401.6 (516.4)A	271.6 (230.2)AB	148.0 (117.5)AB	55.9 (54.7)B
Orthoptera (10–20 mm)	$F_{5,39} = 3.10, P = 0.019$	4.6 (5.0)B	10.0 (10.1)AB	37.1 (47.8)AB	161.8 (278.4)AB	216.3 (241.1)A	107.0 (102.3)AB
Orthoptera (>20 mm)	$F_{5,39} = 2.85, P = 0.027$	0.3 (0.7)B	1.6 (2.6)AB	2.5 (3.3)AB	3.0 (2.0)AB	7.25 (6.5)AB	9.4 (13.3)A
Diptera (>20 mm)	$F_{5,39} = 3.83, P = 0.007$	0.5 (1.1)AB	2.1 (2.0)A	1.0 (1.7)AB	0.1 (0.4)B	0.0 (0.0)B	0.1 (0.4)B
Coleoptera adult	$F_{5,39} = 3.56, P = 0.010$	32.9 (15.2)B	41.8 (14.9)AB	64.8 (45.1)A	40.0 (20.3)AB	44.5 (22.4)AB	30.9 (13.0)B

TABLE 2. Proximate nutrient composition (SD in parentheses) of common arthropods from central Nebraska prairies. Crude fat, crude protein, ash, and total dietary fiber (TDF) is presented on a percent dry matter basis.

Group	Size (mm)	% Crude fat	% Crude protein	% Ash	% TDF	% Moisture	Gross energy (kJ/g)
Tettigoniidae	<10	17.17 (0.02)	67.61 (0.67)	5.40 (0.16)	11.14 (0.08)	67.66 (0.10)	23.36
	10–20	19.73 (0.27)	67.64 (0.26)	4.59 (0.05)	11.43 (0.41)	68.51 (0.08)	22.74
	>20	14.43 (0.01)	68.37 (0.21)	4.87 (0.22)	**	70.68 (0.00)	20.90
Acrididae	<10	7.64 (0.04)	73.72 (0.41)	5.71 (0.04)	11.02 (0.88)	67.58 (0.07)	20.50
	10–20	7.29 (0.08)	75.62 (0.12)	5.27 (0.04)	10.67 (0.13)	69.66 (0.02)	16.54‡
	>20	6.74 (0.03)	76.00 (0.18)	4.45 (0.08)	10.28 (0.46)	69.16 (0.00)	22.22
Chrysomelidae		10.88 (0.00)	60.32 (0.00)	4.45 (0.12)	12.65 (0.13)	68.98 (0.04)	**
Gryllidae		10.95 (0.05)	62.46 (0.03)	5.49 (1.01)	**	68.09 (0.03)	22.34
Lepidoptera larvae		15.70 (0.17)	60.65 (0.32)	8.29 (0.04)	21.18 (0.06)	73.88 (0.27)	22.77

**Insufficient sample for analysis.
‡The low concentration of gross energy in medium-sized Acrididae should be interpreted with caution as it likely reflects an analytical error.

TABLE 3. Mineral concentrations of dried, ground samples of 2 families of common grasshoppers from central Nebraska prairies. No replicates were possible due to insufficient sample size.

Group	Ca[a]	P[a]	Mg[a]	Na[a]	K[a]	Fe[b]	Zn[b]	Cu[b]	Mn[b]
Tettigoniidae	0.13	0.83	0.01	0.09	1.11	61	110	24	77
Acrididae	0.27	0.79	0.11	0.06	1.13	62	155	39	15

[a]Percent dry matter
[b]Parts per million

concentrations between differently sized Tettigoniidae and Acrididae (Table 2). In the present study, Chrysomelidae, with their hard elytra, contained more TDF than did either family of Orthoptera. However, between Acrididae and Tettigoniidae, we observed slightly greater fiber concentration in the relatively soft-bodied Tettigoniidae compared with the relatively hard-bodied Acrididae. Caloric concentration was approximately 20 kJ/g for all arthropod groups, except for medium-sized Acrididae (Table 2). The low caloric concentration of medium-sized Acrididae reported here likely represents an analytical error, and we do not consider these data further. Caloric concentration only fluctuated approximately 11% among arthropod groups and sizes.

Macromineral concentration of Acrididae and Tettigoniidae (all size classes combined) varied inconsistently between the 2 orthopteran groups and in magnitude (Table 3). Calcium concentration of Acrididae was over 100% greater than that of Tettigoniidae, yet phosphorous concentration of these 2 groups varied by only 5% (Table 3). Phosphorous and sodium concentration differed by 3% and 33%, respectively, between the 2 orthopteran groups, while magnesium concentration of acridid grasshoppers was 1000% greater than that of tettigoniid grasshoppers. Trace minerals also differed inconsistently between the 2 groups, with iron concentration differing by <2% between the groups, while zinc, copper, and manganese differed by 41%, 63%, and 81%, respectively.

DISCUSSION

The nutritive value of prey items may affect their selection by predatory species. Prey size is known to influence selection by insectivorous birds (Kaspari 1991), especially when adult birds are provisioning nestlings (van Balen 1973). Although past work used handling times to explain this selectivity (Royama 1966, Banbura et al. 1999), nutritional differences among prey items may also be important. We found little evidence for size-mediated nutritional differences in orthopterans. Where differences were apparent, they were either small in magnitude or their relationship to body size was nonmonotonic. Several factors could be responsible for this lack of effect. First, although body growth (measured as length in this study) is associated with a decline in surface-area-to-volume ratios, this change in body size may be independent (or largely so) from a change in body composition (e.g., Lease and Wolf 2010, 2011). Second, our pooling of species into common size classes may have masked any possible size-mediated differences that would have appeared had grasshopper species been analyzed independently. Although this is a possibility, Studier and Sevick (1992) found minimal differences among moisture, dry matter, and mineral concentration of mixed-species and single-species samples of Orthopterans. Further, our decision to lump species into broad categories based on size is likely consistent with how foraging birds would approach selection of prey items.

Development from hatching to fledging is rapid in grassland passerine birds, and this rapid development requires great energetic, nutritional, and mineral inputs. Our analysis of the nutritive concentrations of common grassland arthropods suggests that many groups differ only slightly in nutritional composition. Exceptions to this observation exist though, with some groups or size classes having great disparity in particular nutrients (e.g., fat concentration of Tettigoniidae and Acrididae). It is worth noting that even the slight differences in nutrient concentration of arthropods presented in Table 2 may translate to large differences in nutrients delivered to offspring when the provisioning rate of parent birds is considered. In our study area, Bobolinks and Grasshopper Sparrows have per nestling provisioning rates of approximately 2.5 to 4 provisions per hour 6 d after nestlings hatch (Skipper and Kim 2013). When this rate is considered, even

small differences in the nutrient concentration of individual arthropods have the potential to translate to slower or more rapid growth, depending upon the arthropods selected. Additionally, we acknowledge that our study did not address variation in nutrients such as carotenoids, vitamins E and D, and individual amino and fatty acids, among others, which all may be important for nestling growth. Variation in these and other nutrients not assessed in the current study may be important considerations for passerines provisioning young. Therefore, we caution against disregarding the slight differences in nutrient concentration among arthropod groups or size classes.

Calcium requirements for developing wildlife are high, and Robbins (1993) gives calcium requirements for young birds as 0.5%–1.3% of dry diet. Additionally, Ca:P ratios of 1:1 or 2:1 are suggested as ideal for birds (Fowler 1978, Robbins 1993). We observed both Acrididae (0.27% Ca) and Tettigoniidae (0.13% Ca) to be insufficient suppliers of dietary calcium to developing birds. Similarly, Ca:P ratios were unfavorable, with Acrididae and Tettigoniidae having ratios of 1:2.9 and 1:6.4, respectively. We further evaluated tettigoniids and acridids as sources of trace minerals in comparison to the nutritional needs of wild birds published by Robbins (1993). Both tettigoniids and acridids provided sufficient Fe, Zn, and Cu to meet the nutritional requirements of birds. Tettigoniids, but not acridids, provided sufficient Mn and Na, while acridids, and not tettigoniids, provided sufficient Mg. Neither group provided sufficient K to meet the demands of wild birds.

Nutritive, mineral, and energy concentrations of sampled arthropods were generally within the ranges reported in other studies (e.g., Robel et al. 1995, Barker et al. 1998, Oonincx and van der Poel 2011, Punzo 2003, Finke 2002). Taxonomic differences, methodological differences in sample preparation and analytical methods, or both can likely explain where differences exist between our data and those of other studies.

We found grassland arthropods to be abundant on managed prairies in central Nebraska. As a whole, arthropod abundance followed the expected phenological progression for arthropods throughout the growing season. When considered individually and by body size, some arthropod groups displayed seasonal trends while others did not. These differences may reflect our choice of sampling methodology (sweep nets) rather than the lack of seasonal trends. For example, we frequently observed lepidopteran adults during sampling, but our samples appear to underestimate their abundance. Alternatively, some arthropod groups may experience seasonal increases in number before or after our sampling effort. Where we observed seasonality in abundance, most arthropod groups peaked near sample period 2 (medium and large lepidopteran larvae, large dipterans) or period 3 (small orthopterans and coleopteran adults). Within our study area, these sampling periods overlap the mean hatching dates for 2 abundant grassland birds, Bobolink and Grasshopper Sparrow (13 June and 12 June, respectively [Kim unpublished data]), and items at peak abundance at this time are frequently fed to the nestlings of these species (Skipper and Kim 2013).

In conclusion, our data suggest synchronicity between the breeding activities of Bobolinks and Grasshopper Sparrows and the peak abundance of small, palatable orthopterans. Additionally, our data suggest that, for the nutrients and arthropods examined, nutrient contents differ minimally among arthropod groups and sizes. The integration of nutritional concentrations of prey items and their seasonal abundance affords a new perspective on annual variation in settlement decisions, prey selection, and nesting success of birds. This new perspective also informs longer-term processes such as timing of arrival on the breeding ground and nest initiation. The predictable phenology of arthropod groups, from hatch in the early season through instar and larval forms to adults later in the season, provides a reliable source of food for insectivorous birds and their offspring.

with sample preparation and analysis. We thank 2 anonymous reviewers for their comments and criticisms of an earlier draft.

LITERATURE CITED

[AOAC] ASSOCIATION OF OFFICIAL ANALYTICAL CHEMISTS. 2003. Total dietary fiber in foods, enzymatic-gravimetric method. Method 985.29 *in* W. Horwitz, editor, Official methods of analysis. 17th edition. AOAC International, Gaithersburg, MD.

BANBURA, J., M.M. LAMBRECHTS, J. BLONDEL, P. PERRET, AND M. CARTAN-SON. 1999. Food handling time of Blue Tit chicks: constraints and adaptation to different prey types. Journal of Avian Biology 30:263–270.

BARKER, D., M.P. FITZPATRICK, AND E.S. DIERENFELD. 1998. Nutrient composition of selected whole invertebrates. Zoo Biology 17:123–134.

BRUST, M.L., W.W. HOBACK, AND R.J. WRIGHT. 2008. The grasshoppers (Orthoptera: Acrididae and Romaleidae) of Nebraska. [Accessed 12 September 2013]. http://extensionpublications.unl.edu/assets/pdf/eb3.pdf

FINKE, M.D. 2002. Complete nutrient composition of commercially raised invertebrates used as food for insectivores. Zoo Biology 21:269–285.

FOWLER, M.E. 1978. Metabolic bone disease. Pages 55–76 *in* M.E. Fowler, editor, Zoo and wild animal medicine. Saunders Press, Philadelphia, PA.

HENSZEY, R.J., K. PFEIFFER, AND J. KEOUGH. 2004. Linking surface- and ground-water levels to riparian grassland species along the Platte River in central Nebraska, USA. Wetlands 24:665–687.

KASPARI, M. 1991. Prey preparation as a way that Grasshopper Sparrows (*Ammodramus savannarum*) increase the nutrient concentration of their prey. Behavioral Ecology 2:234–241.

KASPARI, M., AND A. JOERN. 1993. Prey choice by three insectivorous birds: reevaluating opportunism. Oikos 68:414–430.

LACK, D. 1968. Ecological adaptations for breeding in birds. Chapman and Hall, London, United Kingdom. 409 pp.

LEASE, H.M., AND B.O. WOLF. 2010. Exoskeletal chitin scales isometrically with body size in terrestrial insects. Journal of Morphology 271:759–768.

LEASE, H.M., AND B.O. WOLF. 2011. Lipid content of terrestrial arthropods in relation to body size, phylogeny, ontogeny and sex. Physiological Entomology 36:29–38.

MARTIN, T.E., AND G.R. GEUPEL. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. Journal of Field Ornithology 64:507–519.

NOCERA, J., G. FORBES, AND G.R. MILTON. 2007. Habitat relationships of three grassland breeding bird species: broadscale comparisons and hayfield management implications. Avian Conservation and Ecology 2(1): art7. 19 pp.

OONINCX, D.G.A.B., AND E.S. DIERENFELD. 2012. An investigation into the chemical composition of alternative invertebrate prey. Zoo Biology 31:40–54.

OONINCX, D.G.A.B., AND A.F.B. VAN DER POEL. 2011. Effects of diet on the chemical composition of migratory locusts (*Locusta migratoria*). Zoo Biology 30:9–16.

PROSKY, L., M.G. ASP, T.F. SCHWEIZER, J.W. DEVRIES, I. FURDA, AND S.C. LEE. 1994. Determination of soluble dietary fiber in foods and food products: collaborative study. Journal of AOAC International 77:690–694.

PUNZO, F. 2003. Nutrient composition of some insects and arachnids. Florida Scientists 66:84–98.

RENFREW, R., A.M. STRONG, N.G. PERLUT, S.G. MARTIN, AND T.A. GAVIN. 2015. Bobolink (*Dolichonyx oryzivorus*), version 2.0. *In:* P.G. Rodewald, editor, The birds of North America. Cornell Lab of Ornithology, Ithaca, NY. https://doi.org/10.2173/bna.176

ROBBINS, C.T. 1993. Wildlife feeding and nutrition. 2nd edition. Academic Press, London, United Kingdom. 366 pp.

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

ROTENBERRY, J.T. 1980. Dietary relationships among shrubsteppe passerine birds: competition or opportunism in a variable environment. Ecological Monographs 50:93–110.

ROYAMA, T. 1966. Factors governing feeding rates, food requirements and brood size of nestling Great Tits *Parus major*. Ibis 108:313–347.

SKIPPER, B.R., AND D.H. KIM. 2013. Provisioning rate, dietary composition, and prey selection of breeding Bobolink and Grasshopper Sparrows. Western North American Naturalist 73:35–40.

SLAGSVOLD, T., AND K.L. WIEBE. 2007. Hatching asynchrony and early nestling mortality: the feeding constraint hypothesis. Animal Behaviour 73:691–700.

STUDIER, E.H., AND S.H. SEVICK. 1992. Live mass, water content, nitrogen and mineral levels in some insects from south-central lower Michigan. Comparative Biochemistry and Physiology Part A: Physiology 103:579–595.

VAN BALEN, J.H. 1973. A comparative study of the breeding ecology of the Great Tit *Parus major* in different habitats. Ardea 61:1–93.

VICKERY, P.D. 1996. Grasshopper Sparrow (*Ammodramus savannarum*), version 2.0. *In:* A.F. Poole and F.B. Gill, editors, The birds of North America. Cornell Lab of Ornithology, Ithaca, NY. https://doi.org/10.2173/bna.239

VISSER, M.E., AND C. BOTH. 2005. Shifts in phenology due to global climate change: the need for a yardstick. Proceedings of the Royal Society B 272:2561–2569.

WIEBE, K.L., AND T. SLAGSVOLD. 2014. Prey size increases with nestling age: are provisioning parents programmed or responding to cues from offspring. Behavioral Ecology and Sociobiology 68:711–719.