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# Dietary choices and their implication for survival and development of omnivorous mole crickets (Orthoptera: Gryllotalpidae)



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## ABSTRACT

Omnivory is a common feeding strategy in terrestrial arthropods, and omnivores that partake of a mixed diet often gain developmental and reproductive advantages. We determined the palatability and preference of plant and animal foods for two omnivorous mole crickets, *Scapteriscus vicinus* Scudder and *Scapteriscus borellii* Giglio-Tos. Adults of both species fed more readily on carrots than bermudagrass blades, rhizomes, and roots. When given a choice, *S. vicinus* preferentially fed on carrots (plant diet) whereas *S. borellii* preferred mealworms (animal diet). Nymphs of both species were reared on animal, plant, or mixed (plant–animal rotation) diets. *S. borellii* fed mealworms developed faster, with greater body mass and survival, and a longer pronotal length compared to individuals fed only carrots. Nymphs of *S. vicinus*, however, performed slightly better when fed mealworms, and poorer when given a mixed diet. Omnivory among *Scapteriscus* mole crickets may be a beneficial adaptation for insects in low nitrogen, grassland environments. This work suggests that these two species respond differently to plant and animal diets. *S. borellii* has a survival and developmental advantage by ingesting animal tissue. Diet will influence the age distribution of field populations, and this may influence interactions with their grass host and natural enemies.

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## 1. Introduction

Omnivory, utilizing food from two or more trophic levels (Denno and Fagan, 2003), is widespread among insects (Coll and Guershon, 2002; Singer and Bernays, 2003). Purported benefits of omnivory include decreased sensitivity to limited food resources (Pearson et al., 2011), acquiring balanced nutrients (e.g. C:N ratio; Behmer, 2009; Denno and Fagan, 2003), dilution or sequestration of toxins, and reduced interspecific competition (Coll and Guershon, 2002; Singer and Bernays, 2003). Physiological and behavioral mechanisms associated with nutrient regulation can evolve in response to a changing or unpredictable nutritional environment (Behmer, 2009). Omnivory, facilitated by dietary self-selection, often results in enhanced survival, growth rate, and fitness (Waldbauer and Friedman, 1991; Coll and Guershon, 2002; Behmer, 2009). Although dietary self-selection behavior has been demonstrated in generalist herbivores such as grasshoppers, locusts, and caterpillars that non-randomly select among different suitable plant species when given a choice (Waldbauer and Friedman, 1991; Behmer, 2009), only a few studies have investigated this behavior in omnivores.

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Those have mainly been with omnivorous thrips (*Frankliniella* spp.), hemipteran species (Coll and Guershon, 2002), and cockroaches (*Supella longipalpa* Fabricius; Waldbauer and Friedman, 1991).

Mole crickets (Orthoptera: Gryllotalpidae), as subterranean orthopterans, can be a useful model system to enrich our limited understanding of the feeding behavior of hypogeal omnivores. The tawny mole cricket, *Scapteriscus vicinus* Scudder, and the southern mole cricket, *Scapteriscus borellii* Giglio-Tos, are two introduced species that cause severe damage to turfgrass in the southeastern United States (Potter, 1998). As a subterranean omnivore that is mobile below ground in both nymphal and adult stages, mole crickets have access to a variety of food sources. Potential host plants range from above-ground grass leaves (Walker, 1984), seedlings of vegetables (Hayslip, 1943; Schuster and Price, 1992) to belowground roots and developing peanuts (Hayslip, 1943). Mole crickets also feed on earthworms (Hudson, 1987), soil arthropods (Fowler et al., 1985), and have cannibalistic behavior (Hayslip, 1943).

Several studies (Taylor, 1979; Matheny, 1981; Fowler et al., 1985; Silcox and Brandenburg, 2011) have used dissections to determine the types of food consumed by field-collected mole crickets. Based on gut contents, *S. borellii* consumes both plants and animals with animal tissues dominant (Taylor, 1979), whereas gut contents of *S. vicinus* are mainly plant-based. Gut dissection studies, so far the only insight into mole cricket feeding ecology, are limited because they may reflect abundance of a particular food in the habitat of that specimen or differential rates of digestion (Taylor, 1979;

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Matheny, 1981), and not necessarily dietary choices. Notably, no published studies have quantified consumption of prescribed diets by mole crickets. Dietary choice tests, therefore, can reveal preferences for particular foods that will provide insight on the foraging behaviors and their consequences for individual fitness.

Mole crickets, being predominately soil- and grass-inhabiting, could seemingly benefit from incorporating animal food into a plant-dominated diet. Long-term feeding trials (Godan, 1964) with the omnivorous European mole cricket, *Gryllotalpa gryllotalpa* L., showed that nymphs continuously fed an animal diet (larvae of *Galleria*) had lower mortality, reduced cannibalism, faster development, and higher fecundity compared to the ones reared on a plant diet (i.e. carrot, potato, lettuce). Such comparisons have not been done for the pest species (*Scapteriscus* spp.) in North America. Omnivory among these two *Scapteriscus* spp. may be either an intentional effort for individuals to balance nutrients or an opportunistic response to higher quality food in the environment. In either scenario, omnivory should result in higher rates of survival and faster development.

In this study, we addressed the following questions: (i) are diet choices of omnivorous mole crickets consistent with previously published gut dissection studies with *Scapteriscus* spp.? and (ii) does an omnivorous diet provide fitness benefits for *Scapteriscus* mole crickets compared to carnivory or herbivory? Acceptance of animal and plant diets by adult *S. borellii* and *S. vicinus*, and their respective feeding preferences, were studied in the laboratory by no-choice and choice trials. Furthermore, the effects of an animal, plant, or mixed animal and plant diets on survival and development of mole cricket nymphs were examined.

#### 2. Materials and methods

#### 2.1. Sources of insects

Adult S. borellii were collected from 16 May to 6 June 2011 using a modified acoustic trap (Thompson and Brandenburg, 2004) from a driving range at Grand National Golf Course, Opelika, AL (32°67′64″ N, 85°41′90″ W). Hybrid bermudagrass ('Tifway 419', Cynodon dactylon (L.) Pers × Cynodon transvaalensis Burtt-Davy), was the predominant plant in the driving range. Adult S. vicinus were collected by soap flush (30 mL of Joy liquid detergent in 8 L of water) on 14 March 2012 from the driving range, also predominant hybrid bermudagrass ('Tifway 419'), at Shell Landing Golf Club, Gautier, MS (30°39′04″ N, 88°67′70″ W). All collected individuals were immediately washed with fresh water upon emergence, and then placed into 473 mL of plastic cups (Dart, Mason, MI). The cups contained autoclaved, moistened sand and had ventilated lids. Mole crickets were provisioned with a mixed diet of organic carrot strips (Inter-American Products, Cincinnati, OH) and freeze-dried mealworms (Coleoptera: Tenebrionidae; Fluker Farms, Port Allen, LA), and held in a growth chamber (Percival Scientific Inc., Perry, IA) at 27 °C with a 14:10 (L:D) photoperiod in the laboratory at Auburn University before the experiments started.

#### 2.2. Relative acceptance of plants

Laboratory no-choice tests with different plant diet treatments were conducted using mixed sex *S. borellii* and *S. vicinus* adults on 31 August 2011 and 6 April 2012, respectively. Mole crickets were provisioned with 100 mg of organic carrot strips, bermudagrass blades, bermudagrass rhizomes, or bermudagrass roots. Carrots are used as a surrogate food for other grass-root feeding insects (e.g. *G. gryllotalpa* and scarab grubs, Godan, 1964; Popay et al., 2003). Grass parts (blades, rhizomes, and roots) were hybrid bermudagrass 'Tifway 419' harvested from the Auburn University Turf Research Unit, Auburn, AL. Cores of grass were washed free of soil and were separated into blades, rhizomes and roots (each individual part was approximately 3–5 cm long) before exposing to mole crickets.

Experiments with S. borellii were conducted in plastic containers (34.2 cm  $\times$  20.9 cm  $\times$  11.8 cm; Kis, Brampton, Canada) with one half (lengthwise) of the container filled with autoclaved, moistened sand for the mole crickets to reside, whereas S. vicinus was placed in a paper food container (1.89L; Solo, Highland Park, IL) filled with 470 mL of sand. Different containers were used to make our experimental conditions more suitable for S. vicnus, which did not respond in our preliminary tests in the plastic containers. Before each assay, one mole cricket was introduced to the sand in the test arena and starved for 24 h in the growth chamber. Each plant diet treatment was placed on a  $5 \text{ cm} \times 5 \text{ cm}$  piece of filter paper (Whatman, Piscataway, NJ) and added into each container. It was placed on the other side of the plastic container for S. borellii, and on the surface of sand for S. vicinus. The containers were placed in a dark growth chamber at 27 °C. After 12 h (one feeding bout), diets were reweighed, then corrected for background weight change using a set of untreated diets that were held in the same condition without mole crickets. Each diet treatment was replicated seven times for each species. Insects were tested with only one diet treatment. The amounts (mg) of consumed food were analyzed using GLM procedure with LSmeans test (SAS 9.2; SAS Institute, 2008) for mean separations to determine the relative consumption of the different plant parts. Data for each species were analyzed separately.

## 2.3. Feeding preference between plant and animal diets

Laboratory choice and no-choice tests were conducted using both sexes of *S. borellii* and *S. vicinus* from 19 May to 9 June 2011 and from 18 to 29 March 2012, respectively. Choice tests provided mole crickets with 145 mg of a plant and an animal diet, whereas no-choice tests determined consumption of each diet treatment (290 mg) independently. The plant diets were organic carrot strips and animal diets were freeze-dried mealworms. The experimental procedure and test arenas for determining feeding preference were the same as previously described for relative acceptance of plants tests.

Choice and no-choice tests were replicated with 30 and 10 mole crickets per diet treatment, respectively. Mole crickets that did not consume any diet in choice tests were excluded before analysis. The amount (mg) of consumed food in choice tests was analyzed using TTEST procedure (SAS 9.2) for paired *t*-tests to determine adult mole cricket feeding preference. The amount (mg) of consumed food in no-choice tests was analyzed using TTEST procedure for two-sample *t*-tests to determine the acceptability or palatability of the diets to adult *S. borellii* and *S. vicinus*. Data for each species were analyzed separately.

## 2.4. Fracture force, nitrogen and water content

Toughness of bermudagrass blades and carrot strips were measured on 15 October 2011, after being freshly collected from ten different individuals (replicates), using a penetrometer (QA Supplies, Norfolk, VA) to compare the fracture force of grass blades and carrots used in mole cricket feeding studies. Fracture force (g) were analyzed using TTEST procedure for two-sample *t*-tests using SAS 9.2.

For nitrogen and water contents, samples consisting of 0.5 g of organic carrot strips, hybrid bermudagrass blades, roots, or freezedried mealworms were collected from five different individuals (replicates). Samples were weighed freshly, oven dried at  $60 \,^{\circ}$ C for 24 h, and then reweighed to calculate water content. Nitrogen content was determined from a 0.1 g sample of each tissue by modified Kjeldahl analysis (McKenzie and Wallace, 1954) in Auburn University Soil Testing Laboratory, Auburn, AL. Water (%) and nitrogen content (%) data of each tissue were square root transformed prior to statistical analyses, and compared by GLM procedure with LSmeans test for mean separations using SAS 9.2.

## 2.5. Effects of diet on survival and development

Laboratory experiments were separately conducted to evaluate how different diet treatments affect survival and development of *S. borellii* and *S. vicinus* nymphs from July 2011 to May 2012 and from April to June 2012, respectively. For each species, field-collected males and females were paired randomly in the laboratory, and each pair was held in separate 473 mL transparent plastic cups containing approximately 450 mL of autoclaved, moistened sand until females oviposited (Xu, 2012). Each cluster of newly laid eggs was transferred into a 473 mL plastic cup filled with moistened vermiculite (Sun Gro Horticulture, Bellevue, WA) and incubated in a growth chamber at 27 °C until eggs hatched. Newly hatched nymphs were transferred to separate 473 mL plastic cups with ventilated lids containing approximately 150 mL of autoclaved, moistened sand and reared separately in a growth chamber at 27 °C with a 14:10 (L:D) photoperiod.

Every 2d, each nymph was provisioned with a comparable amount (80 mg) of either a plant (organic carrot strips), animal (freeze-dried mealworms), or diet rotation (alternating plant and animal diets every 2 d). The amount of diets was increased as mole crickets developed such that they were being provisioned with 160 mg of each diet as 6th instars. Starved nymphs were a negative control. Each of the four treatments was replicated eight times for each species. Nymphs in each replicate were hatched from the same egg cluster. To determine the impact of diet treatments on longevity and growth, survival of mole cricket nymphs was recorded every 2 d and they were weighed weekly. Nymphs were marked with white fingernail polish (Bari Cosmetics, Greenwich, CT) on the pronotum as an indicator to determine the molt event and calculate the instar duration from molt to molt (developmental time). After each molt, the pronotal length (Hudson, 1987) was also measured using a digital caliper (Absolute Digimatic, Mitutoyo, Aurora, IL).

Survival analyses were conducted using the Kaplan–Meier method (LIFETEST procedure; SAS 9.2). Pairwise comparisons of the survival distribution function between treatments were made using the log-rank test. Statistical significance was determined with the Bonferroni adjustment for multiple comparisons ( $\alpha = 0.05/6 = 0.0083$ ). A repeated measures analysis of variance (ANOVA) was separately performed using the MIXED procedure (SAS 9.2) with LSmeans test for mean separations to determine the effects of diet treatments on body weight (mg), developmental time (days), and pronotal length (mm) of *S. borellii* for weeks 0–40 and *S. vicinus* for weeks 0–8. Body weight and developmental time data were log<sub>10</sub> transformed prior to statistical analysis. Data for each species were analyzed separately.

### 3. Results

#### 3.1. Relative acceptance of plants

Among four plant diet treatments, *S. borellii* adults consumed significantly more mass of carrot strips (Fig. 1;  $F_{3,24}$  = 12.98, P < 0.0001). No bermudagrass rhizomes were consumed within 12 h. Consumption of bermudagrass blades and roots was statistically similar. For adult *S. vicinus*, consumption of the three grass parts was similar. However, *S. vicinus* also consumed significantly more weight of carrot strips (Fig. 1;  $F_{3,24}$  = 9.96, P = 0.0002).



**Fig. 1.** Mean ( $\pm$ SE) consumption of four plant materials (carrot strips, bermudagrass blades, rhizomes, roots) by adult *S. borellii* and *S. vicinus* within 12 h. There was no consumption of bermudagrass rhizome by *S. borellii*. Each diet treatment was replicated seven times for each species. Bar graphs with different letters are significantly different within a species (P < 0.05).

#### 3.2. Feeding preference between plant and animal diets

Out of 30 individuals, three *S. borellii* did not consume either diet, but eight individuals consumed a mixed diet of carrots and mealworms within 12 h in choice tests. Meal size for individuals of *S. borellii* that consumed both diets (mean = 132.5 mg) was, on average, double that for individuals that consumed a single diet (56 mg) (t = 6.8, d.f. = 25, P < 0.0001). Adult *S. borellii* consumed similar amounts of the carrots and mealworms in no-choice tests (Fig. 2A; Satterthwaite's test: t = -1.1, d.f. = 11.681, P = 0.2942). However, when given a choice, *S. borellii* consumed about two times more weight of mealworms than carrots in 12 h (Fig. 2A; t = 3.03, d.f. = 26, P = 0.0054).

Out of 30 adult *S. vicinus*, two individuals did not consume either diet whereas 12 *S. vicinus* consumed a mixed diet of carrots and mealworms within 12 h in choice tests. Meal size for individuals of *S. vicinus* that consumed both diets (mean = 132.5 mg) was, on average, double that for individuals that consumed a single diet (60 mg) (t= 3.9, d.f. = 26, P < 0.0001). Adult *S. vicinus* consumed four times more weight of carrots than mealworms in no-choice tests (Fig. 2B; Satterthwaite's test: t= -4.41, d.f. = 9.8332, P=0.0014). However, when given a choice, *S. vicinus* consumed similar amounts of each diet (Fig. 2B; t= -1.82, d.f. = 27, P= 0.0797). We also separately performed analyses on the consumption of males and females for both species, and found no difference in dietary preference between sexes (Xu, 2012).

#### 3.3. Fracture force, nitrogen and water content

Fracture force was significantly different between bermudagrass blades and carrot strips (Table 1). Carrot strips had the greatest water content but lower nitrogen content compared to the other diets (Table 1). Bermudagrass blades were intermediate in both water and nitrogen content. Bermudagrass roots had similar amount of water content with blades but the lowest nitrogen content. Nitrogen content of mealworms was approximately

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**Fig. 2.** Mean (±SE) consumption of carrots and mealworm diets by adult *S. borellii* (A) and *S. vicinus* (B) within 12 h in no-choice and choice tests. Asterisk over the bar denotes that significantly different consumption of diet (*P*<0.05). There were 30 replicates in choice test and ten replicates in no-choice test. Three *S. borellii* and two *S. vicinus* did not consume either diet treatment within 12 h in choice tests were excluded before analysis.

nine times higher than that of carrot strips and bermudagrass roots (Table 1).

#### 3.4. Effects of diet on survival and development of S. borellii

Nymphs fed mealworms ( $\chi^2 = 14.42$ , P = 0.0009) lived significantly longer than starved individuals (Fig. 3A). Nearly half of *S. borellii* could survive for 4 wk without food provisioned (starved) but died eventually at the end of 5 wk. All starved *S. borellii* nymphs (control) remained in 1st instar stage and died without molting. Thus, these observations were excluded before development data analysis.

At the termination of this experiment (week 40), 50% and 40% of *S. borellii* nymphs developed to adults in the mealworm and diet rotation groups, respectively (Fig. 4A;  $F_{2,18} = 10.44$ , P = 0.001 for main effects of diet treatment). However, none of the nymphs fed carrots developed to adults during the 40 wk experiment. From the 2nd to 5th instar stage, development was significantly slower for the group fed carrots than for the other groups. The duration of 2nd–5th instars in the carrot diet was generally twice as long as nymphs in the mealworm and diet rotation (Fig. 4A). Generally, 50% of *S. borellii* fed on mealworms reached wing pad stage at 7th instar and developed to adults at 9th instar. In contrast, only 12.5% of nymphs fed carrots presented wing pads at 9th instar and never developed to adults at the end of 40 wk.

Body weight of *S. borellii* increased weekly ( $F_{40,525}$  = 75.65, P < 0.0001 for time effect) in all diet treatments (Fig. 3B). Weight gain among *S. borellii* nymphs was significantly influenced by diet ( $F_{3,28}$  = 112.29, P < 0.0001), with significantly greater weight gain by nymphs that included animal tissue (mealworm and diet rotation treatments) than those fed a carrot only diet (t = 17.45 and 14.09, for mealworm and diet rotation, respectively; d.f. = 28, P < 0.0001). Although the growth curve of *S. borellii* fed the diet rotation intersected the one of nymphs fed mealworms at 16 wk (Fig. 3B), the body weight of nymphs fed mealworms was significantly greater (t = 2.5, d.f. = 28, P = 0.0185).

Pronotal length was significantly influenced by diet treatment ( $F_{2,18}$  = 93.29, P < 0.0001), instar stage ( $F_{9,111}$  = 290.07, P < 0.0001), and diet × stage interaction ( $F_{17,111}$  = 11, P < 0.0001). After the 1st and 2nd instar stages, pronotal length was significantly shorter for nymphs fed carrots than for the other two diet groups (Fig. 4B). The differences increased with each successive instar.

## 3.5. Effects of diet on survival and development of S. vicinus

Survival of *S. vicinus* was significantly influenced by diet treatment ( $\chi_3^2 = 11.79$ , *P*=0.0081). Nearly half of *S. vicinus* could survive for 3 wk without food provisioned (starved) but died eventually at the end of 5 wk (Fig. 5A). Overall, nymphs in the diet rotation died faster than starved individuals from 0 to 4 wk. At the termination

## Table 1

Mean (±SE) values of fracture force, nitrogen and water content of different diet treatments.

Diet treatment	Nitrogen (mg/g dry wt)	Water (%)	Fracture force (g)
Mealworms	$8.96 \pm 0.24$ a	$3.60 \pm 0.40$ c	N.A.
Bermudagrass blades	$1.41 \pm 0.13 \text{ b}$	$71.20 \pm 0.49$ b	$108.00 \pm 9.35$
Bermudagrass roots	$0.76\pm0.04~d$	$70.00 \pm 1.10 \text{ b}$	N.A.
Carrot strips	$1.09 \pm 0.01 \text{ c}$	$90.80 \pm 0.49$ a	$213.00 \pm 13.15$
Test statistics	$F_{3,8} = 781.50$	$F_{3,16} = 2501.19$	$t_{18} = -6.51$
Р	<0.0001	<0.0001	<0.0001

Means (±SE) presented are actual means. Within a column, values followed by the different letters are significantly different (P<0.05). N.A., not available.

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**Fig. 3.** Observed survival probabilities (A) and mean (±SE) weight (B) of *S. borellii* raised on different diet treatments in the laboratory over a 40 wk period. There was a significant heterogeneity among the survival curves of *S. borellii* provisioned with different diet treatments (A;  $\chi_3^2 = 26.46$ , *P* < 0.0001). There were initially eight replicates with each diet treatment. The numbers in the brackets represent the number of mole crickets analyzed at 0, 10, 20, 30, and 40 wk (B).

of the experiment (week 8), 37.5% of *S. vicinus* nymphs survived in both carrot and mealworm diet groups (Fig. 5A). Due to the low survival, the results for developmental time and pronotal length are excluded for *S. vicinus*.

Body weight of *S. vicinus* nymphs increased weekly ( $F_{8,90}$  = 31.08, P < 0.0001, for time effect) only in mealworm and diet rotation treatments (Fig. 5B). There were significant main effects of diet treatment ( $F_{3,28}$  = 18.33, P < 0.0001) and a diet × time interaction ( $F_{20,90}$  = 5.44, P < 0.0001). Overall, nymphs fed diets that included animal tissue (mealworm and diet rotation treatments) started to gain weight consistently at 2 wk, whereas nymphs fed only carrots had negligible (average 3.7 mg) weight gain over 8 wk. Starved nymphs lost approximately 2 mg of weight on average at 3 wk, compared to initial weight (Fig. 5B).

## 4. Discussion

#### 4.1. Dietary choices of Scapteriscus mole crickets

Despite their status as pests in grassland systems (Frank and Walker, 2006), both species of *Scapteriscus* mole crickets fed sparingly on bermudagrass blades and roots in our acceptance test. *S. borellii* and *S. vicinus* are omnivores as nymphs and adults, which verifies the gut contents of field-collected mole crickets (Taylor, 1979; Matheny, 1981; Fowler et al., 1985; Silcox and Brandenburg, 2011). Based on the proportion of plant and animal tissue in the guts, *S. vicinus* is presumed to be an herbivore and *S. borellii* is an alleged predator. In our laboratory experiments, *S. vicinus* adults



**Fig. 4.** Mean ( $\pm$ SE) values of developmental time (A) and pronotal length (B) of *S. borellii* provisioned with either a carrot, mealworm, or rotation (alternating carrot and mealworm diets every 2 d) in the laboratory. Asterisks, significant differences among treatments at each instar stage (*P*<0.05).

showed no preference for carrots (surrogate plant diet) but consumed significantly more carrots under no-choice conditions. Plant diets (carrots and grass parts) have greater water content than mealworms, which may make those plant tissues more palatable for S. vicinus. Alternatively, adult S. borellii preferred mealworms but had no difference in meal size suggesting both diets were similar in palatability. Per gram of dry weight, mealworms have >6× greater nitrogen content than the plant parts evaluated. Greater nitrogen is expected in animal tissue compared to plant tissues (Schoonhoven et al., 2005). In the field, grasses are an abundant, but nitrogen-limited resource for Scapteriscus spp. Plant tissues, even well managed and fertilized turfgrasses, available to mole crickets would not be comparable in nitrogen content to animal tissue as prey (Schoonhoven et al., 2005). Graminivory may be a consequence of availability of grass relative to prey in their habitat (Coll and Guershon, 2002). A habitat that is nitrogen-limited is one possible route for the evolution of omnivory (Coll and Guershon, 2002).

#### 4.2. Effects of diet on omnivore survival and development

Although both *S. borellii* and *S. vicinus* are subterranean omnivores, the extent and benefits of omnivory were species dependent. Diet quality was not a main factor of survivorship of *S. vicinus* nymphs, but weight gain was greatest when animal protein (mealworms and diet rotation) was added to the diet. Adult *S. borellii* prefer mealworms in choice tests and the availability of mealworms higher in nitrogen content had a positive impact on longevity, growth, and body size of *S. borellii*. This suggests that development

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**Fig. 5.** Observed survival probabilities (A) and mean (±SE) weight (B) of *S. vicinus* raised on different diet treatments in the laboratory over an 8 wk period. There was a significant heterogeneity among the survival curves of *S. vicinus* provisioned with different diet treatments (A;  $\chi_3^2 = 11.79$ , P = 0.0081). There were initially eight replicates with each diet treatment. The numbers in the brackets represent the number of mole crickets analyzed at 0, 4, 5, 6, 7, 8 wk (B).

of S. borellii is nitrogen limited, which is common for orthopteroids such as grasshoppers (Joern and Behmer, 1997). Instar duration, through the 5th instar, was significantly less for S. borellii fed either mealworms or the diet rotation compared to the carrot diet, but there was no difference in later instars (Fig. 4A). Wing pads were beginning to develop in the late-instar (7th or 8th instar) nymphs, which may reflect other physiological changes. Immature insects may require greater protein content from foods for amino acids needed for new cuticle formation (Behmer and Joern, 2012). Thus, the optimal diet of young mole crickets may be protein biased, changing to a more carbohydrate-rich diet once wing pads are formed and the insects are nearly mature. Increased carbohydrate intake among penultimate instars is also suggested to create reserves for mating flights or to supply additional energy for males during courtship behaviors (Ulagaraj, 1975). This change in diet may explain the increased tunneling and turfgrass injury by large nymphs and adults in spring preceding oviposition.

Omnivores, like generalist herbivores, should engage in optimal foraging and would benefit from maximizing or optimizing nutrient intake (Coll and Guershon, 2002; Behmer and Joern, 2012). We hypothesized that forced omnivory would increase survival and hasten development. Neither species of *Scapteriscus*, however, seemed to benefit from diet mixing per se. In the choice test, less than half of the adults of either species consumed both food types and those that did mix food types consumed about twice the amount of those that had meals of a single food type. Increased consumption may have resulted from the difficulty or novelty of the choice (Bernays, 2001) among food types that vary in carbohydrate

and nitrogen content. It is also possible that mole crickets encountered a non-preferred diet first and then switched to a preferred diet. We did not attempt to quantify such behaviors during choice tests but provided both diets ad libitum so diet mixing did not result from a shortage of either diet.

Unexpectedly, *S. vicinus* nymphs fed the diet rotation did not perform well as *S. borellii*. In fact, they died faster than the starved individuals (Fig. 5A). This is difficult to explain. Diets did not appear to be hazardous to adult *S. vicinus* in short-term choice and nochoice tests, and survival of nymphs fed single diets of carrots and mealworms were comparable. Therefore, we do not suspect toxic effects of carrots or mealworms. Nymphs in all treatments were handled similarly between groups and species of mole crickets with the same frequency of disturbance for meal replacement. For these reasons, we do not suspect disturbance/handling mortality or some other experiment-specific condition. We are left only to attribute this result to some unknown species-specific response of *S. vicinus* in captivity. Among field collected mole crickets, *S. vicinus* are more sensitive to mortality in captivity than *S. borellii* (YX and DWH, personal observations).

#### 4.3. Implications of results for the turfgrass ecosystem

This is one of only a few papers (e.g., Hudson, 1987) to consider variability in development of Scapteriscus mole crickets. Results for S. borellii raise concerns about how the instar distribution of fieldsampled mole crickets is scored. Previous rearing studies (Hudson, 1987; Braman, 1993) assigned nymphal instars on the basis of pronotal length. Those studies used a standard diet (e.g., cricket chow or dog food). Pronotal length of S. borellii nymphs can vary widely depending on the diet choice. Hudson (1987) reported an average pronotal length for 7th instar S. borellii fed cricket chow as 5.65 mm. Because diet influences both developmental rate and pronotal length of S. borellii, pronotal lengths based on mole crickets fed a single diet in the laboratory may be misleading when applied to the field populations having more diverse diets (Taylor, 1979; Matheny, 1981; Fowler et al., 1985; Silcox and Brandenburg, 2011). The size of mole crickets in the field can impact the success of their biological control agents. The ectoparasitoid, Larra bicolor Fabricius (Hymenoptera: Crabronidae) attack only large nymphs or adult mole crickets (Portman et al., 2009) and the entomopathogenic nematode Steinernema scapterisci Nguyen & Smart (Rhabditida: Steinernematidae) can only enter the spiracles on larger nymphs and adult mole crickets (Hudson and Nguyen, 1989). Mole crickets that hasten development by feeding on animal tissue with greater nitrogen content should be more susceptible to these biocontrols.

It is common for both species of mole crickets to share a local habitat as well as geographic range in North America, and both are know to be cannibalistic (Hayslip, 1943; Frank and Walker, 2006). S. borellii benefits significantly from consumption of prey, so it would benefit from actively hunting prey perhaps even other mole crickets. Seeking prey by herbivores can be risky (Coll and Guershon, 2002), so omnivory by S. vicinus may involve scavenging or a 'sit and wait' approach (Denno and Fagan, 2003). Furthermore, the presence of prey may increase local activity of omnivores (Eubanks and Denno, 1999). The turfgrass ecosystem provides abundant populations of microarthropods and earthworms (Potter et al., 1990) that are potential prey for omnivorous mole crickets (Potter, 1998). It is logical therefore to predict that abundant prey may increase localized damage to turfgrass especially by S. borellii. In related research, Xu et al. (2012) found significantly more injury to bermudagrass infested with mole crickets when earthworms were present compared to mole cricket only controls. In the last 20 years, newer, target-selective insecticides have all but replaced more broad spectrum insecticides. These newer insecticides have minimal impacts on soil microfauna (Larson et al., 2012) and therefore may increase foraging by mole crickets and damage to turfgrass.

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