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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.

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. 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 × 20.9 cm × 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 (1.89 L; 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 cm × 5 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 freeze-dried mealworms were collected from five different individuals (replicates). Samples were weighed freshly, oven dried at 60 °C for 24 h, and then reweighed to calculate water content. Nitrogen content was determined from a 0.1 g sample of each tissue