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Authors: Squitier, Jason M., and Capinera, John L.

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HOST SELECTION BY GRASSHOPPERS (ORTHOPTERA: ACRIDIDAE) INHABITING SEMI-AQUATIC ENVIRONMENTS

JASON M. SQUITIER AND JOHN L. CAPINERA
Department of Entomology and Nematology, University of Florida, Gainesville, FL 32611-0620

ABSTRACT

Through laboratory choice tests involving 19 plant species, we assessed the host selection behavior of six grasshopper species: *Stenacris vitreipennis* (Marschall) (glassywinged toothpick grasshopper), *Leptysma marginicollis* (Serville) (cattail toothpick grasshopper), *Gymnoscirtetes pusillus* Scudder (little wingless grasshopper), *Paroxya clavuliger* (Serville) (olivegreen swamp grasshopper), *Paroxya atlantica* Scudder (Atlantic grasshopper), and *Romalea microptera* (Beauvois) (eastern lubber grasshopper). This grasshopper assemblage is commonly associated with semi-aquatic habitats in the southeastern United States. These poorly studied species display both graminivorous (*S. vetreipennis* and *L. marginicollis*) and mixed graminivorous-forbivorous feeding habits (the remaining species), the nature of which are fairly predictable based on examination of mouthpart morphology, but not entirely consistent with the tendency of cyrtacanthacridine species to feed on forbs.

Key Words: host preference, plant acceptance, mouthpart morphology

RESUMEN

Por medio de pruebas de selección de laboratorio utilizando 19 especies de plantas, evaluamos el comportamiento de selección de hospederos de seis especies de saltamontes: *Stenacris vitreipennis* (Marschall), *Leptysma marginicollis* (Serville), *Gymnoscirtetes pusillus* Scudder, *Paroxya clavuliger* (Serville), *Paroxya atlantica* Scudder, y *Romalea microptera* (Beauvois). Este grupo de saltamontes, esta comúnmente asociado con habitats semiacuáticos, en el sureste de los Estados Unidos. Estas especies poco estudiadas demuestran hábitos de alimentación graminívora (*S. vetreipennis* y *L. marginicollis*) y de alimentación mixta graminívora y de hierbas (las especies restantes), la naturaleza de los cuales son suficientemente predecibles basándose sobre la examinación de la morfología del aparato bucal, pero no totalmente consistentes con la tendencia de las especies cirtacanthacridines para alimentarse de plantas herbaceas.

Although often viewed as polyphagous herbivores, most grasshoppers are selective to some degree, exhibiting definite plant preferences (Mulkern 1967). In previous studies, it has been shown that grasshoppers are conveniently classified as grass-feeders (graminivorous), forb-feeders (forbivorous), or a mix of the two (ambivorous or mixed feeders) (Isely 1944). Phylogenetic differences exist among grasshoppers in relation to host plant preferences (Dadd 1963, Joern 1979). For example, members of the acridid subfamily Gomphocerinae tend to have a preference for grasses, Cyrtacanthacridinae (Melanoplinae in part) prefer forbs, and Oedopodinae eat both grasses and forbs (Dadd 1963, Joern & Lawlor 1980, Otte 1981). Joern (1986) points out that most monophagous and polyphagous species are forb-feeders while oligophagous species are grass feeders.

Information on dietary habits of Florida's grasshoppers is growing, though still far from complete. Preference tests (Capinera 1993, Scherer 1997) have been conducted for some of Florida's upland plants and crops, though information on most of Florida's grasshoppers is lacking. Such tests commonly are used to construct preference hierarchies (Lewis and van Emden 1986), but are constrained by experimental design. The investigator must have the wisdom to present the correct array of plants, which should be based on the habitat in which the insect is found. Nevertheless, even good designs are subject to faulty interpretation, as lack of a "preferred" host among the array of choices may force a hungry individual to feed on non-preferred plants which, in nature, might be accepted only if faced with starvation.

A very general method to determine the diet of a grasshopper is by the morphology of the grasshopper's mandibles (Mulkern 1967, Patterson 1984). The morphological characters of the mandibles, incisor and molar surfaces are useful in labeling grasshoppers as grass- or forb-feeders (Chapman 1964, Bernays & Barbehenn 1987, Kang et al. 1999) though most species with forb-feeding mandibles feed on a mixture of grasses and forbs. Isley (1944) suggested that the study of mandibular morphology would aid in understanding grasshopper ecology and their role in terrestrial communities.

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We evaluated host selection behavior by grasshoppers among the plant species abundantly found inhabiting semi-aquatic habitats. Most research on grasshopper feeding behavior has been conducted in arid environments, where grasshoppers most often attain high and damaging levels of abundance. Very little is known concerning species that inhabit moist or wet environments because such species usually do not become pests. The host selection behavior displayed by grasshoppers in choice tests was compared with host preference predictions based on mouthpart (mandible) morphology.

Materials and Methods

Grasshoppers were collected from several wet habitats: freshwater marshes, lakesides, flatwoods and ditchbanks. The grasshopper species included in this study were *Stenacris vitreipennis* (Marschall) (glassywinged toothpick grasshopper), *Leptysma marginicollis* (Serville) (cattail toothpick grasshopper), *Gymnoscirtetes pusillus* Scudder (little wingless grasshopper) *Paroxya clavuliger* (Serville) (olivegreen swamp grasshopper), *Paroxya atlantica* Scudder (Atlantic grasshopper), and *Romalea microptera* (Beauvois) (eastern lubber grasshopper). The grasshoppers were field-collected as large nymphs or adults and maintained in the laboratory during the experimental period. The insects and choice tests were held in an insect growth room at 30-32°C with a photoperiod of 14:10 (L:D) and a relative humidity of 40 ± 10%. Between study repetitions, the grasshoppers fed Romaine lettuce, a plant that seems to have nearly universal acceptance by acridids.

The plant species were presented to the grasshoppers in a series of four-choice tests. The plants were clipped into equal sized portions, the stems wrapped in cotton, and the cuttings were placed into vials filled with water in order to maintain plant turgidity. The 19 plant species were randomly assembled into 6 clusters of 4 plants each, with each cluster containing cattail as a common plant, and the components not varying among grasshoppers species or replicate tests. Each cluster was replicated 7 times, with replicates occurring on different days. Each of the four plants was randomly placed at equal distances from the others and from the sides of screen cages measuring 0.3 m on each side.

The grasshoppers were exposed to the host plants for approximately 24 h followed by estimation of the amount consumed. The scale for determining grasshopper consumption was taken from Capinera (1993): the consumption was determined by a visual estimate of the remaining plant material and assigning it a value of 1 to 5. A value of 1 would be assigned when 0-20% of the plant was eaten, 2 when 21-40% consumed, 3 when 41-60% consumed, 4 when 61-80% consumed and 5 when 81-100% consumed. The feeding trials were conducted under the same environmental conditions mentioned earlier. The temperature and humidity maintained in the laboratory during this experiment was approximately the optimal feeding range for most grasshoppers (Chapman 1957, Mulkern 1967).

The number of grasshoppers per cage was adjusted to reflect the individual appetites of the grasshoppers, thereby allowing measurable consumption without exhausting any of the plant material. Thus, there were 5 *Romalea microptera*, 6 *Paroxya clavuliger,* 6 *Leptysma marginicollis,* 6 *Stenacris vitreipennis,* 10 *Paroxya atlantica*, and 12 *Gymnoscirtetes pusillus* per cage. These grasshopper populations resulted in relatively the same amount of plant material eaten between species over the 24-h test period, an average of about 30%.

We took steps to assure that the grasshoppers had ample opportunity to explore the cages and host plants before registering acceptance of hosts by prolonged feeding. We maintained relatively low densities, and in no case was consumption high enough on one plant species to influence consumption of another plant. The cages were small, allowing the grasshoppers to encounter most or all plant species with relatively little movement. Therefore, we believe that the grasshoppers were fully capable of assessing the host options, and registered "preference" by their host consumption behavior. Observation of the insects confirmed that grasshoppers moved freely and often sampled plants without continuing to feed.

The 19 plants that were evaluated in this study were collected from the same habitats as the grasshoppers, and represented the most abundant floral elements in the semi-aquatic habitats sampled. The study plants included *Typha* spp. (cattail) (Typhaceae); *Eichhornia crassipes* (floating water hyacinth), and *Pontederia cordata* (pickerel weed) (Pontederiaceae); *Urochloa mutica* (para grass), *Leptochloa* spp. (sprangletop), *Panicum repens* (torpedograss), *Sacciolepis striata* (American cupscale) and *Chasmanthium sessiliflorum* (long leaf spikegrass) (Gramineae); *Polygonum punctatum* (dotted smartweed) and *Polygonum hirsutum* (hairy smartweed) (Polygonaceae); *Hydrocotyle* spp. (pennywort) and *Cicuta mexicana* (water hemlock) (Umbelliferae); *Ludwigia octovalvis* (long fruited primrose willow) and *Ludwigia suffruticosa* (headed seedbox) (Onagraceae); *Sagittaria latifolia* (common arrowhead) (Alismataceae); *Cyperus compressus* (poorland flatsedge) and *Cyperus surinamensis* (tropical flatsedge) (Cyperaceae); *Juncus efusus* (softrush) (Juncaceae); and *Sesbania macrocarpa* (hemp sesbania) (Leguminosae). For the purposes of this study the monocot families of Typhaceae, Pontederiaceae, Gramineae, Alismataceae, Cyperaceae and Juncaceae were

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considered grasses and the dicot families Polygonaceae, Umbelliferae, Leguminosae and Onagraceae were considered forbs.

The mean consumption values for each plant from the 6 plant clusters were calculated for each grasshopper species using Graph Pad Software (Instat 1993) one-way analysis of variance (ANOVA). The individual means were then compared in each grasshopper species trial using the Tukey-Kramer multiple comparison test. Simultaneously, mandibles of the grasshoppers were examined visually from preserved specimens and classified as forb- or grass-feeding types according to the descriptions and drawings of Isley (1944).

Results and Discussion

Of the 6 species collected from the wetland plant habitats, 5 were in the subfamily Cyrtacanthacridinae whereas *Romalea microptera*, though closely related to Cyrtacanthacridinae, is placed in the subfamily Romaleinae or in the family Romaleidae. Based on subfamily taxonomy, such cyrtacanthacridines might be expected to be forb-feeders.

Examination of the mandibles revealed that not all species were morphologically equipped to feed on forbs (Fig. 1). Three of the cyrtacanthridines, *Paroxya clavuliger*, *Paroxya atlantica*, and *Gymnoscirtetes pusillus* possessed toothed mandibles, suggesting a tendency to feed on forbs. However, *Leptysma marginicollis* and *Stenacris vitreipenni* were found to possess blunt-toothed mandibles, characteristics of grass-feeding species. *Romalea microptera* displayed mandibles suitable for forb feeding (Isley 1944, Patterson 1984).

The grouping of grasshoppers by mandible type to predict host preference was, for the most part, confirmed with the food choice experiments (Table 1). The cyrtacanthridine species with forb-feeding mandibles proved to be mixed feeders, accepting both grasses and forbs. *Gymnoscirtetes pusillus* displayed a mixed preference by readily consuming 2 grasses and 2 forbs. *Paroxya atlantica* also displayed a mixed preference by selecting 3 grasses and 2 forbs, and *Paroxya clavulger* chose 2 grasses and 2 forbs. *Romalea microptera* also displayed a mixed preference, preferring 2 forbs and 4 grasses. The two species with grass-feeding mandibles, *Stenacris vitreipennis* and *Leptysma marginicollis*, displayed strong preference for grasses. Although in a small number of cases forbs were consumed, in no case was a forb consumed by these latter species more than a grass.

Typha spp. (cattail) was used as a standard in each trial because it is a very common aquatic plant and relative consumption of this species would allow comparison to the other plants. Consumption values for cattail ranged from 1.3 to 5.0 in the various tests. Overall, cattail is one of the most readily accepted hosts for the grasshopper species tested. Other plant species were often consumed about as readily, or more readily, than cattail. *Gymnoscirtetes pusillus* had low consumption values but showed preferences for cattail, long fruited primrose willow, headed seedbox and sprangletop. *Paroxya atlantica* showed preference for cattail, pennywort, common arrowhead, poorland flatsedge and water hemlock. *Paroxya clavuliger* showed preference for cattail, water hyacinth, dotted smartweed, pennywort, water hemlock and sprangletop. *Stenacris vitreipennis* showed preference for cattail and poorland flatsedge. *Leptysma marginicollis* showed preference for cattail, pickerel weed, long fruited primrose willow and softrush. *Romalea microptera* showed preference for cattail, common arrowhead, poorland flatsedge, headed seedbox, sprangletop and hairy smartweed.

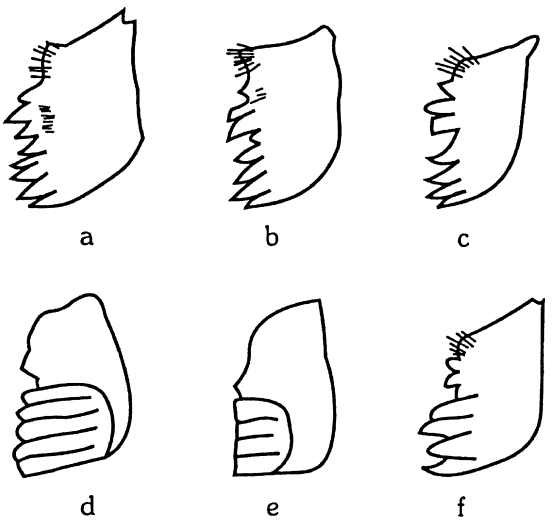


Fig. 1. Diagrams of the left mandible of the grasshopper species: (a) *Romalea microptera* Beauvois, (b) *Paroxya clavuliger* (Serville), (c) *Paroxya atlantica* Scudder, (d) *Leptysma marginicollis* (Serville), (e) *Stenacris vitreipennis* (marschall), (f) *Gymnoscirtetes pusillus* Scudder.

This study provides the first documentation of the host selection behavior of the grasshopper assemblage commonly associated with semi-aquatic habitats in the southeastern United States. These poorly studied species display both graminivorous and forbivorous feeding habits, the nature of which is fairly predictable based on examination of mouthpart morphology, but not entirely consistent with the tendency of cyrtacanthridine species to feed on forbs. The graminivorous feeding behavior of *Stenacris vitreipennis* and *Leptysma marginicollis* is also reflected in modified body form. Both species display unusually long, thin bodies that allow them to blend with narrow emergent grass vegetation. This crypsis undoubtedly makes

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TABLE 1. COMPARATIVE CONSUMPTION OF SEMI-AQUATIC PLANTS BY GRASSHOPPERS IN LABORATORY CHOICE TESTS.

Grasshopper species	Plant species and associated mean consumption values ± SD[a]								F	P	df
Gymnoscirtetes pusillus	cattail	1.7 ± 0.5 a	w. hyacinth	1.0 ± 0.0 b	para grass	1.0 ± 0.0 b	d. smartweed	1.0 ± 0.0 b	15.0	0.0001	3,24
	cattail	1.3 ± 0.5 ab	pennywort	1.1 ± 0.4 ab	p. weed	1.0 ± 0.0 b	p. willow	1.7 ± 0.5 a	4.3	0.0145	3,24
	cattail	1.4 ± 0.5 a	arrowhead	1.0 ± 0.0 a	p. flatsedge	1.6 ± 0.5 a	a. cupscale	1.1 ± 0.4 a	2.7	0.0760	3,24
	cattail	1.4 ± 0.8 a	softrush	1.0 ± 0.0 a	hemlock	1.1 ± 0.4 a	sesbania	1.1 ± 0.4 a	1.0	0.4098	3,24
	cattail	1.7 ± 0.5 ab	torpedograss	1.0 ± 0.0 b	h. seedbox	1.8 ± 0.9 a	t. flatsedge	1.0 ± 0.0 b	5.6	0.0047	3,24
	cattail	1.7 ± 1.0 ab	sprangletop	2.4 ± 1.0 a	h. smartweed	1.0 ± 0.0 b	spikegrass	1.1 ± 0.4 b	5.9	0.0036	3,24
Paroxya atlantica	cattail	3.7 ± 1.4 a	w. hyacinth	1.4 ± 0.5 b	para grass	1.0 ± 0.0 b	d. smartweed	1.1 ± 0.4 b	19.5	0.0001	3,24
	cattail	2.4 ± 1.5 ab	pennywort	3.4 ± 1.3 a	p. weed	1.3 ± 0.5 b	p. willow	2.1 ± 1.0 ab	4.1	0.0170	3,24
	cattail	2.1 ± 1.1 a	arrowhead	1.6 ± 0.5 ab	p. flatsedge	1.3 ± 0.5 ab	a. cupscale	1.1 ± 0.4 b	3.0	0.0491	3,24
	cattail	2.0 ± 1.4 b	softrush	1.4 ± 0.5 b	hemlock	4.3 ± 1.0 a	sesbania	2.7 ± 1.1 b	9.7	0.0002	3,24
	cattail	3.7 ± 1.4 a	torpedograss	1.1 ± 0.4 b	h. seedbox	1.6 ± 1.1 b	t. flatsedge	1.0 ± 0.0 b	13.4	0.0001	3,24
	cattail	2.6 ± 1.5 a	sprangletop	2.0 ± 1.3 ab	h. smartweed	1.1 ± 0.4 ab	spikegrass	1.0 ± 0.0 b	3.8	0.0242	3,24
Stenacris vitreipennis	cattail	3.6 ± 1.1 a	w. hyacinth	1.1 ± 0.4 b	para grass	1.7 ± 0.5 b	d. smartweed	1.0 ± 0.0 b	23.5	0.0001	3,24
	cattail	2.4 ± 1.0 a	pennywort	1.0 ± 0.0 b	p. weed	1.1 ± 0.4 b	p. willow	1.1 ± 0.4 b	10.2	0.0002	3,24
	cattail	2.4 ± 1.5 a	arrowhead	1.0 ± 0.0 b	p. flatsedge	1.7 ± 0.8 ab	a. cupscale	1.0 ± 0.0 b	4.6	0.0113	3,24
	cattail	3.3 ± 1.1 a	softrush	1.1 ± 0.4 b	hemlock	1.0 ± 0.0 b	sesbania	1.0 ± 0.0 b	25.5	0.001	3,24
	cattail	2.4 ± 1.8 a	torpedograss	1.3 ± 0.5 a	h. seedbox	1.7 ± 1.0 a	t. flatsedge	1.3 ± 0.5 a	1.7	0.1846	3,24
	cattail	2.6 ± 1.3 a	sprangletop	1.4 ± 0.4 b	h. smartweed	1.0 ± 0.0 b	spikegrass	1.1 ± 0.4 b	8.1	0.0007	3,24
Leptysma marginicollis	cattail	2.0 ± 0.8 a	w. hyacinth	1.0 ± 0.0 a	para grass	1.3 ± 0.5 a	d. smartweed	1.0 ± 0.0 a	3.9	0.0369	3,12
	cattail	1.8 ± 0.5 a	pennywort	1.0 ± 0.0 a	p. weed	1.3 ± 0.5 a	p. willow	1.3 ± 0.5 a	2.1	0.1522	3,12
	cattail	2.0 ± 0.8 a	arrowhead	1.0 ± 0.0 a	p. flatsedge	1.5 ± 0.6 a	a. cupscale	1.0 ± 0.0 a	3.7	0.0439	3,12
	cattail	1.3 ± 0.5 b	softrush	2.0 ± 0.0 a	hemlock	1.0 ± 0.0 b	sesbania	1.0 ± 0.0 b	14.3	0.0003	3,12
	cattail	1.3 ± 0.5 a	torpedograss	1.3 ± 0.5 a	h. seedbox	1.3 ± 0.5 a	t. flatsedge	1.8 ± 0.5 a	1.0	0.4262	3,12
	cattail	1.5 ± 0.6 a	sprangletop	1.3 ± 0.5 a	h. smartweed	1.0 ± 0.0 a	spikegrass	1.0 ± 0.0 a	1.6	0.2476	3,12
Romalea microptera	cattail	5.0 ± 0.0 a	w. hyacinth	2.3 ± 1.6 b	para grass	1.0 ± 0.0 b	d. smartweed	1.6 ± 1.5 b	16.1	0.0001	3,24
	cattail	3.9 ± 1.7 a	pennywort	3.6 ± 1.9 a	p. weed	2.3 ± 1.9 a	p. willow	4.6 ± 1.1 a	2.3	0.1071	3,24
	cattail	3.7 ± 1.6 a	arrowhead	3.9 ± 1.2 a	p. flatsedge	3.4 ± 1.5 a	a. cupscale	1.1 ± 0.4 b	7.0	0.0015	3,24
	cattail	4.7 ± 0.8 a	softrush	2.7 ± 1.6 a	hemlock	4.5 ± 0.8 a	sesbania	3.3 ± 1.9 a	2.9	0.0589	3,24
	cattail	5.0 ± 0.0 a	torpedograss	1.3 ± 0.5 b	h. seedbox	5.0 ± 0.0 a	t. flatsedge	1.3 ± 0.5 b	201.7	0.0001	3,24
	cattail	5.0 ± 0.0 a	sprangletop	3.8 ± 1.5 a	h. smartweed	4.3 ± 1.6 a	spikegrass	1.5 ± 0.8 b	10.0	0.0003	3,24
Paroxya clavuliger	cattail	3.9 ± 1.7 a	w. hyacinth	2.0 ± 1.7 ab	para grass	1.0 ± 0.0 b	d. smartweed	2.9 ± 0.9 ab	6.3	0.0027	3,24
	cattail	3.0 ± 1.7 b	pennywort	4.9 ± 0.4 a	p. weed	1.1 ± 0.4 c	p. willow	4.0 ± 1.0 ab	16.7	0.0001	3,24
	cattail	3.7 ± 1.0 a	arrowhead	2.3 ± 0.8 b	p. flatsedge	1.9 ± 0.9 bc	a. cupscale	1.0 ± 0.0 c	15.8	0.0001	3,24
	cattail	2.4 ± 1.8 ab	softrush	1.6 ± 1.1 b	hemlock	4.4 ± 1.1 a	sesbania	2.9 ± 1.8 ab	4.5	0.0126	3,24
	cattail	4.0 ± 1.4 a	torpedograss	1.0 ± 0.0 b	h. seedbox	2.1 ± 1.1 b	t. flatsedge	1.1 ± 0.4 b	16.3	0.0001	3,24
	cattail	3.4 ± 2.0 a	sprangletop	4.0 ± 1.3 a	h. smartweed	1.0 ± 0.0 b	spikegrass	1.3 ± 0.8 b	10.3	0.0002	3,24

[a]Means ± SD within rows followed by the same letter are not significantly different ($P = 0.05$) by Tukey-Kramer Multiple Comparison Test. Cattail, floating w(water) hyacinth, paragrass, d(dotted) smartweed, pennywort, p(pickerel) weed, long fruited p(primrose) willow, common arrowhead, p(poorland) flatsedge, a(American) cupscale, softrush, w(water) hemlock, h(hemp) sesbania, torpedograss, h(headed) seedbox, t(tropical) flatsedge, sprangletop, h(hairy) smartweed and long leaf spikegrass.

them difficult to detect and presumably safer from predation. Interestingly, these grass-feeding cyrtacanthacridine species have very slanted faces, thereby physically resembling grass-feeding gomphocerines more than their close relatives, the forb-feeding cyrtacanthacridines.

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