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HOST PLANT SELECTION BY *ROMALEA MICROPTERA* (ORTHOPTERA: ROMALEIDAE)

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ABSTRACT

The eastern lubber grasshopper, *Romalea microptera* (Palisot de Beauvois) (Orthoptera: Romaleidae)[also known as *R. guttata* (Houttuyn)], is known to be polyphagous, but little else is known about its diet. Choice and no-choice tests were conducted to determine plant preference. In choice tests, 104 different plants were presented and relative preference was determined using 'Romaine' lettuce (*Lactuca sativa* L. var. *longifolia*; Asteraceae) as a standard. These included representative plants from several categories, including ornamental plants, weeds, shrubs, trees, vines, aquatic or semiaquatic plants, and vegetable crops. The grasshoppers did not display a statistically significant difference in selection, relative to 'Romaine' lettuce, for 20% of the plants evaluated; these should be considered very susceptible to injury because lettuce is a readily accepted plant. A few plants (3%) were more preferred than lettuce, and of course would also be at high risk for consumption. The majority of plants tested (77%) were significantly less preferred, but even some of these are at risk because, like other polyphagous insects, lubbers sometimes will feed on less acceptable plants when preferred plants are not available. A subset of these (n = 25) was also presented in no-choice tests, and the choice and no-choice responses compared. Plant preference in choice and no-choice tests was significantly correlated. A selection of ornamental plants (n = 10) that scored least-preferred in choice tests was assessed in no-choice 'starvation' tests, and 9 of the 10 proved to be quite resistant to grasshopper feeding. Several plants (n = 5) that produce foliage asynchronously were assessed in choice tests, with the grasshoppers preferring young foliage relative to old foliage. In field cage studies, the acceptability of plants significantly affected the efficacy of insecticide-containing baits, with significantly higher mortality found in cages containing non-preferred plants. Thus, host plant selection affects damage directly by regulating the amount of feeding, and indirectly by influencing acceptance of bait.

Key Words: lubber grasshopper, diets, plant preference, insecticide baits

RESUMEN

El saltamonte torpe del este, *Romalea microptera* (Palisot de Beauvois) (Orthoptera: Romaleidae), es conocido por ser polífago, pero poco más se sabe acerca de su dieta. Se realizaron pruebas de elección y no elección para determinar su preferencia a las plantas. En pruebas de elección, se presentaron 104 plantas diferentes y la preferencia relativa se determinó usando lechuga romana (*Lactuca sativa* L. var *longifolia*;. Asteraceae) como un estándar. Estos incluyen plantas representativas de varias categorías, incluyendo plantas ornamentales, hierbas, arbustos, árboles, enredaderas, plantas acuáticas o semiacuáticos y cultivos vegetales. Los saltamontes no mostraron una diferencia estadísticamente significativa en la selección, en relación con la lechuga romana, para el 20% de las plantas evaluadas; estos deben ser considerados muy susceptibles a daño debido que las plantas de lechuga son fácilmente aceptadas. Unas pocas plantas (3%) fueron más preferidas que la lechuga, y por supuesto también sería un alto riesgo para el consumo. La mayoría de las plantas analizadas (77%) fueron significativamente menos preferidas, pero incluso algunas de ellas se encuentran en riesgo debido a que, al igual que otros insectos polífagos, los saltamontes torpes a veces se alimentan de plantas menos aceptables cuando las plantas preferidas no están disponibles. Un subconjunto de estos (n = 25) también se presentó en las pruebas de no elección, y las respuestas de elección y no elección fueron comparables. La preferencia de plantas en pruebas de elección y no elección se correlacionó significativamente. Una selección de plantas ornamentales (n = 10) que anotó menos preferidas en pruebas de elección se evaluó en pruebas de no elección 'inanición›, y 9 de los 10 demostró ser bastante resistentes a la alimentación de los saltamontes. Varias plantas (n = 5) que producen follaje asincrónico fueron evaluados en las pruebas de selección, y los saltamontes preferían follaje tierno en relación con de follaje viejo. En estudios en jaulas de campo, la aceptabilidad de las plantas afectó significativamente la eficacia de los insecticidas que contienen cebo, con una mortalidad significativamente más alta en las jaulas que tenían plantas no preferidas.

Por lo tanto, la selección de plantas hospederas afecta el daño directamente por medio de la regulación de la cantidad de alimentación, e indirectamente por la influencia en la aceptación del cebo.

Palabras Clave: saltamontes torpes, dietas, preferencia de la planta, cebos insecticidas

Eastern lubber grasshopper, *Romalea microptera* (Palisot de Beauvois) (Orthoptera: Romaleidae)[also known as *R. guttata* (Houttuyn)] is widely dispersed in the southeastern USA. It is exceptionally large (commonly 6-8 cm in length, 8-12 g in weight) and distinctively colored (yellow, black, sometimes pink), and often abundant enough to attract attention and concern. Lubber grasshoppers sometimes damage ornamental plants in the landscape, especially flowers, and occasionally affect vegetable plants in home gardens. They also defoliate newly planted citrus trees, though they rarely cause significant damage to mature citrus groves. They can be very difficult to control with chemical insecticides.

The chemical ecology of eastern lubber grasshopper has been the subject of many studies. *Romalea microptera* is aposomatic and toxic, being emetic to birds and lizards (Yousef & Whitman 1992). They eject a repellent defensive secretion from modified metathoracic spiracles. Both natural plant products and their metabolites are involved in the chemical defenses. The secretion consists principally of phenolics and quinones, but the volume, chemical components, and concentrations vary with their age, sex, and diet (Jones et al. 1987, 1989; Whitman et al. 1991, 1992). Sequestration of allomones from plants by insects is not unusual, but normally associated with monophagous or oligophagous species. However, eastern lubber grasshopper is polyphagous.

Despite the apparent importance of host-plant selection in their defensive chemistry, and the potential of lubber grasshoppers to cause plant damage, the host-plant relationships of this insect are poorly described. Watson & Brantley (1940) and Watson (1941) made observations on the diet of eastern lubber grasshopper, noting that they were found on narcissus, *Narcissus* sp. (Aspargales: Amaryllidaceae); crinum, *Crinum* sp. (Aspargales: Amaryllidaceae); cowpea, *Vigna unguiculata* (L.) Walp. (Fabales: Fabaceae); and peanut, *Arachis hypogaea* L. (Fabales: Fabaceae); and could be reared successfully on narcissus and tread softly, *Cnidoscolus stimulosus* (Michx.) Engelm. & Gray (Malpighiales: Euphorbiaceae), but not on pokeweed, *Phytolacca americana* L. (Caryophyllales: Phytolaccaceae). They also were reported to eat some emergent semiaquatic plants, including pickerelweed, *Pontederia cordata* L. (Commelinales: Pontederiaceae); lizard's tail, *Saururus cernuus* L. (Piperales: Saururaceae); arrowhead, *Sagittaria* sp. (Alismatales: Alismataceae); and a sedge, *Cyperus* sp. (Poales: Cyperaceae) The silk of corn, *Zea mays* L. (Poales: Poaceae), was reportedly injured, but acceptability of the foliage was not mentioned. Jones et al. (1987, 1989) reported that wild onion, *Allium canadense* L. (Aspagales: Amaryllidaceae), was a "favored" food plant, and that the grasshoppers could be reared on a mixture of 26 plant species from 15 families. Whitman (1988) suggested that they would feed on 104 plant species from 38 families, citing unpublished data. Barbara & Capinera (2003) studied suitability of poison bait for lubber control. As part of this investigation, they compared the acceptance of various vegetable crops to bran bait, thus obtaining relative preference values for several crops. Relative to bran, crops in the plant families Brassicaceae, Asteraceae, Cucurbitaceae, and Apiaceae were preferred by lubbers, but Solanaceae were not. Eastern lubber grasshopper clearly will feed on a number of plants from different plant families, but except for the aforementioned observations, the plants particularly susceptible or resistant to feeding largely remain undetermined. Thus, I conducted several studies designed to identify the relative susceptibility of common plants to herbivory by eastern lubber grasshopper. After identifying some preferred and non-preferred plants, I also assessed the influence of representative plants on efficacy of insecticide-containing bait. Bait formulations of insecticides are commonly used for grasshopper suppression, but the baits need to compete with host plants for the attention of the grasshoppers in order to be effective.

Materials and Methods

Colony Maintenance

First instars of eastern lubber grasshopper were field collected in Alachua and Polk Counties, Florida, maintained in screen cages until they attained the fourth or fifth instar, and then used for host feeding tests. They were held at 25-27 °C in screen cages measuring 30 × 30 × 60 cm, but a desk lamp with an incandescent bulb was turned on adjacent to the cage during the 14 photophase to allow them to increase body temperature. They were fed 'Romaine' lettuce (*Lactuca sativa* L. var. *longifolia*; Asteraceae) and wheat (*Triticum* sp.; Poales: Poaceae) bran prior to, and after, testing. Grasshoppers that were used in host plant tests were returned to the 'Romaine' lettuce and bran diet for at least 3 days prior to being used for other tests. Grasshoppers always had access to food, and were never starved prior to evaluation of food preferences, as this can affect food choice (Chapman & Sword 1997).

Choice Tests

Choice tests were conducted using 'Romaine' lettuce as a standard, and preference for other plants was assessed relative to 'Romaine'. Individual fourth or fifth instar hoppers were presented with a leaf or portion of a leaf of a single test plant, and an equivalent amount of lettuce. About 10-12 cm^2 of the test leaf, depending on its natural size, was matched with equivalent 'Romaine' leaf area. Because 'Romaine' leaf tissue varies considerably in leaf thickness (thin apically, thick basally), it was also possible to visually match the test plants with similar 'Romaine' leaf thickness. Each test leaf and the corresponding 'Romaine' leaf section were presented adjacent to each other at the center of a test arena. The test arena was a transparent cylindrical plastic container, 15 cm in diameter and 7 cm high. The arena lid closed very tightly, and each arena was provided with a wet paper towel, so the foliage remained turgid during the test. Each hopper was allowed to feed for 10 h or until it consumed 80-100% of either leaf type. The arenas were monitored regularly and the individual test terminated if either leaf was nearly consumed. I recorded the feeding of hoppers that consumed at least half of one leaf, but as noted previously, I terminated the test before the hopper could be forced into feeding on the alternate host due to lack of preferred food. Leaf consumption was rated from 1-5 based on the proportion of each leaf consumed, where 1 represented 1-20%, 2 was 21-40%, 3 was 41-60%, 4 was 61-80%, and 5 was 81-100%. There were 25 replicate hoppers in individual containers for each plant species, though some did not eat the minimum (approximately half of one leaf) to demonstrate preference. Visual estimates of leaf loss were used in most cases, because this is displays less temporal variation than weight and is the basis for classification of this insect as a pest. However, for finely divided leaves such as carrot and fennel, wet weight was used to determine leaf loss. The number of successful feedings (at least 50% consumption of one plant) for each plant species is shown in Table 1, along with the plant species. Host plant preference was analyzed statistically by comparing the leaf consumption ratings of the test species and 'Romaine' lettuce with the Wilcoxin Matched-Pairs Signed Rank Test using Prism (GraphPad Software, Inc., San Diego, California). This is the nonparametric equivalent of a paired t-test, and makes no assumption about normality of the data. Some of the data were not normally distributed, warranting the nonparametric assessment of the data. Paired analyses are recommended for choice tests (Horton 1995). These analyses allowed me to classify host plant preference into 3 categories: less preferred than 'Romaine' lettuce, about as preferred as 'Romaine', and more preferred than 'Romaine'. Using these consumption ratings, I also calculated an acceptability index (A.I.) that considers feeding on both choices, thereby adjusting for individual differences among grasshoppers in the estimated levels of consumption:

Test plant consumption

$$\text{A.I.} = \frac{\text{Test plant consumption}}{\text{Test plant consumption + 'Romaine' consumption}}$$

This type of acceptability index is commonly used to assess host selection by invertebrates in laboratory environments where the amount and number of host plants is controlled (Cook et al. 1996; Fenner et al. 1999). The A.I. was used to rank the host preference from most to least preferred. Several plant species or cultivars in each of several categories were investigated: 18 vegetables; 43 ornamentals; 22 vines, shrubs, and trees; 14 weeds; and 7 semiaquatic or aquatic plants. These plants were selected because they are commonly planted or naturally occur frequently. Insecticide-free plant material was gathered from The University of Florida Natural Area Teaching Laboratory, campus organic gardens, or provided by faculty from their home gardens. The only exception was 'Romaine' lettuce, which was store purchased, because it is continuously available in consistent quality.

The effect of plant leaf age on hopper acceptance was assessed using 5 plant species for which young and old leaves commonly occur simultaneously and are easily distinguished: laurel cherry, *Prunus carolina* Alton (Rosales: Rosaceae); hophornbeam, *Ostrya virginiana* (Mill.) K.Koch (Fagales: Betulaceae); peregrina, *Jatropha integerrima* Jacq. (Malpighiales: Euphorbiaceae); rose, *Rosa* sp. (Rosales: Rosaceae) and hogbrier, *Smilax tamnoides* L. (Liliales: Smilacaceae). Equal amounts of young (terminal) vegetation were matched with old (basal) vegetation and presented to hoppers using the methods previously described. Leaf consumption ratings were compared between young and old leaves within each plant species using the Wilcoxin Matched-Pairs Signed Rank Test.

No-Choice Tests

At the same time that choice tests were being conducted, no-choice tests were implemented for 25 plant species. The no-choice tests were conducted in the same manner as the choice tests, except that lettuce was not provided. The hoppers were allowed to feed for 10 h, and the same 5 leaf consumption ratings were recorded except for

TABLE 1. PLANTS TESTED FOR RELATIVE PREFERENCE BY *ROMALEA MICROPTERA* AND RANKED BY ACCEPTABILITY INDEX (A.I.) WITHIN EACH PLANT CATEGORY.

Scientific name	Common name	Family	Number tested[a]	A.I.	Significance level[b]
Vegetables					
Pisum sativae	Garden pea	Fabaceae	23	0.59	ns
Lactuca sativa	Lettuce cv butterhead	Asteraceae	20	0.57	ns
Brassica oleraceae cv *Acephala*	Kale	Brassicaceae	18	0.51	ns
Phaseolus vulgaris	Green bean	Fabaceae	22	0.49	ns
Daucus carota	Carrot	Apiaceae	25	0.43	ns
Brassicae oleracea cv Capitata	Cabbage	Brassicaceae	25	0.40	$P < 0.05$
Brassica oleracea cv *Gemmifera*	Brussels sprouts	Brassicaceae	18	0.40	$P < 0.05$
Allium cepeae	Onion	Amaryllidaceae	24	0.39	$P < 0.05$
Cucumis sativa	Cucumber	Cucurbitaceae	20	0.37	$P < 0.05$
Allium sativum	Garlic	Amaryllidaceae	13	0.35	$P < 0.01$
Brassica oleracea cv *Acephala*	Collards	Brassicaceae	18	0.33	$P < 0.05$
Solanum melongea	Eggplant	Solanaceae	20	0.32	$P < 0.01$
Solanum lycopersicum	Tomato	Solanaceae	17	0.29	$P < 0.001$
Capsicum annuum	Bell pepper	Solanaceae	19	0.27	$P < 0.001$
Apium graveolens	Celery	Apiaceae	13	0.25	$P < 0.01$
Abelmoschus esculentus	Okra	Malvaceae	13	0.23	$P < 0.01$
Foeniculum vulgare	Fennel	Apiaceae	12	0.21	$P < 0.01$
Zea mays	Sweet corn	Poaceae	20	0.19	$P < 0.001$
Ornamental plants					
Nerium oleander	Oleander	Apocynaceae	15	0.66	$P < 0.001$**
Hippeastratum sp.	Amaryllis	Amaryllidaceae	22	0.48	ns
Asclepias tuberosa	Butterfly weed	Asclepiadaceae	15	0.47	ns
Jatropha integerrima	Peregrina	Euphorbiaceae	20	0.43	ns
Ruella simplex	Mexican petunia	Acanthaceae	14	0.41	ns
Lantana camara	Lantana	Verbenaceae	20	0.40	ns
Barleria cristata	Philippine violet	Acanthaceae	18	0.38	$P < 0.05$
Trachelospermum jasminoides	Confederate jasmine	Apocynaceae	22	0.38	$P < 0.05$
Tradescantia pallida	Purple queen	Commelinaceae	16	0.38	$P < 0.01$
Canna sp.	Canna	Cannaceae	25	0.33	$P < 0.001$
Begonia sp.	Begonia	Begoniaceae	18	0.33	$P < 0.001$
Gardenia jasminoides	Gardenia	Rubiaceae	19	0.33	$P < 0.001$

[a]Number of successful tests, wherein at least 50% consumption was recorded.

[b]Statistical significance is based on comparison with consumption of 'Romaine' lettuce. Plants that were consumed more readily than lettuce are indicated by a double asterisk (**); plants consumed about as readily as lettuce are indicated by ns; plants significantly less preferred than lettuce display probability values only.

TABLE 1. (CONTINUED) PLANTS TESTED FOR RELATIVE PREFERENCE BY *ROMALEA MICROPTERA* AND RANKED BY ACCEPTABILITY INDEX (A.I.) WITHIN EACH PLANT CATEGORY.

Scientific name	Common name	Family	Number tested[a]	A.I.	Significance level[b]
Hydrangea macrophylla	Hydrangea	Hydrangeaceae	20	0.31	$P < 0.001$
Plumbago auriculata	Plumbago	Plumbaginaceae	19	0.30	$P < 0.001$
Hamelia patens	Firebush	Rubiaceae	17	0.30	$P < 0.01$
Crinum sp.	Crinum	Amaryllidaceae	20	0.29	$P < 0.01$
Tropaeolum sp.	Nasturtium	Tropaeolaceae	15	0.28	$P < 0.001$
Ipomea nil	Japanese morning glory	Convolvulaceae	15	0.29	$P < 0.01$
Tulbaghia violacea	Society garlic	Amaryllidaceae	23	0.27	$P < 0.001$
Antirrhinum majus	Snapdragon	Plantaginaceae	14	0.27	$P < 0.01$
Rosa sp.	Rose	Rosaceae	15	0.27	$P < 0.01$
Viola hederacea	Australian violet	Violaceae	16	0.26	$P < 0.001$
Torenia sp.	Torenia	Scrophulariaceae	15	0.26	$P < 0.01$
Viola tricolor	Pansy	Violaceae	14	0.25	$P < 0.01$
Paspalum notatum	Bahia grass	Poaceae	16	0.25	$P < 0.001$
Neomarica northiana	Walking iris	Iridaceae	18	0.25	$P < 0.001$
Dietes iridioides	African iris	Iridaceae	14	0.23	$P < 0.001$
Pentas lanceolata	Penta	Rubiaceae	16	0.23	$P < 0.001$
Helianthus debilis	Beach sunflower	Asteraceae	16	0.23	$P < 0.001$
Neomarica caerulea	Giant apostle's iris	Iridaceae	13	0.22	$P < 0.01$
Hemerocallis fulva	Daylily	Xanthorrhoeaceae	18	0.22	$P < 0.001$
Hibiscus coccineus	Scarlet rose mallow	Malvaceae	18	0.21	$P < 0.001$
Agapanthus africanus	Lily of the Nile	Amaryllidaceae	20	0.20	$P < 0.001$
Lantana montevidensis	Weeping lantana	Verbenaceae	15	0.19	$P < 0.001$
Stenotaphrum secundatum	St. Augustine grass	Poaceae	16	0.19	$P < 0.001$
Odontonema strictum	Firespike	Acanthaceae	18	0.18	$P < 0.001$
Euryops pectinatus	Bush daisy	Asteraceae	13	0.18	$P < 0.01$
Brugsmania sp.	Angel's trumpet	Solanaceae	15	0.18	$P < 0.001$
Cymbidium sp.	Orchid	Orchidaceae	15	0.18	$P < 0.001$
Callistemon sp.	Bottlebrush	Myrtaceae	14	0.18	$P < 0.001$
Salvia coccinea	Tropical sage	Lamiaceae	12	0.17	$P < 0.01$
Euphorbia pulcherrima	Poinsettia	Euphorbiaceae	19	0.17	$P < 0.001$
Zamia integrifolia	Coontie	Zamiaceae	15	0.17	$P < 0.001$
Vines, shrubs, and trees					
Vitis vulpinae	Frost grape	Vitaceae	18	0.41	ns

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TABLE 1. (CONTINUED) PLANTS TESTED FOR RELATIVE PREFERENCE BY *ROMALEA MICROPTERA* AND RANKED BY ACCEPTABILITY INDEX (A.I.) WITHIN EACH PLANT CATEGORY.

Scientific name	Common name	Family	Number tested[a]	A.I.	Significance level[b]
Prunus carolina	Laurel cherry	Rosaceae	15	0.37	$P < 0.01$
Quercus virginiana	Live oak	Fagaceae	15	0.36	$P < 0.05$
Ostrya virginiana	Hophornbeam	Betulaceae	12	0.35	$P < 0.05$
Carya glabra	Pignut hickory	Jugandaceae	13	0.34	$P < 0.01$
Musa sp.	Banana	Musaceae	19	0.34	$P < 0.01$
Smilax bona-nox	Saw greenbrier	Smilaceae	19	0.33	$P < 0.01$
Vitis rotundifolia	Muscadine grape	Vitaceae	16	0.32	$P < 0.01$
Parthenocissus quinquefolia	Virginia creeper	Vitaceae	22	0.29	$P < 0.001$
Erythrina herbacea	Coralbean	Fabaceae	17	0.29	$P < 0.01$
Liquidambar styraciflua	American sweetgum	Altingiaceae	14	0.28	$P < 0.001$
Prunus americana	American plum	Rosaceae	14	0.28	$P < 0.01$
Magnolia grandifolia	Southern magnolia	Magnoliaceae	13	0.26	$P < 0.01$
Tilia americana	Basswood	Malvaceae	15	0.26	$P < 0.001$
Calicarpa americana	American beautyberry	Limiaceae	16	0.25	$P < 0.001$
Citrus paradisi x *C. reticulata*	Tangelo	Rutaceae	15	0.23	$P < 0.001$
Discorea bulbifera	Air potato	Discoreaceae	18	0.22	$P < 0.001$
Citrus sinensis	Orange	Rutaceae	19	0.21	$P < 0.001$
Rubus cuneifolius	Sand blackberry	Rosaceae	16	0.20	$P < 0.001$
Baccharis halmifolia	Groundsel	Asteraceae	15	0.20	$P < 0.001$
Smilax smalli	Lance-leaf greenbrier	Smilaceae	18	0.19	$P < 0.001$
Passiflora incarnata	Passion vine	Passifloraceae	18	0.19	$P < 0.001$
Weeds					
Poinsettia cyathophora	Painted leaf	Euphorbiaceae	22	0.61	$P < 0.05$**
Cnidoscolus stimulosus	Tread softly	Euphorbiaceae	25	0.52	ns
Phyllanthus urinaria	Chamber bitter	Euphorbiaceae	25	0.51	ns
Desmodium tortuosum	Florida beggarweed	Fabaceae	22	0.46	ns
Oldenlandia corymbosa	Old world diamond-flower	Rubiaceae	15	0.46	ns
Richardia scabra	Florida pusley	Rubiaceae	23	0.45	ns
Digitaria ischaemum	Smooth crabgrass	Poaceae	25	0.43	ns
Chenopodium ambrosioides	Mexican tea	Chenopodiaceae	18	0.37	$P < 0.01$
Phytolacca americana	Pokeweed	Phytolaccaceae	21	0.34	$P < 0.01$
Melothria pendula	Creeping cucumber	Cucurbitaceae	25	0.34	$P < 0.01$

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[b]Statistical significance is based on comparison with consumption of 'Romaine' lettuce. Plants that were consumed more readily than lettuce are indicated by a double asterisk (**); plants consumed about as readily as lettuce are indicated by ns; plants significantly less preferred than lettuce display probability values only.

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Scientific name	Common name	Family	Number tested[a]	A.I.	Significance level[b]
Cyperus globulosus	Globe sedge	Cyperaceae	17	0.29	$P < 0.01$
Bidens alba	Beggarticks	Asteraceae	18	0.28	$P < 0.001$
Ambrosia artemisiifolia	Common ragweed	Asteraceae	13	0.25	$P < 0.01$
Amaranthus hybridus	Smooth pigweed	Amaranthaceae	21	0.18	$P < 0.001$
Semiaquatic or aquatic plants					
Colocasia esculenta	Wild taro	Araceae	15	0.63	$P < 0.05$**
Typha sp.	Cattail	Typhaceae	22	0.45	ns
Pistia stratiotes	Water lettuce	Araceae	23	0.35	$P < 0.01$
Thalia geniculata	Bent alligator flag	Marantaceae	17	0.31	$P < 0.01$
Alternanthera philoxeroides	Alligatorweed	Amaranthaceae	20	0.29	$P < 0.001$
Pontederia cordata	Pickerelweed	Pontederiaceae	15	0.22	$P < 0.001$
Saururus cernuus	Lizard's tail	Saururaceae	20	0.23	$P < 0.001$
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[b]Statistical significance is based on comparison with consumption of 'Romaine' lettuce. Plants that were consumed more readily than lettuce are indicated by a double asterisk (**); plants consumed about as readily as lettuce are indicated by ns; plants significantly less preferred than lettuce display probability values only.

the few cases where the hopper did not feed during the test. Association between leaf consumption ratings in the no-choice tests and those in the corresponding choice test was tested with a Spearman correlation analysis (Prism, GraphPad Software, Inc., San Diego). The plants used for this correlation analysis are shown in Fig. 1.

A final series of 'starvation' no-choice tests was conducted on several ornamental plant species that had very low A.I.s in the choice tests. The stems of 3 clippings from each of several plants were inserted into water, and the clippings were made available for 10 h to mixed populations of about 50 last instar nymphs and adults in cages in the laboratory. Grasshoppers were not provided with alternative food. The cages were as described under 'colony maintenance'. Consumption of these plants by lubber grasshoppers was assessed visually. The plants tested in this manner were: coontie, *Zamia integrifolia* L. (Cycadales: Zamiaceae); poinsettia, *Euphorbia pulcherrima* Willd. ex Klotzsch (Malpighiales: Euphorbiaceae); tropical sage, *Salvia coccinea* Buc'hoz ex Etl. (Lamiales: Lamiaceae); bottlebrush, *Callistemon* sp. (Myrtales: Myrtaceae); cymbidium orchid, *Cymbidium* sp. (Aspargales: Orchidaceae); angel's trumpet, *Brugsmania* sp.; bush daisy, *Euryops pectinatus* (L.) Cass. (Asterales: Asteraceae); firespike, *Odontonema strictum* Kuntze (Lamiales: Acanthaceae), weeping lantana, *Lantana montevidensis* (Spreng.) Briq. (Lamiales: Verbenaceae); lily of the Nile, *Agapanthus africanus* (L.) Hoffmanns (Aspargales: Amaryllidaceae); and scarlet rose mallow, *Hibiscus coccineus* (Medik.) Walter (Malvales: Malvaceae).

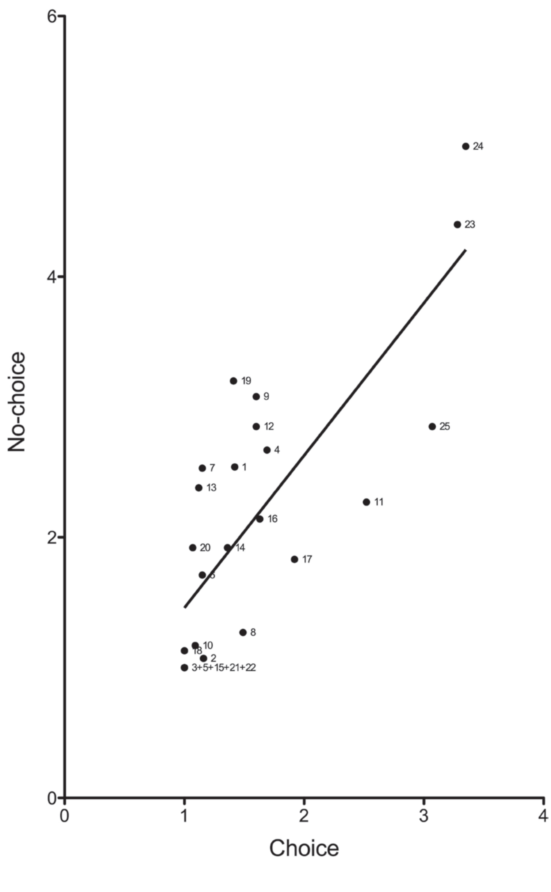

Fig. 1. Correlation of preference ratings for simultaneous two-choice ('Romaine' lettuce and test plant) and no-choice (test plant only) feeding tests. Spearman correlation coefficient = 0.7973; $P < 0.0001$. Plants tested were: 1, hophornbeam; 2, magnolia; 3, basswood; 4, American plum; 5, sweetgum; 6, pignut hickory; 7, live oak; 8, cherry laurel; 9, crinum; 10, daylily; 11, amaryllis; 12, Mexican petunia; 13, snapdragon; 14, pansy; 15, lily of the Nile; 16, canna; 17, society garlic; 18, African iris; 19, walking iris; 20, giant apostle's iris; 21, bush daisy; 22, tropical sage; 23, tread softly; 24, painted leaf; 25, Florida pusley.

Insecticide Interactions

Because host plant availability affects feeding behavior, I also assessed the interaction of host plants with toxicity to insecticide-containing bait. I hypothesized that bait would be more readily consumed in the absence of highly preferred plants. A granular bait formulation containing 5% carbaryl (Mole Cricket Bait, Southern Agricultural Insecticides, Inc., Palmetto, Florida) was tested on adult lubber grasshoppers in field cages after preliminary laboratory tests demonstrated susceptibility of the lubbers to the bait, and acceptance of the bait in the absence of other food. Three cages measuring 61 cm × 61 cm × 61 cm, were formed from 4-mesh galvanized hardware cloth. Cages lacked a bottom and were staked down over bare soil. Each cage contained 1 of 3 treatments: a control without plants or insecticide bait, 2 preferred plants plus insecticide bait, or 2 non-preferred plants plus insecticide bait. The preferred plants were butterfly weed, *Asclepias tuberosa* L. (Gentianales: Apocynaceae) and Mexican petunia, *Ruellia simplex* C. Wright (Lamiales: Acanthaceae) and the non-preferred plants were bush daisy, *Euryops pectinatus* and penta, *Pentas* sp. (Gentianales: Rubiaceae). Each cage with plants contained both of the preferred species or both of the non-preferred plants. The cages receiving bait also received 15 g of bait sprinkled on the soil. Ten adult lubber grasshoppers were introduced per cage. The lubber grasshoppers were allowed to feed for 24 h, then returned to the laboratory, maintained as noted earlier under 'colony maintenance', and monitored for 48 h. This assay, with all treatments conducted simultaneously, was replicated 4 times at 3 day intervals. Percent mortality was analyzed by randomized complete block ANOVA and Bonferroni's Multiple Comparison Test after transformation (arcsine square root of decimal % value plus 0.5) (GraphPad Software, Inc., San Diego, California); non-transformed means are presented.

Results

Lubber grasshoppers displayed varying responses to potential host plants, with both preferred and non-preferred plants occurring among each of the plant categories assessed (vegetables; ornamentals; vines, trees and shrubs; weeds; aquatics). Of the 104 plants tested, 21 (20%) were accepted as readily as 'Romaine' lettuce (Table 1). Surprisingly, 3 plant species (3%: the ornamental shrub oleander [Apocynaceae], the annual weed painted leaf [Euphorbiaceae], and the semiaquatic plant wild taro [Araceae]) were significantly more preferred than lettuce in choice tests. 'Romaine' lettuce is readily accepted and suitable for growth, so these plants are highly attractive. There was approximately a 3-fold difference (generally about 0.2 - 0.6) in A.I. among plants.

In the test of grasshopper response to foliage maturity, young foliage was significantly preferred for all 5 species of plants tested. The mean leaf consumption ratings for old and young foliage, number of insects successfully tested, and statistical significance of the comparison of leaf ages were 1.1 and 4.0, 13, and $P = 0.001$ for laurel cherry; 1.0 and 4.4, 15, and $P < 0.001$ for hophornbeam; 1.8 and 4.1, 15, and $P = 0.01$ for peregrina; 1.3 and 3.4, 11, and $P = 0.003$ for rose; and 1.4 and 4.3, 18, and $P < 0.001$ for hogbrier.

There was a highly significant correlation between preference ratings in choice and no-choice tests ($r = 0.797$, $P < 0.001$) (Fig. 1). As is often the case with correlations, however, the statistical significance is heavily dependent on the extreme (highest and lowest) values. Indeed, plants that were most preferred or least preferred in choice tests often elicited very similar responses by hoppers in no-choice tests. In contrast, some plants that were consumed but not preferred (preference ratings of 1-2 in choice tests) had considerably higher ratings in the no-choice tests, suggesting that the hoppers were adaptable and could eat less-preferred food in the absence of preferred food.

In the no-choice 'starvation' tests, plants with low (< 0.21) A.I. were offered to cages of grasshoppers for 10 h. Except for lily of the Nile, where some leaf injury (< 5%) occurred, little consumption of leaf blades was observed. The grasshoppers thoroughly investigated the plants and in most cases nibbled on the leaf tissue, but there was no significant foliar injury. An interesting anomaly occurred with angel's trumpet and firespike; although the grasshoppers did not eat leaf blade tissue, they fed on petioles, and even severed the petioles on some leaves of angel's trumpet, which has softer petiole tissue than firespike. Thus, a confounding factor of the choice tests is that leaf blade tissues were tested, whereas other tissues such as leaf petioles and blossoms might be more susceptible to injury.

Availability of attractive host plants in field cages significantly affected efficacy of insecticide-containing bait ($F = 48.4$; df = 2,6; $P < 0.001$). Mortality (mean, SD) in the control (insecticide-free) cages (2.5, 5.0%) was statistically the same as in the cages with preferred plants (7.5, 5.0%), whereas mortality was statistically greater (32.5, 9.6%) in cages with non-preferred host plants. Thus, the preferred host plants were attractive enough to reduce consumption of the bait, though non-preferred plants were not.

Discussion

The plants that were readily consumed by grasshoppers represent 14 plant families, confirming earlier reports of eastern lubber grasshopper being a broadly polyphagous herbivore. Complaints about damage to plants in Florida by eastern lubber grasshopper most often involve either 'lilies' or citrus. Formerly, the family Liliaceae was more broadly defined, and included many more plant genera. Many plants still called lilies are not true lilies, as they are not members of the family Liliaceae. Often, the affected plants are in the family Amaryllidaceae (formerly placed in the family Liliaceae), especially amaryllis and crinum. Indeed, in these studies the members of the family Amaryllidaceae were fairly well accepted, especially amaryllis. Quite a number of other ornamental plants appear to be susceptible to feeding, including some that increasingly are finding great favor in residential plantings, such as oleander, butterfly weed, and Mexican petunia. These may be appropriate for certain areas, but in locales where lubber grasshoppers historically are a problem, other less preferred ornamental plants may be more suitable. Though most plants were not as preferred as lettuce, a considerable number of both annuals and perennials were readily accepted, with annuals most commonly accepted in the vegetable and weed categories, and perennials in the ornamental and aquatic categories.

It is interesting to note that the foliage of some perennial trees, shrubs, and vines were consumed; though many are not highly preferred, they are available early in the year, before many annuals germinate. Thus, they may be important in maintaining populations immediately after hopper hatching (often February or March). The tendency of lubbers to climb trees perhaps enhances the suitability of this tall vegetation for these insects. The ability of eastern lubber grasshopper to eat weeds and semiaquatic plants in addition to trees, shrubs, and vines assures their persistence in Florida. In less rural areas, the presence of diverse ornamental plants in addition to some naturally occurring vegetation provides these resilient herbivores with a wide choice of food. Preference of vegetable crops displayed by lubbers in this study was similar to an earlier report (Barbara & Capinera 2003), although not all plants were included in both studies.

Plants that were not as readily accepted as 'Romaine' lettuce should not be viewed as inedible. Plants with an A.I. as low as 0.20 often had at least 50% of the insects consuming greater than 20% of the foliage in choice tests (preference rating of 2 or higher), so only plants with a lower A.I. might be considered unacceptable. Only 14 plants (14.5%) had such low (< 0.20) A.I.s. Thus, under duress, these insects can be expected to graze on a large number of plants, perhaps 85% of plants that they encounter. This could allow them to survive in most environments while searching for more favorable food resources.

In addition to insect hunger, there are other sources of variation that might affect the preference for, and suitability of, potential host plants. The condition of the plant is a major factor, and variables such as nutrient and water availability, prior herbivory, exposure of the plant to disease-causing organisms and plant growth regulators, and light exposure, can all affect insect feeding (Heinrichs 1988; Waring & Cobb 1992; Bernays & Chapman 1994: Zaller et al. 2003). An additional source of variation is prior experience; insects can learn from previous feeding on food plants and be positively or negatively affected by such experiences (Szentesi & Jermy 1990; Courtney & Kibota 1990; Capinera 1993). These aspects of herbivory were not considered in this study.

One of the most important variables affecting host selection is foliage maturity. In nature, most plants have foliage of varying ages, and there may be chemical or structural changes associated with age that influence insect feeding behavior. This was examined by offering lubber grasshoppers old and young foliage from five different plant species in choice tests. For all five species, young foliage was significantly preferred. Thus, it is quite clear that there is variability in acceptance even within a plant, and host acceptance by lubber grasshoppers cannot be entirely predicted. It also suggests that although some vegetation may be readily consumed early in the season, palatability may decline with time (foliage age) and the grasshoppers may change their feeding behavior accordingly.

Based on mouthpart structure and diet, grasshoppers are classified as graminivorous (grass-feeding), with grinding molars consisting of parallel ridges, and incisors typically fused into a scythe-like cutting edge; forbivorous (broad leaf plant-feeding), with a depressed molar region surrounded by raised teeth, and incisors equipped with large, interlocking teeth; and herbivorous (mixed-feeding), with characteristics intermediate between grass-feeding and forb-feeding mouthparts. Eastern lubber grasshopper is classified as forbivorous based on the morphology of their mouthparts (Smith & Capinera 2005). Although only a few graminoids were evaluated (corn, bahiagrass, St. Augustinegrass, smooth crabgrass, globe sedge), as expected from their mandibular morphology, grasses and grass-like plants were not very preferred hosts for lubber grasshoppers. The exception was smooth crabgrass, which has leaf blades not nearly as course as the other graminoids, and bears very thin vascular bundles, which may account for its acceptability. The presence of thick vascular bundles (Kranz leaf anatomy, C_4 plants) is sometimes cited as a resistance factor for grasses (Ehleringer & Monson 1993), and although some species are adapted to feed or even specialize on these plants, eastern lubber grasshopper is not well equipped to feed on most graminoids.

Whitman (1988), citing unpublished data, suggested that eastern lubber grasshopper displayed obligatory host switching, whereby favored plants became less favored following feeding. In the case of 'Romaine' lettuce, this was clearly not the case, as they remained very accepting of 'Romaine'. Earlier (Capinera 1993), I studied host selection in the polyphagous American grasshopper, *Schistocerca americana* (Drury). American grasshopper displays experience-induced changes in plant selection. They became more selective when provided with several alternate hosts, especially if previously provided with non-preferred hosts. Because Whitman's data are not published, it is difficult to know how obligatory the host switching by eastern lubber might be, or if it is related to availability of less favored hosts, as appears to be the case with American grasshopper. What is clear, however, is that lubbers explore and taste plants readily, rejecting some, eating measurable quantities of a great number of hosts, and eating large quantities of some preferred hosts. So although they are polyphagous, not all plants are readily eaten.

The highly significant correlation between preference ratings in choice and no-choice tests indicates that choice tests are strongly indicative of feeding behavior under different conditions of host availability. It also is independent validation of polyphagy in this species. Despite the frequent occurrence of monophagy or oligophagy among insect herbivores, there is considerable survival advantage in being able to adjust the diet, or adapt to differing availabilities of hosts, by being polyphagous. Polyphagous grasshoppers even are reported to display fitness increases when they have opportunity to mix diets; this is attributed to both nutritional benefits and dilution of potential toxins (Chapman & Sword 1997).

Despite the adaptability displayed by eastern lubber grasshoppers, certain plants are poorly accepted as food resources. Nearly all the ornamentals identified as being non-preferred in choice tests, and further evaluated in 'starvation' tests (i.e., coontie, poinsettia, tropical sage, bottlebrush, cymbidium orchid, bush daisy, firespike, weeping lantana, and scarlet rose mallow) would be suitable recommendations for planting where eastern lubber grasshopper was a threat. Lily of the Nile was an exception, exhibiting some injury in the starvation tests. Like most plants in the family Amaryllidaceae, it is fed upon by lubbers. So although not preferred relative to 'Romaine' lettuce, the starvation test indicated that it was susceptible to injury, and therefore cannot be recommended as a lubber-resistant ornamental plant. Obviously, it would be highly advisable to avoid growing ornamental plants with a high A.I. (e.g., oleander, amaryllis, butterfly weed, peregrina, Mexican petunia) in locations where lubbers habitually occur. Even plants with intermediate A.I. values (0.22-0.40) should probably be avoided. Also, due to the relatively polyphagous nature of this insect, interplanting more and less-resistant plants might not prove to be useful to reduce plant damage, because such interplanting strategies are mostly useful for insects with a narrow host range (Stanton 1983).

The only vegetable plant that seemed to be quite resistant to eastern lubber grasshopper was sweet corn. However, as noted previously, lubbers apparently feed on the silk from young ears of corn, so none of the vegetable plants tested are truly free from risk of injury. The susceptibility of vegetables is not surprising, as plant breeders often select for reduction of allelochemicals as part of the process of improving taste for humans, thus making the plants more susceptible to insect feeding injury. As demonstrated earlier (Barbara & Capinera 2003) and in these tests, however, solanaceous crops were less preferred.

Plants that were attractive to lubber grasshoppers interfered with the ability to control them by applying insecticide-treated bait. Though this is not surprising, the level of control attained even in the presence of non-preferred plants was somewhat disappointing because the maximum level of mortality was modest. Unlike some grasshoppers, eastern lubber grasshoppers climb plants readily, which takes them out of contact with bait scattered on the soil. Other grasshoppers are more geophilous, or inhabit areas with short vegetation, making baits more likely to be encountered and therefore more efficacious. These results suggest that for optimal lubber suppression, bait applications should be used in non-vegetated areas surrounding suitable hosts. Lubber grasshoppers, being flightless, would thereby be required to walk through bait treatments before attaining susceptible hosts, enhancing the likelihood of bait ingestion and insecticide-induced mortality.

The choice tests and no choice tests employed in these studies were effective at establishing a general hierarchy of acceptability in several plant categories. Although there are many sources of variation that might slightly modify the feeding of lubber grasshoppers on plants, these studies have produced considerable information on susceptibility of common plants to herbivory by eastern lubber grasshopper. They also demonstrate the potential interference of attractive host plants with bait formulations of insecticide. Host selection behavior regulates plant damage directly by affecting what plants are attacked, and indirectly by affecting consumption of insecticide-treated bait.

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