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Lubber grasshoppers, *Romalea microptera* (Beauvois), orient to plant odors in a wind tunnel

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Abstract

We tested the response of individual adult lubber grasshoppers in a wind tunnel to the odors of 3 plant species and to water vapor. Grasshoppers moved upwind to the odors of fresh-mashed narcissus and mashed Romaine lettuce, but not to water vapor, or in the absence of food odor. Males and females showed similar responses. Upwind movement tended to increase with the length of starvation (24, 48, or 72 h). The lack of upwind movement to water vapor implies that orientation toward the mashed plants was not simply an orientation to water vapor. These results support a growing data base that suggests that grasshoppers can use olfaction when foraging in the wild.

Key words

grasshopper, Romaleidae, *Romalea microptera*, olfaction, host search, wind tunnel, feeding behavior, starvation, food odors, lubber, anemotaxis

Introduction

How grasshoppers find their food has long been of interest to researchers (Uvarov 1977). Acridoids are thought to use visual, chemical, and tactile senses when searching for, identifying, biting, and accepting food (Chapman 1988, 1990). For example, many grasshoppers orient visually to emergent plants, certain colors, or to two-dimensional images drawn on paper; vertical contrasting stripes are especially attractive (Kennedy 1937, 1939; Williams 1954; Wallace 1958; Mulkern 1967, 1969; Bailey & Harris 1991; Szentesi *et al*. 1996).

Evidence that some grasshoppers can use olfaction to orient to food plants comes from many sources (Watson & Bratley 1940, Volkonsky 1942, Slifer 1955, Dadd 1963). In the field, grasshoppers sometimes move upwind toward odorous plants, synthetic plant chemicals, carrion, or baits (Boppré *et al*. 1984; Modder 1984; Bomar & Lockwood 1994b,c; Lockwood *et al*. 2001). For example, Chapman (1990) observed a marching band of *Chortoicetes terminifera* nymphs turn upwind toward fresh grass. Also, grasshopper antennae possess numerous olfactory sensilla (Kang & Chen 1997, Bland 1989, Blaney & Simmonds 1990, Chen & Kang 2000) that respond electrophysiologically to a range of plant odors, including the green leaf odors (Blust & Hopkins 1987, White & Chapman 1990a, Dickens *et al*. 1993, Kang *et al*. 1995, Hansson *et al*. 1996, Njagi & Torto 1996, Chen & Kang 2000). A smaller number of olfactory sensilla are found on grasshopper palps (Blaney 1977, Blaney & Simmonds 1990), and apparently also on all parts of the legs (Slifer 1954, 1956). In addition, rates of turning, antennation, palpation, and biting often increase in the presence of food odors (Kennedy & Moorhouse 1969, Mordue 1979, Chapman 1988, Chapman *et al*. 1988). Grasshoppers will also retreat from the odors of deterrent plants or chemicals (Kennedy & Moorhouse 1969, Chapman 1974). However, the most convincing evidence that grasshoppers use olfaction in food search comes from wind tunnel and olfactometer experiments, showing that grasshoppers can orient upwind in response to food odors. To date, 3 grasshopper species, *Schistocerca gregaria*, *S. americana*, and *Melanoplus sanguinipes*, have been shown, in the laboratory, to move upwind to the odors of damaged plants (Haskell *et al*. 1962, Kennedy & Moorhouse 1969, Moorhouse 1971, Hopkins & Young 1990, Lee *et al*. 1987, Njagi & Torto 1996, Szentesi *et al*. 1996). *Melanoplus sanguinipies* also oriented to various synthetic green-leaf volatiles (Hopkins & Young 1990, Szentesi *et al*. 1996), and *S. gregaria* were attracted to the odors of 3 ammonium salts (Haskell *et al*. 1962). In addition, numerous grasshopper species oriented in wind tunnels to the odors of carrion or fatty acids (Bomar & Lockwood 1994a, Lockwood *et al*. 2001). Movement upwind is assumed to be via odor-induced anemotaxis (Kennedy & Moorhouse 1969, Szentesi *et al*. 1996). However, there is evidence that grasshoppers can also orient to odors in still air (Slifer 1955, Szentesi 1996).

After contacting a potential food item, further identification and acceptance of that plant probably relies primarily on taste (Muralirangan *et al*. 1997, Chapman & Sword 1993). Indeed, nonvolatile plant chemicals can strongly influence grasshopper feeding (Blaney 1975, Mole & Joern 1994). Grasshopper antennae, mouthparts, and tarsi are richly supplied with contact chemosensilla (Chapman 1988, Blaney & Simmonds 1990, White & Chapman 1990b), and prior to biting, grasshoppers typically antennate and rapidly palpate the leaf surface, and touch it with their labrum (Blaney & Chapman 1970, Blaney & Simmonds 1990, Chapman 1990). This brings gustatory sensilla into contact with leaf chemicals, and grasshopper gustatory sensilla respond electrophysiologically to numerous compounds (Blaney 1975; Simpson *et al*. 1990, 1991).

Mechanoreceptors on the palps, labrum, and galeae function to locate and align the mandibles with the leaf edge (Sinoir 1969). Prior to biting, grasshoppers usually glide their heads over the leaf surface while rapidly palpating it, until the leaf edge is located (Chapman 1988). Continued feeding presumably relies on input from gustatory receptors on the mouthparts and in the buccal cavity (Blaney & Simmonds 1990), and mechanoreceptors continue to guide the food into and through the mouth.

The most controversial step in the above scenario is medium- to long-range olfactory orientation (Bailey & Harris 1991). This is because many species in the field appear not to use olfaction in host search. Some grasshoppers remain on their food plants for most of their lives, and therefore appear not to require strong olfactory senses. Other grasshoppers wander on the ground and sample (bite) nearly every plant they encounter, lending support to the idea that most diet selection in acridids begins, not with olfaction, but with random biting (Dadd 1963; Mulkern 1967; Sinoir 1969, 1970; Bland 1981). Few authors have rigorously demonstrated odor orientation to undamaged plants in either the lab or field, and others found little or no evidence of olfactory orientation (Williams 1954, Dadd 1963, Mulkern 1967, Bland 1981).

In this paper we report that adult Eastern Lubber grasshoppers, *Romalea microptera* (Beauvois), orient to the odors of damaged plants in a wind tunnel. This species is excellent for this type of study because it is polyphagous, large, flightless, docile, and easily reared in the laboratory (Matuszek & Whitman 2001). In addition, early reports suggest that *R. microptera* exhibits long-distance orientation to food odors (Watson & Bratley 1940). In 2 successive years, Watson (1941) noted large numbers of *R. microptera* nymphs marching in long columns toward fields planted with narcissus, a favored food. In the 1st year, narcissus was planted about 300 m to the northeast of the hatching site, and the nymphs marched to the northeast. In the 2nd year, narcissus was planted to the west, and the nymphs marched to the west, suggesting that group marching in this species was directed toward a food source.

Methods and Materials

Insects.— Eastern Lubber grasshoppers, *Romelea microptera* (Beauvois) were obtained from the Illinois State University colony, maintained in 1 m^3 wire-mesh cages at 23 to 34 °C and L:D 14:10 photoperiod, and fed Romaine lettuce, wheat bran, and oatmeal *ad libitum*, with supplements of green onion, green bean pods, and carrot leaves and roots, 3 times per week (Chladny & Whitman 1997, Matuszek & Whitman 2001). The colony was established from wild animals captured in Copeland, Florida in 1997. Experimental animals consisted of 9 to 35 d-old adults, and were provided with narcissus for 2 or 3 d prior to starvation.

Wind Tunnel.— We tested the walking response of individual grasshoppers to odors in a 183 × 30.5 × 15 cm wooden wind tunnel, with a transparent plexiglass lid (wind speed: 47 cm/s; air temperature: 30 to 32 °C; light source: eight 40 W fluorescent bulbs, 2 m above and parallel to the chamber). A double layer of black nylon screen at the upwind end of the tunnel allowed air flow, but blocked visual stimuli. During tests, odor sources were placed on the floor, in the center of a separate 15 × 30.5 × 15 cm odor chamber attached to the upwind end of the wind tunnel. A variable-speed fan sucked air through the odor chamber, then the tunnel, and then vented it through a duct outside the room. Preliminary tests using "fog" from dry ice placed in warm water, demonstrated a relatively steady, laminar and turbulence-free air flow, through the wind tunnel, and allowed us to determine wind speed. The floor of the wind tunnel was lined with white paper, which was changed with each new animal. Grid marks allowed us to measure the location of the test insect as it moved up or downwind.

Experiment 1: Response to food odors.— We tested individual adult *R. microptera* to each of 4 odor sources *vs* 3 starvation treatments, for a total of 12 odor × starvation combinations. Five to 10 different animals were used for each combination. Each animal was tested once. Odor sources included 50 g of Romaine lettuce (*Lactuca sativa* L. var. *longifolia*), green onion (*Allium cepa*), narcissus (*Narcissus pseudonarcissus*), and a no-odor (empty chamber) control. Lettuce, narcissus, and onion are favored foods for *R. microptera*. Starvation treatments included animals starved for 24, 48, or 72 h. Animals were starved by keeping them in a food and water-free container, held under similar environmental conditions as described above for the stock colony. During starvation, no cannibalism occurred.

Experiment 2: Response to water vapor.— We tested individual adult *R. microptera* to 2 odor sources *vs* 3 starvation treatments, for a total of 6 odor × starvation combinations. Six different animals were used for each combination. Odor sources used were the presence or absence of 50 g of H_2O. Starvation treatments included animals starved for 24, 48, or 72 h. Animals were starved as per Experiment 1.

Odor preparation.— In a separate room, immediately before the test, 50 g of fresh plant material (leaves of Romaine lettuce, or leaves, stems, and bulbs of green onion or narcissus) were chopped, macerated, and placed into a new clean 1-cm deep × 12-cm diameter plastic tray. For Experiment 2, 50 g of tap water were placed in a similar plastic tray. For no-odor controls, in both Experiments 1 & 2, we used empty clean trays.

Testing procedure.—For both Experiments 1 & 2, individual adult grasshoppers were placed on the floor in the exact center of the wind tunnel, facing the wall and perpendicular to the wind flow. We alternated between male and female grasshoppers for each run. After 15 min, we recorded the upwind (+) or downwind (-) distance moved by the grasshopper.

Statistical Analysis.— In both experiments we first used independent-measures t-tests to test for sexual differences. We then used a 2-way fixed-effect model of the GLM (general linear model) procedure for both Experiments 1 & 2, to analyze the effects of starvation time versus food type or water vapor on grasshopper movement in the wind tunnel. *Post-hoc* testing was conducted using the Ryan-Einot-Gabriel-Welsch (REGWQ) multiple range test. All statistical tests were conducted using SPSS version 9.0 (SPSS Inc.) or SAS (SAS Institute Inc.).

Results

Experiment 1: response to food odors

We pooled the results from males and females because we found no significant difference (two-independent sample t-test $t_{96} = 0.720$, $P>0.05$) in upwind distance traveled by males ($\bar{x} \pm s_{\bar{x}} = 21.7 \pm 6.7$ cm, N=49) *vs* females (29.1 ± 7.7 cm, N=49). We then used a 2-way fixed-effect GLM procedure to examine the effect of both food type and starvation time and to check for potential interactions between starvation time and food type. This analysis demonstrated that there were significant differences among the treatments ($F_{11,86}=2.66$, $P<0.05$), but no significant interaction between food type and starvation time ($F_{6,86}=1.22$, $P>0.05$). Food type demonstrated significant differences among the various treatment groups (food type $F_{3,86}=5.30$, $P<0.05$). *Post-hoc* analysis of the food type groups demonstrated 2 different REGWQ groupings. Significant differences were found in the upwind distance traveled by animals exposed to either Romaine

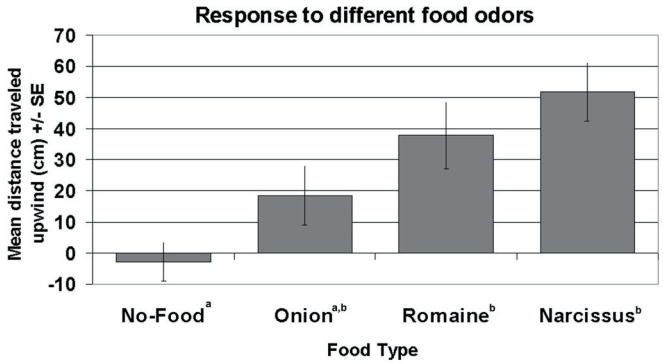

Fig 1. Direction and mean distance traveled ($\bar{x}$+$s_{\bar{x}}$) by adult *R. microptera* grasshoppers in a wind tunnel, when exposed to various food odors (starvation treatments combined). A GLM analysis demonstrated significant differences among treatments ($F_{3,86}$=5.30, P<0.05). *Post-hoc* analysis using REGWQ multiple range test demonstrated two groupings (designated a and b). A significant difference between the mean distance traveled upwind for the narcissus and romaine lettuce-treatments compared to the no-food odor group is clearly seen. The onion-treatment group is a member of both groupings.

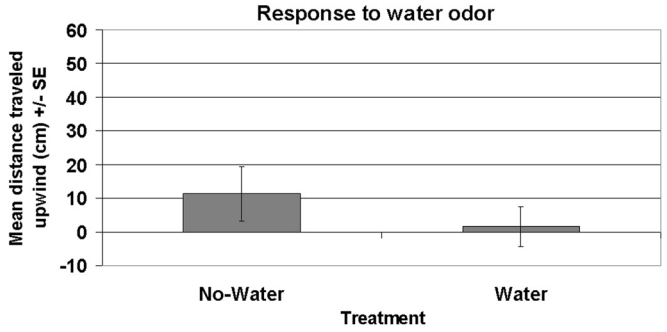

Fig 3. Mean distance($\bar{x}$ +$s_{\bar{x}}$) traveled upwind by adult *R. microptera* grasshoppers in a wind tunnel exposed to either the presence or absence of water vapor (starvation treatments combined). GLM analysis showed no significant difference ($F_{1,30}$=1.10, P>0.05) between the 2 groups.

lettuce or narcissus compared to the no-food controls (Fig 1). There was a strong trend, but no significant difference ($F_{2,86}$=2.41, P>0.05) in mean distance moved upwind between the 24-h starved (17 cm), 48-h starved, (38 cm) and 72-h starved (46 cm) groups (Fig. 2).

Experiment 2: response to water vapor

As in Experiment 1 we pooled the results from males and females, because we found no significant difference (t_{34} = -0.807, P>0.05) in distance traveled upwind by males ($\bar{x}$±$s_{\bar{x}}$ = 11.2 ± 7.2 cm, N=18) *vs* females (0.4 ± 11.3 cm, N=18). We conducted further tests using a two-way fixed effect GLM procedure to examine the effects of both water vapor and starvation time and to check for potential interactions between starvation time and water vapor. This analysis demonstrated that there were significant differences among the treatments ($F_{5,30}$=4.35, P<0.05), but no significant interaction between water vapor and starvation time ($F_{2,30}$=1.71, P>0.05). Further, there was no significant difference between the animals tested in the presence, vs the absence, of water vapor ($F_{1,30}$=1.10, P>0.05) (Fig. 3). However, there were significant differences among the 3 starvation treatments ($F_{2,30}$=8.62, P<0.05). *Post-hoc* analysis of starvation time (for combined water and no-water treatments) demonstrated 2 different REGWQ groupings. The first group demonstrated no significant difference in the mean distance traveled by the 24-h starved (-0.3 cm), and 48-h starved (-18.5 cm), individuals. The 2nd group consisted of the 72-h starved individuals, who traveled significantly further upwind (36.1 cm) than either the 24-h or 48-h starved groups (Fig. 4).

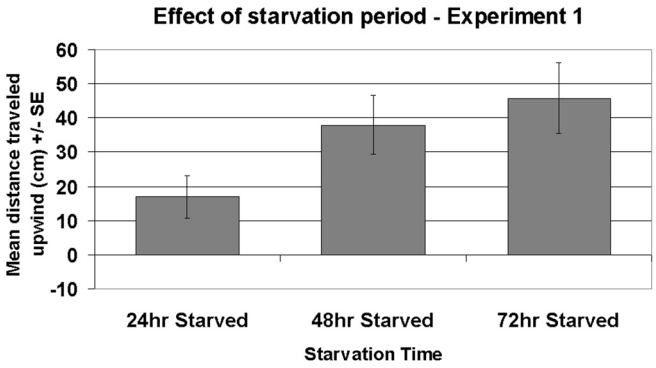

Fig 2. In Experiment 1, GLM analysis of the effect of starvation period on the mean distance traveled by *R. microptera* grasshoppers (food treatments combined) demonstrated a strong trend, but no significant differences among the treatments ($F_{2,86}$=2.41, P>0.05).

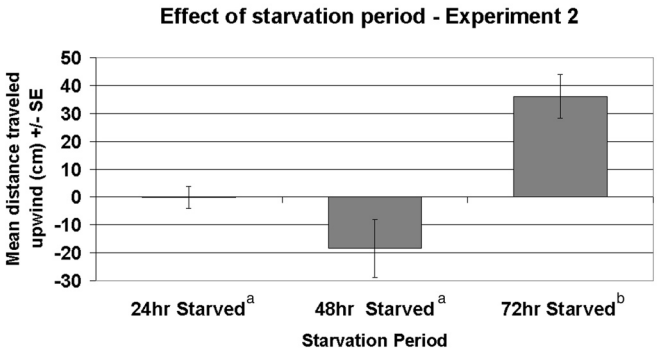

Fig 4. The effect of starvation period on upwind movement of *R. microptera* grasshoppers in a wind tunnel (response to water vapor and no water vapor combined). REGWQ multiple range test demonstrated 2 groupings (designated a & b) with the 72-h starved grasshoppers moving significantly further upwind than either the 24-h or 48-h starved insects.

Discussion

Our study demonstrates that adult lubber grasshoppers can respond to food odors by moving upwind. These results support previous work on the use of olfactory cues in the Acrididae (Chapman 1988). Among grasshoppers, *S. gregaria*, *S. americana*, and *M. sanguinipes* have been shown to move upwind to the odors of crushed or cut plants in wind tunnels or y-tube olfactometers (Kennedy & Moorhouse 1969, Lee *et al*. 1987, Hopkins & Young 1990, Njagi & Torto 1996, Szentesi *et al*. 1996). *M. sanguinipes* also moved upwind toward the odors of undamaged grasses and individual and mixed green leaf volatiles in the laboratory (Hopkins & Young 1990, Szentensi 1996), and *Zonocerus* species oriented in the field to plants releasing pyrrolizidine alkaloids (Boppré & Fischer 1994). In addition, many grasshoppers orient to the odors of carrion or volatile

fatty acids, in the field or in wind tunnels (Lockwood 1989a,b; Bomar & Lockwood 1994a,b,c; Whitman *et al*. 1994; Lockwood *et al*. 2001).

In our tests, odors from fresh mashed narcissus elicited greater orientation responses than did odors from mashed onion, suggesting that plants vary in their attractiveness. Electrophysiological studies demonstrate that grasshopper sensilla can discriminate among odors (Blaney & Simmonds 1990, Njagi & Torto 1996). Haskell *et al*. (1962) and Hopkins and Young (1990) also reported that different plants and individual volatile compounds elicited different levels of orientation in wind tunnels, implying that grasshoppers can discriminate among different plant odors from a distance.

Although grasshoppers possess hygroreceptors (Slifer 1955, Bland 1981, Blaney & Simmonds 1990), we were unable to demonstrate an upwind movement to water vapor alone, suggesting that orientation toward the mashed plants in our study was not simply a response to water vapor, but was in response to other plant volatiles. Although some authors have provided limited evidence that grasshoppers could orient toward or away from water vapors (Bodenheimer 1944; Slifer 1955; Riegert 1959, 1960; Lockwood 1989a), other have suggested otherwise (Kennedy 1937, Aziz 1957, Haskell *et al*. 1962, Bomar & Lockwood 1994a). Clearly, this area requires further study.

In our second experiment, upwind movement increased with starvation time, with 72-h starved individuals demonstrating a significant upwind movement when compared to either the 24-h, or 48-h starved groups. A similar nonsignificant trend was observed in Experiment 1 (Fig. 2). Previous authors have noted that hunger stimulates locomotion (Williams 1954, Kaufman 1968, Mulkern 1969, Bland 1981, Chapman 1988) or odor orientation (Haskell *et al*. 1962, Kennedy & Moorhouse 1969, Moorhouse 1971) in grasshoppers. However, we failed to find a significant odor × starvation interaction, suggesting that in *R. microptera*, increased starvation influenced response to wind, but not to odor.

Do grasshoppers commonly use olfaction when orienting to food plants in nature?— To date, only 4 grasshopper species from 3 subfamilies, have been shown to orient to plants via olfaction in the laboratory, and virtually all of these studies used cut, bruised, or macerated plants. One notable exception was Hopkins and Young (1990) who used both damaged, and whole undamaged plants. It is well known that damaged plants release different and substantially greater amounts of volatiles than undamaged plants, and thus these various laboratory studies may not accurately reflect what occurs in nature. Likewise, although grasshoppers will orient to baits, carrion, or volatile fatty acids in the field, this does not necessarily mean that they normally use olfaction to orient to plants. Observations of olfactory orientation to plants in nature are mostly anecdotal (Watson 1941, Chapman 1990). In contrast, *Zonocerus variegatus* and *Z. elegans* clearly use olfaction to orient to pyrrolizidine alkaloid-containing plants (Boppré *et al*. 1984, Modder 1984), but this orientation may be primarily for purposes of pharmacophagy instead of nutrition (Boppré & Fischer 1994). Hence, at this time, there is strong evidence that grasshoppers use olfaction in host search, but rigorous field confirmation is needed. It will be especially important to test monophagous and oligophagous species from a diversity of subfamilies, communities, and life-forms (geophilous, arboricoles, *etc.*) to odors from undamaged and slightly damaged plants, in the field. Despite these limitations, we believe that the evidence to date makes it highly likely that free-living grasshoppers incorporate at least short-range olfaction when searching for food plants.

In conclusion, our results reaffirm the idea that grasshoppers use not only visual, acoustic, thermal, gustatory, and tactile senses to monitor and orient to the environment, but also olfaction. The growing evidence of orientation to food odors by grasshoppers parallels an increasing awareness of the importance of intraspecific odor communication (pheromones) for both gregarious and solitary grasshoppers (Whitman 1990, Heifetz *et al*.1996, Pener & Yerushalmi 1998, Stauffer *et al*. 1998, Hassanali & Torto 1999, Niassy *et al*.1999, Torto *et al*. 1999, Despland 2001, Njagi & Torto 2002), suggesting that olfaction is more important to grasshoppers than previously realized.

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