

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

Authors: Helms, Jeff B., Booth, Carrie M., Rivera, Jessica, Siegler, Jason A., Wuellner, Shannon, et al.

Source: Journal of Orthoptera Research, 12(2) : 135-140

Published By: Orthopterists' Society

URL: [https://doi.org/10.1665/1082-6467\(2003\)012\[0135:LGRMBO\]2.0.CO;2](https://doi.org/10.1665/1082-6467(2003)012[0135:LGRMBO]2.0.CO;2)

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

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

JEFF B. HELMS, CARRIE M. BOOTH, JESSICA RIVERA, JASON A. SIEGLER, SHANNON WUELLNER, AND DOUGLAS W. WHITMAN

4120 Department of Biological Sciences, Illinois State University, Normal, IL 61790. E-mail: dwwhitm@ilstu.edu

## 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, anten-

tion, 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 sanguinipes* 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 (Murali-rangan *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, *Romelea 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 1<sup>st</sup> year, narcissus was planted about 300 m to the northeast of the hatching site, and the nymphs marched to the northeast. In the 2<sup>nd</sup> 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<sup>3</sup> 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<sub>2</sub>O. 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 ( $\bar{x} \pm s_x = 21.7 \pm 6.7$  cm,  $N = 49$ ) vs females ( $29.1 \pm 7.7$  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

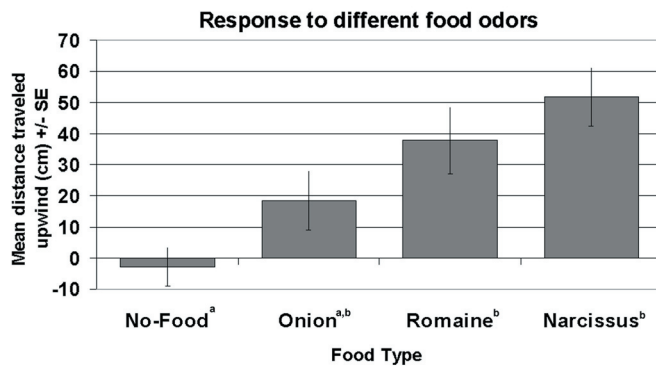


Fig 1. Direction and mean distance traveled ( $\bar{x} \pm s_x$ ) by adult *R. microptera* grasshoppers in a wind tunnel, when exposed to various food odors (starvation treatments combined). A GLM analysis demonstrated significant differences among treatments ( $F_{3,86}=5.30$ ,  $P<0.05$ ). *Post-hoc* 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.

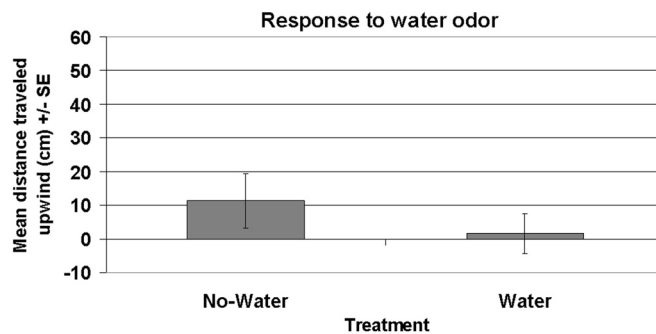


Fig 3. Mean distance ( $\bar{x} \pm s_x$ ) traveled upwind by adult *R. microptera* grasshoppers in a wind tunnel exposed to either the presence or absence of water vapor (starvation treatments combined). GLM analysis showed no significant difference ( $F_{1,30}=1.10$ ,  $P>0.05$ ) between the 2 groups.

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 ( $\bar{x} \pm s_x = 11.2 \pm 7.2$  cm,  $N=18$ ) vs females ( $0.4 \pm 11.3$  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 starva-



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 ( $F_{2,86}=2.41$ ,  $P>0.05$ ).

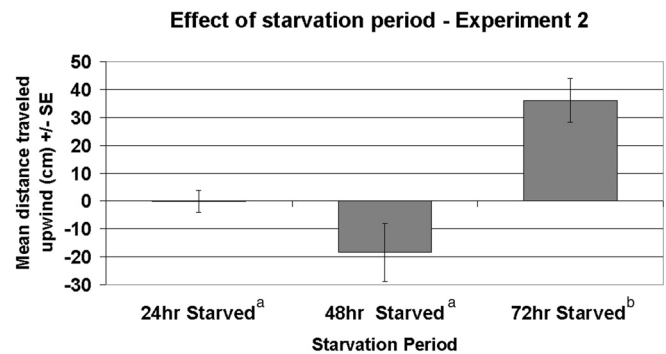


Fig 4. The effect of starvation period on upwind movement of *R. microptera* grasshoppers in a wind tunnel (response to water vapor and no water vapor combined). REGWQ multiple range test demonstrated 2 groupings (designated a & b) with the 72-h starved grasshoppers moving significantly further upwind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

tion 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).

#### 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, Szentesi 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  $\times$  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.

## Acknowledgements

This research was initiated and supported by Dr. Scott Sakaluk's Animal Behavior class and the Undergraduate Research Training (CRUI) Program at Illinois State University, and by NSF grant DBI-9978810.

## References

- Aziz S. A. 1957. The reactions of the Desert Locust, *Schistocerca gregaria* (Forsk.) (Orthoptera: Acrididae), to physical factors, with special reference to relative humidity. *Bulletin of Entomological Research* 48: 515-531.
- Bailey E.V., Harris M.O. 1991. Visual behaviors of the Migratory Grasshopper, *Melanoplus sanguinipes* F. (Orthoptera: Acrididae). *Journal of Insect Behavior* 4: 707-726.
- Bland R.G. 1981. Survival and food detection by first-instar *Melanoplus femurrubrum* (Orthoptera: Acrididae). *Great Lakes Entomologist* 14: 197-204.
- Bland R.G. 1989. Antennal sensilla of Acrididae (Orthoptera) in relation to subfamily and food preferences. *Annals Entomological Society of America* 82: 368-384.
- Blaney W.M. 1975. Behavioural and electrophysiological studies of taste discrimination by the maxillary palps of larvae of *Locusta migratoria* (L.). *Journal of Experimental Biology* 62: 555-569.
- Blaney W.M. 1977. The ultrastructure of an olfactory sensillum on the maxillary palps of *Locusta migratoria* (L.). *Cell and Tissue Research* 184: 397-409.
- Blaney W.M., Chapman R.F. 1970. The functions of the maxillary palps of Acrididae (Orthoptera). *Entomologia Experimentalis et Applicata* 13: 363-376.
- Blaney W.M., Simmonds M.S.J. 1990. The Chemoreceptors, pp.1-37. In: Chapman R.F., Joern A. (Eds) *Biology of Grasshoppers*. John Wiley and Sons, New York.
- Blust M.H., Hopkins T.L. 1987. Olfactory responses of a specialist and a generalist grasshopper to volatiles of *Artemisia ludoviciana* (Nutt.) (Asteraceae). *Journal of Chemical Ecology* 13: 1893-1902.
- Bodenheimer F.S. 1944. Studies on the ecology and control of the Moroccan Locust (*Dociostaurus maroccanus*) in 'Iraq. I. Results of a mission of the 'Iraq Department of Agriculture to N. 'Iraq in spring 1943. *Bull. Dir.-gen. Agric. 'Iraq* 29: 121.
- Bomar C.R., Lockwood J.A. 1994a. Olfactory basis of cannibalism in grasshoppers (Orthoptera: Acrididae): I. Laboratory assessment of attractants. *Journal of Chemical Ecology* 20: 2249-2260.
- Bomar C.R., Lockwood J.A. 1994b. Olfactory basis of cannibalism in grasshoppers (Orthoptera: Acrididae): II. Field Assessment of attractants. *Journal of Chemical Ecology* 20: 2261-2272.
- Bomar C.R., Lockwood J.A. 1994c. Olfactory basis of cannibalism in grasshoppers (Orthoptera: Acrididae): III. Use of attractants on carbyl wheat bran bait. *Journal of Chemical Ecology* 20: 2273-2281.
- Boppré M., Fischer O. W. 1994. *Zonocerus* and *Chromolaena* in West Africa, pp.107-126. In: Krall S., Wilps H. (Eds) *New Trends in Locust Control*. Deutsche Gesellschaft für Technische Zusammenarbeit, Eschborn.

- Boppré M., Seibt U., Wickler W. 1984. Pharmacophagy in grasshoppers? *Zonocerus* attracted to and ingesting pure pyrrolizidine alkaloids. *Entomologia Experimentalis et Applicata* 35: 115-117.
- Chapman R.F. 1974. The chemical inhibition of feeding by phytophagous insects: a review. *Bulletin of Entomological Research* 64: 339-363.
- Chapman R.F. 1988. Sensory aspects of host-plant recognition by Acridoidea: questions associated with the multiplicity of receptors and variability of response. *Journal of Insect Physiology* 34: 167-174.
- Chapman R.F. 1990. Food selection, pp. 39-72. In: Chapman R.F., Joern A. (Eds) *Biology of Grasshoppers*. John Wiley and Sons, New York.
- Chapman R.F., Sword G. 1993. The importance of palpation in food selection by a polyphagous grasshopper (Orthoptera: Acrididae). *Journal of Insect Behavior* 6: 79-91.
- Chapman R.F., Bernays E.A., Wyatt T. 1988. Chemical aspects of host-plant specificity in three *Larrea*-feeding grasshoppers. *Journal of Chemical Ecology* 14: 561-579.
- Chen H.H., Kang L. 2000. Olfactory responses of two species of grasshoppers to plant odours. *Entomologia Experimentalis et Applicata* 95: 129-134.
- Chladny T., Whitman D. 1997. A simple method to culture grasshopper eggs with long egg diapause. *Journal of Orthoptera Research* 6: 82.
- Dadd R.H. 1963. Feeding behaviour and nutrition in grasshoppers and locusts, pp. 47-109. In: Beament J.W.L., Treherne J.E., Wigglesworth V.B. (Eds) *Advances in Insect Physiology*. Academic Press, London.
- Despland E. 2001. Role of olfactory and visual cues in the attraction/repulsion responses to conspecifics by gregarious and solitary Desert Locusts. *Journal of Insect Behavior* 14: 35-46.
- Dickens J.C., Prestwich G.D., Ng C., Visser J.H. 1993. Selectively fluorinated analogs reveal differential olfactory reception and inactivation of green leaf volatiles in insects. *Journal of Chemical Ecology* 19: 1981-1991.
- Hansson B.S., Ochieng' S.A., Grosmaître X., Anton S., Njagi P.G.N. 1996. Physiological responses and central nervous projections of antennal olfactory receptor neurons in the adult Desert Locust, *Schistocerca gregaria* (Orthoptera: Acrididae). *Journal of Comparative Physiology A* 179: 157-167.
- Haskell P.T., Paskin M.W.J., Moorhouse J.E. 1962. Laboratory observations on factors affecting the movements of hoppers of the Desert Locust. *Journal of Insect Physiology* 8: 53-78.
- Hassanali A., Torto B. 1999. Grasshoppers and locusts. In: Hardy J., Minks A. (Eds) *Pheromones of Non-lepidopteran Insects Associated with Agricultural Plants*. CABI, London.
- Heifetz Y., Voet H., Applebaum S.W. 1996. Factors affecting behavioral phase transition in the Desert Locust, *Schistocerca gregaria* (Forsk.) (Orthoptera: Acrididae). *Journal of Chemical Ecology* 22: 1717-1734.
- Hopkins T.L., Young H. 1990. Attraction of the grasshopper, *Melanoplus sanguinipes*, to host plant odors and volatile components. *Entomologia Experimentalis et Applicata* 56: 249-258.
- Kang L., Chen H.H. 1997. Antennal sensilla of grasshoppers (Orthoptera: Acrididae) in relation to subfamily and biological habit. *Metaleptea* 17(2): 15.
- Kang L., Charlton R., Hopkins T.L. 1995. Olfactory response of the grasshopper *Melanoplus sanguinipes* to plant odours and volatile compounds. *Entomologia Sinica* 2: 136-144.
- Kaufmann T. 1968. A laboratory study of feeding habitats of *Melanoplus differentialis* in Maryland (Orthoptera: Acrididae). *Annals Entomological Society of America* 61: 173-180.
- Kennedy J.S. 1937. The humidity reactions of the African Migratory Locust, *Locusta migratoria migratorioides* R. and F., gregarious phase. *Journal of Experimental Biology* 14: 187-197.
- Kennedy J.S. 1939. The behaviour of the Desert Locust (*Schistocerca gregaria*) (Forsk.) (Orthoptera) in an outbreak center. *Transactions Royal Entomological Society London* 89: 385-542.
- Kennedy J.S., Moorhouse J.E. 1969. Laboratory observations on locust responses to wind-borne grass odour. *Entomologia Experimentalis et Applicata* 12: 487-503.
- Lee J.C., Bernays E.A., Wrubel R.P. 1987. Does learning play a role in host location and selection by grasshoppers, pp. 125-127. In: Labeyrie V., Fabres G., & Lachaise D. (Eds) *Insects-Plants. Proceedings of the 6th International Symposium on Insect-Plant Relationships (PAU 1986)*. Dr W. Junk, Dordrecht, Netherlands.
- Lockwood J.A. 1989a. Cannibalism in rangeland grasshoppers (Orthoptera: Acrididae): attraction to cadavers. *Journal Kansas Entomological Society* 61: 379-387.
- Lockwood J.A. 1989b. Ontogeny of cannibalism in rangeland grasshoppers (Orthoptera: Acrididae). *Journal Kansas Entomological Society* 62: 534-541.
- Lockwood J.A. 2001. Canola oil as a kairomonal attractant of rangeland grasshoppers: an economical liquid bait for insecticide formulation. *International Journal of Pest Management* 47: 185-194.
- Matuszek J.V., Whitman D.W. 2001. Captive rearing of Eastern Lubber Grasshoppers *Romalea microptera*. *Invertebrates in Captivity*, pp. 56-63.
- Modder W.W.D. 1984. The attraction of *Zonocerus variegatus* (L.) (Orthoptera: Pyrgomorphidae) to the weed *Chromolaena odorata* and associated feeding behaviour. *Bulletin of Entomological Research* 74: 239-247.
- Mole S., Joern A. 1994. Feeding behavior of graminivorous grasshoppers in response to host-plant extracts, alkaloids, and tannins. *Journal of Chemical Ecology* 20: 3097-3109.
- Moorhouse J.E. 1971. Experimental analysis of the locomotor behaviour of *Schistocerca gregaria* induced by odour. *Journal Insect Physiology* 17: 913-920.
- Mordue A.J. 1979. The role of the maxillary and labial palps in the feeding behaviour of *Schistocerca gregaria*. *Entomologia Experimentalis et Applicata* 25: 279-288.
- Mulkern G.B. 1967. Food selection by grasshoppers. *Annual Review of Entomology* 12: 59-78.
- Mulkern G.B. 1969. Behavioral influences on food selection in grasshoppers (Orthoptera: Acrididae). *Entomologia Experimentalis et Applicata* 12: 509-523.
- Muralirangan M.C., Muralirangan M., Partho P.D. 1997. Feeding behaviour and host selection strategies in Acridids, pp. 163-182. In: Gangwere S.K., Muralirangan M.C., Muralirangan M. (Eds) *The Bionomics of Grasshoppers, Katyids and Their Kin*. CAB International.
- Niassy A., Torto B., Njagi P.G.N., Hassanali A., Obeng-Ofori D., Ayertey J.N. 1999. Intra- and interspecific aggregation responses of *Locusta migratoria migratorioides* and *Schistocerca gregaria* and a comparison of their pheromone emissions. *Journal of Chemical Ecology* 25: 1029-1039.
- Njagi P.B.N., Torto B. 1996. Responses of nymphs of desert locust, *Schistocerca gregaria* to volatiles of plants used as rearing diet. *Chemoecology* 178: 172-178.
- Njagi P.G.N., Torto B. 2002. Evidence for a compound in Comstock-Kellogg glands modulating premating behavior in male Desert Locust, *Schistocerca gregaria*. *Journal of Chemical Ecology* 28: 1065-1074.
- Pener M.P., Yerushalmi Y. 1998. The physiology of locust phase polymorphism: an update. *Journal of Insect Physiology* 44: 365-377.
- Riegert P.W. 1959. The humidity reactions of grasshoppers. Humidity reactions of *Melanoplus bivittatus* (Say.) and *Camnula pellucida* (Scudd.): reactions of normal grasshoppers. *Canadian Entomologist* 91: 35-40.
- Riegert, P.W. 1960. The humidity reactions of *Melanoplus bivittatus* (Say.) (Orthoptera, Acrididae): antennal sensilla and hygro-reception. *Canadian Entomologist* 92: 561-570.
- Simpson C.L., Chyb S., Simpson S.J. 1990. Changes in chemoreceptor sensitivity in relation to dietary selection by adult *Locusta migratoria*. *Entomologia Experimentalis et Applicata* 56: 259-268.
- Simpson S.J., James S., Simmonds M.S.J., Blaney W.M. 1991. Variation in chemosensitivity and the control of dietary selection behaviour in the locust. *Appetite* 17: 141-154.
- Sinoir Y. 1969. Le rôle des palpes et du labre dans le comportement de nourriture chez la larve du criquet migrateur. *Ann. Nutr. Alim.* 23: 167-194.

- Sinoir Y. 1970. Quelques aspects du comportement de prise de nourriture chez la larve de *Locusta migratoria migratorioides* (Rand F). Annales Société Entomologique France (N.S.) 6: 391-405.
- Slifer E.H. 1954. The reaction of a grasshopper to an odorous material held near one of its feet (Orthoptera: Acrididae). The Proceedings Royal Entomological Society of London 29: 177-179.
- Slifer E.H. 1955. The detection of odors and water vapor by grasshoppers (Orthoptera: Acrididae) and some new evidence concerning the sense organs which may be involved. Journal of Experimental Zoology 130: 301-317.
- Slifer E.H. 1956. The response of a grasshopper, *Romalea microptera* (Beauvois) to strong odours following amputation of the metathoracic leg at different levels. Proceedings Royal Entomological Society London A 31: 95-98.
- Stauffer T.W., Hegrenes S.G., Whitman D.W. 1998. A laboratory study of oviposition site preferences in the Lubber Grasshopper, *Romalea guttata* (Houttuyn). Journal of Orthoptera Research 7: 217-221.
- Szentesi A., Hopkins T.L., Collins R.D. 1996. Orientation responses of the grasshopper, *Melanoplus sanguinipes*, to visual, olfactory, and wind stimuli and their combinations. Entomologia Experimentalis et Applicata 80: 539-549.
- Torto B., Assad Y.O.H., Njagi P.G.N., Hassanali A. 1999. Evidence for additional pheromonal components mediating oviposition aggregation in *Schistocerca gregaria*. Journal of Chemical Ecology 25: 835-845.
- Uvarov B. 1977. Grasshoppers and Locusts: A Handbook of General Acridology. Centre For Overseas Pest Research, London.
- Volkonsky M. 1942. Observations sur le comportement du criquet pelerin (*Schistocerca gregaria*) (Forsk.) dans le sahara Algero-nigérien. Arch. Inst. Pasteur Alger 20: 236-248.
- Wallace G.K. 1958. Some experiments on form perception in the nymphs of the Desert Locust, *Schistocerca gregaria* (Forsk.). Experimental Biology 35: 765-775.
- Watson J.R., Bratley H.E. 1940. Preliminary report on Lubberly Locust control. Florida Entomologist 23: 7-10.
- Watson J.R. 1941. Migrations and food preferences of the Lubberly Locust. Florida Entomologist 24: 40-42.
- White P.R., Chapman R.F. 1990a. Olfactory sensitivity of gomphocerine grasshoppers to the odours of host and non-host plants. Entomologia Experimentalis et Applicata 55: 205-212.
- White P.R., Chapman R.F. 1990b. Tarsal chemoreception in the polyphagous grasshopper *Schistocerca americana*: behavioural assays, sensilla distributions and electrophysiology. Physiological Entomology 15: 105-121.
- Whitman D.W. 1990. Grasshopper chemical communication, pp. 357-391. In: Chapman R.F., Joern A. (Eds) Biology of Grasshoppers. John Wiley, New York.
- Whitman D.W., Blum M.S., Slansky F. 1994. Carnivory in phytophagous insects, pp. 161-205. In: Ananthakrishnan T.N. (Ed) Functional Dynamics of Phytophagous Insects. Oxford and IBH Publishing CO. PVT. LTD., New Delhi.
- Williams L.H. 1954. The feeding habitats and food preferences of Acrididae and the factors which determine them. Transactions Royal Entomological Society of London 105: 423-454.