

Specialized parasitoid attracted to a pheromone of ants

DONALD H. FEENER, JR^{*}, LUCIA F. JACOBS[†] & JUSTIN O. SCHMIDT[‡]

^{*}*Department of Biology, University of Utah*

[†]*Department of Psychology, University of California, Berkeley*

[‡]*Carl Hayden Bee Center, Tucson, Arizona*

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Abstract. *Apocephalus paraponerae* (Diptera: Phoridae) parasitizes workers of the giant tropical ant, *Paraponera clavata* (Hymenoptera: Formicidae), in Central America. When female parasitoids locate fighting or injured workers of this species, they deposit one or more eggs in them and feed from wounds. Male parasitoids are also attracted to hosts for feeding and to locate females for mating. In a series of experiments it was demonstrated that males and females of this parasitoid were attracted to two products of the mandibular glands of *P. clavata*, 4-methyl-3-heptanone and 4-methyl-3-heptanol. These compounds are produced in the mandibular glands of numerous ant species and serve as alarm pheromones in some species. Phorid parasitoids of ants may routinely use host-produced pheromones to locate hosts, and behavioural interactions between ants and their parasitoids may have shaped the use of these pheromone systems by both interactants.

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Insect parasitoids use a wide assortment of cues to locate suitable hosts for oviposition (Vinson 1976, 1981, 1984; Godfray 1993). These cues may originate from a variety of sources, including the microhabitat or food plants of potential hosts, the activity of hosts in the microhabitat, or directly from the hosts themselves. Regardless of the origin of these cues and the variation in their information content, selection should favour the use of those cues that allow parasitoids to locate appropriate hosts reliably and accurately (Lewis et al. 1990; Vet et al. 1990). Signals used in intraspecific communication are especially reliable and stable, and it is therefore not surprising that some parasitoids have evolved the means to exploit the communication systems of their hosts successfully (Vinson 1984). The tachinid parasitoid *Trichopoda pennipes*, for example, is attracted to the sex pheromone of its pentatomid host, *Nezara viridula* (Mitchell & Mau 1971; Harris & Todd 1980). Because males produce and release this pherom-

one, they are more likely to be parasitized than females (Mitchell & Mau 1971). Parasitoids exploit other sensory modalities as well. Females of the tachinid *Ormia* (= *Euphasiopteryx*) *ochracea* are attracted to the mating songs of singing male crickets (Gryllidae) and ovolarviposit on or near these males and adjacent females (Cade 1975; Walker 1993). The acoustical organ used by this parasitoid to detect the song of its host is remarkably convergent in form and function with that of its host (Robert et al. 1992).

To a greater extent than perhaps any other group of organisms, social insects have evolved elaborate systems of intraspecific communication and offer abundant opportunities for exploitation by the arthropods associated with them (Hölldobler & Carlin 1987; Hölldobler & Wilson 1990). In ants the primary form of communication is chemical, although tactile, visual and acoustical modalities are used as well. Pheromones in ants serve a number of social functions that include nestmate recognition, alarm, and recruitment of nestmates to enemies, new food sources, and nest sites (Hölldobler & Wilson 1990). Many nest associates of ants use olfactory cues to locate and identify suitable colonies for colonization or to follow the recruitment trails of their hosts (Moser 1964; Akre & Rettenmeyer 1968; Hölldobler 1969,

Correspondence: D. H. Feener, Jr, Department of Biology, University of Utah, Salt Lake City, UT 84112, U.S.A. (email: feener@biology.utah.edu). L. F. Jacobs is at the Department of Psychology, University of California, Berkeley, CA 94720, U.S.A. J. O. Schmidt is at the Carl Hayden Bee Center, 2000 East Allen Road, Tucson, AZ 85719, U.S.A.

1971; Hölldobler & Wilson 1990). The actual substances used by these associates have been identified only rarely, however (Moser 1964). The host-location cues used by non-nest associates of ants, such as parasitoids in the dipteran family Phoridae, are completely unknown (Brown & Feener 1991a).

Recently Brown & Feener (1991a) found that the phorid parasitoid *Apocephalus paraponerae* was attracted to whole body extracts of its host, workers of the giant tropical ant, *Paraponera clavata*. Here we demonstrate that both males and females of *A. paraponerae* are specifically attracted to two products of the paired mandibular glands of workers. Mandibular gland products serve as alarm pheromones in many ant species, including close relatives of *P. clavata* in the subfamily Ponerinae (Duffield & Blum 1973; Blum 1981; Hermann et al. 1984; Hölldobler & Wilson 1990). These products apparently do not elicit alarm behaviour in *P. clavata*, however (Hermann et al. 1984). The results reported here suggest that the reduced response of *P. clavata* workers to the mandibular gland products of co-workers may be an evolved response that decreases the level of parasitism within colonies. In addition, we argue that the realized host range of *A. paraponerae* may largely depend on the taxonomic distribution of these mandibular gland products and the use of hosts as a preferred mating site.

Paraponera clavata is a prominent member of the Neotropical ant fauna, occurring in Atlantic lowland forest from Brazil to Nicaragua (Janzen & Carroll 1983). Colonies typically nest at the base of trees, and the large conspicuous workers forage in both understory and canopy foliage (Janzen & Carroll 1983; Bennett & Breed 1985; Harrison & Breed 1987; Belk et al. 1989). Foraging workers collect extra-floral nectar and invertebrate prey and can recruit nestmates to large food sources via pheromone trails (Young 1980; Breed et al. 1987; Fewell et al. 1992). Males and females of *A. paraponera* are attracted to the nest entrances of *P. clavata*, to disturbed lone workers or those engaged in fighting, and to injured or freshly killed workers; a female's chance of successful oviposition is greatest, however, in injured or freshly killed hosts (Brown & Feener 1991a). Females typically deposit more than one egg per host, and several females may simultaneously deposit eggs in a single host (Brown & Feener 1991b). Egg hatching and larval development

occurs very rapidly, with larvae leaving the host within 3–7 days after oviposition and crawling away from the host to pupariate in the surrounding leaf litter. Adult flies emerge 17–26 days after oviposition (Brown & Feener 1991b). The geographical range of *A. paraponerae* appears to be roughly co-extensive with the range of *P. clavata*.

METHODS

We conducted the study between 23 June and 2 July 1993 at the La Selva Biological Station, Puerto Viejo de la Sarapiquí, Heredia Province, Costa Rica (10°26'N, 83°59'W). The major habitat type at La Selva is lowland rain forest with a mean annual temperature of 26°C and 4 m of annual rainfall (Clark 1988). Both *P. clavata* and *A. paraponerae* are widely distributed at La Selva, occurring in a variety of habitats that range from second growth to deep primary forest. We worked in the Holdridge Arboretum, where colonies of *P. clavata* are common, easily observed and well studied (Breed & Harrison 1987; Brown & Feener 1991a; Fewell et al. 1992).

In the experiments described below, we used workers from a total of seven colonies, which were separated from each other by at least 25 m. We used individuals from a single colony in each experimental replicate, and used no colony more than once during an experiment.

In all experiments we compared the attractiveness of three different treatments. We defined attractiveness as the number of individuals of *A. paraponerae* attracted to each treatment during a 15-min period. Treatments consisted of dissected body parts of *P. clavata* workers or chemical compounds mixed in olive oil in a ratio of 1:10 by volume. Olive oil slows the oxidation of chemical compounds and the rate of release to the air. Treatments with chemical compounds consisted of 1 ml of mixture deposited on a small piece of cotton. During each experimental replication, we placed each treatment on the ground in a plastic petri dish at the vertex of an equilateral triangle, 0.5 m on a side. Each treatment was thus equidistant from the other two treatments, which also made it possible to collect all the flies that were attracted to each treatment. We collected flies with an aspirator as they arrived at a treatment and deposited them into a labelled vial

Table I. Number of *A. paraponerae* attracted to treatments consisting of body parts or extracts of the host, *P. clavata*

Experiment 1				
	Head	Thorax	Abdomen	Total
Male	76	11	0	87
Female	11	4	2	17
Total	87	15	2	104
Experiment 2				
	Mandible	Head without mandible	Abdomen	Total
Male	58	22	5	85
Female	51	22	10	83
Total	109	44	15	168
Experiment 3				
	Extract	Mandible	Body without head	Total
Male	16	21	6	43
Female	26	23	7	56
Total	42	44	13	99
Experiment 4				
	Ketone	Alcohol	Control	Total
Male	23	18	9	50
Female	7	12	4	23
Total	30	30	13	73

Extract in experiment 3 is a 10% solution of the mandibular gland products, 4-methyl-3-heptanone and 4-methyl-3-heptanol. The ketone and alcohol in experiment 4 are 4-methyl-3-heptanone and 4-methyl-3-heptanol, respectively.

containing 80% alcohol. In the laboratory we identified and sexed the flies with the aid of a dissecting microscope.

We compared attractiveness of different treatments to males and females of *A. paraponerae* using one-way and two-way contingency table analysis (Sokal & Rohlf 1981). Tables included all replicates of each experiment. We used one-way contingency tables to compare the response of parasitoids to different treatments. We constructed tables for each sex separately and for both sexes combined. We calculated expected cell frequencies assuming that parasitoids were equally attracted to all treatments. We used two-way contingency tables to detect differential responses of the sexes to treatments (a sex-by-treatment interaction). Expected cell frequencies in these tables were calculated from marginal totals (Sokal & Rohlf 1981). We determined overall statistical significance of these contingency tables by log-likelihood tests (*G*-tests). Single degree-of-freedom tests (*z*-tests) of specific hypotheses within these tables were performed by constructing contrasts in proportions (Kirby 1993). The Bonferroni procedure

was used to adjust α -values, such that $\alpha=0.05$ was maintained across all contrasts within an experiment.

RESULTS

Anatomical Source of Attractant

We located the anatomical source of the attractant by comparing the attractiveness of separate host body parts. In the first experiment we compared the attractiveness of head, thorax and abdomen (Table I). Because only two parasitoids were attracted to isolated abdomens during this experiment, we combined the 'abdomen' and 'thorax' treatments into a single 'body' treatment for statistical analysis. Male parasitoids were strongly attracted to the head of the host relative to the rest of the body ($G=54.55$, $df=1$, $P<0.0001$). Female parasitoids also appeared to favour the head of the host over the thorax and abdomen (Table I), but the difference was not statistically significant when thorax and abdomen were combined ($G=1.49$, $df=1$, $P>0.2$), probably because of the small number of females attracted in the course of this

experiment. A difference in the relative attractiveness of the head to male and female parasitoids was also indicated by the significant sex-by-treatment interaction ($G=4.52$, $df=1$, $P=0.03$). Results of this experiment suggest that the anatomical source of the attractant is in the head capsule of the host, and that male parasitoids are more directly attracted to the source than females.

The most likely source of an attractive odorant in the head capsule of *P. clavata* workers is the mandibular glands. In the second experiment, therefore, we compared the attractiveness of the mandibular glands, the head capsule without the mandibles and associated glands, and the thorax and abdomen combined (Table I). These three treatments differed significantly in the number of male and female parasitoids attracted ($G=54.62$, $df=2$, $P<0.0001$ for males; $G=31.95$, $df=2$, $P<0.0001$ for females). There was no significant sex-by-treatment interaction ($G=2.12$, $df=2$, $P=0.35$), indicating that there was no difference in the response of males and females to the treatments. As expected, the mandibles and their glands were more attractive to *A. paraponerae* than the head capsule without the mandibles ($z=7.72$, $P<0.0001$) and the body without the head ($z=13.04$, $P<0.0001$). The head without mandibles was significantly more attractive than the body without head ($z=4.28$, $P<0.0001$), presumably the result of contamination with mandibular gland products. These results suggest that the substance(s) attractive to parasitoids resides in the host's mandibular glands.

Identity of the Attractant

Having located the source of parasitoid attractant(s) in the mandibular glands of workers, we then compared the relative attractiveness of the two major products of the mandibular gland, 4-methyl-3-heptanone and 4-methyl-3-heptanol (Hermann et al. 1984). These products occur in the ratio 9:1 in the mandibular glands. We first compared the attractiveness of these compounds in their natural ratio to the attractiveness of whole, intact mandibular glands and the attractiveness of the headless body of the host as a control. We then compared the attractiveness of these compounds against one another and against a control consisting of the olive oil alone.

Both male and female parasitoids were differentially attracted to baits consisting of the

combined mandibular gland products, intact mandibular glands and decapitated bodies (Table I; $G=9.11$, $df=2$, $P=0.01$ for males; $G=13.01$, $df=2$, $P=0.001$ for females). The sexes did not respond differently to these three treatments ($G=0.86$, $df=2$, $P>0.6$). When the sexes were combined, both intact mandibular glands and mandibular gland products were significantly more attractive than the body alone ($z=5.19$, $P<0.0001$ for whole glands; $z=4.87$, $P<0.0001$ for gland products). Intact mandibular glands and mandibular gland products, however, did not differ in attractiveness ($z=0.29$, $P>0.7$), which strongly suggests that *A. paraponerae* is attracted to one or both of the compounds, 4-methyl-3-heptanone and 4-methyl-3-heptanol.

Response of parasitoids to the separate products of the mandibular glands and a control appeared to differ by sex (Table I). Males discriminated between the three treatments ($G=6.50$, $df=2$, $P=0.04$), but females apparently did not ($G=4.27$, $df=2$, $P=0.12$). The sex-by-treatment interaction was not significant, however ($G=1.9$, $df=2$, $P=0.4$), probably because of the low number of females attracted in the course of the experiment. When the sexes were combined, 4-methyl-3-heptanol and 4-methyl-3-heptanone were equally attractive to parasitoids (Table I), and both were significantly more attractive than the olive oil control ($z=3.19$, $P=0.001$ for both products). Based on the results of this experiment, both 4-methyl-3-heptanone and 4-methyl-3-heptanol serve as attractants for *A. paraponerae*.

DISCUSSION

Results of this study demonstrate that males and females of the parasitoid *A. paraponerae* are attracted to the two major products of the mandibular glands of the host ant species *P. clavata*. These products, 4-methyl-3-heptanone and 4-methyl-3-heptanol, appear to be released by disturbed, fighting, injured or freshly killed workers, but by themselves or in combination are not sufficient to elicit alarm behaviour in nestmates (Hermann et al. 1984). *Paraponera clavata* is unusual among ponerines in not showing alarm behaviour when exposed to mandibular gland products (Hermann et al. 1984). Hermann et al. (1984) argued that this lack of response to mandibular gland products is due to the absence

of well-developed interactions outside the nest, including group defence behaviour. Recent evidence, however, suggests that workers of *P. clavata* do have well-developed interactions outside the nest, at least during foraging (Breed et al. 1987; Harrison & Breed 1987; Fewell et al. 1992). As an alternative to the hypothesis of Hermann et al. (1984), we suggest that the reduced responsiveness to mandibular gland products observed in *P. clavata* compared to other ponerines is an evolved response to minimize parasitism of workers. Distinguishing between these hypotheses will require detailed comparative studies of alarm behaviour and the extent of parasitism in ponerine ants.

Brown & Feener (1991a) noted that males as well as females of *A. paraponerae* were attracted to freshly killed *P. clavata* workers and suggested that males used hosts as feeding or mating sites. Observations made during the present study confirmed both suggestions. Both males and females imbibed fluid from their injured hosts. Moreover, males vigorously courted females and mated with them while on the body of the host. The rapidity with which males of *A. paraponerae* discovered hosts and the large number of them attracted to a single host suggest that males are under intense selection to locate females for mating. From a male's perspective, a host releasing the mandibular gland products 4-methyl-3-heptanone and 4-methyl-3-heptanol is an excellent predictor of the eventual presence of receptive females. Males may learn to respond to these cues as they gain experience searching for mates, or differential mating success may have favoured genotypes strongly attracted to these compounds. Regardless of the underlying mechanism, it seems likely that hosts act as favoured mate encounter sites for *A. paraponerae* (Parker 1978; Thornhill & Alcock 1983). Such an encounter site convention may act to reinforce host specificity of these parasitoids, because males and females reciprocally reinforce one another's host-seeking behaviour (Parker 1978; Thornhill & Alcock 1983; Futuyma & Moreno 1988). Hosts serve as mate encounter sites in many other phorid parasitoids of ants (D. H. Feener, personal observations), and may partly explain the high level of host specificity found in these parasitoids.

Signals used by parasitoids for host location may broaden or constrain host range depending on the nature and distribution of the signal.

Parasitoids may fail to oviposit in perfectly suitable hosts in the absence of a required cue, or they may mistakenly oviposit in unsuitable hosts if the cue is present. In addition to *P. clavata*, *A. paraponerae* is also sometimes attracted to ants in the ponerine genera *Ectatomma* and *Pachycondyla* (Brown & Feener 1991b; B. V. Brown, personal communication; D. H. Feener, personal observations). Workers of at least one species of *Pachycondyla* produce 4-methyl-3-heptanone and 4-methyl-3-heptanol in their mandibular glands, and show typical alarm behaviour in the presence of these compounds (Duffield & Blum 1973). Mandibular gland products of *Ectatomma* have not yet been examined. In contrast, *A. paraponerae* is not attracted to ants in the ponerine genera *Gnamptogenys* and *Odontomachus* (B. V. Brown, personal communication; D. H. Feener, personal observations). The mandibular glands of workers in these genera contain a variety of compounds (Blum 1981; Hölldobler & Wilson 1990), but not 4-methyl-3-heptanone and 4-methyl-3-heptanol. It is not yet known whether species in any of these genera are suitable hosts for *A. paraponerae*, but we suspect that they are. We hypothesize that the realized host range of this parasitoid is determined by the taxonomic distribution of the olfactory cues it uses in host location and the mutual reinforcement for the use of these cues by males and females seeking mating and oviposition sites.

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REFERENCES

- Akre, R. D. & Rettenmeyer, C. W. 1968. Trail-following by guests of army ants (Hymenoptera: Formicidae). *J. Kans. entomol. Soc.*, **41**, 165–174.
- Belk, M. C., Black, H. L. & Jorgensen, C. D. 1989. Nest tree selectivity by the tropical ant, *Paraponera clavata*. *Biotropica*, **21**, 173–177.
- Bennett, B. & Breed, M. D. 1985. On the association between *Pentaclethra macroloba* (Mimooaceae) and *Paraponera clavata* (Hymenoptera: Formicidae) colonies. *Biotropica*, **17**, 253–255.

- Blum, M. S. 1981. *Chemical Defenses of Arthropods*. New York: Academic Press.
- Breed, M. D., Fewell, J. H., Moore, A. J. & Williams, K. R. 1987. Graded recruitment in a ponerine ant. *Behav. Ecol. Sociobiol.*, **20**, 407–411.
- Breed, M. D. & Harrison, J. M. 1987. Individually discriminable recruitment trails in a ponerine ant. *Insectes soc.*, **34**, 222–226.
- Brown, B. V. & Feener, D. H., Jr. 1991a. Behavior and host location cues of *Apocephalus paraponerae* (Diptera: Phoridae), a parasitoid of the giant tropical ant, *Paraponera clavata*. *Biotropica*, **23**, 182–187.
- Brown, B. V. & Feener, D. H., Jr. 1991b. Life history parameters and description of the larva of *Apocephalus paraponerae* (Diptera: Phoridae), a parasitoid of the giant tropical ant *Paraponera clavata* (Hymenoptera: Formicidae). *J. nat. Hist.*, **25**, 221–231.
- Cade, W. 1975. Acoustically orienting parasitoids: fly phonotaxis to cricket song. *Science*, **190**, 1312–1313.
- Clark, D. B. 1988. The search for solutions: research and education at the La Selva Station and their relation to ecodvelopment. In: *Tropical Rainforests: Diversity and Conservation* (Ed. by F. Almeda & C. M. Pringle), pp. 209–224. San Francisco: California Academy of Sciences.
- Duffield, R. M. & Blum, M. S. 1973. 4-methyl-3-heptanone: identification and function in *Neoponera villosa* (Hymenoptera: Formicidae). *Ann. entomol. Soc. Am.*, **66**, 1357.
- Fewell, J. H., Harrison, J. F., Stiller, T. M. & Breed, M. D. 1992. Distance effects on resource profitability and recruitment in the giant tropical ant, *Paraponera clavata*. *Oecologia (Berl.)*, **92**, 542–547.
- Futuyma, D. J. & Moreno, G. 1988. The evolution of ecological specialization. *A. Rev. Ecol. Syst.*, **19**, 207–233.
- Godfray, H. C. J. 1993. *Parasitoids: Behavioral and Evolutionary Ecology*. Princeton, New Jersey: Princeton University Press.
- Harris, V. E. & Todd, J. W. 1980. Male-mediated aggregation of male, female, and 5th-instar southern green stink bugs and concomitant attraction of a tachinid parasite, *Trichopoda pennipes*. *Entomol. exp. appl.*, **27**, 117–126.
- Harrison, J. M. & Breed, M. D. 1987. Temporal learning in the giant tropical ant, *Paraponera clavata*. *Physiol. Entomol.*, **12**, 317–320.
- Hermann, H. R., Blum, M. S., Wheeler, J. W., Overal, W. L., Schmidt, J. O. & Chao, J.-T. 1984. Comparative anatomy and chemistry of the venom apparatus and mandibular glands in *Dinoponera grandis* (Guérin) and *Paraponera clavata* (F.) (Hymenoptera: Formicidae: Ponerinae). *Ann. entomol. Soc. Am.*, **77**, 272–279.
- Hölldobler, B. 1969. Host finding by odor in the myrmecophilic beetle *Atemeles pubicollis* Bris. (Staphylinidae). *Science*, **166**, 757–758.
- Hölldobler, B. 1971. Communication between ants and their guests. *Scient. Am.*, **224**, 86–93.
- Hölldobler, B. & Carlin, N. F. 1987. Anonymity and specificity in the chemical communication signals of social insects. *J. comp. Physiol. A*, **161**, 567–581.
- Hölldobler, B. & Wilson, E. O. 1990. *The Ants*. Cambridge, Massachusetts: Harvard University Press.
- Janzen, D. H. & Carroll, C. R. 1983. *Paraponera clavata* (bala, giant tropical ant). In: *Costa Rican Natural History* (Ed. by D. H. Janzen), pp. 752–753. Chicago: University of Chicago Press.
- Kirby, K. N. 1993. *Advanced Data Analysis with SYSTAT*. New York: Van Nostrand Reinhold.
- Lewis, W. J., Vet, L. E. M., Tumlinson, J. H., van Lenteren, J. C. & Papaj, D. R. 1990. Variations in parasitoid foraging behavior: essential element of a sound biological control theory. *Environ. Entomol.*, **19**, 1183–1193.
- Mitchell, W. C. & Mau, R. F. L. 1971. Response of the female southern green stink bug and its parasite, *Trichopoda pennipes*, to male stink bug pheromone. *J. econ. Entomol.*, **64**, 856–859.
- Moser, J. C. 1964. Inquiline roach responds to trail-marking substance of leaf-cutting ants. *Science*, **143**, 1048–1049.
- Parker, G. A. 1978. Evolution of competitive mate searching. *A. Rev. Entomol.*, **23**, 173–196.
- Robert, D., Amoroso, J. & Hoy, R. R. 1992. The evolutionary convergence of hearing in a parasitoid fly and its cricket host. *Science*, **258**, 1135–1137.
- Sokal, R. R. & Rohlf, F. J. 1981. *Biometry*. 2nd edn. New York: W. H. Freeman.
- Thornhill, R. & Alcock, J. 1983. *The Evolution of Insect Mating Systems*. Cambridge, Massachusetts: Harvard University Press.
- Vet, L. E. M., Lewis, W. J., Papaj, D. R. & van Lenteren, J. C. 1990. A variable-response model for parasitoid foraging behavior. *J. Insect Behav.*, **3**, 471–489.
- Vinson, S. B. 1976. Host selection by insect parasitoids. *A. Rev. Entomol.*, **21**, 109–133.
- Vinson, S. B. 1981. Habitat location. In: *Semiochemicals: Their Role in Pest Control* (Ed. by D. A. Norlund, R. L. Jones & W. J. Lewis), pp. 51–78. New York: John Wiley.
- Vinson, S. B. 1984. How parasitoids locate their hosts: a case of insect espionage. In: *Insect Communication* (Ed. by T. Lewis), pp. 325–348. London: Academic Press.
- Walker, T. J. 1993. Phonotaxis in female *Ormia ochracea* (Diptera: Tachinidae), a parasitoid of field crickets. *J. Insect Behav.*, **6**, 389–410.
- Young, A. M. 1980. Notes on foraging of the giant tropical ant *Paraponera clavata* (Hymenoptera: Formicidae: Ponerinae). *J. Kans. entomol. Soc.*, **53**, 35–55.