

males in an olfactometer (Fig. 9.8) (Borges and Aldrich, 1994). The role, if any, of minor male-specific *Euschistus* volatiles in reproductive isolation is unknown.

Adults of all the phytophagous pentatomids described above retain small, but active anterior dorsal abdominal glands which, at most, are only slightly sexually dimorphic. The secretions from these glands in *N. viridula* are not particularly remarkable for bugs (2-hexenal, hexanal, hexanol, and tridecane) (Aldrich et al., 1978). However, *Euschistus* spp. emit species-specific blends from these glands that may actually be epideictic pheromones promoting spacing in natural habitats (Aldrich, unpublished). This is a form of communication that may be widespread in terrestrial Heteroptera, judging by the mushrooming number of previously unreported exocines identified from these tiny glands (later in this section and 3.3–5).

One phytophagous stink bug has finally been discovered whose males have gigantic dorsal abdominal glands homologous to the pheromone glands of *Podisus* (James and Warren, 1989). Gland extracts and live males of the Australian spined citrus bug, *Biprorulus bibax*, induced colonization of pesticide-sterilized citrus groves (Table 9.4) (James et al., 1991). The male-specific secretion is dominated by the novel hemiacetal, (1*E*)-3,4-bis(1'-butenyl)tetrahydro-2-furanol, and also includes lesser amounts of linalool, nerolidol, and farnesol isomers (Fig. 9.9) (Oliver et al., 1992). The insect produces only the (3*S*,4*R*)-stereoisomer (Mori et al., 1992). In a shadehouse bioassay permitting flight, synthetic (3*S*,4*R*,1'*E*)-3,4-bis(1'-butenyl)tetrahydro-2-furanol alone is biologically active, but a mixture mimicking the natural blend is significantly more attractive (James et al., 1994a). The unusual hemiacetal may be formed by enzymatic dimerization of 2-hexenal

Table 9.4. *Podisus* spp. and symbionts caught in pheromone-baited traps (Aldrich, 1988b).

	<i>P. neg-lectus</i>	<i>P. maculiventris</i>	<i>E. flava</i>	<i>H. aurata</i>	<i>F. crinita</i>	<i>T. calvus</i>	chloropids ^a & milichiids
H/T/B	0	308	279	41	18	2	163
H/L/B	83	0	19	30	0	5	12
H/L-T/B	41	151	211	19	4	10	41
Totals:	124	459	509	90	22	17	216

^aCompounds: H = (*E*)-2-hexenal, T = α -terpineol, L = linalool, B = benzyl alcohol; blend ratio = 1/20.17 by volume, 2 live- and 2 sticky-traps/treatment, March 27–May 29, 1985; one *P. maculiventris* and no symbionts in a control trap.

^bChloropidae [total # individuals]: *Olella* new sp. near *tigramma* (Loew) [116 females, 32 males], *O. cinerea* (Loew) [3], Genus undetermined new sp. ("puzzling" intermediate between *Aphanotrigonum* and *Conioscinella*) [6], and *Rhopalopteron carbonarium* (Loew) [6].

^cMilichiidae [total # individuals]: *Milichiella* sp. prob. *lacteipennis* Loew [15 females], and *Phyllomyza securicornis* (Fallen) [4 females].

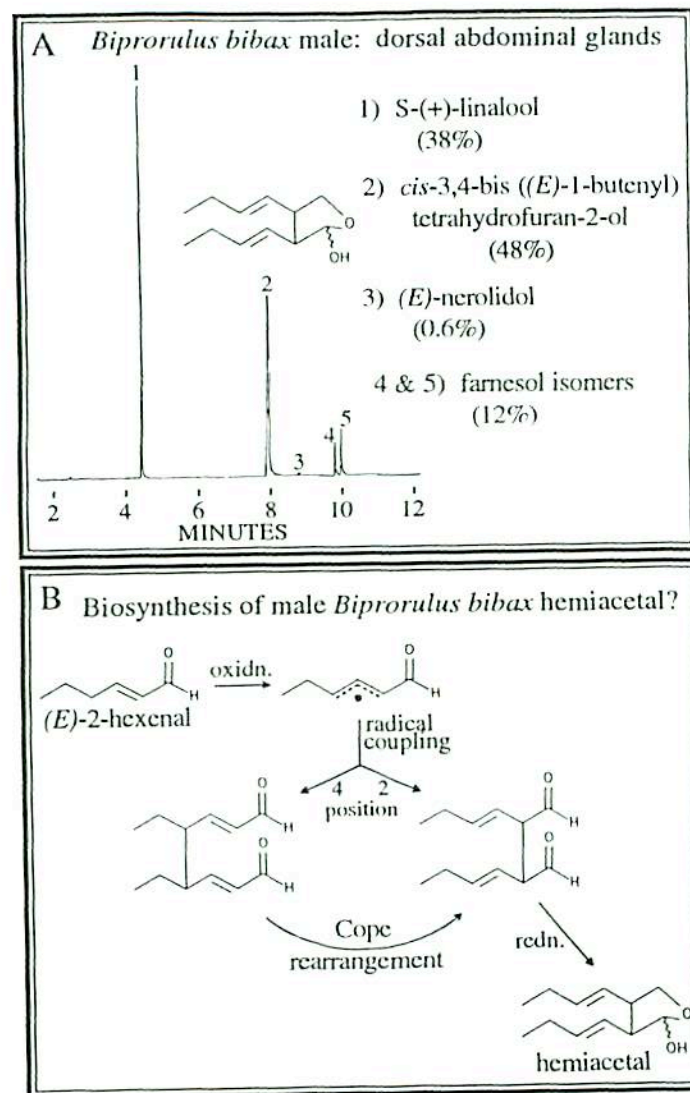


Figure 9.9. (A) Gas chromatogram and chemistry of the attractant pheromone of the spined citrus bug, *Biprorulus bibax*, produced by enlarged dorsal abdominal glands in males. (B) Hypothetical biosynthetic pathways leading from the ubiquitous heteropteran exocrine compound, (*E*)-2-hexenal, to the esoteric hemiacetal that is the key pheromone component.

ceous mirid, *Pilophorus perplexus*, butyl and hexyl butyrates dominate the secretions of both sexes, with octyl acetate and an isomer of (*E*)-2-hexenyl butyrate being female-specific minor constituents (Knight et al., 1984b). Female *Lygus lineolaris* and *L. elisus* produce large and equivalent amounts of (*E*)-2-hexenyl and hexyl butyrates, whereas males produce much less of the unsaturated ester (Aldrich et al., 1988; Gueldner and Parrott, 1978), but no such dimorphism occurs in *L. hesperus* (Aldrich et al., 1988). Terpenyl acetates occur in one mirid; headspace analyses of agitated *Harporocera thoracica* adults showed that female-derived volatiles are enriched with geranyl and neryl acetates (Hanssen and Jacob, 1982, 1983). Male *H. thoracica* may be heavily reliant on a pheromone to find mates because they only live for a week, whereas females are long-lived and disperse acrially before ovipositing (Southwood and Leston, 1959).

From the foregoing account, it seems that mirids are another taxon in which the metathoracic scent gland has acquired a sexual function, with esters being the key components (Knight et al., 1984b; Aldrich, 1988a). However, Graham (1988) presented convincing evidence that pheromone in *L. hesperus* originates near the ovipositor. Judging from the sex pheromone system of the mullein bug, females of other mirids may well attract males with synergistic blends involving trace components. Still, in view of the richness of mirid species (>10,000 species), it is perhaps unrealistic to expect that there is but one type of pheromone system for the group.

3.7. Enicocephalidae

Unique-headed bugs are rare predators, and are the only bugs to form aerial leks (Hickman and Hickman, 1981; Stys, 1981). Males of this group have hypertrophied exocrine glands (Section 2.2). In addition, the anterior dorsal abdominal gland remains active in both sexes of adults (Aldrich, 1988a). Individual genera form male-dominated, female-dominated, or mixed swarms, with male-dominated leks possibly most common (Stys, 1981). Vision is important for mate location as males often have larger eyes than females (Kritsky, 1977). Pheromones of enicocephalids are unknown.

4. Exploitation of Pheromones as Kairomones

Orientation to plant volatiles is often an important step in the host-selection process (Tumlinson et al., 1992; Vinson, 1984), and for some Heteroptera, such as lygaeine specialists on Asclepiadaceae [e.g., Anderson (1991)], this phase is dominant. However, research on Pentatomidae shows that pheromones are exploited as kairomones to a surprising extent. For example, in three seasons, over 17,800 parasitoids were attracted to pheromone-baited traps for *P. maculiventris*—more than five times the number of spined soldier bugs caught (Aldrich, 1985).

4.1. Diptera

Tachinidae, Ceratopogonidae, Milichiidae, and Chloropidae flies are masters of chemical espionage when it comes to pentatomid pheromones (Table 9.3) (Aldrich, 1985, 1988a, 1988b).

4.1.1. Tachinidae

In the eastern United States, two tachinid species, *Euclytia flava* and *Hemyda aurata*, are highly attracted to *P. maculiventris* and *P. neglectus* pheromones (Fig. 9.12; Table 9.3). Both species lay macroeggs, principally on adults. *Hemyda aurata* is a specialist on *Podisus*, whereas *E. flava* also parasitizes several phytophagous stink bugs (Aldrich, 1985). Feral male spined soldier bugs usually have about four times more tachinid eggs on them when collected than do females, and some 10% of overwintered *P. maculiventris* are parasitized by *H. aurata* (Aldrich et al., 1984a). Surprisingly, in eight years of pheromone-trapping, not a single *E. flava* has been reared from spring-collected soldier bugs (Aldrich et al., 1984a, unpublished).

Despite the total absence of *E. flava* from overwintered soldier bugs, this species is invariably the first to appear at pheromone traps in the spring (Fig. 9.12). *Euclytia flava* males frequently perch on or nearby pheromone-baited live traps, but both sexes of *E. flava* are susceptible to sticky traps. Spined soldier bugs apparently modify their behavior to avoid parasitization. For example, *P. maculiventris* captures in live traps abruptly decline, and counts remain low for the rest of the season, once *E. flava* appears, in marked contrast to captures in sticky traps (Fig. 9.12). Spring emergence of *P. maculiventris* is past its peak by the time *E. flava* is present and, likewise, these flies arrive late for the emergence of new-generation *P. maculiventris* adults (Fig. 9.12). In addition, *E. flava* seems to not waste its time on *P. neglectus* (Table 9.3) which, as a univoltine species confined to coniferous forests, is rare compared to *P. maculiventris*. In contrast, the specialist, *H. aurata*, is perfectly synchronized with the upsurge of new-generation adults at the end of May (Fig. 9.12), and attacks *P. neglectus* as well as *P. maculiventris* (Table 9.3).

Curiously, *H. aurata* will not enter live traps, and females greatly outnumber males in sticky traps, even though individuals captured from surrounding foliage are always male. On the other hand, the sexes of *E. flava* are equally susceptible to both types of trap when baited with pheromone containing racemic or (+)- α -terpineol. Nevertheless, these two tachinids behave similarly under natural conditions because in traps baited with live *P. maculiventris* males, the preponderance of *E. flava* are female (Aldrich et al., 1984a). High concentrations of synthetic pheromone appear to superstimulate *E. flava* males causing more of them to be trapped. *Euclytia flava* and *H. aurata* males are territorial around pheromone-calling spined soldier bugs—this interpretation is substantiated by

Aldrich
 1985
 (1982)

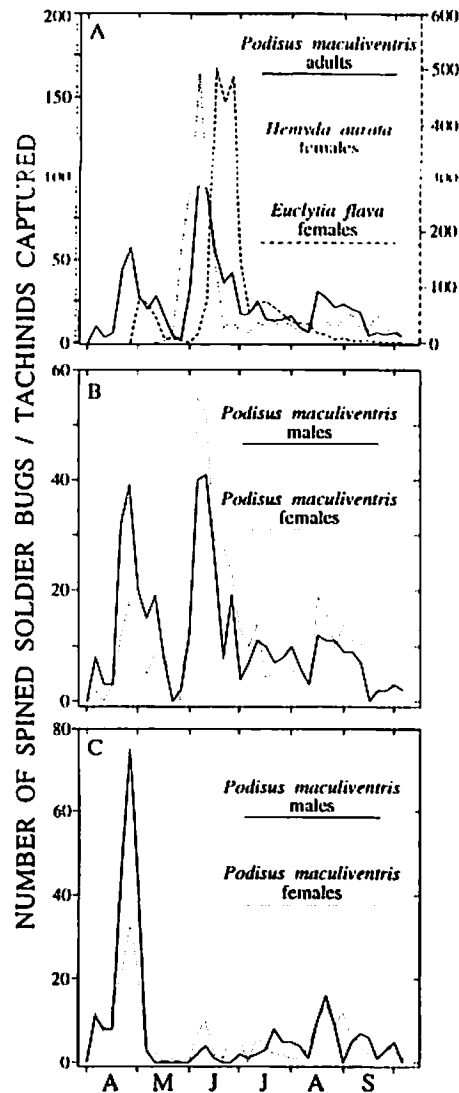


Figure 9.12. (A) Field attraction of *Podisus maculiventris* adults, and females of the tachinid parasitoids, *Euclytia flava* (scale on right) and *Hemyda aurata*, to seven sticky traps baited with synthetic *P. maculiventris* pheromone in 1983. *P. maculiventris* adults caught on or near seven sticky traps (B), or inside five live traps (C) baited with synthetic pheromone in 1983. Each point is the sum of catches for five consecutive days. All tests conducted at the Beltsville Agricultural Research Center (Aldrich et al., 1984a).

the fact that males of each tachinid are significantly larger than females (the opposite is true for *Podisus* spp.) (Aldrich, 1985).

By August, almost no *E. flava* are attracted to traps baited with *P. maculiventris* pheromone (Fig. 9.12); this generalist evidently shifts its attack to plant-feeding pentatomids toward the end of the growing season. For example, more than 90% of adult *Elasmotethus virgatus* (Acanthosomatidae) collected during July and August were parasitized by *E. flava* (Jones and McPherson, 1980), and *E. flava* is one of a complex of tachinids that use the pheromone of *Euschistus* spp. (Section 3.1) as a host-finding kairomone (Aldrich et al., 1991a). Reproduction, as evidenced by pheromone responsiveness (Fig. 9.13), is skewed toward the early season in *P. maculiventris* to take advantage of the onslaught of foliage-feeding larvae, while populations of phytophagous stink bugs build up later in the season as host plants mature. Whether parasitoids switch from responding to one kairomone to another with time, or simply choose the extant kairomone at a given point in time, is an open question.

Other tachinids "home-in" on attractant pheromones of phytophagous stink bugs [e.g., Moriya and Masakazu (1984)], with the best-known case being attraction of *Trichopoda* spp. to pheromone-releasing *N. viridula* males (Aldrich

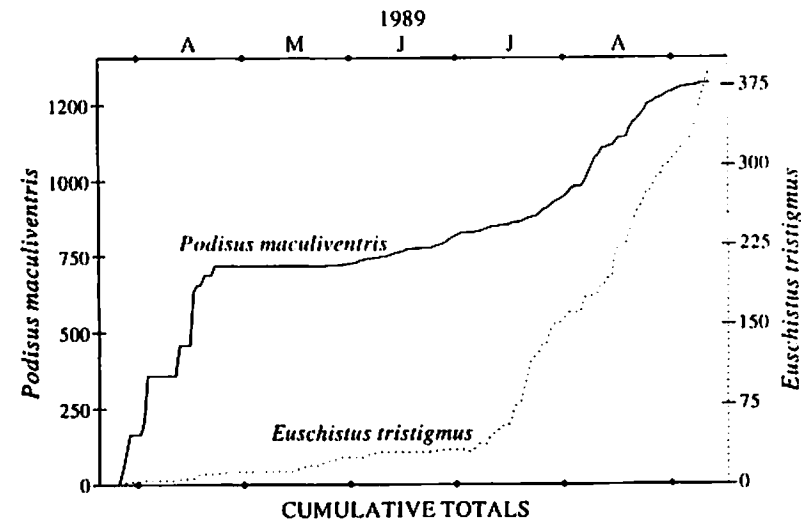


Figure 9.13. Cumulative catches of adult *Podisus maculiventris* (predaceous) and *Euschistus tristigmus* (phytophagous) in live traps baited with synthetic pheromones. Field test conducted at the Beltsville Agricultural Research Center; eight traps/each set; traps for *P. maculiventris* baited every three days with synthetic formulation (Table 3) (Aldrich et al., 1984a); traps for *E. tristigmus* baited every other day with 10 μ l of a 0.3 mg/ μ l solution of methyl (2*E*,4*Z*)-decadienoate in heptane.

et al., 1987, 1989). In fact, the preference of *T. pennipes* females for male bugs, and the specificity of *Trichopoda* spp. for certain geographically isolated *N. viridula* populations, were early indicators that males produce a pheromone and that pheromone strains of *N. viridula* exist (Aldrich et al., 1993a; Todd, 1989). In the Americas, at least six tachinid species have adapted to *N. viridula* and are now more abundant on this exotic host than native hosts (Jones, 1988; Hokkanen, 1986), including *T. giacomellii* in Argentina which parasitizes *N. viridula* in a density dependent fashion (Liljestrom and Bernstein, 1990). *Trichopoda pennipes* is the only Nearctic tachinid to accomplish this host shift. The chemical similarity of native *Acrosternum* spp. and *Nezara* pheromones (Section 3.1) almost certainly facilitated adoption of *N. viridula* by New World tachinids (Aldrich et al., 1989). Moreover, it is possible that pheromone strains of *N. viridula* evolved due to tachinid selection pressure.

Both predaceous and phytophagous pentatomid males risk tachinid attack when they advertise their presence with pheromones. Indeed, the risk of parasitization for *N. viridula* females (and probably females of other bugs) derives primarily from their association with males during courtship and copulation (McLain et al., 1990). *Podisus* males have pheromone glands capable of opening and closing (perhaps itself a response to parasite pressure), and a cheater male counterstrategy has apparently evolved whereby "silent" males respond to the pheromone of conspecifics in order to intercept females without incurring parasitization (Aldrich et al., 1984a; Aldrich, 1985). Parasite pressure is abated on the relatively uncommon *P. neglectus*, which may be the reason the noncalling strategy is depressed (Table 9.3) (Aldrich, 1988b). *Nezara viridula* males cannot precisely control pheromone emission, but in the 200 years since arriving in the United States, parasitism by *T. pennipes* seems to have shortened the preoviposition period and lengthened the fifth nymphal stage, thereby minimizing exposure to tachinids (Hokkanen, 1983).

4.1.2. Ceratopogonidae

Females of the ectoparasitic biting midge, *Forcipomyia crinita*, use the pheromone of *P. maculiventris* as a beacon to find potential hosts (Table 9.3) (Aldrich et al., 1984a). The flies swell with the blood like a mosquito while feeding through thick pronotal cuticle, apparently with little adverse affect on hosts. Bugs seem unaware of the presence of biting midges.

These ectoparasites are supreme generalists and eavesdroppers. A given ceratopogonid species often feeds on hosts from different orders (Wirth and Messersmith, 1971). Some ceratopogonids are attracted to stridulating wood-boring beetles (Wirth and Messersmith, 1971), while others go to cantharidin from blister beetles [ref. in Wirth (1980)]. Biting midges probably respond to different heteropteran pheromones such as that of *A. pennsylvanicum* (Section 3.1), a species also fed upon by *F. crinita* (Aldrich, unpublished).

4.1.3. Milichiidae and Chloropidae

Several species of small milichiid and chloropid flies routinely show up in traps baited with synthetic *P. maculiventris* pheromone (Table 9.4) (Aldrich, unpublished). By far the most frequently encountered is a new species of chloropid in the genus *Olcella* (Table 9.3).

Milichiids and chloropids, including an *Olcella* sp., fly to heteropterans trapped in spider webs when the bugs emit defensive secretion (Section 5.1). As such, there is some question whether attraction of these symbionts to synthetic *Podisus* pheromones is a nonadaptive by-product of the fact that the widespread allomonal component, (*E*)-2-hexenal, is also a *Podisus* pheromone component (Eisner et al., 1991). However, attraction to the soldier bug pheromone appears to be specific and adaptive because significantly more chloropids and milichiids are caught in traps baited with synthetic pheromone for *P. maculiventris* than for *P. neglectus* (Table 9.3; $\chi^2 = 30.7$, $p < 0.005$). The association of some of these symbionts with asopines probably qualifies as kleptoparasitism (Vollrath, 1984) since individuals of *Olcella* n. sp. feed on prey captured by *P. maculiventris* inside live traps (Aldrich, unpublished). *Phyllomyza securicornis* (Milichiidae) is another consistent visitor (Table 9.3), and members of this genus are sometimes phoretic (Robinson and Robinson, 1977). Other milichiids are associated with assassin bugs (Richards, 1953; Robinson and Robinson, 1977).

4.2. Hymenoptera

Females of the egg parasitoid, *Telonomus calvus* (Hymenoptera: Scelionidae), come to the vicinity of *P. maculiventris* or *P. neglectus* males releasing pheromone and wait for a female bug to arrive, whereupon one or more wasps become phoretic on the inseminated bug (Aldrich, 1985; Orr et al., 1986a) (Table 9.3). Host-finding by *T. calvus* is unusual because it entails first orienting to a male-produced pheromone and then recognizing female hosts, possibly by the sex-specific odor from the small dorsal abdominal glands of females (Aldrich et al., 1984b; Aldrich, 1985). *Telonomus calvus* requires *Podisus* eggs <12 hr old to successfully develop (Orr et al., 1986a). Phoresy ensures that fresh eggs are found, and enables *T. calvus* to compete with larger, nonphoretic species having less stringent host-egg age requirements, such as *T. podisi* (Orr et al., 1986b).

Telonomus podisi parasitizes eggs of several phytophagous pentatomids and, in agroecosystems, is the dominant egg parasitoid of the spined soldier bug (Orr et al., 1986b; Orr, 1988). In contrast to tachinids, attraction of *T. podisi*, *Trissolcus basalus*, *T. euschistii*, and other nonphoretic oligophagous scelionids, to sexual pheromones (Section 3.1) must be weak, if it occurs at all (Borges and Aldrich, unpublished; Mattiacci et al., 1993). Nonetheless, a few *T. podisi* females were caught in pheromone-baited traps for *P. maculiventris* (Aldrich, 1985). Even though all previously identified long-range kairomones attractive to parasitoids

are host sex pheromones (Tumlinson et al., 1992), other signals are more important for distant orientation by scelionid parasitoids of Heteroptera (Section 5.2).

5. Exploitation of Allomones as Kairomones

Data demonstrating exploitation of allomones by parasites or predators of Heteroptera are sparse or anecdotal, yet the phenomenon is undoubtedly real for certain Tachinidae, Milichiidae, and Chloropidae (Diptera); and probable for some Braconidae, Sphecidae, and Chrysididae (Hymenoptera). It is difficult to believe that heteropteran allomones are not exploited as kairomones by several species of tarsonemid mites (Prostigmata) which live in the metathoracic scent gland of Coreidae (Fain, 1979).

5.1. Diptera

Tachinids occasionally parasitize *Podisus* nymphs, suggesting that these flies use signals other than sex pheromones to find immature bugs. Since the contents of nymphal scent glands are shed with the exuviae (Section 2.1), an experiment was designed to determine if tachinids respond to the allomone of *P. maculiventris* nymphs (Aldrich, 1988b). Artificial nymphal stink gland secretion attracts both *E. flava* and *H. aurata*, albeit less so than artificial adult pheromone (Table 9.5). It is easy to imagine that responding to secretion leaching from exuviae is highly adaptive for tachinids because, in so doing, the flies find vulnerable hosts that will not ecdyse before their externally laid macroeggs have a chance to hatch.

Milichiid and chloropid flies, including species congeneric with those attracted to *Podisus* pheromones (Table 9.3), also profit by the emission of heteropteran allomones (Eisner et al., 1991; Sivinski and Stowe, 1980; Sivinski, 1984). Bugs

Table 9.5. Attraction of tachinid fly parasitoids to artificial *Podisus maculiventris* adult pheromone^a or nymphal allomone^b (Aldrich, 1988b).^c

Lure ^d	Tachinid Species			
	<i>Euclyptia flava</i>		<i>Hemysda aurata</i>	
	female	male	female	male
(E)-2-hexenal + benzyl alcohol + α-terpineol ^e	249	171	42	35
(E)-4-oxo-2-hexenal + linalool + tridecane ^e	88	8	11	18
linalool	0	0	0	2
unbaited	0	0	0	0

^cSix live-traps and 6 sticky-traps/treatment monitored daily, April 25–June 17, 1986

^dBlend ratios: (E)-2-hexenal/benzyl alcohol/α-terpineol as in Table 8.4, equal volumes of (E)-4-oxo-2-hexenal/linalool/tridecane; 10 μl/trap/day.

snared in webs of orb-weaving spiders. *Nephila clavipes*, spray scent gland secretion to little effect against the attacking spider, but flies zigzag their way from downwind toward the spider to share in the meal (Eisner et al., 1991). This scenario is repeated with *N. viridula* and other pentatomids and coreids producing (E)-2-hexenal; in fact, the synthetic compound alone is significantly attractive (Eisner et al., 1991). The nutritional cost of these symbionts to *Nephila* varies from being inconsequential to substantial, depending on age of the spider and the number of flies stealing food (Eisner et al., 1991). Thus, the relationship blurs the distinction between commensalism and kleptoparasitism (Vollrath, 1984).

Miltogrammine flies that attack sphecid wasps carrying heteropteran nymphs may prove to be an extremely convoluted example of message stealing (Section 5.2).

5.2. Hymenoptera

Peristenus and *Leiophron* spp. (Braconidae) parasitize the nymphs of many mirid species (Day 1987, personal communication), with certain hosts (Day and Saunders, 1990) and habitats (Snodgrass and Fayad, 1991) preferred over others. Circumstantial evidence suggests *Peristenus* spp. use the allomones of nymphs as kairomones. Females of both *P. pseudopallipes* (Lim and Stewart, 1976) and *P. stygius* (Condit and Cate, 1982) sometimes seize lygus bug exuviae and attempt to oviposit in them. Furthermore, *P. stygius* females attack Mirinae, Orthotylinae, and Phylinae species, but totally ignore species of Bryocorinae (Condit and Cate, 1982), a subfamily whose nymphs curiously lack external openings for their dorsal abdominal glands (Aryeetey and Kumar, 1973).

Another situation where allomones might undermine a bug's safety involves sand wasps (Sphecidae: Bembicini), some of which provision their nests exclusively with immature Heteroptera (Evans, 1966). Double espionage may occur here too by distantly related culprits: cuckoo wasps (Chrysididae), and miltogrammine flies (Sarcophagidae). Cuckoo wasps oviposit in heteropteran nymphs, before or after they are captured by stink bug hunters, as a means of ultimately parasitizing the sphecids (Carrillo S. and Caltagirone, 1970). Similarly, swarms of miltogrammine flies commonly larviposit on heteropteran prey as they are flown in the grasp of sphecids returning to their nests (Evans, 1966). The extent to which these wasps and flies rely on allomones to find prey is unknown.

Finally, a concrete case of chemical attraction by a parasitoid to a heteropteran allomone has been discovered for *Trissolcus basalis* (Scelionidae), the most important egg parasitoid of the southern green stink bug, *N. viridula*. Although *T. basalis* females are not appreciably drawn to the attractant pheromone of *N. viridula*, they are attracted to and stimulated by (E)-2-decenal, the main scent gland aldehyde of adult southern green stink bugs (Mattiacci et al., 1993). A second kairomone emanating from the glue used to fasten down egg masses

comes into play at short range for final recognition (Bin et al., 1993). Pentatomids can be grouped according to the chain length of scent gland alkenals (Table 9.1). Therefore, differential long-range attraction to stink bug allomones may explain why some scelionids exhibit clear host preferences in the field [e.g., Orr et al. (1986b); Foerster and de Queiroz (1990)], but are indiscriminate in the laboratory (Orr, 1988; Jones, 1988).

The discovery of long-range parasitoid attraction to the allomone of *Nezara* is puzzling because ovipositing hosts do not normally emit scent gland secretion nor is (*E*)-2-decenal detectable from eggs (Borges and Aldrich, 1992; Mattiacci et al., 1993). It is possible that low levels of scent gland compounds give bugs a body odor sensed by parasitoids. Alternatively, wasps could be attracted to stink bug allomones because they are indicative of dense populations of potential hosts. The distinction between individual versus population-level explanations for parasitoid response to heteropteran allomones is more than an esoteric argument. Intensive efforts are under way to mass produce and to manage wild *T. basalis* for augmentation and conservation. Synthetic oviposition stimulants are essential to artificially rearing *T. basalis* (and other parasitoids) (Volkoff et al., 1992), and attractant kairomones are potentially invaluable tools for husbandry of wild parasitoids (Aldrich, 1991; Tumlinson et al., 1992).

6. Conclusions

Challenges abound for chemical ecologists of the Heteroptera. There is a long list of identified exocines from a smattering of species in the order, and a short list of assigned functions for known molecules. Behavioral research on heteropteran semiochemicals needs to be emphasized, especially in the field. Pheromones of predaceous heteropterans, and kairomones for parasitoids of noxious heteropterans, are potentially powerful semiochemicals for agriculture in the 21st century.

Many true bugs are relatively large, with long-lived adults and, as such, are choice targets for parasites and predators. Protection provided by potent defensive secretions sometimes backfires by exposing Heteroptera to adapted enemies. Except for the Miridae, heteropteran pheromones identified to date come from males in species with large adults. Evolution of males as the attractive sex may, in part, be due to selection pressure from parasitoids. While, predaceous Heteroptera appear to be extremely reliant on pheromones to congregate, they suffer from a tremendous barrage of parasites homing in on their pheromones. Mechanisms allowing control over pheromone release evolved in some heteropteran species, enabling them to restrict exposure to parasitoids. This evolutionary step created the opportunity for males to cheat by retaining their pheromone and intercepting females responding to calling males.

Discovery of the first pheromones for moths renewed hope for biorational pest control. It is increasingly clear that both predators and parasites frequently rely

on semiochemicals to find prey or hosts, and each other. In the Heteroptera, unique opportunities exist for managing beneficials with innocuous chemicals, particularly for key predators conspicuously absent from this discussion: pirate bugs (Anthocoridae), damsel bugs (Nabidae), and bigeyed bugs (Geocorinae).

Acknowledgments

I dedicate this chapter to Thomas R. Yonke who sparked my interest in Heteroptera. I will always be grateful to Murray S. Blum and William S. Bowers for allowing me the freedom to pursue my fascination with bugs. I also thank those who have listened to me talk about bugs over the years, especially my wife Barbara.

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