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BIONOMICS OF THE NABIDAE

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INTRODUCTION

The family Nabidae, or damsel bugs, is a small family of the true bugs (Hemiptera: Heteroptera) containing 31 genera and approximately 380 species (70, 72). While all known species are terrestrial, some species are found in moist areas on the ground or at the edge of streams, ponds, and marshes (fresh and saline) (77, 107). Nabidae prey on a variety of small invertebrates, chiefly arthropods (7, 27, 61, 75). Some plant feeding by nabids may occur, but no development follows (141), and it is likely that moisture is the chief objective (25, 116). The predaceous habit, together with the widespread occurrence of some species in a variety of ecosystems, particularly agroecosystems, has attracted the attention of entomologists.

Much of the world literature on the Nabidae is taxonomic (e.g. 51, 65, 67, 70, 107, 113–115, 135, 139). There have been few summaries of the family, but there are two notable exceptions. Kerzhner (70) dealt primarily with the nabids of the USSR, but he summarized morphology, life stages, parasites, biogeography, fossils, and especially importantly, his own work on the classification and phylogeny of the Nabidae. Pericart (107) dealt with the Nabidae of the western Palearctic, treating each species in detail. Both books have extensive bibliographies. Although many taxa found outside the Holarctic region remain unknown to us biologically, much is now known about the Palearctic species and, to a lesser extent, the Nearctic species. As our knowledge grows, it is certain that we will discern considerable biotic diversity in the habits and habitats of the Nabidae.

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SYSTEMATICS

Position Within the Heteroptera

Leston et al (86) placed the family Nabidae within the superfamily Cimicoidea in the group Cimicomorpha, one of the two subdivisions of the Geocorisae, or land bugs. Earlier, Carayon (16) had compared internal genital organs and adult scent glands of the Nabidae and Reduviidae and concluded that these two families were not closely related as had been suggested by earlier workers (e.g. 114). China & Miller (23) considered the Nabidae close to the Velocipedidae, a taxon sometimes included as a subfamily of the Nabidae. Carayon (20) reviewed the status of the Nabidae and included both the Velocipedinae and the Medocostinae as subfamilies within the family.

Stys (146) considered the Medocostidae a distinct family. Stys & Kerzhner (147) considered both the Medocostidae and the Velocipedidae as families separate from the Nabidae. Kerzhner (70) placed the Nabidae within the Cimicoidea in the Cimicomorpha and retained the Velocipedinae and Medocostinae within the family. Pericart (106) removed the Velocipedinae from the Nabidae and elevated it to family status, but restored it to subfamily status in 1987. Schuh (121) reviewed the impact of cladistics on the classification of the Heteroptera. He presented the current classification of the Heteroptera and considered the cladistic work that had been done on various subgroups. Schuh placed the Nabidae in the Cimicomorpha, and he removed both the Velocipedinae and the Medocostinae and considered them distinct families. He reviewed the Cimicomorpha and presented a cladogram of the group, based in part upon the work of Kerzhner (70).

Family Classification

Stål (135) included three subfamilies in the Nabidae: Nabina, Coriscina, and Pachynomina. Carayon (16) considered the Pachynominae as a taxon closer to the Reduviidae and removed it from the Nabidae. He included the Scotomedinae (=Velocipedinae) as a subfamily of the Nabidae, following Blöte (11). Leston et al (86) concurred with Carayon. China & Miller (23) recognized five subfamilies in the Nabidae: Nabinae, Prostemminae, Arachnocorinae, Gorpinae, and Carthasinae. They considered the Velocipedidae and Pachynomidae as separate families. Carayon (20) included in the Nabidae four subfamilies, the Nabinae, Prostemmatinae, Velocipedinae, and Medocostinae, with the last subfamily intermediate between the Velocipedinae and the Nabinae. Kerzhner (70) recognized the same four subfamilies, with the subfamily Nabinae divided into four tribes (Nabini, Arachnocorini, Carthasini, and Gorpini). Schuh (121) questioned the status of the Velocipedinae and Medocostinae, and felt that additional information is needed to clarify their position within the Cimicomorpha. He considered them as distinct families of uncertain position. Pericart (107) retained the Velocipedinae and Medocostinae in the family Nabidae, along with the Nabinae and Prostemmatinae. Additional work is needed to clarify the uncertainties associated with the major subdivisions of the family.

The chromosomes of a number of species have been characterized (84, 89, 95, 96, 103). The type number for the family is $2n = 18$ ($16A + X + Y$) (84). While most species that have been investigated show this number, several have $2n = 20$, and *Aptus mirmicoides* is known to have $2n = 34$ (84). Supernumerary sex chromosomes have been reported from several species (95). There is considerable disagreement over the mechanisms involved in the increase in chromosome number (see e.g. 152, 153). Thomas (152) suggested that the most likely explanation of autosome increase is aneuploidy.

BIONOMICS

Movement

Southwood (130) defined two types of animal movement, trivial and migratory. Trivial movements occur within the habitat of the population, in contrast to migratory movements, which carry the animal away (140). Most available information on movement in the nabids is confined to members of the subfamily Nabinae (15, 30, 32, 39, 75, 100, 157).

TRIVIAL MOVEMENT Nabids are active shortly after hatching and begin feeding immediately, often on prey considerably larger than themselves (100). Koschel (75) found that early instar nymphs of *Himacerus apterus* lived on forbes and grasses but moved to shrubs and trees later in their life. This species is one of the few that occurs regularly in trees (7, 15, 27, 75, 134, 145), where they have been reported to feed on a variety of prey. Scudder (123) reported *Nabicula vanduzeei* from *Pinus contorta* in North America. On cotton, adult nabids were found higher on the plant than the nymphs (157). The adults also displayed a stronger preference for the fruits than the nymphs. Diel movement occurs in nabids in grasslands; bugs were found in the upper portions of grass at night (39). This movement might be a response to microclimatic conditions rather than a nocturnal activity, since there was no evidence that the nabids were not active during the day. Soybeans sampled by sweeping at different times during the day showed no significant change in numbers (32). Night activity has been documented for *Himacerus mirmicoides* in the United Kingdom (30).

FLIGHT Adult Nabidae are winged insects, and some species are able to move considerable distances (71). *Nabis capsiformis* is the most widespread species and is pantropical in distribution. There is ample evidence that

Nabidae fly. McPherson & Weber (93), working on the seasonal flight patterns of Hemiptera in North Carolina, collected six species of nabids from window traps set at different heights above the ground (1–7 m). The three common species included *Nabis americoferus, Nabis roseipennis,* and *N. capsiformis*. Johnson & Southwood (64) collected *Nabis ferus* 50 ft above the ground in aerial nets. Edwards (36), reporting on arthropods from alpine aeolian ecosystems, mentioned *Nabis alternatus* as one of the five species of insects taken on the summit of Mount Rainier, Washington. A number of genera of nabids are commmonly taken in light traps (128); specimens are always macropterous. Southwood (128) demonstrated Heteroptera showing high levels of flight activity were associated with temporary habitats. A high level of brachyptery may restrict nabids to stable habitats.

Some nabids may be found high in the air. Glick (43) reported *N. roseipennis* from 2000 ft and *Hoplistoscelis sordidus* from 1000 ft in Louisiana. Specimens of *N. capsiformis* have been collected many miles from the nearest land in the Atlantic, Pacific, and Indian Oceans (71). This species lives in open areas, including coastal habitats, and is a generalist in its feeding habits. Leston (83) considered the spread potential and island colonization of the Heteroptera. While the family Miridae ranked highest, the Nabidae ranked eighth of 15 families considered.

WING POLYMORPHISM Although many adult Nabidae have completely developed (macropterous) wings, a number of species show considerable wing polymorphism (microptery and brachyptery) (51, 81, 82, 137). Wing reduction may be slight [e.g. *Nabis brevis* (107)] or greatly reduced [e.g. *Phorticus brevipennis* (68)]. In a few instances the wing reduction is unilateral rather than bilateral (82), although this is an aberrant condition. Nonetheless, wing reduction of some sort is common in the Nabidae. Of the 32 species of nabids found in Europe and the Maghreb (107), 25 (78%) display some form of wing reduction in some individuals. Seven (22%) are known in the macropterous state only. Of the North American taxa in which sufficient specimens were available to constitute an adequate sample, nine (32%) species are known only from macropterous forms and 19 (68%) species have some individuals showing some type of wing reduction. These percentages will change as more information becomes available.

Brachyptery is common in insects on islands, including the Nabidae (66, 158). Zimmerman (158) discussed 26 species of nabids from the Hawaiian Islands, and at least an equal number remain to be described. All known species save one *(N. capsiformis)* are endemic to the islands. Twelve of the 26 species have at least partly modified wings. When the full study on this family has been completed in the Hawaiian Islands, we will have a much better understanding of the role of wing reduction in speciation and habitat utilization. Considerably more species of Nabidae are known from the Hawaiian Islands than from North America or Europe.

Southwood (129) proposed a hormonal theory to explain wing polymorphism in the Heteroptera. He suggested that shortness of wings is a character of the juvenile and is determined by the concentration of juvenile hormone. He considered the reduction of wings in mountain forms of *N. ferus* (136, 137) as a case of metathetely, whereas he cited the occurrence of only four nymphal instars in *Nabicula limbata* (most Heteroptera have five) as an example of prothetely. *Nabicula limbata* is most commonly found in the brachypterous state, but according to Stehlik (136) the long-winged form is found in cooler, mountainous circumstances (in contrast to the short-winged form of *N. ferus*).

The degree of wing development influences dispersal capabilities (53). Many of the species that show strong wing reduction are found in stable habitats, especially on the ground (51, 59, 68, 75, 145). Fully winged individuals (e.g. *N. capsiformis*) are often associated with temporary habitats, including agroecosystems (37, 56, 128, 130, 132). In some instances the brachypterous forms might be considered typical K-strategists and the macropterous species r-strategists. Even though ready dispersal is normally associated with r-strategists, Hamilton & May (48) suggested that dispersal may be expected not only from species occupying patchy environments, but also from those species found in uniform, permanent habitats. McPherson & Weber (93) reported the capture of *Pagasa fusca* in aerial samples taken at 1–3 m in North Carolina. This species is a ground inhabitant and is usually found in the brachypterous state.

Dispersal forms may occur in otherwise immobile populations. For example, Freeman (41) reported a very rare macropterous female of a mirid, *Mecomma dispar*, taken at 300 ft. Normally, only the male of this species is macropterous (134). I collected over 1000 specimens of a species of *Rhagovelia* (Veliidae) on a large river in Oregon. All were apterous except for a single male and female.

INTRODUCTIONS Commercial activities influence the movement of insects, and many species have been introduced into areas well removed from their native range (78). Since the time of Columbus the North American continent has received at least 1683 species, mostly from the western Palearctic region (87, 119, 125); remarkably few species have gone in the opposite direction (some notable exceptions include the grape phylloxera, fall webworm, and Colorado potato beetle). At least two species of introduced Nabidae have been found in North America: *Nabis brevis* and *Anaptus major*. Parshley (104) reported that *N. brevis* was found "on nursery stock imported from England." McAtee (91) objected to the inclusion of this record by Blatchley (10) on the grounds that many insects are detected by agricultural inspectors, but Parshley's citation does provide a specific record of a means of introduction. *Nabis brevis* is usually slightly brachypterous, lives in moist environments, deposits its eggs in grasses, and hibernates as an adult (107). The species does not appear to have become established in North America (57).

Anaptus major is established in North America and is known from California, Oregon, Washington, and British Columbia on the Pacific Coast and from New York and Pennsylvania in the eastern United States (5, 51, 57, 77, 122, 156). There is reasonable evidence that *A. major* was introduced (at least in the Pacific Northwest) via ballast materials brought from Europe, particularly the United Kingdom (77, 122). Southwood & Fewkes (133) reported this species as ". . . common on wastelands" in England. Specimens have been collected on disturbed sites around ports in Oregon, including areas close to known ballast dump sites (J. D. Lattin, personal observations). *Anaptus major* is fully winged, but its favored habitats are the ground and low vegetation (107). In Europe this species may occur along the water's edge together with *Nabicula lineata* (107, 134). A North American analog of *N. lineata*, *Nabicula propinqua*, was collected with *A. major* in a coastal salt marsh in Oregon (77).

Nabis ferus is a common, widespread species in the Palearctic region (70, 107). Before 1960 it was regarded as one of the most widespread species in North America and was thought to represent an introduction from the Old World (51). Then Carayon (19) demonstrated that the North American species was actually distinct from *N. ferus;* he named the species *N. americoferus*. It is curious that only *A. major* appears to have become established in North America, and that none of the many Old World species of the genus *Nabis* have done so. Careful attention to disturbed environments along both coasts of North America may yet disclose exotic species.

Nabis capsiformis is a special case. This pantropical species is the most widespread nabid known (52, 70, 71). It occurs only in the macropterous state (107). Kerzhner (71) reported it as the only species recovered from aerial samples taken over the Atlantic, Indian, and Pacific Oceans. Its status as an immigrant is less certain, but Zimmerman (158) considered it so in Hawaii. Collection of this species in Central Europe has been reported only occasionally (69, 107, 138). While human activities may have had little or no role in the dispersal of *N. capsiformis*, its ability to disperse is well established.

Mortality Factors

PARASITES A variety of organisms parasitize the eggs, nymphs, and adults of Nabidae. Carayon (17) found protozoans and bacteria in the digestive tract of nabids. He considered both groups to be parasitic. Further, he felt that the bacteria were not of the symbiotic type found in some other Heteroptera (usually phytophagous taxa). Morrill (98) reported the presence of nematode parasites in *N. alternatus* in the United States. Rubtsov (118) described a new species of Mermithidae parasitizing a nabid from the far eastern Soviet Union. Both parasitic (phytoseiid) and phoretic (trombidiiform) mites have been found associated with Nabidae (22, 51, 70, 100). Chant & Lindquist (22) described the otopheidominid (76) mite *Nabiseius duplicisetus* from the dorsal surface of the abdomen of a nabid from Chile. Mundinger (100) observed a trombidiid mite attached to a second-instar nymph of *N. roseipennis*. Pericart (107) reported that only about 1% of the specimens of nabids that he examined had ectoparasitic mites associated with them.

Two families of parasitic flies have been reported from nabids, the Chloropidae (70, 127) and Tachinidae (e.g. 70, 107). Smith (127) observed a species of *Elachipteron* on the back of a nabid, inserting its ovipositor beneath the hemelytra. Representatives of at least three genera of Tachinidae have been reported parasitizing Nabidae: *Leucostoma simplex*, a Holarctic species, has been reported from *A. mirmicoides* (58), *N. ferus* (35), *N. alternatus* (24, 98, 143, 150, 151, 154), *N. americoferus* (2, 55, 143), and *N. capsiformis* (143); *Hyalomya aldrichii*, a species that sometimes parasitizes the lygaeid *Geocoris* (24), was commonly encountered in *N. alternatus*, *N. americoferus*, and *N. capsiformis* in Arizona (143); and *Athrycia cinerea* was reared from *N. alternatus* or *N. americoferus* (2). Parasitization by the last species was 3% (2). This is quite low compared to parasitization rates recorded for *L. simplex* of 24% in nymphs and 44% in adults of *N. alternatus* and *N. americoferus* (24) and 6–28% in *N. alternatus* (98). Stoner et al (143) recorded parasitism varying from 0 to 48.2% in Arizona for both *L. simplex* and *H. aldrichii* on *N. alternatus* and *N. americoferus*. Percent parasitism was high in January, low in the spring, high in midsummer, low in the fall, and then high again in the winter. The nabids had two peaks in their populations, one in May and another in November. The degree of parasitism lagged behind these population peaks.

Hendrick & Stern (55) provided a detailed study of the development of *L. simplex* on *N. americoferus* in California. The egg is inserted through the intersegmental membrane of the abdomen, usually between the convexium and the sternites. Both nymphs and adult bugs are attacked. The eggs hatch three days later (at 80°F). There are three larval instars, and the total larval period is about 26 days. Although superparasitism did occur in the laboratory, it was rarely encountered in the field. The mature larva exits the bug quickly, usually through the dorsal surface between the terminal abdominal tergites. The host generally dies shortly thereafter. Pupation occurs quickly outside the host and lasts for about 9 days before the adult emerges.

Three families of Hymenoptera parasitize Nabidae: Scelionidae and Mymaridae on eggs and Braconidae on nymphs and adults. Southwood &

particularly birds. The size of nabids makes them potential prey for many invertebrate and vertebrate predators.

DISEASE The entomophagous fungus *Verticillium lecanii* has a wide geographical range and attacks a variety of insects although the fungus controls aphids, it is also a potent killer of *N. alternatus*, a major predator of aphids (50). The mortality rate of nabids dipped in a spore suspension was 82% (50).

Feeding

PLANTS Although the basic feeding strategies of Heteroptera have been the subject of some debate (25, 26, 148), the nabids are known to be largely predaceous. Some plant feeding has been observed, however (73, 116, 141). Ridgway & Jones (116) used cotton plants labeled with ^{32}P to demonstrate plant feeding. Their experiments indicated that nabids could be exposed to systemic insecticides applied to cotton plants. Indeed, systemic chemicals have reduced *Nabis* populations (80). Stoner (141) noted plant feeding but indicated that, while longevity increased, no nymphal growth occurred. The plant-feeding habits of *N. alternatus* have been implicated in the possible spread of a yeast *(Nematospora coryli)* found in *Brassica juncea* seed grown in Canada (13). The yeast was recovered from the nabids during the summer, but overwintering individuals tested negative; however, the test sample of bugs was small. The relationship between the bug and the yeast is not clear; the bug may acquire the yeast by feeding on insects that have fed on the plants.

ANIMAL PREY The mandibles of the Nabidae project ahead of the maxillae during penetration of animal prey (25). Both mouthparts have serrated tips. Arnold (3) observed nabids touching their potential prey with the foreleg several times prior to inserting the mouthparts; he proposed that this action accustomed the prey to the predator's touch.

Feeding is essential to growth and development, but the insect is able to survive short periods without food (75). At 17°C, the average survival time without food for nymphs of *H. apterus* was 15.9 days (75); younger nymphs died earlier than older nymphs. Most nabids overwinter in the adult stage and thus are able to go long periods without food.

Most of the prey of Nabidae are small invertebrates, chiefly insects (15, 70, 107). Collyer (27) reported *H. apterus*, a tree-inhabiting nabid, as an occasional predator of the red spider mite in orchards. The same nabid is a known predator of many insects in trees (75, 145). Most types of insect prey of nabids are plant-feeding species, but nabids sometimes attack predaceous insects, including members of their own species (63, 75). *Nabis alternatus* feeds on the lygaeid *Geocoris punctipes*, an important predator in some agroecosystems (4). Several genera within the nabid subfamily Prostemmatinae (e.g. *Prostemma, Alloeorhynchus,* and *Pagasa*) are known predators of other Lygaeidae, particularly members of the Blissinae, Geocorinae, and Rhyparochrominae (20, 42, 51, 70, 107, 112). These particular nabids and lygaeids live on the ground. Froeschner (42) and Reinert (112) reported two *Pagasa* species feeding on two different species of chinch bugs, both pests of considerable importance. A number of nabid species are predators of Miridae, and especially the genus *Lygus* (108, 109, 149, 155). Smaller nymphal nabids can handle smaller prey; the larger damsel bugs can handle all life stages of *Lygus*. Immunological techniques have been used to demonstrate that *N. americoferus* (like *N. ferus*) is a predator of *Lygus* spp. (155).

Nabids are confirmed predators of leafhoppers in all stages, including the beet leafhopper and the potato leafhopper (40, 74, 90). Nabids also prey upon aphids of many different species, including a number of species of economic importance (9, 21, 47, 63, 79, 111, 117). The polyphagous feeding habits of the nabids make them less effective than species-specific predators against specific prey species.

Among the Coleoptera, species of the Chrysomelidae have been reported as prey for nabids, including the Colorado potato beetle (38, 44, 94, 105). Two nabid species were considered major predators on two species of goldenrod leaf beetles (94). Eggs and larvae of Lepidoptera constitute common prey for many Nabidae, with feeding usually concentrated on the smaller stages (31, 92, 120, 126). Several native nabids attack the introduced *Hyphantria curea* in the Soviet Union (7). One of these, *H. apterus* (F.), one of the few tree-inhabiting nabids, was reported as a predator of the gypsy moth *(Lymantria dispar)* in the Ukraine (29) and on a variety of geometrid larvae in Poland (145). As was the case with other prey, younger stages of nabids were able to handle smaller prey, and the larger damsel bugs attacked most prey sizes.

Polyhedral inclusion bodies of a nuclear polyhedrosis virus of the moth *Heliothis punctigera* were found in the feces of *Nabis tasmanicus,* one of the predators of *H. punctigera* in Australia (6). A bioassay showed no loss of infectivity during the passage through the nabid's gut. Cooper (28) reported that 39% of field-collected *N. tasmanicus* adults contained polyhedra in their feces. He considered this predator and a predatory pentatomid as potential agents for disseminating infective polyhedra in the field.

Functional Role in Ecosystems

NATURAL ECOSYSTEMS The Nabidae are members of a guild of arthropod predators found in different terrestrial ecosystems. They are often associated with representatives of several other predaceous families of Heteroptera such as Anthocoridae, Lygaeidae (*Geocoris* spp.), Miridae (Deraeocorinae and others), Pentatomidae (Asopinae), and Reduviidae. Although the Nabidae is a small family of about 380 species (72) displaying rather modest ecological diversity, there is some apparent ordering of habitat preferences. Southwood (131) discussed the influence of the habitat on ecological strategies and provided a good discussion of the r-K selection spectrum. Most known nabids seem to be K strategists, particularly in regard to dispersal, since a high percentage show some sort of wing reduction. Further, some species display restricted niche breadth. For example, the Prostemmatinae are found on the ground and in the litter layer, usually closely associated with their prey, ground-inhabiting Lygaeidae (20, 107). *Himacerus apterus* lives in the grass-forbe zone in the first several nymphal instars and then moves up into trees (75). *Arachnocoris albomaculatus* is adapted to live in spider webs, where it apparently feeds on trapped insects (101). The usually brachypterous *Nabicula subcoleoptrata* is a predator of several species of Chrysomelidae within its range (38, 94). As discussed above, most of the prey species belong to certain insect taxa, although nabids appear to have the capacity to attack a number of other arthropods. Indeed, some species are generalist feeders and can be considered r-strategists.

AGROECOSYSTEMS Much of what we know about the habits of nabids has come from a large number of studies involving their functional role as predators in various agroecosystems (e.g. 12, 14, 46, 102, 110, 120, 143). The number of species is quite small, and most belong to the genus *Nabis*. Most, if not all, would be considered r-strategists according to Southwood's definition (131, 132). He posited that polyphagous predators are likely to be important in the temporary habitats often created by agriculture, where habitats may not be stable enough for K-strategists to become established. Ehler & Miller (37) provided support for the idea that r-selected natural enemies can provide control for r-selected pests; they cited *N. americoferus* as an example of such an enemy.

There is considerable evidence that nabids respond to habitat manipulation such as that occurring in agroecosystems. Intercropped fields of bean and maize supported more nabids than monocultures (97). Although differing maturity dates, locations, and row spacing in soybeans had little impact on predator populations, grassy soybean fields had more nabids than broadleaf-weed and weed-free fields (124). In conservation tillage systems in soybean fields, nabids were most numerous in no-till fields previously planted with soybeans that had not received an insecticide application (49).

Carayon (18) proposed that predatory Heteroptera (including Nabidae) could have an important role in the natural control of pest species, but felt it would be difficult to utilize them because of their polyphagy, cannibalism, and their variation in numbers over time and space. He recognized two size classes of predaceous Heteroptera. Since nabids are generally part of a group of predators, it is the summed effort of this predator guild that is important. The size classes of the Anthocoridae, Lygaeidae, Miridae, Nabidae, Reduviidae, and Pentatomidae provide a continuum able to cope with wide size range of prey (61).

RESEARCH NEEDS

Any review discloses potential areas for productive research. For the Nabidae, important areas include the compilation of comprehensive manuals on the fauna of most areas of the world. Such publications would stimulate biological studies. One region that deserves special attention is the Hawaiian Islands; a detailed study of the fauna of this region would be likely to enrich our ideas about insular evolution. Biological studies of almost any tropical species of nabid would be of special interest, since most existing information is for temperate species. The role of nabids in natural and manipulated ecosystems, including their varying feeding strategies, needs much additional attention. Special features of the nabids, such as the common occurrence of reduced wing development, might have potential value in manipulated ecosystems; the reduced mobility of the adults might be of value in reducing pest populations (54). There seems to be an interesting series of interactions between the ground-inhabiting Prostemmatinae and the ground-dwelling Lygaeidae, which include some pest taxa (e.g. *Blissus*). Finally, much progress is being made on the chemical ecology of many insect groups, but we know almost nothing about the importance of semiochemicals in the family Nabidae (1).

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