

## **XIII International Entomophagous Insects Workshop**

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## XIII International Entomophagous Insects Workshop

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### Organized by

Molly Hunter, Department of Entomology, University of Arizona, Tucson, AZ, and James Hagler, USDA-ARS, Western Cotton Research Laboratory, Phoenix AZ.



**Figure 1.** Participants in the XIII International Entomophagous Insects Workshop

**Abstracts are listed in alphabetical order by the last name of the senior author.**

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A growing number of studies suggest that plants can dramatically influence the interactions between herbivorous insects that feed on them and the natural enemies of these herbivores. Features of plants, such as morphology, nutritional quality, and allelochemistry can affect herbivore-enemy interactions. Although these studies provide ample evidence for the role of plants in determining the performance of parasitoids, no study has established an effect of plant characteristics on their genetic population structure and genetic differentiation of the third trophic level. In this study we examined the influence of host plant species and habitat characteristics on parasitoid genetic population structure. The model system comprises beans of the genus *Phaseolus* (*P. vulgaris*, *P. coccineus* and *P.*

*lunatus*), two bruchid beetles (*Zabrotes subfasciatus* and *Acanthoscelides obtectus*), and a complex of three hymenopteran parasitoids, *Horismenus* sp. (Eulophidae), that attack these beetles. Molecular markers (microsatellites) were developed and used to estimate the genetic heterogeneity within and among parasitoid populations from different habitats and on the three bean species. Geographic isolation and plant species appeared to be the most important factors influencing the genetic structuring of parasitoid populations. Additionally, the parasitoid species composition varied greatly between plant species, suggesting a high degree of specialisation of the parasitoids on the first trophic level.

### Effects of host age, female parasitoid age and host plant, on parasitism of *Ceratogramma Etiennei* (Hymenoptera: Trichogrammatidae)

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The parasitism of *Diaprepes abbreviatus* (L.) eggs by *Ceratogramma etiennei* Delvare as influenced by host age, age of the parasitoid, and host plant preference was evaluated. Percent parasitism of *D. abbreviatus* eggs by *C. etiennei* decreased as eggs matured under laboratory and greenhouse tests. One to 2 d old *C. etiennei* females parasitized more hosts than older females. Host plant leaf thickness, leaf pubescence and plant strata affected parasitism by *C. etiennei*. This parasitoid is diurnal and spends approximately 5 min probing, 46 min in actual parasitism per egg mass and 24 min resting.

### Natural enemies and the evolution of host range expansion in herbivorous insects

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Some recent theoretical research has suggested that natural enemies can retard or accelerate the rate of evolution of host range expansion in an herbivorous insect. Other theoretical results imply that natural enemy induced mortality may have little influence on the rate of evolution of host range expansion. This issue has attracted some interest when considered in the context of the evolution of resistance to transgenic Bt crops. I provide an overview to the various theoretical approaches to the problem and outline a set of circumstances where natural enemies could exert considerable selection pressure on an herbivorous insect to expand its host range.

### **Colorado potato beetle hemolymph effects on the parasitic nematode *Heterorhabditis marelatus***

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The Colorado potato beetle (*Leptinotarsa decemlineata* Say) (CPB) is the key pest of potatoes and other solanaceous crops in the United States and much of Europe. The beetle rapidly develops resistance to most pesticides used against it, and transgenic crops are not currently favored by the general public for pest control. Hence, we examined biological control of the beetle, using the entomopathogenic nematode *Heterorhabditis marelatus* Liu & Berry and its symbiotic bacteria. The nematode kills nearly 100% of beetles in field trials, but does not reproduce in the beetle. Previous research indicated the symbiotic bacteria switched rapidly to a secondary form when placed in CPB hemolymph. Unlike the primary form of the bacteria, the secondary form does not provide nutrients or protection against competing pathogens for the nematode. The research discussed here examines the host's immune system and hemolymph chemistry effects on the nematode and its symbiotic bacteria. We found that the immune system rarely inhibits bacterial or nematode growth. However, a toxic protein, which may be the previously identified 57kD leptinotarsin, appears to cause the bacterial switch to the secondary form. When the protein is denatured, the nematodes still cannot reproduce. Addition of a variety of lipids indicates that a lipid source is not available to the nematodes or the symbiotic bacteria in CPB hemolymph, limiting reproduction. We hypothesize that the glycoalkaloids from the plants on which the CPB feeds bind to the lipid-transport proteins in the hemolymph, halting the movement of cholesterol in the hemolymph, and thus negatively affecting the nematodes.

### **Ecological and evolutionary implications of oosorption by *Eretmocerus eremicus* (Hymenoptera: Aphelinidae)**

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Oosorption (egg resorption) in parasitic wasps is thought to be limited to strongly synovigenic taxa due to the high time cost associated with the process. We have discovered, however, that the strongly pro-ovigenic species *Eretmocerus eremicus* resorbs oocytes linearly between 2 and 8 d of adult life. Furthermore, it appears that the oosorption mechanism in this wasp differs ultrastructurally from those previously reported in hymenopterans. While the mechanism of yolk degradation follows the general "islands of degeneration" model, it is unusual in that this process begins and progresses while the chorion and vitelline membranes remain as barriers to contact by the follicular epithelium. The egg membranes, which in previous studies are completely digested by enzymes from the follicle cells prior to yolk breakdown, are instead broken down concurrently. The synchrony between these two phases of the oosorption process of *E. eremicus* may be an adaptation to decrease the time required to resorb each oocyte, thus lowering the time cost of the process to this short-lived insect. Additionally, this is the first unequivocal example of an ultrastructural mechanism for autolytic oosorption in insects. From an evolutionary perspective, this may explain how many members of the Encyrtidae and at least one ichneumonid are capable of resorbing oocytes with no apparent breakdown of the chorion.

### **Impact of *Eretmocerus eremicus* (Hymenoptera: Aphelinidae) on open-field *Bemisia tabaci* (Hemiptera: Aleyrodidae) populations.**

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The effect of three different release rates (1x, 10x, and 20x the recommended rate of 25,000/ha) of *Eretmocerus eremicus* Rose and Zolnerowich on *Bemisia tabaci* (Gennadius) populations found in open-field cantaloupe, *Cucumis melo* L., was evaluated against populations in untreated control plots. Parasitoids were released from a point source in the center of each of nine treatment plots. Whitefly population growth, encompassing all developmental stages, and rates of parasitism were monitored within a 10-m annulus surrounding the center point in all 12 plots over a 52-d period. The rates of *B. tabaci* population increase during this time were equivalent regardless of the parasitoid release rate. Whitefly densities were not limited in any of our treatment plots when compared to those found in the control plots. Moreover, mean rates of parasitism did not increase with time nor did they differ among the three treatments or control plots. Finally, estimated rates of parasitism were density dependent responding positively to increasing host numbers. The ineffectiveness of this parasitoid in controlling whitefly populations in the field may be due to its high propensity to disperse at low host

densities or to influxes of immigrating whiteflies. Hence, the use of *E. eremicus* alone is not an efficient means to reduce whitefly populations in melon crops in the southwestern United States.

### **Inter-population variation in performance of insects in a tri-trophic system**

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Many species of parasitoids are distributed over populations in a variety of habitats in which they may experience different environmental conditions. If gene flow among these populations is limited and natural selection operates differently in the different habitats, this should lead to genetic divergence and local adaptation. Our study examines the effects of plant variation and the existence of local adaptation in a tri-trophic interaction. The system comprises four wild populations of the bean *Phaseolus vulgaris*, the bruchid beetle *Zabrotes subfasciatus* and the braconid parasitoid *Stenocorse bruchivora*. Transplant experiments revealed that bruchid performance varies among bean populations. Beetles from one site performed better on the seeds of their original site than on seeds of the other populations. A nutritional analysis of the seeds showed that seeds from this site are nutritionally superior as they have a higher nitrogen content. We then examined the consequences of bruchid variation on the performance and potential for local adaptation of the parasitoid. The results did not show evidence for local adaptation, but they showed behavioural and performance differences among parasitoid populations with respect to their origin and the origin of the seeds in which they developed. We currently study the role of the plant in determining genetic differences among populations.

### **Patch quality, life expectancy and patch residence time in female egg parasitoids**

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The Marginal Value Theorem predicts that female parasitoids should exploit host patches until their instantaneous rate of gain reaches a marginal value. Patch residence time was measured in an egg parasitoid, *Anaphes victus* (Hymenoptera: Mymaridae), when patch quality and travel time varied. The effect of female age on patch residence time was also tested while keeping travel time constant. The females *Anaphes* stayed longer and exploited the patch to a higher level when patch quality and travel time increased. However,

the marginal value at which females left the patch decreased with these parameters. Contrarily to *Trichogramma* species, *Anaphes* females appear to base their patch quality estimate on the first patch encountered rather than on a fixed innate estimate. Such strategy may be optimal when inter-generation variability in patch quality is high. Independently of travel time, the age of females influenced their patch residence time. Patch residence time increased exponentially as the life expectancy of females decreased. The probability of finding another patch diminishes with a female life expectancy and it is therefore adaptive to exploit the current patch to a higher level.

### **The molecular phylogenetics of the Figitidae (Hymenoptera: Cynipoidea)**

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The figitids are a diverse assemblage of parasitic cynipoids. Intense systematic research over the past two decades has revealed much about this ubiquitous group, both taxonomically and phylogenetically. To aid in the study of figitid phylogenetics, I have sequenced the 28S D2+D3, COI and 16S gene regions while placing a premium on taxon sampling that represents the maximum diversity of the Figitidae. Additionally, several members of other cynipoid families have been included. The results to date find the majority of figitid subfamilies monophyletic. The goal of this research is a robust phylogeny that future studies on the classification and evolution of this group can be based upon.

### **Migration by the sweet potato whitefly, *Bemisia tabaci*, and its aphelinid parasitoid *Eretmocerus eremicus***

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Information has been gathered for several years on the migration habits of the sweet potato whitefly, *Bemisia tabaci*. Empirical evidence demonstrates that this relatively small insect is easily capable of migrating several kilometers during a single morning. Anecdotal evidence indicates it can disperse much farther. Contrastingly, one of its principle natural enemies in the Southwest, *Eretmocerus eremicus*, seems less capable of moving even these modest distances. Regardless, an examination of their flight behavior has provided useful information. For example, when examined in the laboratory the ability of *E. eremicus* to sustain flight is linked to gender and mating status. Unmated females fly for significantly longer periods of time than mated females and females fly for significantly longer periods than males. Conclusions concerning flight behavior were substantiated in field trials where female dispersal had a strong directional component while males apparently

diffused away from release points. Taken collectively (see Bellamy presentation) these data provide insight into host/parasitoid relationships.

### **The induction of volatiles in bean plants by feeding and oviposition of *Nezara viridula* that attract the egg parasitoid *Trissolcus basalus*: Behavioral and chemical ecology investigations.**

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The ability of parasitic arthropods to locate and attack hosts, and consequently their efficacy, is a result of sequential host selection steps that are regulated by physical, infochemical, and biochemical factors. A series of cues mediate the host selection process, and among them, volatile compounds emitted by plants as a consequence of herbivore activities play a significant role. When these volatiles recruit natural enemies, they have been termed host-induced synomones and they are regarded as an indirect chemical defense reaction by the plants. The ability of hymenopteran parasitoids to locate their hosts using these induced synomones has been well documented for adult and larval parasitoids, i.e., for those host instars whose feeding activities induce qualitative and quantitative changes in the plant's volatile profile. However, variations in plant volatiles are not only induced by insects that damage plant tissues while they feed, but also by egg deposition, and these volatiles also serve as host-induced synomones for their egg parasitoids. Previous investigations showed that broad bean leaves (*Vicia faba*) damaged by feeding activity of *Nezara viridula* (Heteroptera: Pentatomidae) and on which an egg mass had been laid, produced host-induced synomones that attracted the egg parasitoid *Trissolcus basalus* (Hymenoptera: Scelionidae). In contrast, undamaged leaves or leaves damaged only by feeding did not attract wasp females. Comparisons of the headspace analysis of broad bean plants revealed differences in the blends emitted by undamaged plants and feeding damaged plants carrying an egg mass. Dichloromethane extracts of feeding damaged plants carrying an egg mass attracted *T. basalus* females in Y-olfactometer tests, and after preparative gas chromatography fractionation of these extracts, we obtained a terpenoid fraction that was attractive to the parasitoid.

### **Identification of synomones induced by feeding and oviposition of *Nezara viridula* on bean plants.**

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Several studies have demonstrated that herbivores can induce host plants to produce volatiles that can attract arthropod natural enemies which parasitize or prey on the herbivores, reducing further damage to the plants. To date, studies that have investigated herbivore-induced volatiles have primarily focused on defoliating insects that damage plants by chewing. There is much less information available about volatiles induced by herbivores having phloem-feeding or stylet-sheath-feeding habits, such as Heteroptera. Furthermore, volatiles may be produced in response to insect egg deposition and these volatiles also may serve as host-induced synomones for egg parasitoids. Here we present results of analyses of headspace odors from broad bean (*Vicia faba*) and French bean (*Phaseolus vulgaris*) plants induced by adults of *Nezara viridula* (Heteroptera: Pentatomidae) as a result of their feeding activity, oviposition activity, and feeding and oviposition activity combined. Undamaged plants produced relatively small amounts of “green leaf volatiles” (hexanal, (*Z*)-3-hexenol and (*Z*)-3-hexenyl acetate) and traces of monoterpenes and sesquiterpenes (linalool,  $\beta$ -caryophyllene and (*E,E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene). Feeding and oviposition by adults of *N. viridula* induced a significant increase in terpenoids, reaching a peak during the first day after bug feeding and oviposition. No differences were detected in the volatiles profiles of undamaged plants and plants on which bugs were allowed only to lay eggs. Furthermore, water extracts of *N. viridula* salivary glands induced the emission of the same volatile blend produced by plants damaged by both feeding and oviposition. Bioassays revealed that the volatiles blend produced by plants damaged by both stink bug feeding and oviposition was more attractive to the egg parasitoid *Trissolcus basalus* than volatiles from undamaged plants, or plants with only feeding damage.

### **Provisioning of an enemy-free space for an oligophagous insect herbivore: Direct effect of a recently acquired host plant on parasitoids**

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Enemy-free space (EFS) is a potentially important factor affecting host plant use by phytophagous insects. In this study we first tested whether tomato plants provide *Phthorimaea operculella* larvae with an EFS. Compared to potato, tomato is a sub-optimal host for *P. operculella*. Yet in a few areas, high population densities of *P. operculella* were reported on tomato plants in the last 15 years or so. Berdegue et al. (1996) proposed three conditions for EFS. Through field experiments in Ethiopia, we demonstrated that natural enemies are an important mortality factor on the potato host; a significantly higher proportion of larvae survive on caged potato plants than on exposed ones. We then found that in the presence of natural enemies, larval survival was significantly higher on tomato than potato plants, implying that the herbivore is more protected

from its enemies on tomato than potato plants. Finally, we found that larval survival was significantly higher on caged potato than caged tomato plants. Yet the cost involved in feeding on the sub-optimal novel host (Berdegue et al.'s third condition) was observed only on one of the three tested tomato genotypes and only at the preblossom stage. These variations were not related to trichome density or tomatine concentration. Results however show for the first time that a lack of fitness cost may not necessarily be due to herbivore adaptation to feed on the novel host but may also depend on plant genotype and phenology. We conclude that tomato plants provide EFS for this oligophagous herbivore because all of Berdegue et al.'s conditions were met in our system. Laboratory experiments show that the EFS is due primarily to the direct and negative effect of tomato plants on *Diadegma* larval parasitoids. An intensive field survey provides further support for this conclusion; unlike larvae on nearby potato, *P. operculella* larvae on tomato plants were not parasitized.

### **Consequences of intraspecific interference for competitive displacement and biological control in a community of Hawaiian fruit-fly parasitoids**

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Using a laboratory experiment and a stage-structured population dynamic model, we attempted to explain a historic pattern of competitive displacement in tephritid parasitoids in Hawaii. We sought to understand the simultaneous occurrence of three phenomena following the introduction of the egg parasitoid *Fopius arisanus*: (1) a 10-fold decline in tephritid densities, (2) decline in abundance of four previously established larval parasitoids in the genus *Diachasmimorpha*, and (3) current and historic coexistence of three of the *Diachasmimorpha* species with *F. arisanus*. In a laboratory experiment with *F. arisanus*, we investigated a form of intraspecific interference that arose from "host-egg killing" by adult female *F. arisanus*. We hypothesized that this mechanism of intraspecific interference might explain coexistence, whereas other aspects of *F. arisanus*' biology would explain competitive displacement. We developed a stage-structured population-dynamic model that incorporated the results of our study and other studies of the system. Contrary to our expectations, the model failed to predict the pattern of competitive displacement observed in Hawaii. Competitive displacement, coexistence and enhanced biological control of fruit flies never occurred for the same set of parameter values. The model probably does not incorporate additional competitive advantages of *F. arisanus* and/or other important coexistence-promoting mechanisms.

### **Nutritional implications and differential gene expression in the wing morph differentiation of *Melittobia digitata*.**

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Wing morph development is a developmental plasticity associated with species inhabiting unpredictable or unstable environments. It is a widespread phenomenon among insects and it represents a trade-off between dispersal or migratory behavior and reproduction. The concept of the existence of trade-offs among traits that dictate shifts in the organismal life history has been one of the central paradigms for evolutionary biologists and wing dimorphism is considered a strategy to maximize the development of the reproductive organs by diverting nutrient resources that would be otherwise allocated to the development and maintenance of flying structures. A variety of environment-derived cues such as crowding, host plant condition, temperature and photoperiod, are among the most common factors to elicit wing form differentiation. However, density, especially if coupled to an unsuitable nutritional medium, has been described as the trigger for the development of wing morphs of several species. Although diverse cues may trigger wing morph development, changes in hormone levels is considered to be the underlying mechanism and is likely to be evolutionarily conserved. An increase in titers of juvenile hormone (JH) is the most accepted mechanism to lead to short wing morph (SWM) development through the blockage of changes normally induced by ecdysone-mediated metamorphosis. We discuss the nutritional implications and the differential gene expression in the morph differentiation of the ectoparasitoid *Melittobia digitata*.

### **Expression and molecular characterization of a putative chitinase from teratocytes of *Toxoneuron nigriceps*.**

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Parasitoids are a very diverse group in which their nutritional and physiological interactions will depend on the evolutionary history of a particular host-parasitoid association. They have a natural arsenal to help them to subdue the host immune response, alter and regulate host metabolism, development, and synthesis of host proteins, such as maternally-born secretions (venom, calyx fluids), larval secretions, associated symbiotic virus (PDVs), and/or secretions from teratocytes (a particular cell type derived from the developing embryo). Teratocytes are cells derived from the serosal membrane of parasitoid eggs that may have a dual function in the parasitoid-host interaction serving not only as a source of substances that alter the host internal environment, but also of proteins that might have a nutritional role for the developing parasitoid. *Toxoneuron nigriceps* is a larval endoparasitoid in which teratocytes were shown to secrete several proteins into the host hemocoel and regulate the host endocrine system. In here we analyze the expression pattern, provide the molecular characterization of a putative chitinase

produced by teratocytes and released into the host hemolymph, and discuss its possible implications for the developing parasitoid.

### **Strategies involved in host location of *Telenomus busseolae* and *Trichogramma turkestanica*, egg parasitoids of *Sesamia nonagrioides***

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The noctuid stemborer *Sesamia nonagrioides* (Lepidoptera: Noctuidae) is an important pest of maize in the Mediterranean Basin. The egg clusters of *S. nonagrioides*, concealed under the leaf sheaths or the ear bracts, are attacked by *Telenomus busseolae* (Hymenoptera: Scelionidae) and *Trichogramma* spp. (Hymenoptera: Trichogrammatidae), but only *T. busseolae* exerts an effective natural control. A possible explanation is based on the different strategies used to reach and parasitize the concealed host eggs. *T. busseolae* is dorso-ventrally flattened (depressed) and crawls under the leaf sheath or ear bracts, whereas *Trichogramma* spp. does not show any specialized adaptation. Bioassays were conducted to verify whether such difference of efficacy can be explained also by a different response to semiochemical cues from *S. nonagrioides*. Behavioral responses of *T. busseolae*, reared on *S. nonagrioides*, and *Trichogramma turkestanica*, reared on *S. nonagrioides* or *Ephestia kuehniella* for 1, 5 and 10 generations, were compared. In olfactometer, *T. busseolae* females were attracted by the sex pheromone of *S. nonagrioides* as already reported. Instead, none of the two strains of *T. turkestanica* reared on *S. nonagrioides* and *E. kuehniella* responded to *S. nonagrioides*. In an open arena, *T. busseolae* and both strains of *T. turkestanica* showed an arrestment response to host scales. Specifically, *T. busseolae* response was higher compared to that of both *T. turkestanica* strains. Finally, response by *T. turkestanica* reared on both hosts declined with increasing number of generations. The potential of *T. busseolae* as biological control agent of noctuid stemborers is discussed.

### **Parasitoid and host movement and population dynamics in a heterogeneous prairie landscape.**

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Landscape-level experiments with insect hosts and their parasitoids are virtually non-existent. Here, we studied an egg parasitoid (*Anagrus columbi*) of a planthopper (*Prokelisia crocea*) that exists among discrete patches of prairie cordgrass (*Spartina pectinata*);

the sole food source for the planthopper. We experimentally tested the effects of the landscape matrix (i.e., non host-plant habitat) on the movement and population dynamics of the planthopper and parasitoid. Based on a small-scale experiment in which cordgrass patches were embedded in three different matrix types (3 m between patches), we found that emigration and immigration of planthoppers were highest in a matrix composed of the introduced grass smooth brome, intermediate in native grasses, and lowest in mudflats. The egg parasitoid exhibited an identical response to the three matrix types at this spatial scale. Moreover, the parasitoid's pattern of movement through the matrix was fundamentally different between mudflat and non-host grasses. Adult parasitoids spread diffusively through non-host grasses but exhibited highly directional outward movement in a mudflat. A larger scale field experiment (e" 25 m between patches), corroborated these smaller scale results: Brome facilitates higher connectivity than mudflat. Finally, preliminary data from this large-scale field experiment suggest that local planthopper and parasitoid populations are more prone to extinction in a mudflat and have significantly more asynchronous population densities in space than populations embedded in a brome matrix. These results are expected from metapopulation theory and suggest that the invasion of brome into the tall-grass prairie may greatly affect the stability of this host-parasitoid interaction.

### **Systematics of an enigmatic wasp family: Evaniidae (Hymenoptera)**

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Ensign wasps (Hymenoptera: Evaniidae) develop as solitary egg predators within the oothecae of cockroaches. This interesting family encompasses 20 genera and more than 450 described species, but evaniids have long been neglected taxonomically. The generic relationships within Evaniidae (Hymenoptera) are explored for the first time using both morphological and molecular (16S, 28S) data. We also examined relationships within Apocrita using mixed models in MrBayes; these analyses revolved around Sharkey and Roy's (2002) morphological matrix and Downton and Austin's (2001) molecular (16S, COI, 28S) dataset, with several new taxa added. Our results demonstrate that Evanioidea is monophyletic and sister to Ceraphronoidea + Proctotrupeoidea + Platygastroidea + Cynipoidea + Chalcidoidea.

### **Early nutrition and embryonic development in two congeneric parasitoids, *Encarsia formosa* and *E. pergandiella* (Hymenoptera: Aphelinidae)**

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The availability of amino acids was analyzed in the eggs of the endoparasitoids *Encarsia formosa* and *E. pergandiella* after oviposition and near the end of embryonic development. Newly laid eggs of *E. formosa* appear to contain the full complement of amino acids required for embryonic development while those of *E. pergandiella* absorb greater than 30-fold more amino acids from host hemolymph during embryonic development than are present at the time of oviposition in the host. Only *E. pergandiella* eggs were capable of absorbing and utilizing [<sup>14</sup>C]-labeled lysine in an *in vitro* system. An analysis of embryonic development in the two species revealed that *E. pergandiella* embryos become surrounded by a multinucleate, syncytial membrane early in development while *E. formosa* embryos do not. The membrane around *E. pergandiella* embryos contains large numbers of golgi, mitochondria and rough endoplasmic reticulum. The precise role of the membrane in the development of the embryo is unclear at present, however, the tremendous growth observed in *E. pergandiella* during embryonic development suggests the membrane plays a major role in nutrient acquisition from the host.

### **The role of the germ cell line in caste determination in the polyembryonic wasp, *Copidosoma floridanum* (Hymenoptera: Encyrtidae)**

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A single egg of the polyembryonic wasp, *Copidosoma floridanum*, gives rise to thousands of embryos. These embryos develop into two distinct larval castes. Reproductive larvae possess germ cells and develop into adult wasps, while precocious larvae lack germ cells and function as soldiers that defend the host from competitors. Germ line determinants localize to a single blastomere at the four-cell stage of development. To determine if inheritance of germ cells plays a role in caste formation, we compared development of eggs in which we ablated the progenitor germ cell to eggs in which we ablated other blastomeres. Our results indicate that inheritance of germ cells is a key factor involved in caste formation in *C. floridanum*.

### **Predator and parasitoid response to sequestered secondary compounds.**

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predators and parasitoids. Among these protective features, chemical defenses appear to be the most effective against predators but do not function as well against parasitoid wasps and flies. Our multiple-species comparisons in both temperate and tropical caterpillar rearing studies support this pattern. Thus, chemically defended caterpillars can provide enemy free space for parasitoids. But how do parasitoids avoid toxins that are clearly defensive to predators? Our studies on specific caterpillar-parasitoid interactions provide preliminary support for several complementary toxin-avoidance hypotheses. Parasitoids may develop on tissues where toxins are not sequestered or they may process toxins using metabolism very similar to caterpillar adaptations to plant toxins. In addition to these potential responses to a toxic host, sequestered toxins may also compromise encapsulation in caterpillar hosts, leading to greater parasitism success on toxic caterpillars.

### **Biological control of obscure scale in northern California**

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One of the oldest controversies in classical biological control of insects concerns the need for ecological investigations in the native home of a target pest in order to determine an appropriate introduction strategy for the pest in the exotic home. However, there has been limited progress on this issue because of the sense of urgency that often attends exotic pest problems. Over twenty years ago, I found an exceptional case: An infestation of obscure scale (*Melanaspis obscura* [Comstock]), an exotic diaspidid on native and introduced oaks (*Quercus* spp.) in Sacramento, California that was localized and not expected to spread. Because there was no “need for speed,” I conducted pre-introductory investigations in the native home of the pest (eastern USA), with emphasis on the structure of the scale’s parasite guild. This information was used to derive an introduction strategy designed to maximize the ecological impact of one particular natural enemy—i.e., the aphelinid *Encarsia aurantii* (Howard). The parasite was released in 1988-89; it established, increased in numbers from year to year, and now has reduced the obscure-scale population to a level that no longer requires chemical control (i.e., complete biological control). This case illustrates how “guild analysis” can be used to derive introduction strategies in biological control.

### **Evidence of conserved genes involved in host physiological regulation in bracoviruses.**

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Lepidopteran larvae possess a diverse array of defenses against

Bracoviruses are obligatorily associated with at least 17500 species of endoparasitoid wasps that constitute a clade -the microgastroid complex. They are essential for successful parasitism. Mature virions are produced in the ovaries, and injected by female wasps during oviposition into the host lepidopteran larvae. The virus particles enter host cells where viral genes are expressed, causing several alterations to the host physiology, comprising disruption of the immune defenses, retarded growth and inhibition of metamorphosis. We have undertaken the characterization of *Cotesia congregata* viral genes expressed in the parasitized host *Manduca sexta* and the sequencing of the virus genome. The analysis of the DNA sequences obtained so far and the screening of a cDNA library of parasitized *M. sexta* have allowed us to characterize several multigenic families. Some of the genes recently identified genes contain conserved protein domains found in other parasites or pathogens which are known to be involved in the suppression of the immune response of mammals. This suggests a convergent evolution between parasitoids, bacterial pathogens, and parasitic nematodes (filariae) to face the host cellular response. The characterization of genes conserved in the virus genome of different parasitoid species will also be an essential tool to understand the role played by bracoviruses in the tremendous diversification of the microgastroid complex.

### Nutritional quality of aphid-produced honeydew for non-aphid parasitoids

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Aphid-produced honeydew might be an alternative food source of fundamental importance for adult parasitoids in the context of biological control. Honeydew is likely to be particularly important in crops where nectar is not available, and is expected to increase longevity and fecundity, as well as attraction and retention of adult parasitoids in a target area. We studied the importance of honeydew produced by the aphid *Rhopalosiphum maidis* for the longevity of the solitary larval endoparasitoids *Cotesia marginiventris*, *Camponotus sonorensis*, and *Microplitis rufiventris*, natural enemies of important lepidopteran pests. Honeydew-fed females of all three species lived longer than females provided only with water, but significantly shorter than females that were fed with sucrose. When investigating the effect of honeydew feeding on the parasitism rate of *C. marginiventris* over eight days we found that honeydew-fed females parasitized significantly more caterpillars than non-fed females. Further experiments demonstrated that *C. marginiventris* is able to learn honeydew associated odours. Females that had 2x 15seconds feeding experience with honeydew on aphid-infested barley were more attracted to odours of such plants compared to naïve females and females that had experience with the odour of infested plants only. The results show that aphid-produced honeydew has the potential to serve as a food source for parasitoids and

increases longevity and fecundity. Furthermore, parasitoids can learn to respond to honeydew associated odours, which should increase their foraging efficiency.

### Mass production of *Coccus spp.* and *Saissetia spp.* and their parasitoids

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Reduction of organophosphate and carbamate use in traditional citrus pest management has allowed a secondary pest, citricola scale, *Coccus pseudomagnoliarum* (Kuwana), to re-emerge as a key pest in San Joaquin Valley citrus. Currently, we are evaluating augmentative biological control as a potential alternative pest management tactic to maintain citricola scale populations below economic concern. Commercial methods currently used to produce its parasitoids are uneconomic and cannot meet existing demand. Thus, we have developed an alternative method for rearing the scale and its parasitoids using detached yucca leaves as the host substrate. The leaves are inoculated passively (crawlers freely walk onto new leaves) and are maintained hydroponically while the scales develop. When the scales are 26-30 days old, a portion of them are exposed to the parasitoids for 96 hrs. We collect the emerging parasitoids from these leaves on days 14, 17, and 24 post-exposure, using a specially designed "sting box" which yields 160 female *Metaphycus* sp. per leaf on average. The remaining scale-infested leaves are retained for crawler production to infest additional leaves for subsequent parasitoid production.

### Synchronized development of *Encarsia scapeata* and its univoltine whitefly host, *Trialeurodes lauri*

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Previous life history studies of *Encarsia* species were conducted on multivoltine host species. The present work deals with the developmental adaptations of *Encarsia scapeata*, which develops on a univoltine whitefly host, *Trialeurodes lauri* on *Arbutus andrachne* trees inhabiting the Mediterranean hills of central and northern Israel. The tree has one flush of leaves each year during April and May and the whiteflies respond by emerging during that time, laying eggs and within ca. 3 weeks, developing to the 4th instar. The whiteflies pass the next 10-11 months of the year as 4<sup>th</sup> instar nymphs (in diapause), rather than as pharate adults. Parasitoid emergence occurs at two separate times. Some female emergence occurs in the fall (group 1) whereas most females and all males emerge in the spring (group 2). The mated females of group 2 lay female-producing eggs in the new whitefly generation during May.

A few of these will emerge in the fall and give rise to group 1 females which are virgins and will lay male-producing eggs in parasitized hosts. Most female parasitoids develop to adults only from January through April, probably after inducing premature development of their hosts. These parasitoid females will constitute group 2 and will emerge in the spring together with the males that develop from the eggs laid by group 1 females. Thus, there is considerable developmental synchrony between the parasitoid and its host requiring a complex series of interactions between the two insects.

### **Confirming the role of yeast symbionts in green lacewings, *Chrysoperla* spp. (Neuroptera: Chrysopidae)**

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As larvae, lacewings in the genus *Chrysoperla* are voracious predators of aphids and other soft-bodied insects. Unlike many other lacewings, *Chrysoperla* spp. adults are non-predaceous and feed on pollen, nectar and aphid honeydew. Earlier studies observed that *Chrysoperla* spp. adults house symbiotic yeasts in their crops and indicated that the yeast may supplement amino acids missing in the largely carbohydrate diet (Hagen KS et al. 1970. *Bollettino Laboratorio di Entomologia Agraria Filippo Silvestri* 28:113-34; Hagen KS, RL Tassan. 1972. In J.G. Rodriguez (ed.) *Insect and Mite Nutrition*. North Holland, Amsterdam, The Netherlands). They suggested that lacewings eclose without their yeast symbionts and must obtain them from the environment. In our research, attempts to cure adult *Chrysoperla* spp. of yeast using Hagen et al.'s (1970) protocol, as well as several other fungicides and heat treatment, have been unsuccessful. Furthermore, preliminary data suggests that yeast may also be vertically transmitted. Our research indicates that the functional significance of yeast in green lacewings requires further study.

### **Parthenogenesis-inducing microorganisms in *Encarsia* parasitic wasps: Different mechanisms of sex manipulation**

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In the genus *Encarsia* (Hymenoptera: Aphelinidae) thelytokous reproduction appears to be caused by two different groups of maternally inherited bacteria, namely an  $\alpha$  proteobacteria, *Wolbachia*, and members of the Cytophaga-Flexibacter-Bacteroid (CFB) group, that are located in the reproductive tissues. Although several karyological studies have been performed on thelytokous and arrhenotokous species of *Encarsia*, no data are available on the ploidy level of males obtained by treating parthenogenetic females

with antibiotics, in order to eliminate sex determining symbionts. In this study, male larvae of *E. hispida*, a species with CFB, and *E. formosa*, the only species of *Encarsia* infected by *Wolbachia*, were karyotyped. Chromosome preparations revealed diploid complements ( $2n=10$ ) in the former species and haploid complements ( $n=5$ ) in the latter (in which diploid nuclei were also present). These results suggest that parthenogenesis-inducing microorganisms manipulate sex in two different ways. *Wolbachia* alters the ploidy level of unfertilized eggs in *E. formosa*, whilst CFB does not in *E. hispida*. Consequently, *E. formosa* follows the general haplodiploid sex determination mechanism of Hymenoptera and the genic balance model could apply, as for other microbe-associated thelytokous species of chalcidoids. Conversely, in *E. hispida* diploidy has become fixed in both sexes and unfertilized eggs are feminized by CFB probably through a genomic imprinting.

### **Molecular differentiation of closely related *Encarsia* species (Hymenoptera: Aphelinidae) based on mitochondrial COI gene**

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The genus *Encarsia* includes species that are parasitoids of whiteflies and armored scale insects. Many species are considered effective natural enemies of agricultural pests and their correct identification is fundamental for successful biological control programmes. Recently, due to unreliability of morphological characters in separating closely related species of *Encarsia*, new identification techniques are being investigated. In this study, a 850 bp long region of the mitochondrial COI gene was sequenced from 5 species of *Encarsia* belonging to *luteola* (*E. formosa*, *E. luteola* and *E. hispida*) and *strenua* (*E. protransvena* and two strains of *E. sophia*, from Pakistan and Spain respectively) species groups. A parsimony analysis resolved two monophyletic clades supporting the two groups of species considered. The nucleotide sequence divergence between the two *E. sophia* strains was greater than that found among the species of the *luteola* group, suggesting that the two strains could be actually sibling species. PCR-RFLP analysis produced restriction patterns which discriminate *E. formosa* from *E. luteola* (*DraI* and *TaqI*), that are similar morphologically, and the Pakistani from the Spanish strain of *E. sophia* (*DraI* and *XhoI*), that are indistinguishable morphologically. In conclusion, the COI region could be a useful marker to characterize and separate species within the genus *Encarsia* otherwise indistinguishable on a morphological basis.

### **Inter-clone conflicts in the parasitoid wasp *C. floridanum*: Do precocious larvae mediate competition between broods in a single host?**

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When should interacting organisms compete and when should they cooperate? This has been an enduring topic in many areas of evolutionary ecology. Cooperation will be favored when there are material benefits to both parties but not when they are material costs. However, the balance between cooperation and competition will be more complex if interacting individuals experience both costs and benefits. Our study aims to explore proximate mechanisms underlying the evolution of conflicts in the polyembryonic wasp *C. floridanum* by testing the importance of two key components of evolutionary conflicts among individual: Mating opportunities and genetic relatedness. *C. floridanum* is obligately polyembryonic with each egg laid into a host developing clonally into an average of 1200 adults. The majority of embryos develop into 'reproductive' larvae that develop into adults, while a minority of embryos develop into 'soldiers' larvae (precocious larvae) that always die when the host is consumed by the reproductive larvae. Previous studies investigating brood responses to completely unrelated competitors showed that soldiers protect the evolutionary interests of their clone mates by attacking the competitor but with no influence of genetic relatedness or other benefits such as mating opportunities. Here, by injecting intraspecific competitors labeled with a vital tracer into hosts parasitized by *C. floridanum* and by conducting *in vitro* experiments, we characterize the behavioral response of resident soldiers to conspecifics. The genetic background and the sex of the introduced brood are manipulated in order to study how 'soldiers' larvae respond to these two different factors and if precocious larvae are able to mediate competition between two conspecifics broods.

### **The adaptive significance of sibling egg cannibalism in the Coccinellidae: Comparative evidence from three species.**

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Egg cannibalism is common among aphidophagous coccinellids that lay clustered eggs. Neonate larvae may improve their survival probability by cannibalizing sibling eggs prior to dispersal in search of prey. Egg-clustering facilitates sibling egg cannibalism and may represent a form of maternal care that improves the survival of early-hatching larvae at the expense of late-hatching larvae. We examined sibling egg cannibalism behavior in three aphidophagous coccinellid species that lay clustered eggs: *Cycloneda sanguinea* L., *Harmonia axyridis* Pallas, and *Olla v-nigrum* Mulsant. Newly hatched larvae of all three species delayed dispersal from clusters when sibling eggs were available for cannibalism and consumed all late-hatching and/or non-viable eggs within clusters before dispersing. There was significant variation among species in 1) the proportion of eggs laid singly versus in clusters, 2) the proportion of eggs cannibalized by early-hatching larvae and, 3) the physiological consequences of egg cannibalism for developing larvae. Both male and female larvae that cannibalized eggs molted to the second instar sooner than did their non-cannibalizing counterparts in all three species, and this

translated into reduced total developmental time for both sexes in *H. axyridis*, but only for males in *C. sanguinea* and only for females in *O. v-nigrum*. Adult females weighed significantly more than adult males in all three species and increases in adult weight as a consequence of egg cannibalism were sex-specific. Female cannibals were heavier as adults than were non-cannibalizing females in *H. axyridis* and *O. v-nigrum*, but males had similar weights. Egg cannibalism had no detectable effect on adult weight in *C. sanguinea*. Therefore, our results revealed substantial life history benefits for sibling egg cannibalism behavior in all three species, although in many cases the benefits were sex-specific.

### **Flight response of *Aphidius ervi* to tomato plant volatiles**

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Plants can be attractive towards natural enemies of insects that attack them. This common feature is termed indirect resistance and can be exploited to increase biological control of insect pests. The attractiveness of two tomato ecotypes towards *Aphidius ervi* has been studied in wind tunnel bioassay. This parasitoid has proved to be the most effective biocontrol agent of *Macrosiphum euphorbiae*, the key pest of tomato grown in open field in Southern Italy. It has been found that a high level of attractiveness can be either constitutive (ecotype AN5), i.e. recorded in absence of infestation by *M. euphorbiae*, or induced (ecotype AN7), i.e. produced after several days of aphid infestation. In AN5, aphid infestation did not enhance attractiveness towards *A. ervi*, probably due to its higher level of direct resistance to aphids. The F1 obtained by crossing AN5xAN7 followed the response recorded for AN7, suggesting that the inducibility of high level of attractiveness is inherited according to dominant fashion. As a consequence, it appears that this character may be introgressed efficiently into commercially valuable varieties of tomato.

### **Foraging behavior, host stage selection and gut content analysis of field collected *Drapetis nr. divergens* (Diptera: Empididae): A predatory fly of *Bemisia argentifolii***

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Little information is published about the biology of the predatory fly, *Drapetis nr. divergens* Loew. A laboratory investigation of the

foraging behavior and host stage selection of field collected *D. nr. divergens* presented with a surfeit of silverleaf whitefly, *Bemisia argentifolii* Bellows & Perring eggs, nymphs and adults was undertaken. The foraging behavior of *D. nr. divergens* resembled that of an ambush attack strategist, frequently exhibiting motionless behavior and feeding exclusively on mobile adults. A gut content evaluation of *D. nr. divergens* using a whitefly-specific enzyme-linked immunosorbent assay (ELISA) was conducted on field collected flies. The analysis revealed that 15% of the individuals collected contained whitefly remains in their guts.

### **Impacts of exotic parasitoid foraging strategies on a native Hawaiian community: A detailed simulation**

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A quantitative food webs and simulation modeling are useful tools in the study of community structure and dynamics. We used these tools to examine the ways in which exotic species invasions can affect an entire food web, both qualitatively and quantitatively. Starting with detailed life-history data from a plant-moth-parasitoid quantitative food web from the Alaka Swamp, Kaua, we constructed a detailed simulation model which allows us to reveal potential dynamical consequences for species invasions. We included insect behavior as part of the model, which is not generally done in simulations of complex food webs. The simulations indicate that the ability of exotic parasitoids to use learning to enhance foraging success has repercussions throughout the food web.

### **Field oviposition rates of sugar-fed and sugar-starved parasitoids**

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We compared estimates of fecundity of parasitoids foraging freely in the field that were either sugar-fed or sugar-starved. Fecundity was estimated by first tracking changes in egg loads of parasitoids captured throughout the day to obtain a rate of change in the egg load. This rate was then adjusted using egg load changes of parasitoids kept in field cages that contained either sugar sources or not, but no hosts, throughout the foraging day. The result is an estimate of oviposition rate that takes into account egg maturation and resorption. This estimate was applied to samples of field-caught parasitoids that were classified as either sugar-fed or not using the cold anthrone test. We made this comparison for three species of parasitoid Hymenoptera: *Diadegma insulare* (Ichneumonidae), which attacks diamondback moth, *Macrocentrus grandii*

(Braconidae), which attacks European corn borer, and *Aphelinus albipodus*, which attacks soybean aphid. Our results from *D. insulare* and *A. albipodus* are consistent with a higher oviposition rate for sugar-fed parasitoids. Results for *M. grandii* have not been analyzed at the time of this writing.

### **How parasitoids can estimate habitat quality and respond to information cues within and between patches**

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Patch time allocation in insect parasitoids has mainly been studied as a function of host density and host encounters in single-patch experiments. From such experiments we know that parasitoids respond to host kairomones and encounters with unparasitized hosts. Whether they should and do respond to encounters with parasitized hosts has been debated, but experimental evidence has been equivocal. Moreover, whether host density of a given patch and patch encounter rate influence the patch time allocation on subsequent patches has largely remained unanswered. Using the *Drosophila* parasitoids *Leptopilina heterotoma* and *Asobara tabida*, we investigated behavioral responses of wasps to information cues for estimating patch quality and habitat quality. In our patch-quality experiments we tested responses towards staged encounters with unparasitized vs. parasitized hosts. Corresponding with predictions, we found that wasps use information from encounters with both, unparasitized and parasitized hosts, to allocate their patch time. Moreover, we found that host-encounters influenced the walking speed of wasps within and outside of patches, and thus presumably impact the probability of host and patch encounters. In our habitat-quality experiments we found that wasps did not respond on test patches to variation in host density experienced on pre-test patches. However, wasps responded strongly to variation in patch encounter rates in their patch time allocation and patch exploitation level.

### **Host patch exploitation by competing parasitoids: An asymmetric generalized war of attrition?**

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A recent study used a game theoretical approach to model patch leaving and oviposition behavior of two solitary parasitoid females depleting one patch. Optimal decisions on when to start

superparasitizing and when to leave the patch were addressed in terms of a war of attrition. Superparasitism causes the reward of foraging on a patch to change in time, which makes the game a generalized war of attrition. In addition, differences in arrival time between the two females induce superparasitism to affect their expected payoffs from the patch asymmetrically. Predictions from the model are that a female arriving later on a patch will start superparasitizing and leave a patch sooner than a female arriving earlier on a patch. To study a similar problem empirically, we allowed pairs of females of the solitary braconid parasitoid *Asobara persimilis* to compete for hosts in standardized patches, while we assessed patch residence time and oviposition behavior. Treatments consisted of varying the difference in arrival time and the number of competitors simultaneously present in a patch. The results will be presented and discussed referring to the model.

### Evolution of host use and courtship in sibling species of parasitoids

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*Aphelinus varipes* is reported to have a wide host range, attacking more than 40 species of aphids, and a wide geographic distribution, being endemic throughout Eurasia and perhaps in North America. However, we found that *Aphelinus varipes* from different hosts (*Aphis glycines*, *Diuraphis noxia*, *Rhopalosiphum padi*) and countries (France, Georgia, Israel, China, and Japan) showed different patterns of parasitism when exposed to seven aphid species on four host plant species. Some host species were not attacked at all by some wasp populations. When we attempted to cross these populations, most females from most populations rejected males from other populations. The only crosses where some females accepted alien males involved those from allopatric populations. Although these populations are very similar morphologically, they differ subtly morphometrically, and there are small, fixed differences in DNA sequences among them (see companion paper by Woolley et al). Together our data suggest that these populations are sibling species that have diverged greatly in host use and courtship, but much less so in morphology and putatively highly variable DNA sequences. Despite a weak phylogenetic signal from molecular data, host use and mate acceptance do map well on the molecular phylogeny, with a pattern of increasing specialization in host use and with females more likely to mate with males from more closely related species.

### Host finding abilities increased by cleptoparasitism in bark beetle parasitoids

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The braconid *Coeloides bostrichorum* and the pteromalid *Rhopalicus tutela* are two ectoparasitoid wasps attacking the late instar of the spruce bark beetle *Ips typographus*. *R. tutela* is a polyphagous species attacking numerous bark beetles on pine and spruce while *C. bostrichorum* has been reported as the most efficient parasitoid of *Ips typographus*. Both species search for hosts from the bark surface, preferentially in the upper section on tree. Therefore interspecific encounters between foraging females might be frequent. The host searching efficiency of each species, alone or in the presence of the other, was investigated in the laboratory using the “phloem sandwich” technique. When the females searched alone for hosts, *C. bostrichorum* had better host searching abilities than *R. tutela*. In the presence of *C. bostrichorum*, *R. tutela* increased its host finding abilities through direct displacement and stealing of hosts discovered by *C. bostrichorum*. This cleptoparasitic behavior did not seem to affect the success in host location and parasitism of *C. bostrichorum*. However, cleptoparasitism had a disturbing influence on *C. bostrichorum* as the females only probed at bark locations without a host in the presence of *R. tutela* and as they were observed to fly away from the bark after several acts of aggression from *R. tutela*. This study suggests that cleptoparasitism could partly explain the success of the polyphagous *R. tutela* in coexisting with the specialist *C. bostrichorum*.

### Feeding behavior of *Lygus hesperus* and *L. lineolaris* on whitefly life stages

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*Lygus* spp. are known to feed on, and cause economic loss to a number of important agriculture crops, including cotton alfalfa, vegetables, fruits, and ornamentals. However, they are also facultative predators on insect eggs, aphids, whiteflies, lepidopterous larvae, and other insects. We made observations on instars 3 – 5 and adults of *Lygus hesperus* and *L. lineolaris* in leaf arenas in the laboratory to quantify the behavior and predation on whitefly life stages. Feeding occupied 23 – 60% of the total activity budget for *L. hesperus* and 51 – 64% of the time for *L. lineolaris*. Feeding on the cotton leaves was 70 – 84% of the feeding budget for the different stages of *L. lineolaris* and 34 – 84% for *L. hesperus*. When we reared *L. hesperus* on a meridic diet, more than 50% of the feeding budget was eating whiteflies. The amount of time that *Lygus* spp.

spent on each type of behavior occurred in the following order; fed on plants > fed on whitefly adults (mostly dead or disabled) > fed on nymphs > rested > groomed > walked > fed on eggs > probed adults = probed nymphs = probed eggs. *Lygus* spp. fed 3.3 times on the cotton leaves for each time they fed on whiteflies (all stages combined). All stages of both *Lygus* spp. ate more whitefly nymphs than adults. Very few whitefly eggs were consumed.

### **The effect of Phloxine B and Spinosad combined with protein baits on three species of fruit fly parasitoids**

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Abstract: Laboratory bioassays were conducted to evaluate the effect of Phloxine B and spinosad bait (GF-120) on three species of tephritid fruit fly parasitoids, *Fopius arisanus* (Sonan), an egg-larval parasitoid of oriental fruit fly, *Bactrocera dorsalis* (Hendel), *Diachasmimorpha tryoni* (Cameron), larval parasitoid of *Ceratitidis capitata* (Wiedemann), and *Dirhinus giffardii* Silvestri pupal ectoparasitoid of *Bactrocera cucurbitae* (Coquillet). The first 2 braconids were more susceptible to phloxine B than the third one. Results suggest that rates of 0.017%, 0.023% and 0.025% of phloxine B were enough to kill 50% of male and female *D. tryoni* and *F. arisanus* after 24 hours of exposure, respectively. Testing GF-120 showed that 12.5 ppm, 14.1 ppm, 13.9 ppm, 12.6 ppm of spinosad were enough to kill 50% of female and male *D. tryoni* and *F. arisanus* after 24 hours of exposure, respectively. These results may have important implications for decisions concerning best chemicals suited for reducing pest damage while conserving natural enemies in agricultural systems.

### **Brochosomes: A novel defense mechanism deterring egg parasitism of the glassy-winged sharpshooter**

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Brochosomes are lipo-protein particles produced in the Malpighian tubules of certain Cicadellidae. In several genera of Proconiini, these particles are produced by sexually mature females that collect them in reservoirs as conspicuous white spots on each forewing. Following oviposition, females use their hind legs to transfer the white particles around and on their egg masses. The proposed function of brochosomes applied to eggs has been a source of speculation. While observing oviposition behavior of the native egg parasitoid, *Gonatocerus triguttatus* Girault (Hymenoptera: Mymaridae) on the eggs of the glassy-winged sharpshooter, *Homalodisca coagulata* (Homoptera: Cicadellidae; Proconiini), it was observed that the brochosome particles readily adhered to the tarsi and antennae of the parasitoids during examination of the host eggs. Large

brochosome accumulations caused the parasitoids to stop parasitization behavior, leave the egg mass, and spend much time preening in attempts to remove the particles. Experiments demonstrated that little or no time was spent grooming when brochosomes were removed prior to exposure to parasitoids. SEMs of parasitoids showed large accumulations of brochosome particles adhering to tarsi, antennae, mandibles and other body parts. Since the morphology of brochosomes can differ dramatically between sharpshooter genera and even species, there may be limitations to the efficiency of egg parasitoids currently being imported from other host genera for possible release for management of *H. coagulata* in California. The effects of *H. coagulata* brochosomes on native and exotic parasitoids will be compared.

### **Microsatellites illustrate tritrophic relationships of the parasitoid, *Cotesia congregata* (Say) [Hymenoptera: Braconidae]**

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Eight microsatellite loci were developed and tested for usefulness in determining population structure by assaying two groups of the insect parasitoid, *Cotesia congregata* (Say) [Hymenoptera: Braconidae]. One group originated from *Manduca sexta* L. and *Manduca quinquemaculata* (Haworth) on tomato and tobacco ("solanaceous group") and the other from *Ceratonia catalpa* (Boisduval) on catalpa ("catalpa group"). One locus was monomorphic and seven were polymorphic. Allelic distributions differed significantly between the solanaceous and catalpa groups ( $P=0$  for each locus and overall, Fisher's exact test).  $F_{ST}$  was  $<1$  for within-group comparisons across all loci;  $F_{ST}$  was  $>0.47$  for between-group comparisons across all loci. These results lend support to the hypothesis that host plant association is a significant factor influencing population structure of this species. Wasps from the solanaceous and catalpa groups were examined further for mtDNA and rDNA variation to investigate their status as sibling species. One conserved mtDNA gene (16S) showed considerable population genetic variation and a single fixed nucleotide difference between the two groups. Investigation of the more variable mtDNA D-loop is now underway to evaluate the possibility that these groups are incipient species.

### **Olfactory responses by *Metaphycus* sp. nr. *flavus* to semiochemicals released from one of its hosts, *Coccus hesperidum***

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Successful parasitoid-host associations depend on a parasitoid's ability to locate and recognize its hosts in a complex and heterogeneous environment, and to produce offspring from those hosts it locates and accepts. In 1996, we imported *Metaphycus* sp. nr. *flavus* (Howard) (Hymenoptera: Encyrtidae) into California from Turkey for release against citricola scale, *Coccus pseudomagnoliarum* (Kuwana) (Hemiptera: Coccidae), in San Joaquin Valley citrus as a classical and/or augmentative biological control agent. We rear *M. sp. nr. flavus* on excised *Yucca* sp. leaves infested with brown soft scale, *Coccus hesperidum* L. The infested leaves are maintained hydroponically in the University of California, Riverside, Insectary. To improve our mass rearing, we sought to determine whether *M. sp. nr. flavus* recognizes soft brown scale as a host. Using a Y-olfactometer, we tested whether *M. sp. nr. flavus* was attracted to; 1) leaves infested with 26, 27, 28, 29, or 30 d-old scale versus uninfested leaves, 2a) leaves previously infested with brown soft scale but with the scale removed and the leaves washed with distilled water versus leaves infested with brown soft scale, 2b) unwashed versus washed leaves after the brown soft scale had been removed and 3) filter paper disks impregnated with the wash water from the preceding bioassay versus filter paper disks impregnated with distilled water. The bioassays showed that *M. sp. nr. flavus* was preferentially attracted to; 1) leaves infested with 26, 27, 28 and 29 d-old scale but not to leaves infested with 30 d-old scale; 2) leaves infested with soft brown scale or their residue, but not to leaves from which the scale had been removed and the leaves washed with distilled water; and 3) to filter paper disks impregnated with distilled water used to wash off the scale residue after the brown soft scale had been removed from the leaf but not to disks impregnated with distilled water. We conclude that *M. sp. nr. flavus* is equally attracted to 26 to 29 d-old brown soft scale or their residues. These are the scale ages we use to mass-produce the parasitoid in the insectary.

#### **Host habitat location mediated by olfactory stimuli by *Anaphes iole* (Hymenoptera: Mymaridae), an egg parasitoid of *Lygus hesperus* (Hemiptera: Miridae)**

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*Anaphes iole* Girault is the most commonly encountered parasitoid of *Lygus* eggs in the U.S. Chemicals derived from adult hosts, and physical properties of protruding eggs are used as host recognition and acceptance cues by this parasitoid. However, it is unknown whether *A. iole* relies on volatile cues to locate hosts. Therefore, olfactometer and flight chamber experiments were conducted to assess the attractiveness of *A. iole* towards volatiles derived from various host plant complexes. The responses of female parasitoids

to odors emanating from host plants harboring *Lygus hesperus* eggs (infested plants) were measured in a four-arm olfactometer, and their attraction to cotton plants harboring different numbers of eggs were measured in a flight chamber. The olfactometer was similar to that described by Vet et al. (1983), and the flight chamber consisted of a rectangular Plexiglas cage (65 x 35 x 40cm) with two compartments at one end where infested and uninfested plants were placed. Results showed that *A. iole* females spend significantly more time in odor fields corresponding to infested host plants (common groundsel, annual ragweed, redroot pigweed, alfalfa and cotton) compared to control odor fields in the olfactometer, though differences were not detected among host plant species. Significantly more wasps arrived to cotton plants with medium (48.4 eggs) and high (95.9 eggs) infestation levels compared to uninfested plants, while similar numbers were recovered on cotton plants with low infestation (8.7 eggs) compared to uninfested plants. These results represent the first report indicating that *A. iole* are attracted at a distance to plants harboring *Lygus* eggs.

#### **Key predators of *Helicoverpa armigera* in Australian cotton crops.**

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Australian cotton crops have a significant community of native insect predators with potential to control the key pest *Helicoverpa armigera*. The abundance of predatory arthropods increases over the growing season (November to February) when the use of broad-spectrum insecticides is avoided. The rising costs of chemical control and widespread development of insecticide resistance have led to increased interest in conservation biological control. However for biological control to be successful, the key predators of *H. armigera* must be identified and their impact on pest populations measured. The development of a serological test (ELISA) to detect predation on *H. armigera* eggs and larvae has played a major role in this process. Protocols have been developed for a predatory beetle, *Dicranolaius bellulus* (Melyridae), and the predatory bug, *Pristhesancus plagipennis* (Reduviidae). Predators were collected from commercial cotton farms in northern NSW during the 2001-02 and 2002-03 seasons and predation of *H. armigera* quantified for *D. bellulus*. This technique will be extended to additional predator species in the future.

#### **Olfactory responses of *Dicyphus hesperus* Knight (Heteroptera: Miridae) to prey and plant odors.**

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*Dicyphus hesperus* Knight (Heteroptera: Miridae) is an omnivorous generalist predator that is being developed for biological control of arthropod pests of greenhouse-grown tomatoes and peppers in British Columbia, Canada. Responses of female *D. hesperus* to pairs of odor sources were determined in the laboratory using a y-tube olfactometer. Females chose the odor of greenhouse whitefly (*Trialeurodes vaporariorum* Westwood (Homoptera: Aleyrodidae)) on tomato foliage significantly more frequently than the odor of clean tomato foliage. However, no differences in the number of responses were recorded when the odors of two-spotted spider mites (*Tetranychus urticae* Koch (Acari: Tetranychidae)) on tomato foliage and clean tomato foliage were compared or the odors of whitefly on tomato foliage and mites on tomato foliage were compared. Females also chose the odor of green-peach aphids (*Myzus persicae* (Sulzer) (Homoptera: Aphididae)) on pepper foliage significantly more frequently than the odour of clean pepper foliage. No differences in the number of responses were recorded when the odors of cabbage looper eggs (*Trichoplusia ni* (Huebner) (Lepidoptera: Noctuidae)) on pepper foliage and clean pepper foliage were compared or the the odours of green-peach aphids on pepper foliage and cabbage looper eggs on pepper foliage were compared. These results are discussed as they relate to the use of *D. hesperus* for biological control in vegetable greenhouses.

### **The adaptive significance of sibling egg cannibalism in the Coccinellidae: Comparative evidence from three species.**

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We examined sibling egg cannibalism behaviour and its consequences in three aphidophagous coccinellid species that all lay clustered eggs: *Cycloneda sanguinea* L., *Harmonia axyridis* Pallas, and *Olla v-nigrum* Mulsant. There was variation among species in the proportion of eggs laid singly versus in clusters (*C. sanguinea* > *H. axyridis* = *O. v-nigrum*), the synchronicity of egg hatch within clusters (*H. axyridis* > *C. sanguinea* = *O. v-nigrum*) and the proportion of eggs cannibalised by early-hatching larvae (*O. v-nigrum* > *C. sanguinea* > *H. axyridis*). The dispersal of neonate larvae from their egg clusters was delayed by the availability of sibling eggs for cannibalism. Egg cannibals survived to adulthood at the same rate as control larvae in *H. axyridis* and *O. v-nigrum*, and at a higher rate in *C. sanguinea*, suggesting that the *Ephestia* egg diet was sub-optimal for this species. In all three species, larvae that cannibalised eggs as neonates molted to the second instar sooner than did their non-cannibalising counterparts, regardless of gender. This translated into reduced total developmental time for both sexes in *H. axyridis*, but only for males in *C. sanguinea* and only for females in *O. v-nigrum*. Adult females weighed significantly more than adult males in all three species and female cannibals were heavier as adults than were non-cannibalising females in *H. axyridis* and *O. v-nigrum*, whereas males had similar weights. Egg cannibalism had no effect on adult weight in *C. sanguinea*. We hypothesize that the benefits of sibling egg cannibalism accrue in a

gender-specific manner such that females potentially gain more than males, but only if the subsequent larval diet is of high quality.

### **The developmental strategy of an aphidiine parasitoid: Is host quality influenced by temperature or endosymbionts?**

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Host size is commonly considered to be an important determinant of host quality for insect parasitoids. While this is clearly the case for idiobionts parasitoids, host size at the time of oviposition would seem a less predictable indicator of host quality for koinobiont parasitoids. Aphidiine parasitoids are unusual among koinobionts in that they can attack the full range of host developmental stages, and thus a very broad range of host sizes, and frequently show a pattern of increasing progeny size and sex ratio with host instar (and size). These characteristics are more typical of idiobiont parasitoids. By manipulating aphid size in relation to stage of development through rearing *Aphis fabae* at either 15°C or 30°C, cohorts of 30 aphids of each instar were exposed to parasitism by individual mated female *Aphidius transcaasicus* at 22.5°C for a period of 5 h. Parasitized aphids were subsequently reared at the intermediate temperature of 22.5°C until parasitoid progeny emerged. We show that at an initial rearing temperature of 15°C parasitoid progeny sex ratio and size increased linearly with the fresh weight of the successive aphid instars at the time of attack. In contrast, at a rearing temperature of 30°C, this pattern was reversed, with both progeny sex ratio and size declining with fresh weight at the time of attack. The effect of temperature on the nutritional status of aphids, the activity of their obligate endosymbionts, and their future growth potential following parasitism are considered as possible determinants of host quality in aphid hosts for aphidiine parasitoid development.

### **Glassy-winged sharpshooter biological control in California – research and application**

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The biological control of the glassy-winged sharpshooter, *Homalodisca coagulata*, has received considerable attention over

the past three years. Much of the research into biological control has now been applied and ongoing research is being employed to optimize biological control efficacy. Work carried out in conjunction with the California Department of Food and Agriculture has led to the release of four species of Mymarid parasitoid into California. The current status and future directions for improving biological control are also presented.

### **Avoidance of intraguild predators by parasitoids: Chemically mediated behavioural mechanisms and field evaluation**

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In the parasitoid-predator-herbivore system, intraguild (IG) predators can affect parasitism in two ways: Firstly, IG predators prey on parasitized hosts, i.e. intraguild predation (IGP), and secondly, parasitoid females avoid oviposition in host patches where IG predators are present. Some studies on parasitoid-predator interactions have reported that IGP leads to a reduction of parasitism. However, the effects of IG predator avoidance on parasitism and characteristics of chemical compounds which mediate the avoidance behaviour of parasitoids have not clearly been determined. We investigated the effect of IGP by the seven-spot ladybird, *Coccinella septempunctata*, on aphids parasitised by *Aphidius ervi*, and the effect of IG predator avoidance by adult female *A. ervi* on parasitism rates of the pea aphid, *Acyrtosiphon pisum*. To estimate the effects of IGP and IG predator avoidance, we conducted both field and laboratory experiments.

In the field, we found that parasitism rates were lower in patches containing larger IG predator populations. Laboratory experiments showed that parasitoid females avoided plant surfaces on which IG predators had recently foraged. Non-volatile fractions in chemical trails left by foraging ladybirds on plant surfaces significantly induced avoidance behaviour by *A. ervi*. Parasitism rates of aphids on broad bean plants that had been sprayed with a mixture of the chemicals were significantly lower than those on control plants. IGP is not likely to affect parasitism rates negatively, because IG predators didn't show preference for either unparasitized or parasitized hosts. Thus, we conclude that in this system IG predator avoidance by parasitoid females may have more important effects on parasitism.

### **The role of conservation in biological control of *Bemisia tabaci*: A life table approach**

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Within agricultural systems there are multiple abiotic and biotic mortality forces acting on pest insect populations. These forces may be naturally-occurring, as in the case indigenous natural enemies, or man-made as exemplified by insecticides or cultural manipulations. Estimating the contribution and effect of each mortality factor may be difficult because of interactions between factors resulting in mortalities that may be either replaceable or indispensable. From the perspective of conservation biological control, estimating mortality caused by extant natural enemies within the context of other mortality agents is important to understanding the base contribution of biological control to pest suppression, and to evaluating the benefits of manipulating the habitat and other system inputs. Field studies examined the role of natural enemy conservation in cotton within the context of alternative management strategies for *Bemisia tabaci* (Gennadius) based on selective and non-selective insecticides. *In situ*, cohort-based life tables were used to structure, quantify, analyze and interpret the effects of natural enemies relative to the effects of other simultaneous mortality factors acting on pest populations in these systems. Results showed that single applications of selective insecticides initially functioned by replacing some mortality from predation and parasitism, and contributing an immediate, and essential, level of irreplaceable mortality. However, because these selective materials did not significantly disrupt natural enemies populations, parasitoids, and especially predators, were able to supply irreplaceable mortality that contributed to pest suppression for the remainder of the season. In contrast, repeated applications of conventional insecticides were required for pest control because natural enemy populations were reduced and unable to contribute significant irreplaceable mortality. This study demonstrates the role of multiple mortality factors in managing *B. tabaci* and provides a mechanistic understanding of the important contribution of conservation biological control.

### **Surface lipids of whitefly parasitoids**

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Surface lipids from 3 collections of *Encarsia formosa* and *Eretmocerus emeratus*, *E. hayati* and *E. mundus* were characterized by gas chromatography-mass spectrometry. The surface lipids were largely hydrocarbons, mainly methyl-branched alkanes, ranging in size from about C23 (tricosane) to C49 (dimethylheptatetracontane). *Encarsia* hydrocarbons were 15-23% *n*-alkanes but *Eretmocerus* species had 2% or less *n*-alkanes. Trace amounts (<1%) of *n*-alkenes were only detected in the surface lipids of *E. formosa*. All *Eretmocerus* species had similar GC-MS profiles and the major peaks ranged from C31 (2-methyltriacontane) to C37 (dimethylpentatriacontane). The average composition of

*Eretmocerus* hydrocarbons was: *n*-alkanes (2%), 2-methylalkanes (19%), 3-methylalkanes (4%), internally branched monomethylalkanes (14%), 5,X- and internally branched dimethylalkanes (58%), and trimethylalkanes (3%). Major peaks were 2-methyltriacontane (14%), 15-, 13- & 11-methylhentriacontanes (6%), 11,15- & 13,17-dimethylhentriacontanes (18%), 11,15- & 13,17-dimethyltrtriacontanes (22%), and 11,15- & 13,17-dimethylpentatriacontanes (10%). *Encarsia* had more hydrocarbon classes than *Eretmocerus*: Major components ranged from C27 (heptacosane) to C33 (dimethylhentriacontane). Average composition of *Encarsia* hydrocarbons was: *n*-alkanes (17%), 4-methylalkanes (1%), 2-methylalkanes (<1%), 3-methylalkanes (25%), internally branched monomethylalkanes (29%), 5,X- and internally branched dimethylalkanes (21%), 3,X-dimethylalkanes (4%), and trimethylalkanes (1%). Major individual peaks were C27 (5%) and C29 (8%), 3-methylheptacosane (13%) and 3-methylnonacosane (10%), 15-, 13-, 11-, 9- & 7-methylnonacosanes (15%), and 9,13- & 13,17-dimethylnonacosanes (10%). Notable differences in the relative amounts of hydrocarbon classes between [*Encarsia*]-(*Eretmocerus*) were: *n*-alkanes [high]-(low), 2-methylalkanes [low]-(high), 3-methylalkanes [high]-(low), 4-methylalkanes [low]-(none), internally branched monomethylalkanes [high]-(low), internally branched dimethylalkanes [low]-(high), 3,X-dimethylalkanes [high]-(low), and internally branched trimethylalkanes [low]-(high).

### **The hunt for Mymarommatidae in Costa Rica, or the density of microhymenoptera in a tropical forest.**

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Despite an intensive sampling programme for Hymenoptera in Costa Rica since 1985 the family Mymarommatidae has yet to be found there. The family has a virtually cosmopolitan distribution including the New World but is infrequently collected. Adults are relatively small, less than 1mm in length and surprisingly easy to overlook when sorting samples. Specimens have been collected in North America and several Neotropical countries including Belize, Venezuela and Brazil. During a recent visit to Costa Rica in February 2003, a determined effort was made to find Mymarommatidae using a sweep-net fitted with a detachable 4mm screen. This produced a single female specimen of an undescribed species that was collected in seasonal dry forest in Guanacaste Province in the northwest of Costa Rica (Bosque Humedo). The resulting samples could be used to estimate the relative abundance and even densities of smaller Hymenoptera in the lower vegetation of several forest types that were visited. The 4mm screen allowed fairly large insects to pass through, the largest being a 12mm long wasp whilst 8mm long worker ants were not uncommon in the samples. Results are presented in Table 1 and Fig. 1 and show that, in most samples, Chalcidoidea are the dominant smaller Hymenoptera representing slightly more than half of all individuals collected whilst ants make

up about one-half of the remainder. Within the Chalcidoidea, parasitoids of eggs, armoured scales and whiteflies were by far the most numerous, with the genus *Encarsia* representing about 10% of the total Hymenoptera in some samples. From these samples, estimates of the density of smaller Hymenoptera per unit area from ground level to 2.3m ranged from two individuals per sq.m. in drier habitats to 18 per sq.m. in open secondary vegetation with the “normal” density at about 7.7 individuals per sq.m. in moist forest between 50m and 600m above msl.

### **Tritrophic effects of host plant chemistry on the polyembryonic parasitoid *Copidosoma sosares*.**

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While tritrophic effects of host plant chemistry on host finding and acceptance have been well-documented in parasitoids, far fewer studies have examined the potentially negative relationships between plant defensive chemistry and fitness correlates of herbivore natural enemies. We examined the effects of host plant chemistry in a tritrophic system native to Eurasia consisting of three apiaceous host plants (*Pastinaca sativa*, *Heracleum sphondylium*, and *H. mantegazzianum*), the parsnip webworm (*Depressaria pastinacella*), and the polyembryonic encyrtid, *Copidosoma sosares*. In field populations in The Netherlands, two furanocoumarins (known to confer resistance against parsnip webworms) are negatively correlated with the probability of parasitism, clutch size, and survivorship. Dutch parsnip populations produce higher constitutive levels of furanocoumarins than introduced, naturalized populations in the Midwestern US. These parsnip populations harbor webworms, but *C. sosares* (as well as any other natural enemies of the webworm) is notably absent. That Dutch parsnip populations produce significantly lower furanocoumarin levels than Midwestern US parsnip plants suggests *C. sosares* reduces webworm herbivore pressure sufficiently to allow Midwestern US parsnip plants to invest less in physiologically-costly furanocoumarins. Lower numbers of webworms per parsnip plant in Dutch parsnip populations compared to Midwestern US populations supports this contention. Recent discovery of *C. sosares* in parsnip populations in the western US provides a unique opportunity to explore how tritrophic relationships are altered during the course of introduction in situations where the trophic structure is intact (western US) and where the third trophic level is absent (Midwestern US).

### **Identification of tachinid parasitoids (Diptera: Tachinidae) of Nearctic *Choristoneura* species (Lepidoptera: Tortricidae)**

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Leafrollers of the genus *Choristoneura* (Lepidoptera: Tortricidae) comprise 17 species in the Nearctic region and include such serious agricultural and forestry pests as the spruce budworm (*C. fumiferana*), western spruce budworm (*C. occidentalis*), large aspen tortrix (*C. conflictana*), jack pine budworm (*C. pinus*) and obliquebanded leafroller (*C. rosaceana*). Natural control factors that help to keep populations of these pests in check include endoparasitoids of several insect families, in particular the Tachinidae (Diptera), Braconidae (Hymenoptera) and Ichneumonidae (Hymenoptera). There are about 25 species of Tachinidae that have been reported from Nearctic *Choristoneura* species but only about half of these are commonly recorded; the other half represent rare or accidental parasitism of *Choristoneura* species or dubious records. An illustrated identification guide is under preparation to separate the adults and puparia of the confirmed tachinid parasitoids of Nearctic *Choristoneura* species. The guide will include an illustrated key, digitally enhanced images of the adult and puparium of each species, and information on the life history of each species.

#### **Bacterial symbionts in aphids confer resistance to parasitic wasps**

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Molecular diagnostic tools have recently shown that bacterial symbionts of arthropods are extremely common, yet the effects of these symbionts on their hosts are largely unknown. We have found that facultative, vertically transmitted symbionts of the pea aphid, *Acyrtosiphon pisum*—called secondary symbionts (SS) to distinguish them from the obligate symbiont *Buchnera aphidicola*—confer resistance to the dominant natural enemy of pea aphid, the hymenopteran parasitoid *Aphidius ervi*. Isolates of two of the three types of symbionts tested, the T- and the R-type (both independent lineages in the  $\gamma$ -Proteobacteria, and also called PABS and PASS, respectively), confer resistance to parasitoid attack by causing mortality of developing parasitoid larvae. Furthermore, parasitized R- and T-infected aphids produce more early offspring than parasitized uninfected controls indicating a direct fitness benefit to infection. Other work is focused on exploring the generality of this phenomenon, including examining the effects of multiple infections on host-parasitoid interactions. This interaction between a symbiotic bacterium and a host natural enemy provides a mechanism for the spread and persistence of these symbionts, and may be an important component of the widespread variation in susceptibility of pea aphid clones to parasitoid attack.

#### **Presence of teratocytes in Hymenoptera Aphelinidae: Comparative development in *Encarsia berlesei* and *Encarsia citrina***

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In several hymenopteran parasitoids, belonging to Ichneumonoidea and Platygastroidea, the extraembryonic membrane dissociates at hatching into individual cells, known as teratocytes. Teratocytes have never been reported in the Chalcidoidea, although peculiar extraembryonic membranes have been often described. We report for *Encarsia berlesei* and *Encarsia citrina* (Hymenoptera: Chalcidoidea: Aphelinidae) the dissociation of the extraembryonic membranes into cells possessing morphological and embryological features of teratocytes. In *E. berlesei* the membrane dissociated at larval eclosion into 4-9 larger cells and about ten smaller cells, which scarcely doubled their size during maturation. In *Encarsia citrina* the membrane dissociated into five large cells which did not appreciably increase in size during larval development. The dissociated cells of *E. berlesei* presented microvilli on their surface, and cytoplasm provided with abundant rough endoplasmic reticulum and vesicles. These findings provide the first evidences for the presence of teratocytes in the superfamily Chalcidoidea.

#### **Recovery of parasitoids (Hymenoptera: Eulophidae and Trichogrammatidae) released for biological control of *diaprepes abbreviatus* (Coleoptera: Curculionidae) in Florida**

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A biological control program was initiated to develop and implement strategies to manage *Diaprepes abbreviatus* (L.) in response to the spread of this weevil in Florida and the latest infestations in Texas and California. This classical biological control effort is collaborative, involving state, federal, private institutions and

international cooperators in foreign exploration, quarantine, mass production, release, and recovery efforts. A lack of native parasitoids attacking this weevil in Florida (Hall et al., 2001) and past failures to establish exotic parasitoids against it (Beavers et al., 1980) motivated these new efforts to introduce, release and evaluate candidate egg parasitoids (Schauff, 1987; Peña et al., 1998; Peña and Amalin, 2000; Hall et al., 2003). The parasitoids released were, *Ceratogramma etiennei* (Delvare) (Hymenoptera: Trichogrammatidae), *Quadrastichus haitiensis* (Gahan) and *Aprostocetus vaquitarum* (Wolcott) (Hymenoptera: Eulophidae). Here we summarize parasitoids tested in quarantine, recoveries, and relative abundance of parasitoids from release sites in citrus, ornamentals and natural plant habitats.

### **A CFB-group bacterial symbiont induces cytoplasmic incompatibility in the parasitoid wasp *Encarsia pergandiella***

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Many vertically-transmitted symbionts of arthropods increase in frequency by altering reproduction in their hosts. These host reproductive manipulations are diverse, and include cytoplasmic incompatibility, induction of parthenogenesis, male-killing, and feminization of male hosts. Examples of the first three of these four manipulations are known in the parasitic Hymenoptera, the most common type being parthenogenesis induction. One symbiont lineage in the  $\alpha$ -Proteobacteria, *Wolbachia*, is the only bacterium known to cause all of these effects, and has been thought to be unique in causing cytoplasmic incompatibility, in which the fecundity of uninfected females is reduced after mating with infected males. Here we provide evidence that an undescribed symbiont in the *Cytophaga-Flexibacter-Bacteroides* (CFB) group causes cytoplasmic incompatibility in a sexual population of the parasitic wasp *Encarsia pergandiella* (Hymenoptera: Aphelinidae). We established an asymbiotic line of wasps by treating adults with antibiotics for three generations. Wasps were crossed in all four possible combinations of infected and uninfected individuals. In the cross predicted to be incompatible, infected (I) males x uninfected (U) females, progeny production was severely reduced, with these females producing only 12.5% of the number of progeny in other crosses. The incompatibility observed in this haplodiploid species was the female mortality type (and not the male development type); dissections showed that most progeny from the incompatible cross died as eggs. The 16S rDNA sequence of this symbiont is 99% identical to a parthenogenesis-inducing symbiont in other *Encarsia*, including a Brazilian lineage of parthenogenetic *E. pergandiella*, and 96% identical to a feminizing symbiont in haplodiploid *Brevipalpus* mites. Thus, this recently discovered symbiont lineage is capable of inducing three of the four principle manipulations of host reproduction known to be caused by *Wolbachia*.

### **Visually partitioning nocturnal and diurnal predation of lepidopteran eggs: Lessons in the determination of key predators**

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Studies of predators (and predation) have focused largely on field studies of predator populations in certain crops and laboratory studies of predators observed in the field crops; relatively few have attempted to accurately document the predators responsible for mortality of particular pests in the field. The studies that have been conducted have used a variety of techniques including radio-isotopes to label prey, visual observation, and molecular techniques. In many cases these studies have resulted in small samples sizes and/or there are biases associated with these techniques that have not been adequately addressed. I conducted studies to more carefully describe the guild of predators that feed on eggs of lepidopteran pests of field crops, particularly *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae) using visual observation. A primary focus of these studies was to partition diel patterns of predation and more accurately characterize nocturnal predation. Visual observations on predation of lepidopteran eggs were conducted in 1993 and 1994 in corn and soybean grown in Kentucky and from 2001 to 2003 in cotton, corn and soybean grown in south Texas. Results were compared to those from studies using other techniques. In both locations predator taxa, primarily nocturnal, were observed that had previously been unknown or underestimated in their importance as predators of lepidopteran eggs. The wandering spiders and the Phalangidae are two examples of important predators of eggs that have been typically unrecognized. Several diurnal predators that have been studied extensively appeared to be less important than previously believed. Predator complexes will be described and compared to those observed in other studies and the implications for biological control of lepidopteran pests discussed.

### **Do parasitoids of the apple fruit moth attack their host when it is developing on a secondary host plant?**

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Is it possible to develop a strategy for conservation biological control of a pest insect that has a non-crop plant as primary host? The apple fruit moth, *Argyresthia conjugella* (Yponomeutidae), is only a pest problem in population peak years and when its primary host rowan, *Sorbus aucuparia* (Rosaceae), has a low fruit production. However, *A. conjugella* is then causing a severe reduction in the quality of the apple fruit crop, *Malus domestica* (Rosaceae). In spring, adult *A. conjugella* emerge, mate and then lay eggs during June and July on developing fruits of apple and rowan. The larva burrows into the fruit and feeds on developing seeds until maturity where it leaves

the fruit, usually during August and September. Pupation takes place in a cocoon made in the vegetation or soil surface during autumn. *A. conjugella* is univoltine in Sweden. A suite of parasitoids is known to be associated with the apple fruit moth on its primary host, rowan. Usually, 10-15 % of *A. conjugella* larvae developing in rowan are parasitized, but up to 80% parasitism has been reported from Norway. So far we know, nothing is known about the parasitoids impact on *A. conjugella* on apples. There are a few morphological differences between apples and rowan that may influence parasitoid oviposition behavior; first of all fruit distribution differs; rowan berries are in clusters of up to 200 berries, whereas apples are in clusters of a few fruits. One rowan berry will usually host a single *A. conjugella* larvae, whereas a few larvae can develop within an apple. Also the size of the host fruit differs markedly; the distance from the fruit surface to the developing seed and the developing *A. conjugella* larvae is at least 5 times as long in apples compared to rowan berries. *A. conjugella* is known to migrate long distances (several km), but are the parasitoids able to move between the different host plants? Is *A. conjugella* able to attract the parasitoids to apple orchards? Will plantation of flowering perennials and bushes in the orchard attract the parasitoids of *A. conjugella*?

#### **Biological observations and predation behavior of *Mulsantina mexicana* (Coleoptera: Coccinellidae) fed with *Aconophora elongatiformis* (Homoptera: Membracidae)**

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*Aconophora elongatiformis* is a sap-sucking insect that causes damage in tender branches of *Tecoma stans* L. (H.B.K.), a valuable ornamental tree of Bogotá. Observations of frequency and abundance of natural enemies of *A. elongatiformis* in attacked trees in Bogotá revealed that *Mulsantina mexicana* contributed to the natural regulation of this pest. Since there was no information related to this species of Coccinellidae in the country, preliminary work was necessary to confirm its identification, biology and predation behavior. Both prey and predator were maintained under semi-controlled laboratory conditions. The number of nymphs of *A. elongatiformis* consumed per day, as well as the development time of larval instars and longevity of adult stage of *M. mexicana* were determined. Under laboratory conditions, all four larval instars and the adult stage of *M. mexicana* fed on all the nymphal stages of *A. elongatiformis*. The number and size of the prey consumed differed according to the size of the predator. Larval development and adult longevity of *M. mexicana* fed with *A. elongatiformis* averaged 90 days. In the field *A. elongatiformis* is not the only prey consumed by *M. mexicana*, however the duration of the development time and number of prey that it is able to consume justify the recommendation for development of practices conducive to the conservation of *M. mexicana* populations in *T. stans* trees.

#### **Host-shifts from ooparasitism to sessile Sternorrhyncha, in the Proctotrupomorpha: Are chalcids primitively egg-parasitoids?**

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The monophyly of the Chalcidoidea is agreed upon by most authors, despite our current poor understanding of the internal relationships between the families comprising it. The relationships (Mymarommatoidea + (Mymaridae + (remaining Chalcidoidea))) have been proposed by several authors on morphological evidence. A sister-group relationship to the clade comprising (Mymarommatoidea + (Mymaridae + (remaining Chalcidoidea))) has been proposed for Platygastroidea. This paper examines the frequency and apparent ease of host-shifting from ooparasitism to sessile Sternorrhyncha among the chalcidoids and platygastroids. One hypothesis proposes that the basal biology for the Chalcidoidea was that of egg parasitism. The possibility that a shift from ooparasitism to nymphal Sternorrhyncha resulted in an explosion of available niches leading to the current morphological and biological diversity of the chalcidoids has also been proposed. These hypothetical scenarios are discussed in the light of new molecular evidence for proctotrupomorpha relationships.

#### **Determination of plant foraging preferences in the aphid parasitoid *Aphidius colemani*: Emergence conditioning, learning and memory.**

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Female *Aphidius colemani* showed a preference for foraging on the plant on which they were reared. This preference disappeared when the parasitoid pupae were dissected from their mummy cases prior to emergence but, when they were given a mummy case taken from a different plant to examine immediately after emergence they showed a distinct preference for the plant on which this mummy had developed, indicating that chemical information on the surface of the mummy (i.e. the skin of the dead aphid) induced plant foraging preferences. Thus, a female parasitoid is conditioned at the time of emergence by chemical information on its own mummy case, relating to the plant on which it has developed. However, this preference can be changed through learning experiences during subsequent encounters with aphid hosts or mummy cases from a different plant, allowing plasticity in foraging behaviour. When

given a sequence of mummy cases, taken from a range of different plants, to examine after emergence, the plant relating to the last mummy encountered was always preferred but, if this plant was not available, preference reverted to the plant associated with the penultimate mummy encountered. This indicates retained memory for a series of experiences. However, exposure to low temperatures (chilling) shortly after the final encounter nullified preference for the associated plant and preference again reverted to the plant associated with the penultimate mummy encountered. This suggests that both short-term and long-term memories are involved and that the former can be disrupted by cold treatment.

### **Identification and impact of parasitoids on tarhished plant bugs (*Lygus* spp.) in Central and Northern Sweden**

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*Lygus* spp. are generalist herbivores and occur as pests on a wide range of crops in Northern Europe and North America. In the development of conservation biological control strategies for *Lygus* spp. in Sweden more information is needed on the impact of different natural enemies. Initially we have determined the occurrence and the impact of parasitism on adults and nymphs of the most common *Lygus* species in alfalfa, barley, red clover and oil seed rape. Nymphs and adults of *Lygus* spp. were collected by sweep netting in several fields in Central and Northern Sweden for estimation of their parasitisation rate (by dissection) and identification of parasitoid species (from reared *Lygus* specimens). The dominant *Lygus* species was in both locations *L. rugulipennis* (75-97 %). The only parasite species emerging from adult *Lygus* spp. was the tachnid fly *Phasia obesa*. All examined *Lygus* specimens had developed the previous year and hibernated before parasitism was determined. Parasitisation rate was significantly higher in *Lygus* populations from Northern Sweden reaching up 38 % compared with a maximum of 13 % from Central Sweden. From nymphs of *Lygus* spp. the hymenoptera *Peristenus pallipes* was the only species emerging. The overall nymph parasitism in Northern Sweden was 10% in red clover and between 7 % and 10 % in barley fields. In Central Sweden *P. relictus*, *P. pallipes* and *P. varisae* emerged from *Lygus* nymphs. In Central Sweden the overall nymph parasitism was differing more between the crops; with the lowest parasitisation rate in alfalfa (1.4 %) and highest in spring sown oil seed rape (20.6 %). No parasitism was recorded in specimens from barley fields in Central Sweden.

### **Morpho-functional features of antennal multiporous gustatory sensilla in female parasitic Hymenoptera**

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Various kind of sensory structures have been described in insect parasitoids, among which olfactory and gustatory sensilla are the most studied because of their involvement in sex and host recognition mechanisms. Numerous studies have been focused on olfactory sensilla, and sometimes these structures have been misinterpreted being in fact release site of glands or involved in gustation. In the latter case, these sensory structures (which have been found only ventrally on female antennae in the most important parasitoid families, i.e. Trichogrammatidae, Mymaridae, Scelionidae, Platygastriidae, Eulophidae, Diapriidae) show peculiar morphological features, i.e. a cuticular apparatus consisting of a basiconic shaft with a localised multiporous area; cellular components made up of a number of sensory neurons ranging from 6 up to 400. In some cases (Scelionidae) these multiporous sensilla have tubular accessory glands that release their secretion through the sensillum socket. The number of these gustatory sensilla is variable, and it seems to be correlated with the number of sensory neuron found per sensillum. These morphological characters, combined with behavioural observations, strongly suggest a gustatory function, although electrophysiological studies are still needed to confirm this hypothesis. We propose for these sensory structures the term “Multiporous Gustatory Sensilla” (MGS), based on their morpho-functional features.

### **Lifetime reproductive success of adult herbivores and parasitoids in the field**

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Insect parasitoids and insect herbivores with parasite-like life histories have proved to be excellent model systems for developing theory in behavioral and evolutionary ecology and for testing theoretical predictions in the laboratory. Tests of predictions in nature have proven to be much more difficult, however, in large part because reproduction by adult females is distributed widely over space and time. Tests in nature are now critical to advancing our knowledge of parasitoid biology. Here we report a new approach to measuring realized lifetime oviposition success of individual female herbivores and parasitoids in nature. Our approach is based upon (1) studies of strictly proovigenic species (i.e., species that mature all their eggs before emerging as adults) that also do not resorb eggs and (2) a simple technique for capturing adult females at the end of their lives and quantifying their residual egg load. We use this technique to assess the roles of egg limitation, time limitation, predation risk, and body size in shaping female reproductive success in nature. Early empirical results from two systems will be presented, including a parasite-like herbivore (the

gall midge *Rhopalomyia californica*) and a parasitoid (*Anagrus* sp.).

### **Differences in antennal multiporous gustatory sensilla in *Trissolcus basalis* and their possible involvement in the host selection process**

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*Trissolcus basalis* female (Hymenoptera :Scelionidae) carry Multiporous Gustatory Sensilla (MGS) on the antennae. Morphological investigations carried out on these structures showed differences on the external cuticular features of the apical multiporous area between the sensillum on the apical antennomere and the other sensilla. *T. basalis* host acceptance is induced by host recognition kairomone present in the host egg glue. *T. basalis* female starts antennation when it comes into contact with the egg (encounter), then it mounts the egg-masses and continues more extensively, standing on the host (examination). Host acceptance or rejection then can follow. The encounter and examination behaviours are affected by the progressive ablation of the MGS-bearing antennomeres varying the allocation time of the encounter and of the examination behaviour. With amputations the encounter duration increases, while the examination time decreases. Significant time shifts start after the ablation of A11 and A10 antennomeres. These first results suggest that host recognition occurs during the encounter, and host discrimination during the examination. MGS play an important role in host recognition and host discrimination behaviour, mainly in the encounter and the examination phases respectively.

### **A database on host-parasitoid associations in pentatomid bugs**

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Given the economic importance of pentatomid bugs (Heteroptera: Pentatomidae), a database of pentatomid-parasitoid associations is provided on a world-wide scale and analysed in order to evaluate the limits of taxonomic association records in defining host specificity in parasitoids. Some associations from the literature were then compared with laboratory data on parasitoid response to host semiochemicals. A total of 1733 records with 1165 host-parasitoid associations is provided. Out of 306 parasitoid species, belonging

to Hymenoptera, Diptera and Strepsiptera, egg parasitoids are the most represented, followed by imaginal and larval parasitoids. Among the Diptera the large majority of species belong to Tachinidae whereas among the Hymenoptera, the Scelionidae are most common, with *Trissolcus* and *Telenomus* as the genera containing most species and showing, in average, a wider host range. Focusing on *Trissolcus* species, the total number of associations is reported on a world-wide scale and separately per each zoogeographical region. Although laboratory data confirm most of the association tested, some literature associations were proved to be unreliable because the parasitoid did not show a complete response to host semiochemical cues. Potential and limits of literature databases for evaluation of host range is discussed. Most limits could be overcome if a characterization of the “host unit”, considered as the complex of the components affecting host selection by the parasitoid, is also provided.

### **Tritrophic interactions between a Bt plant, the diamondback moth and a braconid endoparasitoid**

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Studies of the interactions between transgenic plants and natural enemies of pest insects are not only important to assess the risks associated with these new crops but also to assess the role of natural enemies in delaying pest adaptation to the transgenic plants. We have studied the effect of transgenic *Brassica napus* (canola, oilseed rape), expressing the Cry1Ac toxin of *Bacillus thuringiensis* (Bt), on the solitary larval parasitoid *Cotesia plutellae*. This parasitoid is an important natural enemy of the diamondback moth, *Plutella xylostella*, a pest of brassicas that has developed resistance to a wide range of insecticides and is one of the main model species for the study of Bt resistance. Although normal *P. xylostella* larvae are highly susceptible to Cry1Ac, laboratory-selected highly resistant strains of this pest are able to survive on Bt plants. We present evidence that although *C. plutellae* larvae that were forced to develop in Bt-treated susceptible *P. xylostella* larvae inevitably died with their hosts, behavioural factors may limit the scale of this effect under field conditions. *Cotesia plutellae* mortality in susceptible hosts was not due to a direct toxic effect of Cry1Ac but due to premature host mortality since *C. plutellae* larvae developed normally in Bt-resistant hosts on Bt plants. Adult *C. plutellae* females were also highly attracted to Bt plants damaged by Bt-resistant hosts suggesting that parasitoids, such as *C. plutellae*, could assist with delaying the build-up of Bt-resistant pest populations.

### **Information processing and constraints on adaptive sex**

### allocation in *Nasonia vitripennis*

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Sex allocation in parasitoid wasps provides a powerful tool for studying constraints on adaptation. With a strong theoretical framework, we are increasingly able to partition variation around predicted sex ratios into non-adaptive deviations due to constraints (e.g. genetic, behavioural), or adaptive variation due to subtle and precise sex allocation decisions. *Nasonia vitripennis* provides one of the best examples of the effects of Local Mate Competition (LMC) on facultative sex allocation, with females decreasing the number of males produced as competition within broods for mates increases. However, there is variation around the predicted optimal sex ratio that needs explaining. Here we describe experiments that consider what sources of information female *N. vitripennis* utilise when making sex ratio decisions, and how processing that information influences deviations from predicted sex ratios produced by simple LMC models. Sources of information we consider include whether a female is mating with kin, how many other hosts in a patch will produce offspring, and the interaction between social environment (other foundresses) and host environment (superparasitism). The results show that female *N. vitripennis* are adaptive in some contexts but not in others, illustrating behavioural constraints on adaptive sex allocation.

### San Jose scale and its natural enemies in California orchards

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San Jose scale (Diaspididae: *Diaspidiotus perniciosus*) is a pest in stone fruit and nut orchards in California, especially in the warmer southern parts of the San Joaquin valley. Field studies aimed at developing a biological control program have shown that the scale can be controlled by three parasitic wasps, *Encarsia perniciosi*, *Aphytis aonidiae*, and *A. vandenboschi* (Aphelinidae). Their abundance and effectiveness vary, however, and the field data suggest that these species differ in foraging patterns, phenology, and climate preference. To explain these observations, we conducted a series of laboratory studies of the biology of these wasps, including investigations of host feeding, host-stage preference, responses to temperature, and possible competition among them. The results will guide mass rearing and augmentative-release strategies and their integration with orchard management practices.

### Natural selection by parasitoids on host-plant use by a polyphagous caterpillar.

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Natural selection from entomophagous insects may influence the evolution of host-plant use by phytophagous insects. A practical problem in studying the evolutionary ecology of herbivore diet is separating the influence of plant defenses alone (bi-trophic interactions) from the combined effects of natural enemies and plant defenses (tri-trophic interactions). Experimentally separating these factors is especially challenging with specialist herbivores that typically gain defense or refuge as well as physiological benefits from a single host-plant. In this study, we use the individually polyphagous caterpillar *Grammia geneura* (Lepidoptera: Arctiidae) to separate performance and defensive benefits from different host-plant species. Previous work showed that certain single host-plant diets (e.g. *Malva parviflora*) enhanced performance and that other single host-plant diets (e.g. *Ambrosia confertiflora*) enhanced resistance against parasitoids. Here, we specifically hypothesized that this caterpillar's natural habit of feeding on a mixture of toxic plant species provides the benefit of resistance against parasitoids at a performance cost to the caterpillars. We collected late instar caterpillars from nature (85% on the preferred host, *Senecio longilobus*), and, assuming some proportion was already parasitized, randomly assigned them among two diet treatments for the duration of development in the laboratory. As expected, caterpillars reared on *Malva* grew more efficiently than those offered a mixture of *Malva*, *Ambrosia*, and *Senecio*. This performance difference was offset, however, by differences in parasitoid resistance. Caterpillars in the *Malva* treatment suffered 46% mortality from parasitoids, while those reared on the mixture suffered only 26% mortality from parasitoids. The probability of mortality from parasitoids was negatively associated with the proportion of toxic plants (*Ambrosia* and *Senecio*) in the diet of individual caterpillars. Parasitoid resistance is probably achieved via defensive pharmacophagy, as caterpillars are stimulated to feed by plant toxins (e.g. pyrrolizidine alkaloids) and sequester them. In the experiment described above, caterpillars offered the mixed diet had approximately twice the concentration of sequestered pyrrolizidine alkaloids (from *Senecio*) as caterpillars given *Malva* only. We conclude that host-plant use by this caterpillar species is an adaptation to tri-trophic interactions involving parasitoids.

### The paternal sex ratio chromosome (PSR) is not involved in maintaining low Parthenogenesis Inducing *Wolbachia* infections in *Trichogramma deion*.

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The PSR chromosome found in the species *Trichogramma kaykai* is only transmitted through males and causes eggs fertilized with PSR sperm to develop into males that are again carriers of the PSR

chromosome. This extremely selfish genetic element is found in approximately 7% of all the males of the species *T. kaykai*, a common egg parasitoid found in the Mojave Desert. These wasps parasitize eggs of the Desert Metalmark butterfly (*Apodemia mormo deserti*). Another sex ratio distorter found in this species is the Parthenogenesis Inducing *Wolbachia*, which causes infected females to produce exclusively female offspring both from fertilized and unfertilized eggs. In *T. kaykai* the presence of PSR in the population causes the PI-*Wolbachia* infection among females to remain at a relatively low level of approximately 7%. Approximately 85% of the parasitized *A. mormo deserti* eggs contain broods of *T. kaykai* and about 15% contain broods of another *Trichogramma* species: *T. deion*. The infection frequency with PI-*Wolbachia* in *T. deion* is approximately 1%. In a low percentage of the host eggs both species can be found. In laboratory experiments we showed that *T. kaykai* PSR males are capable of mating with *T. deion* females and in these crosses the PSR chromosome is passed on to *T. deion*, where it can be maintained and functions in a similar way as in *T. kaykai*. Here we present field data to show that the PSR is not found in the *T. deion* field population and we present a model which shows that it is practically impossible for PSR to maintain the PI *Wolbachia* infection level at 1%. We conclude that other factors such as suppressors must play a role in keeping the PI-*Wolbachia* infection frequency in *T. deion* at the level found in the field populations.

### **Odour-mediated long-range avoidance of interspecific competition by a solitary endoparasitoid may optimize its foraging success**

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Solitary endoparasitoids, of which only one can develop per host, are expected to avoid hosts that have already been parasitized by another wasp if it is likely that they will lose the intrinsic competition. We propose, however, that parasitoids that are not egg-limited - they carry more eggs than they would normally lay in their lifetime - should only reject such inferior hosts if they save considerable time that they then have available for the search of more suitable hosts. The competition between sympatric solitary parasitoids allows testing of this time saving host discrimination hypothesis. For this reason, we studied the outcome of competition between the two parasitoids *Cotesia marginiventris* (Cresson) (Hymenoptera: Braconidae) and *Campoletis sonorensis* (Cameron) (Hymenoptera: Ichneumonidae). They are the most common parasitoids of larvae of the moth *Spodoptera frugiperda* (Smith) (Lepidoptera: Noctuidae) in Mexico and throughout the Americas. In a first experiment, both wasps readily accepted hosts that had already been parasitized by the other species. In these double parasitized hosts, *C. sonorensis* was found to be the superior intrinsic competitor, independently of the sequence in which the two species parasitized a host and of the time difference between the respective ovipositions. In a second experiment, we studied the outcome of

the competition in cages where the wasps could freely forage for 1 day among small maize plants carrying host larvae. Parasitism in these cages with both wasps was compared with parasitism in cages with only one of the two species present. Again *C. sonorensis* was superior in cases of competition, whereas both species showed similar efficiency in parasitism in the cages in which they were confined alone. In a final experiment, we tested the responses of the wasps to the odour of their competitor in a six-arm olfactometer. Female wasps were confronted with the odours of three sources; 1) maize plants damaged by host larvae, 2) similar plants combined with *C. marginiventris* females, or 3) similar plants combined with *C. sonorensis* females. It was found that *C. marginiventris* females avoided the odour source with *C. sonorensis* females, whereas *C. sonorensis* was attracted to all three odour combinations equally. These results are in accordance with our hypothesis of time optimization. Both wasps carry ample eggs and should therefore, upon contact, readily accept inferior hosts, because oviposition takes only seconds. However, by avoiding the odour of *C. sonorensis*, female *C. marginiventris* may evade the intrinsic competition, which it almost always loses, and may save considerable time that it can allocate to the search for more profitable hosts.

### **Environment specific responses to foraging information in insect parasitoids**

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Thelytokously and arrhenotokously reproducing strains of the parasitoid *Venturia canescens* (Gravenhorst) (Hymenoptera: Ichneumonidae) occur in different environments within the same geographical area. While in one type of habitat hosts are in general regularly distributed and scarce, host density as well as host distribution is highly variable in the other. We used the ecological differences between the two parasitoid groups to test a major assumption of learning theory. This theory predicts that animals should only respond to valuable information and that the value of a piece of information depends upon the predictability of the environment. We therefore expected the wasps originating from a variable habitat to respond quickly to information indicating current habitat quality while the wasps from the stable habitat should show a much reduced response pattern or no response at all. This expectation was tested in multi-patch experiments with ten different populations of wasps, five from each type of habitat. Our results reveal that the responsiveness to information cues in these wasps is indeed a function of the variability of the habitat and thus of the potential value of the foraging information available.

### **Influence of gall wasps and their parasitoids on fitness of native prairie perennials (Asteraceae: *Silphium*)**

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By protecting plants from herbivores, generalist predators, such as ants, can influence plant reproduction. Recent studies have shown that parasitoids also can influence reproduction of plants by killing herbivores, reducing damage to photosynthetic or reproductive tissues. In this study, we evaluated the impact of the gall wasp *Antistrophus rufus* Gillette (Hymenoptera: Cynipidae) on its host plant *Silphium laciniatum* Gillette (Asteraceae: *Silphium*) and the mediating influence of the parasitoid *Eurytoma lutea* Bugbee (Hymenoptera: Eurytomidae). Plants exposed to gall wasps had reduced reproductive output, producing shorter flowering stems and smaller seeds. By killing gall wasp larvae, *E. lutea* “rescued” plant reproduction, resulting in production of larger seeds that were more likely to germinate. Using olfactometry bioassays, we also determined that *E. lutea* was significantly attracted to galled plants, suggesting that plants may attract parasitoids using a synomone. These findings suggest that parasitoids can have important influences on plant reproduction and fitness, perhaps imposing selection pressures on plants to facilitate parasitoids, such as by producing synomones.

#### **Encapsulation: Is it a relative thing?**

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We examined the host suitability of *Psytalia concolor* (Szepligeti), an opiine braconid parasitoid of fruit-infesting pests of the family Tephritidae. One measure of suitability for a koinobiont endoparasitoid is the ability to avoid encapsulation. We report levels of encapsulation on different tephritid hosts, and discuss this in terms of phylogenetic relationships amongst the hosts.

#### **Is it possible to enhance the attractiveness of maize plants for parasitoids?**

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When maize plants are damaged by caterpillars they initiate the release of a blend of specific volatiles. This odorous blend is used as an effective host location cue by parasitoids of the caterpillars.

We study ways to exploit and improve this indirect plant defense for biological pest control. Field assays with plants that were treated to release induced volatiles showed higher attraction of parasitoids to these plants. We obtained less conclusive results with field experiments using maize inbred lines that show clear differences in the induced odors they emit, but found promising differences in parasitism rates and indications that particular plant compounds may be responsible for these differences. I will discuss our current research approach in which we make use of a six-arm olfactometer that allows the testing of multiple maize varieties for attractiveness while simultaneously collecting part of the odor of these plants for subsequent chemical analyses. The purpose of these experiments is to determine the compounds that are most important for attraction and are likely candidates for successful manipulation of parasitoid attraction.

#### **Retrospective probabilistic non-target risk assessments for insect biological control agents**

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Biological control of invasive species is an attractive and frequently used strategy for the management of invasive species, but has attracted considerable criticism as a potential ecological risk. We describe here a novel approach to assessing potential risks of new introductions for biological control, using probabilistic-risk assessment methods. This method requires quantification of key ecological traits of the candidate introduction, and the use of “precision trees” to evaluate potential risk. A number of biological control introductions were retrospectively analyzed to test the validity of this procedure. A major obstacle was the dearth of adequate pre-release data for early introductions. Cases with sufficient data appear to be amenable to this type of analysis, validating the procedure, and we propose that this approach has the potential to contribute significantly to improving risk-assessment for new biological control introductions.

#### **Parasitism of aphids by *Endaphis maculans* (Diptera: Cecidomyiidae) in Hawai'i**

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A large number of adventive aphid species are pests of crops and indigenous plants in Hawai'i. Limited introductions of biological control agents have been made to control aphids in the islands, although great potential exists to introduce new natural enemies, primarily because of the limited potential for non-target impacts as there are no endemic aphids in the Hawai'i archipelago. This paper

reports parasitism levels of aphids by *Endaphis maculans*, a little-known aphid parasitoid. It is not known how this parasitoid was introduced to Hawai'i – it was not introduced purposefully and presumably was translocated accidentally. *E. maculans* attacks banana aphids (*Pentalonia nigronervosa*). Parasitism levels in banana plantations were variable, and evidently inadequate to suppress aphid populations in banana. On other plants (e.g. Ti (*Cordyline terminalis*)), parasitism levels were greater, possibly because of soil properties below the plants. The fly pupae exit the parasitized aphids to pupate in the soil, and it is possible that the dense layers of trashed banana leaves and pseudo-stem trunks in banana plantations make pupation difficult. For this parasitoid to be an effective biological control agent in bananas, it may be necessary to modify cultural practices in the plantations.

### **Spatial learning (or something else) allows a parasitoid to use a host that is available for an extremely short time**

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The parasitoid wasp *Hyposoter horticola* parasitizes a nearly fixed fraction of its host butterfly larvae (*Melitaea cinxia*) throughout a large host metapopulation of 300 to 500 local populations in a 50 x 70 km area. I show, using laboratory observation, that the wasp lays eggs in fully developed larvae that have not yet hatched from the egg, constraining the period of host vulnerability to several hours out of the host's one year lifecycle. The parasitoid achieves a persistent high rate of parasitism over the entire host range in spite of the extremely limited period of host vulnerability in part by being extremely mobile. In addition, I show using a field experiment and observation of marked wasps foraging for hosts in natural populations, that the wasps find virtually all host egg clusters in the weeks before the hosts become vulnerable to parasitism, and then later return to parasitize them. By locating the hosts prior to their vulnerability the wasp extends the time available for searching from hours to weeks. After parasitizing about 1/3 of the larvae in a host cluster the wasp stops, apparently leaving a mark that deters further parasitism by other individuals. The result of this novel combination of mobility and local foraging behavior is a stable population size despite an unstable host that is vulnerable during about one thousandth of its lifecycle.

### **Residence time on plants is determined by both prey and plant species in the omnivore *Dicyphus hesperus* (Heteroptera: Miridae)**

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*Dicyphus hesperus* is a native generalist predator currently used by the greenhouse vegetable industry in Canada. While this omnivore feeds on a variety of prey, it also requires plant resources for nutrition. Previous research from our lab has demonstrated specific plant and prey preferences exhibited by this insect. Our current study examined retention time of the omnivore under different plant and prey conditions. Cages were set up with nine plants in a 3x3 grid placed so that plants did not touch or overlap. The plants used were either mullein, *Verbascum thapsus* L. (Scrophulariaceae), tomato, *Lycopersicon esculentum* Mill. (cv. Patio hybrid) (Solanaceae), pepper *Capsicum annum* L. (cv. Enza 444) (Solanaceae), or chrysanthemum *Chrysanthemum coronarium* L (Compositae). In addition, prey were added to the center plant. The prey were either no prey, flour moth eggs, *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae), greenhouse whitefly pupae *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae) or two-spotted spider mite adults *Tetranychus urticae* Koch (Acari: Tetranychidae). Satiated female *D. hesperus* were placed on the center plant and checked daily to determine the length of time taken to move to a new plant under the different plant-prey treatments. There was no interaction between plant type and prey type. Mean retention time of *D. hesperus* across the treatments ranged from 2.5 to 6 days. Female *D. hesperus* remained longer on more preferred plants such as mullein and tomato, compared with chrysanthemum and pepper. Females remained longer on plants with flour moth eggs, than any other prey type. Surprisingly, females remained longer on plants with spider mites than those with whiteflies, despite previous preferences for whiteflies over spider mites in other experiments. Females spent the shortest amount of time on plants with no prey. These results are being incorporated into a model of movement for *D. hesperus* in greenhouses.

### **Periodic boreal moths: Population dynamic consequences of interaction with natural enemies**

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Periodic insects with a fixed multiannual life cycle emerge synchronously in large numbers at intervals of the length of their development time. *Xestia* moths with a two-year life cycle are strikingly abundant in boreal forests around the Northern Hemisphere every second year but scarce in the alternate years. Many hypotheses have been put forward to explain their periodic occurrence, including interaction with natural enemies. We present biological, numerical and modeling evidence suggesting that the

scarcity of the even-year cohorts of eight coexisting *Xestia* species in eastern Finnish Lapland is due to regulation by the parasitoid wasp *Ophion luteus*, possibly reinforced by parasitism by the ichneumonid wasp *Meloboris collector* and by predation by shrews.

### **Ecological parameters that affect the behavioral response and efficiency of *Ganaspidium utilis* as a bio-control agent of *Liriomyza trifolii***

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*Ganaspidium utilis*, introduced to Hawaii as a biological control agent of the leaf mining flies in the genus *Liriomyza*, can successfully parasitize its host in a variety of crops. It is not clear, however, on what crop and under what conditions is this parasitoid most efficient. Using individual leaves as "patches" we investigated how certain ecological parameters, including structural defenses of the host plant, host larval maturity and density affect the parasitoid's behavior and efficiency. Female *Ganaspidium utilis* were able to evaluate "patch quality" and preferentially visit leaves with higher larval density. Maturity of the host larva is not as strong a predictor of female visitation to a leaf. *G. utilis* exhibits a flexible search response when encountering novel crops. Females were quick to exploit the newly introduced host plant species, this in spite of large differences in structural defenses among the crops. The effect of trichomes (presence and density) on the quality of a patch was also studied.

### **Effects of *Toxoneuron nigriceps* on juvenile hormone hemolymph titers of its host, *Heliothis virescens*.**

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Last instar *H. virescens* larvae previously parasitized by *T. nigriceps* do not pupate and remain as prepupae for an extended period of time. This developmental arrest has been shown to be the result of the injection of polydnviruses and venom during oviposition that results in the disruption of the prothoracicotropic hormone (PTTH) signal transduction pathway. As a result ecdysone titers are depressed. At this same time the hemolymph protein titers are elevated and this elevation in protein is thought to be important to the parasitoids development. What is responsible for the elevated

protein titers is not clear. One possible factor that is influencing hemolymph protein titers is the titer of juvenile hormone. In some other host - parasitoid systems juvenile hormone titers are elevated, in others juvenile hormone titers are depressed. Here we report on the effects of *T. nigriceps* on the juvenile hormone titer of last instar parasitized *H. virescens* larvae.

### **Rapid radiation, or bad data: Why is the phylogeny of microgastrine wasps genera so difficult to estimate?**

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The generic classification of the braconid wasp subfamily Microgastrinae has had a controversial history, in part due to different philosophies of systematists, and in part due to conflict among several morphological character systems. Recent molecular studies have not improved the situation, despite the application of data from three genes totaling 2300bp for each genus (many represented by multiple species). Further analyses provide support for the existence of truly short internal branches deep within the tree, implying a rapid early evolutionary radiation of the genera. Alternative explanations, such as conflicting data, poor selection of genes, poor taxon sampling, etc. have been explored, and so far do not appear to explain the poor internal branch support within the subfamily. Split decomposition analysis, for example indicates strong treelike structure in the data at both the species level (within genera) and subfamily level (within the "microgastrid complex"), but shows essentially a "star phylogeny" among genera rather than a network of conflicting signals or a tree. Some directions for continuing investigation are discussed, including the addition of taxa, sequencing of new genes, and the use of mixed-model Bayesian analysis of data, enhanced by the use of parallel processing on supercomputers.

### **No adverse affect of Coleopteran-specific Cry3bb1 toxin from transgenic corn pollen on *Coleomegilla maculata* (DeGeer)**

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Laboratory studies were conducted to determine the effect of a coleopteran specific toxin (Cry3Bb1) expressed in transgenic corn pollen (event MON 863) on *Coleomegilla maculata* (DeGeer) survival and development. *C. maculata* larvae were reared on either Bt pollen, non-Bt pollen, artificial diet or greenbugs. The duration of larval and pupal stages, developmental time from egg hatching to adult emergence, percent (%) survival and elytra length were compared among all treatments. There were no significant differences in developmental time of larvae fed on pollen, artificial diet, or greenbug during the first two larval instars. However,

prolonged development of the 3rd instar (1 day) and 4th instar (2 days) was observed for larvae fed greenbugs. No significant differences were observed in duration of the pupal stage and % survival. The elytra length of beetles reared on artificial diet was significantly shorter than those reared on other treatments, which did not differ significantly from each other. Larvae fed on greenbugs had a longer total development time compared to all other treatments. The results indicate pollen from Bt corn (MON 863) has no effect on *C. maculata* survival and development.

### **Effect of herbivore-induced plant volatiles on *Anaphes iole* (Hymenoptera: Mymaridae) and *Lygus* spp. (Hemiptera: Miridae): electrophysiological and behavioral studies**

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Plants respond to herbivory by producing volatiles that attract natural enemies of the herbivores responsible for the damage. Early studies of this phenomenon have focused on lepidopterous larvae and mites, but more recent work has included other arthropods as well. For several years we have studied plant response to exogenous elicitors and to herbivory by *Lygus* spp., a crop pest with piercing-sucking mouthparts. The blend of herbivore-induced plant volatiles (HIPVs) emitted after *Lygus* feeding is a complex mixture of compounds that vary in concentration. Little is known about the perception of these compounds by *Lygus* or its natural enemies, or the subsequent influence of these chemicals on their behavior. This poster describes our work on the perception of HIPVs by two economically important *Lygus* species, and by *Anaphes iole* Girault, an egg parasitoid of *Lygus*. Our ultimate goal is to apply knowledge of HIPV-insect interactions toward biological control of *Lygus*. We conducted electrophysiological and behavioral studies to address the following questions: 1) Do *A. iole* and *Lygus* spp. exhibit differential perception of individual plant volatiles induced by *Lygus* feeding? and 2) Do individual plant volatiles induced by *Lygus* damage influence the behavior of *A. iole*? We recorded electroantennograms of male and female *A. iole*, *L. lineolaris* (Palisot de Beauvois), and *L. hesperus* Knight to four concentrations of 12 individual HIPVs and green leaf volatiles. Peak EAG responses varied from ca. 0.2 to 3.0 mV. Overall, female wasps were more sensitive to the volatiles than were males. Female wasps were most responsive to (*Z*)-3-hexenyl acetate, (*Z*)-2-hexenyl acetate, 1-hexanol, linalool, and  $\beta$ -ocimene. Male *A. iole* were most responsive to *c*-3-hex-1-ol,  $\alpha$ -farnesene, and (*Z*)-3-hexenyl acetate. For *L. lineolaris* and *L. hesperus*, both genders were most responsive to green leaf volatile alcohols. The terpenoid  $\alpha$ -farnesene also elicited a strong response by *L. lineolaris*. Results from behavioral trials in a four-armed olfactometer indicated that female *A. iole* were significantly ( $P < 0.0001$ ) attracted to (*Z*)-3-hexenyl acetate. Ongoing behavioral trials will test the response of *A. iole* to other HIPVs. Our results suggest that *A. iole* and *Lygus* spp. exhibit differential

perception of plant volatiles. *Anaphes iole* appeared to be responsive to most of the compounds tested; *Lygus* spp., however, exhibited little response to several compounds. For *A. iole*, differential selectivity and sensitivity between the genders suggests the importance of different chemicals for male and female wasps. Males may be more responsive to chemicals involved in sexual communication than to plant-produced compounds. Heightened sensitivity by female antennae to several of the HIPVs suggests roles in host habitat location. For *Lygus*, our results suggest that green leaf volatiles and  $\alpha$ -farnesene might play roles in plant host finding and acceptance. Green leaf volatiles, relatively common plant volatiles, may be important for general host plant orientation, while  $\alpha$ -farnesene, induced by *Lygus* feeding, may play a role in host acceptance. The effect of these volatiles on *Lygus* behavior remains to be studied.

### **Cryptic species in the *Aphelinus varipes* complex: Taxonomic background, phylogenetic relationships and morphometric study of morphological differentiation.**

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Species of *Aphelinus* in the *varipes* complex have been imported into the US and released for biological control of *Schizaphis graminum* and *Diuraphis noxia*. Several different names have been applied to these species including *Aphelinus varipes*, *albipodus*, *nigritus* and *hordei*. Here we concentrate on sympatric pairs of populations reared from *Rhopalosiphum padi* and *D. noxia* from France and Georgia (former USSR). A companion paper by Hopper et al. presents evidence that all four of these forms are reproductively isolated and have different patterns of host utilization. A complex of cryptic species is clearly involved. Portions of COI and COII (mitochondrial genes) and ITS1 and 28sD2 region (nuclear ribosomal genes) show little differentiation among these four species but the majority of nucleotide substitutions and insertion-deletion events that are present occur as autapomorphies in single species. Morphometric study of size and shape differences in the antennae, wings and mesosoma of these four species reveals that they are differentiated from one another by subtle, but consistent differences in the shape of antennal segments, the shape of the delta region in the forewing, and the shape of the lateral lobes of the mesoscutum. In general, both males and females of all four species are significantly different from one another with respect to each body region. Species that have more autapomorphic genetic differentiation are more strongly reproductively isolated, show more morphological differentiation in antennae, wings and mesoma, and have narrower host ranges than species with less autapomorphic genetic differentiation.

## Marking and tracking the glassy-winged sharpshooter, *Homalodisca coagulata* (Say), in field studies

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We developed a technique to mark-release-recapture adult glassy winged sharpshooters (GWSS), *Homalodisca coagulata* (Say) and we tracked field movements of 42,600 adult GWSS in three different field experiments in southern California (Riverside, Kern county and Moreno Valley) during the years of 2000 and 2002. The use of colored dust to mark GWSS has proven to be a reliable, and cost and time effective technique for mark-release-recapture studies in this insect. No differences in mortality between marked and unmarked (control) insects were observed over a 30-day period. We recovered insects with easily recognizable marking 78 days after release in the field. In barren field conditions adult GWSS are able to fly beyond 100m within minutes of their release. Marking did not significantly affect overall flight behavior. Wind speeds above 5 meters per second showed a strong effect on the insects' flight behavior. In the absence of any significant disturbance, GWSS showed localized movement, most of them apparently remaining within 45 meters from the release point after 4 weeks. No preference of GWSS dispersal between orange and lemons trees was observed.

## Sequence-based evidence for horizontal transmission of a *Bacteroidetes* group endosymbiont

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Over the last 20 years, a large number of symbiotic bacteria have been discovered that manipulate the reproduction of insects. In many cases these bacteria gain a transmission advantage by favoring the production of female offspring over male offspring, and generally insect species with haplo-diploid sex determination are more vulnerable to the influence of such sex ratio distorting factors. Inherited bacterial symbionts are therefore important evolutionary forces in parasitoid evolution, as can be inferred from their wide distribution and the diversity of effects they have on the fitness and reproduction of their hymenopteran hosts. While the  $\alpha$ -Proteobacteria *Wolbachia* is well known, an unrelated bacterium in the *Bacteroidetes* group has recently been found to be associated with parthenogenesis, cytoplasmic incompatibility, and feminization in parasitoids and mites. The prevalence of that bacterium in arthropods was assessed by screening about 100 species of insects and Acari. Each specimen was tested using PCR primers specific for the 16S rDNA gene of either *Wolbachia* or the newly described

bacterium. Of the insects screened, 6% and 18% tested positive for the presence of the *Bacteroidetes* bacterium and *Wolbachia* respectively. The distribution of bacteria among the different insect orders differed markedly between the two bacteria, while *Wolbachia* was detected in each of the seven orders tested, the *Bacteroidetes* bacterium was found only in the Hymenoptera and Hemiptera. In order to test the possibility that the *Bacteroidetes* bacterium, like *Wolbachia*, is horizontally transmitted among different insect species, the products from the PCR with the specific primers were cloned, sequenced and compared. The data show that the 16S rDNA gene of the *Bacteroidetes* bacterium found in the insects exhibit over 96% similarity, and therefore suggest horizontal transmission of that bacterium. Among other insects, the *Bacteroidetes* bacterium was detected in the cactus scale *Diaspis echinocacti*, its parasitoid *Plagiomerus diaspis* and the hyperparasitoid *Marietta* sp.. Possible horizontal transmission of the bacterium within that tri-trophic system will be discussed.

## Sequence-based evidence for horizontal transmission of a CFB group endosymbiont

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Over the last 20 years, a large number of symbiotic bacteria have been discovered that manipulate the reproduction of insects. In many cases these bacteria gain a transmission advantage by favoring the production of female offspring over male offspring, and generally insect species with haplo-diploid sex determination are more vulnerable to the influence of such sex ratio distorting factors. Inherited bacterial symbionts are therefore important evolutionary forces in parasitoid evolution, as can be inferred from their wide distribution and the diversity of effects they have on the fitness and reproduction of their hymenopteran hosts. While the  $\alpha$ -Proteobacteria *Wolbachia* is well known, an unrelated bacterium in the *Cytophaga-Flexibacter-Bacteroides* (CFB) group has recently been found to be associated with parthenogenesis, cytoplasmic incompatibility, and feminization in parasitoids and mites. The prevalence of that bacterium in arthropods was assessed by screening about 100 species of insects. Each specimen was tested using PCR primers specific for the 16S rDNA gene of either *Wolbachia* or the newly described bacterium. Of the species screened, 16% and 18% tested positive for the presence of the CFB bacterium and *Wolbachia* respectively. Although the overall percent prevalence seems similar, the distribution of bacteria among the different insect orders differed markedly. *Wolbachia* was detected in each of the seven orders tested, while the CFB bacterium was found only in the Hymenoptera and Hemiptera. In order to test the possibility that the CFB bacterium, like *Wolbachia*, is horizontally transmitted among different insect species, the products from the PCR with the CFB bacterium -specific primers were cloned, sequenced and compared. The data show that the 16S rDNA gene of the CFB bacterium found in 11 out of the 13 insects exhibit over 96% similarity, and therefore suggest horizontal

transmission of that bacterium. Among other insects, the CFB bacterium was detected in the cactus scale *Diaspis echinocacti*, its parasitoid *Plagiomerus diaspis* and the hyperparasitoid *Marietta* sp.. Possible horizontal transmission of the CFB bacterium within that tri-trophic system will be discussed.