
CHAPTER 6. PARAMETERS USED IN LABORATORY HOST RANGE TESTS

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INTRODUCTION

Here, we discuss specific parameters that can be used to characterize the responses – oviposition, feeding, survival, and development – of parasitoids and predators in tests to estimate their host ranges. For any such tests to give reproducible results, both the physical setup, the prey, and the predator must be held to a defined set of conditions. Such factors and how they can affect results of laboratory host range tests are considered in Chapter 5. In Chapter 7, we discuss the various test designs that have been used in host range estimation.

IF YOU ARE WORKING WITH PREDATORS

Unlike parasitoids, for predators, both adults and larvae are mobile and can actively seek prey. Thus, each stage's host range must be assessed, as they may differ. When working with predators, four processes can be observed: (1) feeding (by adults or larvae), (2) adult survival, (3) oviposition (including oogenesis), and (4) larval development. We also discuss likely effects of predator fidelity to habitat type or host plant species on field prey range.

FEEDING (ADULTS AND LARVAE)

Using standard conditions, the quality of a prey species for the predator can be quantified by measuring the number of prey eaten per predator per unit of time (Parameter 1). For both adults and larvae, prior experience with a prey may condition the response in a test. Consequently, both naïve insects and ones conditioned to the target pest should be examined as separate treatments (see Chapter 5)

Parameter 1: Number of prey eaten per predator per unit of time

For easily counted prey, the most direct measure of prey acceptance by the predator is to count the number eaten in a laboratory assay in a standard amount of time (usually 24 hours or some lesser period) and compare this to the number of the target pest, or other test species, consumed. For example, Miller and Williams (1983) compared the number of eggs of each of nine prey species eaten by the staphylinid beetle *Atheta coriaria* (Kraatz) in choice tests where the predator was offered one egg of each of three host species for 24 hours. Similarly, Zilahi-Balogh *et al.* (2002) compared the number of eggs eaten by the derodontid beetle *Laricobius nigrinus* Fender when adults were presented with eggs of either the target pest (*Adelges tsugae* Annand), other adelgids, or scales. They found that the numbers of nontarget prey eggs eaten in a three-day no-choice test were only 14 to 51% of the number of target pest eggs eaten under the same conditions. In such tests, it is important to include negative controls (arenas with no predators) to estimate numbers of prey that die or disappear from causes other than predation and positive controls (arenas in which the predator is presented with the target pest) to demonstrate the predator was physiologically ready to consume prey.

Prey consumed by predatory larvae can be measured using methods similar to those discussed above. Prey choices, however, may differ between young and old larvae; therefore, larvae of different ages should be tested as separate treatments (see Chapter 5). Young larvae, for example, may require a more particular prey species or even prey life stage, while older larvae may feed on a wider range of prey. In chewing species, for example, this may be due in part to lower biting strength of young larvae.

ADULT SURVIVAL

If prey are not easily counted, it may be more effective to measure survival times of predators fed pure diets of single test species (Parameter 2). This approach is useful, for example, (1) for prey such as scales that occur in congested colonies, (2) when prey molt to the next life stage during the test (e.g., Causton *et al.*, 2004), or (3) when uncountable reproduction occurs during the test period (such as with some adelgids), changing the number of prey presented (Butin, 2003).

Parameter 2: Predator survival (in days) when fed only a given prey

For adult predators, another measure of the value of a potential prey is the average number of days a newly emerged, naïve adult predator lives when confined with that test species and water, compared to the survival when confined with (1) the target pest and water or (2) water only. For larvae, this test is approximated by measuring survival to the next life stage (as discussed below in parameter 4a). A test species should be considered a prey only if eating it raises the predator's survival to values higher than on water alone. A test species would be considered a prey of lesser value if predator survival on the test species was greater than on water alone, but less than that on the target pest. Lopez and Kairo (2003), for example, found that survival times for both adults and larvae of the coccinellid *Nephaspis bicolor* Gordon fed only non-whitefly prey were no better than those of starved controls held on moist filter paper. These data suggest that the prey range of this coccinellid is limited to whitefly species.

OVIPOSITION

The value of a test species for predator oviposition can be assessed by answering three questions. (1) Can the predator develop mature eggs when fed only the test species (Parameter 3a)? (2) Does the test species stimulate the predator to lay its eggs (Parameter 3b)? (3) How many eggs does the predator lay when provided access only to the test species compared to when provided access only to the target pest (Parameter 3c)? Since predators may produce fewer eggs when very young or old, predator age should be considered in test design.

Parameter 3a. Egg development (oogenesis) by adults

The nutritional value of a prey species can be measured by its ability to support the development of mature eggs when it serves as the sole food of the adult predator. This can be determined by holding two groups of newly emerged adults (reared as larvae on the target pest) under the physical conditions and length of time that would lead to oviposition on the target pest, giving one group access to only the target pest and confining the other group with a different prey species. Periodically, a subsample of the predators can be dissected and egg development compared between the two groups. The group with access to the target pest serves as the positive control. A third group, held only with water and non-prey foods such as honey, serves as the negative control.

Parameter 3b. Ability of prey to elicit predator oviposition

Many predators lay eggs when they contact stimuli from particular prey. Lopez and Kairo (2003), for example, found that the coccinellid *N. bicolor* lays its eggs in response to wax from its whitefly prey. If a predator only oviposits in response to such a stimulus, its larvae will have access only to prey with those characteristics; larvae of *N. bicolor*, for example, would therefore be expected to be found eating whiteflies in nature. When key kairomones are lacking, oviposition (on a novel prey) is likely to be absent or much reduced. Albuquerque *et al.* (1997) found that oviposition by the specialist green lacewing *Chrysopa slossonae* Banks on novel prey (aphids other than the woolly alder aphid, *Prociphilus tessellatus* [Fitch]) was one-third of that on its usual prey, woolly alder aphid. The key to effective use of this test is recognizing some substance associated with a prey species that is a specific releaser of oviposition. Proof of its nature can be had if transfer of that substance to a related species not normally used by naïve predators for oviposition induces them to lay eggs on the amended nonhost species.

DEVELOPMENT OF IMMATURE STAGES

Host ranges of larvae sometimes differ from those of adults of the same predator species and should be determined separately. The prey range of predator larvae can be measured in terms of larval survival and development (Parameter 4a) and size and fecundity of the adults obtained (Parameter 4b) when reared as larvae on a test species.

Parameter 3c. Numbers of eggs laid

Finally, the number of eggs laid in response to the presence of a test species in a no-choice design provides further information on the likelihood that the species would be used as a prey. To measure this effect, predators with developed eggs should be placed in a standard test arena with a prey species and the number of eggs laid in a fixed period counted and compared to the number laid in the presence of the target pest under the same conditions. Since prior exposure to the pest species is a confounding effect, such conditioned predators should be used only if this is the only means to obtain predators with mature eggs; otherwise, naïve predators should be used. A control treatment (no prey of any species) should also be used to account for the potential for egg dumping in the absence of prey-related cues (e.g., Causton *et al.*, 2004). Zilahi-Balogh *et al.* (2002) found that, in no-choice tests with various nontarget species, field-collected derodontid beetles (*L. nigrinus*) laid on average only 16% of the number of eggs laid when exposed to the target pest (*A. tsugae*) under the same conditions; in paired choice tests, this dropped further to only 6%. Since field collected beetles had previously fed on the target pest, the results of both tests are confounded by preconditioning to the preferred prey.

Parameter 4a. Larval survival and rate of development

The quality of a prey species to a larval predator can be assessed by measuring the percentage of a larval cohort that survive to pupation (or for hemimetabolous insects, molt to the adult) on a diet of the test species versus on the target pest (the positive control) or on water alone. Zilahi-Balogh *et al.* (2002) found that 14% of eggs of the derodontid beetle *L. nigrinus* survived to the adult stage when larvae were fed on hemlock woolly adelgid, but this dropped to zero for all the other five species of prey tested. The time needed for 100% development of the immature stage (at a standard constant temperature) can also be used as an index of prey suitability, as slower development is expected on prey of lower quality.

Parameter 4b. Weight and fecundity of adults reared on test species

As better foods should lead to heavier body weights – and therefore greater fecundity – larval, pupal and adult weights of predators fed as larvae on various test prey can be compared to that of predators reared on the target pest species as an estimate of prey quality. As it may be difficult to weigh very small predators without killing them, this assessment may need to be done by weighing groups of a fixed number of predators taken from batches reared on different larval diets.

Effects of larval diet on adult fecundity can be measured by offering adults reared as larvae either on the target pest or on a non-target test species batches of the target species for oviposition and comparing the number of eggs laid between the groups with different larval diet histories. Tests should be kept short (24 and 48 hours) to avoid influences due to any consumption of the target pest during the test.

EFFECTS OF PREDATOR FIDELITY TO HABITAT OR PLANT SPECIES ON FIELD PREY RANGE

As with parasitoids, if a predator exhibits high fidelity to particular habitats or plants, then these features can act as filters narrowing the predator's field prey range. This is the case, for example, with some species of phytoseiid mites. Beard and Walter (2001) found that species of *Neoseiulus* in inland Australia, while considered to be generalist predators, in fact showed high fidelity to particular tree species or small groups of species. Of the 73 examples of *Neoseiulus eremitus* Beard that were collected, all were from only one tree species (*Eremophila mitchelli* Benth.), and all of the 149 specimens of *Neoseiulus buxens* Beard were collected from *Eucalyptus populnea* F. Muell. Fidelity at the habitat level has been shown by Walter *et al.* (1998), who deployed spider mite prey colonies in tropical Australian habitats to map the presence of the introduced predator mite *Phytoseiulus persimilis* Athias-Henriot and found that this predator, while established in the wild in Australia, did not enter forested habitats.

Laboratory tests are not easily used to observe these processes, especially habitat fidelity. Olfactometers might be useful in establishing the level of responsiveness of particular predators to particular plants. Even a simple choice test in which two plant species are presented together in a small arena and the predator's later position noted can suggest potential predator ties to particular plant species or groups. However, in a still air assay, mixing of volatiles from several test plants may occur and blur the difference between the treatments. Demonstration of plant fidelity is likely to require larger scale tests, with moving air.

Investigation into habitat or host plant selectivity would be needed, especially in cases in which field surveys recorded the predator only in specific habitats or on certain host plants but feeding or oviposition was observed in the laboratory on prey from other habitats or plants.

IF YOU ARE WORKING WITH PARASITOIDS

For most parasitoid species, hosts are found by adult females. The adult's host searching process, therefore, determines which host species are attacked. A great deal has been learned since the 1960s about the mechanisms by which female parasitoids locate and choose hosts (see Godfray, 1994; Jervis and Kidd, 1996; Quicke, 1997). This process can be broken into several steps – host finding, host acceptance, and regulation of host physiology – each of which offers opportunity for measurements useful in assessing a species' host range.

HOST FINDING

Detection of a suitable host can be divided into a series of stages, the first being habitat location; the second, finding of the insect's particular host plant; and the last, discovery of the insect itself on the host plant. At each step, physiologically suitable hosts may be omitted from the host range if a particular species' habitat is not searched, its host plant is not located, or the host is not found when the agent is foraging on the host plant.

Finding the habitat Parasitoid habitat preferences can determine which species are encountered by a parasitoid. For example, the braconid *Cotesia glomerata* (L.), a species introduced to North America from Europe, does not attack the native nontarget woodland butterfly *Pieris*

virginiensis Edwards in New England because this parasitoid does not enter woods to search for hosts (Benson *et al.*, 2003a). In contrast, another native woodland species, *Pieris napi oleracea* Harris, has its second brood in meadows and is attacked by *C. glomerata* (Benson *et al.*, 2003b).

There is, however, no obvious way to determine a parasitoid's habitat preferences in the laboratory before introduction. A partial determination can be made by pre-introduction studies of habitat associations in the parasitoid's native range, as in the case of studies of European mirid bug parasitoids being conducted in support of their possible introduction into North America (Kuhlman *et al.*, 2000). In field surveys, however, the effects of habitat itself may be confounded by plant and host insect effects. If, for example, a certain habitat in the native range lacks suitable plants to support hosts, then surveys in that habitat will likely not detect any parasitoids. However, if suitable plants are present in the same habitat in the receiving country, then the parasitoid may enter that habitat. In some cases, if there is a known volatile attractant from the plant/host complex of the typical host of a parasitoid, that compound can be used to bait traps to survey habitats to detect a target parasitoid. *Cotesia glomerata*, for example, can be detected with yellow sticky cards baited with beta-glucosidase (Mattiacci *et al.*, 1995).

One should not assume that, just because the target pest is found in an agricultural habitat, a parasitoid used against it will also be limited to such agricultural areas. The braconid *Microctonus aethiopoulos* Loan, for example, after its introduction to New Zealand for control of pest weevils in alfalfa fields, was found in a variety of habitats, including modified native grasslands in subalpine zones, where it parasitized several native weevils (Barratt *et al.*, 1998) (see also Chapter 9).

Responding to the insect/plant volatiles A large body of research over the last 40 years has elaborately demonstrated that plant chemistry and morphology affect host finding by natural enemies, especially parasitoids (Cortesero *et al.*, 2000). Parasitoids' abilities to orient towards hosts from a distance are often based on detection of volatile compounds produced by plants, often in response to herbivore feeding (e.g., Read *et al.*, 1970; Navasero and Elzen, 1989; Roland *et al.*, 1989; Turlings *et al.*, 1991; Wickremasinghe and van Emden, 1992; Romeis *et al.*, 1997; Rutledge and Wiedenmann, 1999). Consequently, the plant that the herbivore feeds on can mediate the insect's risk of discovery and parasitism. The same herbivore on different plants can trigger the release of different volatile blends, as can different herbivores on the same plant. This process means that some physiologically acceptable hosts will escape parasitism simply because the right volatiles are not present for the parasitoid to detect. For example, colonies of green peach aphid (*Myzus persicae* [Sulzer]) feeding on collards (*Brassica oleracea* L.) were parasitized by the braconid *Diaeretiella rapae* (McIntosh) at a markedly higher rate than was the same aphid species on sugar beet (*Beta vulgaris* L.) because of this parasitoid's attraction to the essential constituent of mustard oil (allyl isothiocyanate), which is present in collards but not beets (Read *et al.*, 1970).

Similarly, variation between plant species in such physical features as leaf trichome density can mean that parasitism is absent or much less frequent in hosts on plants with unfavorable features, even if the insects are detectable by foraging parasitoids (e.g., Turner, 1983; Hua *et al.*, 1987).

Finally, variation in secondary compounds can render herbivores on some plant species unacceptable for oviposition (Sime, 2002) or unsuitable for development of immature parasitoids (Kester and Barbosa, 1991) due to the sequestration of toxic plant compounds by the insect larvae as they feed. For example, Sime (2002) found that the ichneumonid *Trogus pennator* (Fabricius) did not parasitize the Troidini swallowtail butterfly *Battus philenor* (L.) even though its frass did attract the parasitoid. Rejection of larvae was attributed to the presence of ethanol-soluble compounds (in part, at least, aristolochic acids sequestered from the host plant), which were found on the external surface of the larval integument. Furthermore, in those few cases in which the parasitoids could be induced to oviposit in *B. philenor* larvae, parasitoid progeny died. This case illustrates the likely role of plant chemistry in shaping the parasitoid associations of swallowtails, since *Trogus* spp. readily attack species in two of the three papilionid tribes, but not those in the Troidini, whose members are distinguished by their use of plants in the Aristolochiaceae, which contain aristolochic acids. (The same phenomenon occurs with predators: the Vedalia beetle [*R. cardinalis*] does not feed on prey that have fed on plants with certain alkaloids [Quezada, 1969; Mendel *et al.*, 1992]).

The consequence of these plant effects is twofold. On one hand, some native herbivores that are in a parasitoid's physiological host range will not be used as hosts in the field if they occur on unattractive or morphologically unsuitable plants. Conversely, native herbivores that expand their own host ranges by moving onto introduced plants may become new field hosts of additional parasitoids that search those plants. Babendreier *et al.* (2003a) found that some combinations of influences of host plant species and habitat complexity lowered parasitism by *Trichogramma brassicae* Bezdenko on sentinel eggs of the rearing host (*Ephestia kuehniella* Zeller) in meadows, compared to corn fields.

In laboratory tests designed to predict which native insects might become field hosts for a candidate natural enemy, it is important to (1) test native herbivores on their typical host plants and (2) use test arenas large enough that long-distance host finding is a required step in parasitism. Wind tunnels provide enough space for active upwind flight of parasitoids and are a good arena for assessing the above points (Parameter 5).

Parameter 5: Successful upwind flight to a herbivore/plant complex

The ability of a native herbivore on a native plant to attract upwind parasitoid flight leading to host discovery can be scored as the percentage of female parasitoids that succeed in reaching a bait (consisting of the correct herbivore stage on its native host plant) in a wind tunnel, together with the time taken to reach the bait (Keller, 1990, 1999; Geervliet *et al.*, 1996). Species that do not elicit oriented upwind flight and high discovery rates are unlikely to be exploited in the field. Using this test, species that are physiologically suitable as hosts but are not associated with sufficiently attractive volatiles can be recognized as nonhosts. For species feeding on several plants, parasitism may be high on some species (ones producing attractive volatiles) and low or absent on others (not producing attractive volatiles) (Read *et al.*, 1970; Roland *et al.*, 1989). Oviposition by the tachinid *Cyzenis albicans* (Fall.) was low on apple trees with winter moth (*Operophtera brumata* [L.]) because attractive volatiles produced by oaks were not produced by apple. Spraying of apple trees with oak leaf extracts in small field plots doubled the number of parasitoid eggs laid on the treated apple trees compared to untreated controls (Roland *et al.*, 1989).

Host kairomone effects Once a parasitoid has found a plant with a potential host insect on it, the parasitoid engages in intensified local search to reach the actual insect. Responsiveness to chemicals (Parameter 6) found in such materials as insect body parts (scales, setae, cast skins), excretions (honeydew, silk), and herbivore-damaged plant tissue helps the parasitoid locate the host. Contact with these chemicals (kairomones) induces parasitoid behaviors such as more frequent turning, slower walking, and lower rates of departure by flight, which have the effect of keeping the parasitoid searching the local area.

Parameter 6: Parasitoid responsiveness to a test species' kairomones

Parasitism of a test species in nature at high levels is unlikely unless the parasitoid is responsive to the species' contact kairomones (any source of non-volatile chemical cues perceived by physical contact), which often are what guide the parasitoid to the host's exact location after the parasitoid lands on an infested plant. Potency of a species' kairomones can be assessed in the laboratory by determining the degree to which they arrest parasitoid movement and/or induce oviposition, compared to those of the target pest.

HOST ACCEPTANCE

After physical contact is made with a host, the parasitoid continues to gain further information by examining the potential host with her antennae. If the parasitoid is sufficiently stimulated, she will attempt to oviposit in or on the host (Parameter 7). For example, the aphelinid *Aphytis melinus* DeBach, a parasitoid of California red scale, *Aonidiella aurantii* (Maskell), recognizes its host by detecting the chemical *O*-caffeoyltyrosine on the scale cover. Parasitoids acquire sensitivity to this compound by contacting it when adults emerge from their natal hosts. Subsequent contact with this chemical on scales triggers host acceptance in ovipositing females (Hare, 1996). During ovipositor insertion, further information about the host is gained by parasitoids through sensilla on the ovipositor, and hosts may be rejected even at this stage.

Parameter 7: Parasitism rate

If test results have shown that (1) a parasitoid is able to detect odors from a test species on its natural host plant and fly upwind or in some other way orient to it from a distance and (2) that the parasitoid is responsive to the species' kairomones, then parasitism is a meaningful parameter to measure as an assessment of host range. Rates of parasitism in various kinds of tests (choice, no-choice, sequential, see Chapter 7) can be measured and compared to that on the target pest. For example, Babendreier *et al.* (2003b) assessed rates of parasitism by *T. brassicae* in a variety of nontarget species using no-choice, small arena, dead air tests.

REGULATION OF THE HOST'S PHYSIOLOGY

Once a parasitoid has found and parasitized a host, it must defeat all attempts of the host to destroy it and also regulate the host's physiology in ways that render it favorable for the survival and growth of the immature parasitoids. Host defenses such as encapsulation (Parameter 8) provide several more points at which measurements can be made that describe the quality of a species as a host for a particular parasitoid. In general it is assumed that, if a host species is not

suitable for the survival and growth of the immature parasitoid, the species is not threatened because it will not support a population of the parasitoid. Keller (1999), for example, found parasitism was unsuccessful in many of the test species in which the parasitoids deposited eggs.

Parameter 8: Rate of encapsulation by the host

Encapsulation is a common reaction in which hosts attempt to kill eggs or larvae of internal parasitoids by entombing them inside a layer of material formed from blood cells (Nappi, 1973). This layer of collapsed blood cells often turns dark, and thus can easily be observed. Rates of encapsulation determine if a particular host is suitable or not for a given parasitoid. Blumberg and Van Driesche (2001), for example, found that the obscure mealybug (*Pseudococcus viburni* [Signoret]) was able to encapsulate all of the eggs of *Leptomastix dactylopii* Howard, making this a nonhost for the parasitoid, in contrast to the complete absence of encapsulation in the normal host, citrus mealybug (*Planococcus citri* Risso). Encapsulation rates are readily measured in the laboratory by dissecting test species after exposure to parasitoids. Rates of encapsulation, however, are affected by the exact host life stage (instar) and rearing temperature, in addition to the host species, and these factors must be either considered or held constant. Furthermore, wasps in the families Braconidae and Ichneumonidae have viral symbionts (Polydnviridae species) that can suppress host encapsulation responses (Edson *et al.*, 1981; Beckage, 1998), and thus are a further influence in determining the usual host range.

One might think that it would be possible to predict the rate of host encapsulation in a particular host based on rates seen in that host with other parasitoids. Similarly, it might seem feasible to predict encapsulation probability for a given parasitoid based on data from other hosts. Neither of these propositions, however, turn out to be true. Closely related hosts can differ widely in their response to the same parasitoid, and a single host can respond quite differently to closely related parasitoids (see Alleyne and Wiedenmann, [2001] for a case study). Thus encapsulation rates are useful measures of host suitability but are not predictable and require the testing of each host-parasitoid combination of interest.

Conversely, not all hosts in which the parasitoid develops successfully in the laboratory are actual field hosts. This is especially true for idiobiont hymenopteran parasitoids and some dipterans (phorids and some tachinids), which interact less intimately with their hosts' physiology than do larval koinobiont parasitoids, which must survive the host's internal defenses. For example, Morehead and Feener (2000) found that the phorid *Apocephalus paraponerae* Borgmeier, which in the field is monophagous on the ant *Paraponera clavata* Fabricius, can develop in at least seven other species in the Ponerinae if eggs are artificially placed in hosts.

Finally, the rate of parasitoid emergence from a test host and the size of the emerging parasitoids (Parameter 9), as well as the sex ratio and fecundity of the emerging parasitoids (Parameter 10) are means to assess the quality of the test species as a host.

Parameter 9: Emergence and size of parasitoid progeny

Hosts that are successfully parasitized and that lack high rates of encapsulation, may still vary in their nutritional value for parasitoid immature stages. Rates of survival of these stages can be measured in laboratory rearings. Three values can be assessed: (1) the proportion of oviposition attempts that result in actual oviposition, (2) the number of progeny per host (for gregarious parasitoids), and (3) the size of the progeny (often using hind femur length as a correlate of body size). If a parasitoid fails to develop on a species in such a laboratory test, the species is likely not a host. The meaning, however, of differing levels of survival is harder to interpret.

Parameter 10: Sex ratio and fecundity of parasitoid progeny

Sex ratio and fecundity of parasitoid progeny reared from a given test host can be used as a further measure of the quality of that species as a host. Male-biased sex ratios suggest low host quality, as does reduced female size compared to size of females reared from the target pest. Smaller females, or ones with shorter lifespans, will produce fewer progeny of their own.

REFERENCES

- Albuquerque, G. S., M. J. Tauber, and C. A. Tauber. 1997. Life-history adaptations and reproductive costs associated with specialization in predacious insects. *Journal of Animal Ecology* 66: 307-317.
- Alleyne, M. and R. N. Wiedenmann. 2001. Suitability of lepidopteran stemborers for parasitization by novel-association endoparasitoids. *BioControl* 46: 1-23.
- Babendreier, D., D. Schoch, S. Kuske, S. Dorn, and F. Bigler. 2003a. Non-target habitat exploitation by *Trichogramma brassicae* (Hym.: Trichogrammatidae): what are the risks for endemic butterflies? *Agriculture and Forest Entomology* 5: 199-208.
- Babendreier, D., M. Rostas, M. C. J. Höfte, S. Kuske, and F. Bigler. 2003b. Effects of mass releases of *Trichogramma brassicae* on predatory insects in maize. *Entomologia Experimentalis et Applicata* 108: 115-124.
- Barratt, B. I. P., A. A. Evans, C. M. Ferguson, M. R. McNeill, J. R. Proffett, and G. M. Barker. 1998. Curculionoidea (Insecta: Coleoptera) of New Zealand agricultural grassland and lucerne as potential non-target hosts of the parasitoids *Microctonus aethiopoulos* Loan and *Microctonus hyperodae* Loan (Hymenoptera: Braconidae). *New Zealand Journal of Zoology* 25: 47-63.
- Beard, J. J. and G. H. Walter. 2001. Host plant specificity in several species of generalist mite predators. *Ecological Entomology* 26: 562-570.
- Beckage, N. E. 1998. Parasitoids and polydnaviruses. *Bioscience* 48: 305-311.
- Benson, J., A. Pasquale, R. G. Van Driesche, and J. Elkinton. 2003a. Assessment of risk posed by introduced braconid wasps to *Pieris virginiensis*, a native woodland butterfly in New England. *Biological Control* 26: 83-93.
- Benson, J., R. G. Van Driesche, A. Pasquale, and J. Elkinton. 2003b. Introduced braconid parasitoids and range reduction of a native butterfly in New England. *Biological Control* 28: 197-213.
- Blumberg, D. and R. G. Van Driesche. 2001. Encapsulation rates of three encyrtid parasitoids by three mealybug species (Homoptera: Pseudococcidae) found commonly as pests in commercial greenhouses. *Biological Control* 22: 191-199.

- Butin, E. E. 2003. Biological control and cold hardiness of the hemlock woolly adelgid (Homoptera: Adelgidae). MS thesis, University of Massachusetts, Amherst, Massachusetts, USA.
- Causton C. E., M. P. Lincango, and T. G. A. Poulson. 2004. Feeding range studies of *Rodolia cardinalis* (Mulsant), candidate biological control agent of *Icerya purchasi* Maskell in the Galápagos Islands. *Biological Control* 29: 315-325.
- Cortesero, A. M., J. O. Stapel, and W. J. Lewis. 2000. Understanding and manipulating plant attributes to enhance biological control. *Biological Control* 17: 35-49.
- Edson, K. M., S. B. Vinson, D. B. Stoltz, and M. D. Summers. 1981. Virus in a parasitoid wasp: suppression of the cellular immune response in the parasitoid's host. *Science* 211: 582-583.
- Geervliet, J. B. F., L. E. M. Vet, and M. Dicke. 1996. Innate responses of the parasitoids *Cotesia glomerata* and *C. rubecula* (Hymenoptera: Braconidae) to volatiles from different plant-herbivore complexes. *Journal of Insect Behaviour* 9: 525-538.
- Godfray, H. C. J. 1994. *Parasitoids: Behavioral and Evolutionary Ecology*. Princeton University Press, Princeton, New Jersey, U.S.A.
- Hare, J. D. 1996. Priming *Aphytis*: behavioral modification of host selection by exposure to a synthetic kairomone. *Entomologia Experimentalis et Applicata* 78: 263-269.
- Hua, L. Z., F. Lammes, J. C. van Lenteren, P. W. T. Huisman, A. van Vianen, and O. M. B. de Ponti. 1987. The parasitoid-host relationship between *Encarsia formosa* Gahan (Hymenoptera, Aphelinidae) and *Trialeurodes vaporariorum* (Westwood) (Homoptera, Aleyrodidae). XXV. Influence of leaf structure on the searching activity of *Encarsia formosa*. *Journal of Applied Entomology* 104: 297-304.
- Jervis, M. and N. Kidd. 1996. *Insect Natural Enemies: Practical Approaches to their Study and Evaluation*. Chapman and Hall, London.
- Keller, M. A. 1990. Responses of the parasitoid *Cotesia rubecula* to its host *Pieris rapae* in a flight tunnel. *Entomologia Experimentalis et Applicata* 57: 243-249.
- Keller, M. A. 1999. Understanding host selection behaviour: the key to more effective host specificity testing, pp. 84-92. In Withers, T. M., L. Barton Browne, and J. Stanley (eds). *Host Specificity Testing in Australasia: Towards Improved Assays for Biological Control*. Queensland Department of Natural Resources, Coorparoo, DC, Queensland, Australia.
- Kester, K. M. and P. Barbosa. 1991. Behavioral and ecological constraints imposed by plants on insect parasitoids: implications for biological control. *Biological Control* 1: 94-106.
- Kuhlmann, U., P. G. Mason, and R. G. Footitt. 2000. Host specificity assessment of European *Peristenus* parasitoids for classical biological control of native *Lygus* species in North America: use of field host surveys to predict natural enemy habitat and host ranges, pp. 84-95. In Van Driesche, R. G., T. Heard, A. McClay, and R. Reardon. *Proceedings of Session: Host Specificity Testing of Exotic Arthropod Biological Control Agents – the Biological Basis for Improvements in Safety*. US Forest Service, Forest Health Technology Enterprise Team, Report FHTET-99-1, August, 2000. Morgantown, West Virginia, U.S. A.
- Lopez, V. F. and M. T. K. Kairo. 2003. Prey range of *Nephaspis bicolor* Gordon (Coleoptera: Coccinellidae), a potential biological control agent of *Aleurodicus dispersus* and other *Aleurodicus* spp. (Homoptera: Aleyrodidae). *International Journal of Pest Management* 49: 75-88.
- Mattiacci, L., M. Dicke, and M. A. Posthumus. 1995. β -glucosidase: an elicitor of herbivore-induced plant odor that attracts host-searching parasitic wasps. *Proceedings of the National Academy of Sciences of the United States of America* 92 (6): 2036-2040.
- Mendel, Z., D. Blumberg, A. Zehavi, and M. Weissenberg. 1992. Some polyphagous Homoptera gain protection from their natural enemies by feeding on the toxic plants *Spartium junceum* and *Erythrina corallodendrum* (Leguminosae). *Chemoecology* 3: 118-124.

- Miller, K. V. and R. N. Williams. 1983. Biology and host preference of *Atheta coriaria* (Coleoptera: Staphylinidae), an egg predator of Nitidulidae and Muscidae. *Annals of the Entomological Society of America* 76: 158-161.
- Morehead, S. A. and D. H. Feener, Jr. 2000. An experimental test of potential host range in the ant parasitoid *Apocephalus paraponerae*. *Ecological Entomology* 25: 332-340.
- Nappi, A. J. 1973. Parasite encapsulation in insects, pp. 293-326. In Maramorosch, K. and R. E. Shope (eds.). *Invertebrate Immunity*. Academic Press, New York.
- Navasero, R. C. and G. W. Elzen. 1989. Responses of *Microplitis croceipes* to host and nonhost plants of *Heliothis virescens* in a wind tunnel. *Entomologia Experimentalis et Applicata* 53: 57-63.
- Quezada, J. R. 1969. Population biology of the cottony cushion scale, *Icerya purchasi* Maskell (Homoptera: Coccidae) and its natural enemies in southern California. PhD dissertation, University of California, Riverside, California, U.S.A.
- Quicke, D. L. J. 1997. *Parasitic Wasps*. Chapman and Hall. London.
- Read, D. P., P. P. Feeny, and R. B. Root. 1970. Habitat selection by the aphid parasite *Diareteretiella rapae* (Hymenoptera: Braconidae) and hyperparasite *Charips brassicae* (Hymenoptera: Cynipidae). *The Canadian Entomologist* 102: 1567-1578.
- Roland, J., W. G. Evans, and J. H. Myers. 1989. Manipulation of oviposition patterns of the parasitoid *Cyzenis albicans* (Tachinidae) in the field using plant extracts. *Journal of Insect Behavior* 2: 487-503.
- Romeis, J., T. G. Shanower, and C. P. W. Zebitz. 1997. Volatile plant infochemicals mediate plant preference of *Trichogramma chilonis*. *Journal of Chemical Ecology* 23: 2455-2465.
- Rutledge, C. E. and R. N. Wiedenmann. 1999. Habitat preferences of three congeneric braconid parasitoids: implications for host-range testing in biological control. *Biological Control* 16: 144-154.
- Sime, K. 2002. Chemical defence of *Battus philenor* larvae against attack by the parasitoid *Trogus pennator*. *Ecological Entomology* 27: 337-345.
- Turlings, T. C. J., J. H. Tumlinson, F. J. Eller, and W. J. Lewis. 1991. Larval-damaged plants: sources of volatile synomones that guide the parasitoid *Cotesia marginiventris* to the microhabitat of its host. *Entomologia Experimentalis et Applicata* 58: 75-82.
- Turner, J. W. 1983. Influence of plant species on the movement of *Trissolcus basalis* Woolaston (Hymenoptera: Scelionidae) – a parasite of *Nezara viridula*. *Journal of the Australian Entomological Society* 22: 271-272.
- Walter, D. E., G. N. Azam, G. Waite, and J. Hargreaves. 1998. Risk assessment of an exotic biocontrol agent: *Phytoseiulus persimilis* (Acari: Phytoseiidae) does not establish in rainforest in southeast Queensland. *Australian Journal of Ecology* 23: 587-592.
- Wickremasinghe, M. G. V. and H. F. van Emden. 1992. Reactions of adult female parasitoids, particularly *Aphidius rhopalosiphi*, to volatile chemical cues from the host plants of their aphid prey. *Physiological Entomology* 17: 297-304.
- Zilahi-Balogh, G. M. G., K. T. Kok, and S. M. Salom. 2002. Host specificity of *Laricobius nigrinus* Fender (Coleoptera: Derodontidae), a potential biological control agent of the hemlock woolly adelgid, *Adelges tsugae* Annand (Homoptera: Adelgidae). *Biological Control* 24: 192-198.