

## CHEMICALS IN HOST-PARASITOID AND PREY-PREDATOR RELATIONS

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### Summary

Chemicals which may affect the host-parasitoids and prey-predator relations are semiochemicals, pesticides, and chemical defenses. Semiochemicals are involved in the host seeking process. Parasitoids and predators may primarily search for the host habitat or seek the host directly. In the host habitat location, the semiochemicals involved are synomones produced by the host plant. These plant volatiles are produced in large quantities and they have a high detectability but a low reliability. The host location can be at long or short range. At long distance, semiochemicals involved can be plant volatiles induced by host activity such as feeding damage, a blend of plant and host compounds, or volatile kairomones from the host itself. At short distance, semiochemicals involved are contact kairomones produced by the host and they act as arrestant stimuli for parasitoids and predators. Natural enemies also produce semiochemicals with different functions such as marking patches that repel competitors. Semiochemicals, therefore, are directly involved in the spatial distribution of parasitoids and predators in relation to the host populations. Potential applications of semiochemicals in pest control are currently being explored. In relation to pesticides, their use can produce different results on the population equilibria of host and

parasitoids. Depending on whether the pesticide is applied before or after parasitism, and on the stage of the pest life cycle where equilibrium population is measured, host depression or resurgence can be obtained. The relative toxicity of pesticide to pests, immature and adult parasitoids is important to the level of resurgence produced. Finally chemical defenses are produced by host and prey to avoid being attacked by their natural enemies. These chemicals include compounds that are forcefully ejected at attackers, substances that are present in the cuticle, distasteful internal tissues or regurgitated secretions, and semiochemicals such as alarm pheromones.

## 1. Introduction

Basically, chemicals which may affect host–parasitoid and prey–predator relations are of three different kinds: semiochemicals, pesticides, and chemical defenses. Semiochemicals such as kairomones and synomones are involved in the process of host and prey location, acting as an important factor in the behavior of the searching predators and parasitoids.

When hosts and prey are crop pests, they may be exposed to pesticides to reduce their populations. Often the pesticides affect non-target species, including the pests' natural enemies, whose populations are also reduced. Therefore the host–parasitoid and prey–predator population dynamics may be altered by the presence of pesticides.

In relation to chemical defenses, hosts and natural enemies are in continuous coevolution. Hosts and prey try to develop mechanisms to avoid being attacked by parasitoids and predators. One of these mechanisms is based on the production of chemicals such as venoms and distasteful substances.

Before analyzing the implications of the different chemicals in host–parasitoid and prey–predator relations, it is necessary first to comment on some general features of predators and parasitoids, and of their interaction with their prey and hosts.

Predators are found in all parts of the animal kingdom and they follow different strategies for securing prey: to pursue (lions, cheetahs), to trap (spiders), to ambush (birds of prey), even to steal the prey (some birds), among others. In general, predation occurs when the predators eat their prey, thereby causing the death of the latter. According to this definition, parasitoids are often considered a special kind of predator rather than a parasite because, unlike true parasites, they kill their hosts.

Parasitoids are some of the most abundant of all animals, probably comprising 10% or more of all metazoan animals. They are insects belonging mainly to two orders, Diptera (two-winged flies) and Hymenoptera (ants, bees, and wasps). Within the Diptera, most species occur in the families Tachinidae and Bombyliidae. Within the Hymenoptera there are about 45 families containing parasitoids including such familiar groups as the ichneumonids, braconids, chalcids, pteromalids, and fairy flies.

The biology of insect parasitoids is well known. Adult female parasitoids search for their hosts, responding to physical and/or chemical stimuli such as host vibrations, visual and acoustic signals, or volatile substances from the host habitat or from the host

themselves. The female parasitoids lay their eggs on (ectoparasitoids) or in (endoparasitoids) the body of the host, usually an immature stage of another insect, which is then consumed by the feeding parasitoid larvae. The behavior of parasitoids varies considerably between species. There are parasitoids that develop on dead hosts (idiobionts) or in living hosts that will die when the parasitoids are fully developed (koinobionts); parasitoid species in which only one individual develops in a single host (solitary) or others in which more than one individual (of a single species) develops in a single host (gregarious); parasitoids that attack other parasitoid species (hyperparasitoids); and parasitoids that attack hosts previously parasitized by the same species (superparasitism), or by a different species (multiparasitism).

Predation and parasitism are the two interactions most studied, for two main reasons. First, predators and parasitoids affect the distribution and abundance of populations and the structure of communities, so they have been of central interest to the ecologist who attempts to unravel the complex factors driving the dynamics of species interaction. Second, they play an important part in the natural control of other insect populations, being used in biological control programs of insect pests. This fact has stimulated a large amount of empirical and theoretical work to identify and quantify the attributes that enhance the effectiveness of predators and parasitoids as pest-control agents.

The study of the interactions between natural enemies and their host populations has frequently been carried out by the construction of mathematical models. The reason for this is that the use of models permits the exploration of the significance of different components, independently or in combination with the behavior of interacting host–natural-enemy systems. In this way, models serve as generators or clarifiers of hypotheses about how populations interact, formalizing the structure of the hypothesis in term of axioms (assumptions of the models) and results (outcomes of the models). The mathematical study of population dynamics dates from the 1920s with the appearance of the first models such as the Thompson, Nicholson-Bailey, and Lotka-Volterra. These models explored the consequences of very simple interactions between hosts and parasitoids and prey and predators and formed the basis for the development of mathematical descriptions of these interactions. Since then, the models and their underlying assumptions have become more complex in order to reflect ever increasingly detailed knowledge of the behavior of natural enemies and the other features of populations. Here, we are only going to analyze briefly some of them.

A general model, which defines the host–parasitoid and prey–predator interactions is:

$$N_{t+1} = F N_t f(N_t, P_t) \quad (1)$$

$$P_{t+1} = N_t [1 - f(N_t, P_t)] \quad (2)$$

where  $N$  and  $P$  are the host and parasitoid populations respectively, in successive generations  $t$  and  $t+1$ ,  $F$  is the rate of increase of the host population, and the function  $f$  gives the probability of a host escaping parasitism. This model assumes discrete generations. Depending on the components included, the function of  $f$  acquires different forms. For example the form:

$$f(N_t, P_t) = [1 + a P_t / (k (1 + a T_h N_t))]^k \quad (3)$$

describes the effect of the host density through the handling time,  $T_h$ , and parasitoid aggregation through the exponent of the negative binomial distribution,  $k$ , in the interaction. The host density produces changes in the parasitoid attack rate ( $a$ ) a process called functional response. There are different functional response types. In insect parasitoids, Type II or curvilinear up to the asymptote (the response rises at a constantly decreasing rate towards a maximum value) is widespread, and it is the consequence of the handling time ( $T_h$ ) or time spent by the parasitoid from the encounter with the host until it is oviposited, which reduces the time available for search.

In the real world, the host population is not a single homogeneous unit, but has a heterogeneous distribution in patches or units of spatial distribution. The patches have different host densities and parasitoids may be more attracted to patches of higher host density and therefore concentrate in these areas. The exponent of the negative binomial distribution,  $k$ , defines the aggregative response component, which is strongest when  $k \rightarrow 0$  and weakest when  $k \rightarrow \infty$  (random). For small  $k$  values, the model provides stability, which defines the aggregative response as a stabilizing component, in contrast to the functional response; high values of  $T_h$  introduce instability.

Therefore, according to this model, parasitoids and predators are density-dependent on their hosts and prey and they tend to aggregate in some host or prey patches rather than others. However, when their density in a patch becomes high, individuals meet one another. It has been observed that parasitoids interrupt the search and leave the immediate vicinity after an encounter with other searching conspecifics or with a host that is already parasitized in this patch. Thus, aggregative response and mutual interference may act as a mechanism of spatial redistribution of parasitoids.

Under this framework, we are now going to analyze how chemicals affect host–parasitoid and prey–predator relations. First, we shall analyze the chemicals involved in the search for host and prey habitats, and for hosts and prey within patches, by parasitoids and predators; second, the effect of pesticides in the population dynamics of host–parasitoid and prey–predator; and finally, the chemicals involved in the defense mechanisms of hosts and prey against their parasitoids and predators.

## 2. Semiochemicals Influencing the Behavior of Parasitoids and Predators

As mentioned above, in host–parasitoid and prey–predator relations, semiochemicals intervene in the host or prey seeking process. In this process, parasitoids or predators either directly locate the host or prey (host location), or they first locate its habitat, such as host food plant (host habitat location). The first situation often occurs at short distance, for example when natural enemies and hosts share the same habitat, although some parasitoids and predators also directly locate the host from long distances. However, natural enemies usually search for the host habitat first when they are far from the host.

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### Biographical Sketch

Carlos Lozano was born in Granada, Spain, where he received his PhD (1993) from the University of Granada for studies of biological control of insect pests of olive trees. He then travelled to the University of Cardiff (Wales, UK) for a postdoctoral period (1994–1995). In Cardiff, Carlos studied the role of parasitoids in the population dynamics of bark beetles through the construction of mathematical models. After that he came back to Granada, where he is working as a researcher in the Consejo Superior de Investigaciones Científicas (CSIC) since 1996. In this time, Carlos has concentrated in the role of semiochemicals in the relations between insect-pests with their host-plants and with their parasitoids, publishing the results of these studies in 32 research articles.