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Elicitation of superparasitization behavior from the parasitoid wasp *Leptopilina boulardi* by the organophosphorus insecticide chlorpyrifos

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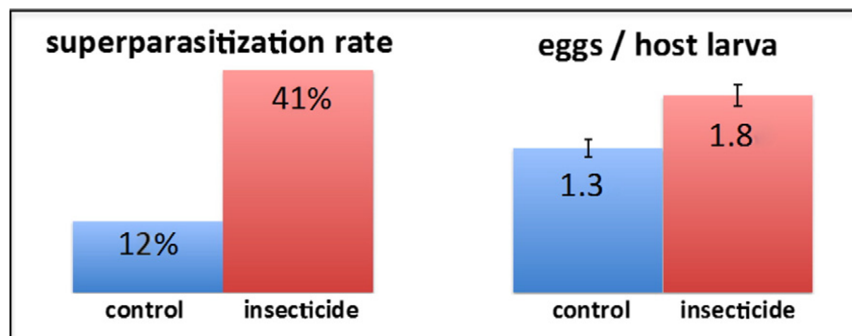
HIGHLIGHTS

- Parasitoids are key species because they control insect populations.
- Chlorpyrifos is one of the most used insecticides worldwide.
- Chlorpyrifos increased the rate of superparasitization by parasitoids.
- This effect involves acetylcholine concentration and is equivalent to that of LbFV.
- This effect may jeopardize the equilibrium of wild insect communities.

GRAPHICAL ABSTRACT



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ABSTRACT

Chlorpyrifos is an organophosphorus insecticide that largely contributes to environmental pollution. Parasitoids, as any other non-target species, can be exposed to insecticides through environmental pollution. Parasitoids are key species because they regulate natural populations of other insects. The hymenopterous parasitoid *Leptopilina boulardi*, whose larvae develop inside *Drosophila* larvae, is a solitary parasitoid; thus, only one larva can successfully develop per host. Therefore, females generally lay only one egg per host because any increase in the number of eggs laid will decrease its fitness. The effects of an LC20 of chlorpyrifos on the parasitization behavior of two strains (NS and S) of *L. boulardi* were evaluated. The NS and S strains were genetically identical but differed in that the S strain was infected by a virus, LbFV, which modifies the parasitization behavior of the parasitoid. In control conditions, parasitoid females from the NS strain rarely superparasitized (laid more than one egg per host) their host whereas females from the S strain frequently superparasitized their host. When parasitoids were exposed to an LC20 of chlorpyrifos, the rates of host larvae superparasitized by females and the mean numbers of eggs laid per host larva increased for both NS and S strains. Therefore, both the insecticide and the virus induced an increase in the superparasitization of the host. The effect of the insecticide on the superparasitization behavior of the parasitoid is discussed according to its mode of action.

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1. Introduction

Hymenopteran parasitoids are ecologically important natural enemies because they control the development of the populations of other insect species by killing the host inside of which their larvae

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develop. Some hymenopteran parasitoid species are strictly proovigenic. This is the case of *Leptopilina boulardi* Barbotin, Carton and Kelner-Pillaut (Hymenoptera: Figitidae) whose females emerge with their total stock of eggs and do not mature more eggs afterwards (Jervis et al., 2008). Therefore, the management of their egg load is an important feature of their fitness. To maximize their fitness, females must maximize the number of eggs that will successfully develop into adults. However, different factors may modify the fecundity, and therefore, the fitness of these parasitoids.

The larvae of the hymenopteran parasitoid *L. boulardi* develop inside *Drosophila* larvae. *L. boulardi* females, which find their host larvae by probing the host substratum with their ovipositor (Vet and Bakker, 1985; Visser et al., 1992), can discriminate if the host larva is already parasitized or not through gustatory receptors present on their ovipositor (Le Ralec, 1991; Le Ralec et al., 1996). The capacity to detect if the host larva has already been parasitized enables *L. boulardi* females to avoid parasitized hosts (Van Lenteren, 1981); this behavior, called host discrimination, is an important trait because *L. boulardi* is a solitary parasitoid, i.e. only one parasitoid per host can successfully develop.

Host discrimination relies on the perception of stimuli (odors) by receptors that transmit their stimulation through nervous pathways (Ruschioni et al., 2015). Because neurotoxic insecticides interfere with nervous transmission (Casida and Durkin, 2013), the perception of these stimuli may be modified. It was shown, for example, that the organophosphorus insecticide chlorpyrifos interferes with pheromonal communications within hymenopteran parasitoid species (Delpuech et al., 1999). Chlorpyrifos has also been shown to interfere with the discrimination of sexual pheromones between species of hymenopterous parasitoids (Dupont et al., 2010). By interfering with the perception of odors, insecticides may interfere with host discrimination. Delpuech and Leger (2011) and Delpuech and Delahaye (2013) have shown that chlorpyrifos and the pyrethroid insecticide deltamethrin inhibited the perception by the hymenopteran parasitoid *Trichogramma brassicae* Bezdenko (Hymenoptera, Trichogrammatidae) of an already parasitized host. Organophosphorus insecticides may interfere with host discrimination not only because they perturb nervous transmissions along neurons but also because these perturbations are caused by an increase in the concentration of acetylcholine in synapses (Casida and Durkin, 2013). Indeed, it has been shown that acetylcholine intervenes in odor perceptions (D'Souza and Vijayaraghavan, 2014) and odor discriminations (Chapuis and Wilson, 2013).

Besides insecticides, any other factor interfering with the parasitization process by parasitoids may also modify their fecundity and, therefore, their fitness. Viruses capable of manipulating the parasitization behavior of parasitoids are such factors. Varaldi et al. (2003, 2006a) have analyzed the parasitization behavior of parasitoid females from two different *L. boulardi* strains. The two strains were genetically identical and only differed by the fact that one was infected by a virus named *L. boulardi* Filamentous Virus (LbFV) and the other was not. Authors demonstrated that the virus induced an increase in the superparasitization behavior (i.e. laying more than one egg per host larva) of female parasitoids.

In this paper, the possible effect of the organophosphorus insecticide chlorpyrifos on the parasitization behavior of the parasitoid *L. boulardi* was tested. For this, the previously mentioned strains were used. The strain not infected by LbFV (NS strain) rarely superparasitized its hosts in control conditions whereas the strain infected by LbFV (S strain) frequently superparasitized the host larvae in control conditions. Therefore, the use of these two strains enables to evidence a possible effect of the insecticide either toward an increase or a decrease in the parasitization behavior of the parasitoid. The results obtained with the strain infected by LbFV will also possibly bring useful knowledge for further investigation and understanding of the mode of action of the virus in increasing the superparasitizing behavior of *L. boulardi*. Furthermore, because every organophosphorus insecticide has the same mode of action (inhibition of acetylcholinesterase in the central nervous system of insects), the results obtained with chlorpyrifos may also be valid for any other organophosphorus insecticide.

2. Materials and methods

2.1. Biological material

Two strains of *L. boulardi* were used for the experiments, a non-superparasitizing strain, called NS, and a superparasitizing strain, called S. The NS strain was an inbred line (8 generations of brother-sister mating, 82% of homozygosity, origin: Sienna, Italy) (Varaldi et al., 2006a). The S strain was derived from the NS strain by injecting extracts containing the LbFV, inducing superparasitization, into *Drosophila* larvae previously parasitized by the NS strain (Varaldi et al., 2006b). Thus, the two parasitoid strains, NS and S, shared the same genetic background, but were either uninfected (non-superparasitizing phenotype, NS) or infected (superparasitizing phenotype, S) by LbFV. Parasitoid strains were reared on larvae of a *Drosophila melanogaster* strain Sainte Foy.

2.2. Determination of lethal concentrations

Newly emerged parasitoids (males and females) were maintained in vials (9.5 cm long, 2.5 cm of diameter) containing 10 ml of agar medium with sugar and nipagin at 25 °C, 70% relative humidity, 12 h:12 h light:dark until they were exposed to the insecticide. Parasitoid females, one to 4 days old, were exposed to the insecticide in groups of ten in glass vials (length 7.5 cm, width 12 mm) containing a piece of paper (length 5 cm, width 8 mm) on which 12 μl of the insecticide diluted in acetone were deposited (pure acetone was used for controls). The pieces of paper were left 1 h on the lab bench for evaporation of the acetone before placing in vials. A small drop of honey was placed on the side of the vial to feed the parasitoids and vials were kept at 25 °C, 70% relative humidity, 12 h:12 h light:dark. The mortality of *L. boulardi* was assessed after 24 h of contact with the treated piece of paper. For each strain (NS and S), 5 different concentrations of insecticide were used and, for each concentration, 50 adults were exposed to the insecticide. The lethal concentration for 20% of the parasitoids (LC20) was estimated from the regression line of mortality determined by the log-probit program of Raymond (1985), based on Finney (1971) after two replicates. The insecticide used was chlorpyrifos (99% certified purity; Cluzeau Info Labo, Sainte-Foy-La-Grande, France).

2.3. Exposure to the insecticide and parasitization

Newly emerged parasitoids were maintained and exposed to the LC20 as described in Section 2.2 (pure acetone was used for controls). After 24 h of exposure to the LC20 of insecticide, females that survived were separately placed in petri dishes. One female was deposited per petri dish (1.3 cm height, 5.5 cm of diameter) that contained 10 ml of agar medium (with sugar and nipagin), a drop of about 0.1 ml of living bakery yeast deposited on the center of the agar medium and 12 *Drosophila* eggs deposited in each petri dish 24 h before parasitoid females. The delay of 24 h was sufficient enough for allowing eggs to hatch into larvae before parasitoid females were placed inside the petri dishes. Parasitoid females were allowed to parasitize *Drosophila* larvae in the petri dishes during 24 h, and then, were removed. From the moment *Drosophila* eggs were deposited to the moment parasitoid females were removed, the petri dishes were stored at 21 °C. After that, the petri dishes were stored at 14 °C until the dissection of *Drosophila* larvae performed the following 3–7 days to count the parasitoid larvae and encapsulated parasitoid eggs and larvae per *Drosophila* larva used for the calculation of the percentage of encapsulation (i.e. the number of encapsulated eggs and larvae over the total number of parasitoid eggs and larvae present in the *Drosophila* larva).

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