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Infectious Behavior in a Parasitoid

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Solitary parasitoid insects usually lay only one egg per host and reject already parasitized hosts, as only one offspring can successfully develop (1). Despite the constraints, superparasitism is commonly observed. A body of theoretical works has explained that the decision of a parasitoid to lay extra eggs can be advantageous and selected for when host's are rare (2). However, superparasitism in a solitary *Drosophila* parasitoid was not determined by parasitoid nuclear genes but caused by an infectious extra-chromosomal factor. This microparasite takes advantage of the wasp's superparasitism behavior for its own transmission. This leads to reconsider the evolutionary interpretation of this behavior.

A comparison of seven laboratory strains of *Leptopilina boulardi* (3) showed clear between-population variation in superparasitism behavior (a mean of 1.00 to 3.56 eggs/parasitized host, $P < 0.0001$, table S1). This trait was also highly variable within strains, even in the Sienna strain that was initiated from a single female. To investigate the origin of such variability, 20 inbred lines were established from the Sienna strain (8 generations of sib-mating, homozygosity > 0.996). Stable lines were obtained: some of them never caused superparasitism (NS lines), while others laid up to 15 eggs in the same host [S lines, see two typical S and NS lines in Fig. 1A, see also fig. S1 and supporting online material (SOM) text]. Crosses between S and NS inbred lines (3) revealed strict maternal transmission of the phenotypes (Fig. 1A; fig. S2): both F1 and back-crosses behaved similarly to their maternal ancestors. The same result was obtained when crossing two natural populations (Antibes and Madeira) also showing contrasting superparasitism behavior (table S1). Variability in superparasitism behavior appeared to be induced by an extra-chromosomal factor that is vertically transmitted through maternal lineage.

To investigate whether this extra-chromosomal factor was infectious, we first parasitized *Drosophila* larvae by NS females (from Madeira) and subsequently superparasitized the larvae by S females (from Antibes). At emergence of the adult parasitoids, females were individually tested for their behavior and for their genotype using a molecular marker that allows to distinguish the two strains [second internal

transcribed spacer of the ribosomal DNA, see (4) for PCR conditions]. They were compared to control females emerging from hosts parasitized only by Madeira females, or by Antibes females (within-strain competition), respectively (3). All controls behaved as expected: Madeira females never allowed superparasitism, while Antibes did (Fig. 1B). Among the winners of the between-strain competition, all Antibes females favored superparasitism as expected, while 71% (46/65) of Madeira females also favored superparasitism in spite of their genotype (Fig. 1B). This result showed that superparasitism behavior was horizontally transmitted and is probably regulated by an infectious extra-chromosomal factor present in the S line. Superparasitism behavior of newly infected lines was stable over generations, suggesting that the infectious factor settled durably (table S2).

The apparent infectiousness of superparasitism behavior strongly suggests the involvement of a replicating particle in S females. Preliminary electron microscopy suggests a virus is involved, since particles were observed in S females (8/9) and not in NS females (0/6) (Fig. 1 C; SOM text). Because superparasitism in *L. boulardi* is not determined by parasitoid's genes but by a microparasite, the adaptive significance of this behavior for the parasitoid needs to be reconsidered. Modification of the wasp's behavior makes it more likely that hosts will be infested with both uninfected and infected females, favoring horizontal transmission of the particles. However, consequence of this behavioral modification for the fitness of the microparasite is not so evident since it suffers a trade-off between horizontal and vertical transmission. Several parameters of the association (physiological cost of infection, efficiency of vertical transmission, parasitoid/*Drosophila* ratio) need to be estimated before we can decide whether this phenomenon should be interpreted as a mere pathological effect or as a true adaptive manipulation (5).

References and Notes

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Fig. 1. (A) Distribution of number of parasitic eggs / host larva in S and NS parental lines and back crosses illustrating two generations of introgression (mother x father: BC1: (NS x S) x S, BC2: (S x NS) x NS). (B) Horizontal transmission of superparasitism: behavior and genotype (*M/A*) of females emerging from hosts initially parasitized by Madeira females only (exp 1), Antibes females only (exp 2), both strains (exp 3). Surface of circles is proportional to number of individuals (3). (C) Transmission electron microscopy (3) showing viral particles (arrow) in S oviducts. l: lumen of the oviduct where eggs transit during oviposition. Bar, 500 nm. The insert shows a cross section of a group of nucleocapsids within the nucleus. Bar, 200 nm.

