



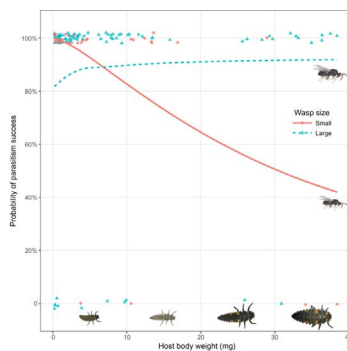
Fitness consequences of body-size-dependent parasitism in a gregarious parasitoid attacking the 7-spot ladybird, *Coccinella septempunctata* (Coleoptera: Coccinellidae)



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GRAPHICAL ABSTRACT



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ABSTRACT

Variation in body size of hosts and their parasitoids poses a significant challenge for gregarious parasitoid females to make their decisions to optimally utilize a range of hosts. In the present study, we investigated the combined effect of host size across successive host larval stages and maternal wasp size on fitness-correlated performances of offspring parasitoids, using the larval-pupal gregarious parasitoid *Oomyzus scaposus* attacking the 7-spot ladybird *Coccinella septempunctata*. The probability of parasitism success decreased with ladybird body weight at the time of parasitism when small sized wasps made the attack, but maintained a high level across the full range of host weights when large sized wasps made it. Offspring development time to adulthood decreased, while brood size increased, asymptotically with host body weight, but they did not vary with maternal wasp size. Sex ratio was female-biased and did not vary with ladybird body weight or maternal wasp size. Body size of F1 adult parasitoids did not vary with ladybird body weight or maternal wasp size. Our findings suggest that small 7-spot ladybird larvae are preferred hosts for small *O. scaposus* females, while large sized ladybird larvae appeared to have little or no effect on parasitism success of large female parasitoids.

1. Introduction

The relationship between adult body size and evolutionary fitness is fundamental for understanding behavioral evolution and life history

traits of a wide range of organisms (Peters, 1983). Many life history traits are correlated with body size (Stearns, 1992), which is a key feature of organisms and varies continuously because of the effects of natural selection on mortality rates and the size-dependency of resource

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acquisition (Chown and Gaston, 2010). Predatory animals are often considerably larger than their prey (Cohen et al., 1993), whereas parasites and pathogens are generally much smaller than their hosts (Memmott et al., 2000). Parasitoids lie between these extremes (Cohen et al., 2005). Relative sizes of parasitoids and their hosts are often fixed for the two parasitoid life history strategies (Askew and Shaw, 1986). While idiobiont parasitoids are often larger in body size than their hosts, which stop growing at the time of parasitism, koinobiont parasitoids are often smaller than their hosts, which continue growing after parasitism (Quicke, 1997).

Body size is strongly favored over other fitness correlates in many parasitoids (King, 1987; Machauer and Sequeira, 1993; Godfray, 1994; Harvey and Strand, 2002; Harvey, 2005). Numerous studies have documented that host size at the time of parasitism is positively correlated with parasitoid size emerged from the host (Godfray, 1994), which in turn is known to affect fitness by influencing searching efficiency, longevity, or egg supplies (Mayhew and Heitmans, 2000; Milonas, 2005; Jervis et al., 2008; Kasamatsu and Abe, 2015). In addition, wasp size may also influence the quality of host attacked. A small female wasp may not be able to use a large, good quality host that is more effective in defense against attacks (Godfray, 1994; Henry et al., 2009). So, body size becomes the most prominent fitness measure in predictive models of clutch size and progeny sex allocation in parasitoids (Charnov, 1982; van Alphen and Visser, 1990; Visser, 1994).

Oomyzus scaposus (Thompson) (Hymenoptera: Eulophidae) is a widely distributed parasitoid of predatory ladybirds (Ceryngier and Hodek, 1996; Noyes, 2016). It attacks a broad range of ladybird species, such as the 7-spot ladybird *Coccinella septempunctata* as a major host in the native range of the ladybird (Li, 1984; Triltsch, 1996; Kuznetsov, 1987) and the multicolored ladybird *Harmonia axyridis* as a minor host in the ladybird's invaded Europe and North America (Riddick et al., 2009; Comont et al., 2014). Previous observations suggested that female wasps may prefer to parasitize 7-spot ladybird third and fourth instar larvae, though they occasionally attack pupae (Iperti, 1964; Klausnitzer, 1969) and younger larvae (Filatova, 1974). A single bout of oviposition lasts from 2 to 5 min (Li, 1984), and a maximum of three bouts of oviposition may occur to a host larva (Semyanov, 1986). Many offspring parasitoids can develop successfully within a single host (Semyanov, 1986), with a record of as many as 47 from a 7-spot ladybird pupa (Li, 1984). The emerging wasps are sexually mature and mate between siblings within a few minutes after emerging (Iperti, 1964; Filatova, 1974). Parasitism rates by *O. scaposus* attacking aphidophagous Coccinellidae may vary widely, fluctuating considerably from month to month (Li, 1984) and from year to year (Dean, 1983; Semyanov, 1986; Pankanin-Franczyk and Ceryngier, 1999). What is known so far about this parasitoid is fragmentary, mostly from rearing ladybirds collected from the field (Ceryngier et al., 2012). Detailed laboratory studies on the interaction between this parasitoid and its ladybird hosts are necessary for understanding the fluctuated population dynamics in the field.

In this study, we examined the combined effect of host and maternal wasp size on parasitism success, developmental time, the number of offspring adults emerged, sex ratio and body size of emerging adults. We individually exposed 7-spot ladybird larvae across all instars to *O. scaposus* females of varying body sizes. Previous studies often focused on either host or maternal wasp size (e.g. Vet et al., 1994; Visser, 1994; Nakamura and Noda, 2002; Silva-Torres et al., 2009; Gao et al., 2016), while few addressed both (but see Henry et al., 2006 for the study of a solitary aphid parasitoid). By determining the interaction effect between host and maternal wasp sizes on parasitism can progeny production we better understand the flexibility in oviposition strategy of gregarious parasitoids.

2. Materials and methods

2.1. Insect rearing

The 7-spot ladybird and its prey vicia aphid *Megoura japonica* (Matsumura) were collected from the crop field margins, at Jiangpu farm, northern suburbs of Nanjing, eastern China. From about 100 ladybird larvae collected in a few field trips, 30 or so were parasitized and came up with scores of *O. scaposus* parasitoids. Two female and one male parasitoids were randomly sampled from each brood to establish the parasitoid stock. The ladybird stock was established from 20 unparasitized ladybirds selected at random and maintained in insectary ($25 \pm 1^\circ\text{C}$, $60 \pm 5\%$ RH, photoperiod L16: D 8 h), using vicia aphids as food. The aphid colonies were maintained on potted bean plant *Vicia faba* L. Bean seeds were planted in a plastic pot (8 cm diameter and 10 cm height) with peat moss-sand mixed soil. When the seedlings grew to a height of approximately 20 cm, they were infested with aphid virginoparae from aphid stock colonies. Bean leaves with aphids were excised and provided to ladybird larvae in a plastic food box (10 cm in diameter and height) with a mesh-screen lid. Ladybird age cohorts were obtained for the experiment after three generations in insectary. To maintain the parasitoid colony, parasitism was made by releasing a female parasitoid into a glass tube (1.5 cm diameter and 8 cm long) where a 7-spot ladybird 2nd or 3rd instar larva was subjected to parasitization. As soon as the wasp made an attack on and left from the host, the wasp was returned to the stock colony. The parasitized ladybird larva was provided with aphids *ad libitum* as food until pupation. The pupa was transferred to a glass tube for the emergence of offspring adult parasitoids. Emerged adult parasitoids from the host were collected in a vial to be allowed mating and provided with honey liquid as supplementary food via a piece of fine cotton thread on the vial wall. Female wasps were identified from males by their antennae; males have long hairs on each segment and females lack these hairs. The female wasps used in the experiment were 1–2 days old, mated, and naive.

2.2. Experimental protocol

To examine the quality of 7-spot ladybird larvae as hosts for *O. scaposus*, we tested all larval instars (L1–L4) of the ladybird for their body size effects. The ladybird larvae were obtained at two points in time (on the 1st and last day) within each instar, specifically on the 1st and 2nd day of L1–L3 while on the 1st and 4th day of L4. Each larva was tested once. Body weight (Mean \pm SD) and sample size (n) for the successive age cohorts were 0.29 ± 0.05 mg ($n = 16$) for Day 1/L1, 0.75 ± 0.11 mg ($n = 15$) for Day 2/L1, 1.09 ± 0.25 mg ($n = 16$) for Day 1/L2, 2.23 ± 0.29 mg ($n = 25$) for Day 2/L2, 3.53 ± 0.64 mg ($n = 23$) for Day 1/L3, 7.86 ± 0.95 mg ($n = 14$) for Day 2/L3, 12.24 ± 1.98 mg ($n = 19$) for Day 1/L4, and 31.99 ± 1.99 mg ($n = 19$) for Day 4/L4.

Ladybird larvae were individually exposed to parasitism after being weighted (Mettler Toledo, model AL204-IC, to an accuracy of 0.01 mg). A host larva was transferred to a petri dish containing 2 aphid nymphs as food and then a female wasp was released into the petri dish. When the wasp left the host after making oviposition, it was kept in 75% alcohol and then measured under a microscope (OLYMPUS-DP12, Tokyo, Japan) in the hind tibia length (HTL) as a body size correlate. The attacked ladybird larva was reared in a vial where vicia aphids were provided *ad libitum* as food until its pupation. The F1 parasitoid adults emerged from the host pupa were counted as brood size and sexed by their antennal characteristics. Proportion male of F1 adult parasitoids was used as a measure of sex ratio. Body size of F1 adult parasitoids was measured according to sex in HTL, which was averaged over a maximum of 5 F1 parasitoids sampled at random from a brood. If the attacked ladybird larva came up with emerging adult parasitoids, it was defined as a successful parasitism; If the host larva came up with emerging a ladybird adult, it was recorded as a failed parasitism.

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