

Developmental interactions between *Spodoptera exigua* (Noctuidae: Lepidoptera) and its uniparental endoparasitoid, *Meteorus pulchricornis* (Braconidae: Hymenoptera)

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Abstract

A single choice test was performed to examine developmental strategies in the uniparental endoparasitoid *Meteorus pulchricornis* and its host, the beet armyworm, *Spodoptera exigua*. The results support the hypothesis that a compromised developmental strategy is pursued by solitary koinobiont endoparasitoids in the Braconidae and Ichneumonidae, where a trade-off between offspring body size and development time was exhibited. All five larval instars of *S. exigua* were susceptible to parasitism by *M. pulchricornis*, but rates were higher in intermediate-aged hosts than in hosts at opposite ends of the age continuum. Conversely, parasitoid mortality from egression to adult eclosion was higher in the youngest and oldest host larvae. Adult parasitoid size increased significantly in line with host size at time of parasitism, but development time from oviposition to adult eclosion was greater when intermediate-aged hosts were selected than in when hosts at opposite ends of the age continuum were used. Developmental flexibility and host regulation appeared to be important to the parasitoid, in that the host instar from which parasitoid larvae emerged varied depending on when parasitism took place in the L₁ through L₃ host instars. The duration of the final instar of parasitized host larvae was significantly prolonged compared with unparasitized larvae under most circumstances, but was shortened when the host was parasitized in instar L₂ or L₃, with parasitoids emerging from the L₅ host larvae.

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1. Introduction

Among the most important trade-offs in life history evolution is whether to grow larger at the cost of longer development time, or to develop more rapidly at the cost of reduced size (Harvey and Strand, 2002). The intimate relationship between a host and its parasitoid provides an ideal model system to evaluate this trade-off, where the parasitoid compromises between offspring development rate and body size. This is especially so for koinobiont parasitoids, where the host continues to develop after being parasitized.

Koinobiont parasitoids can extend the range of vulnerable stages in hosts through either host regulation (Harvey et al., 1999; Jones, 1985, 1986; Vinson and Iwantsch, 1980) and/or developmental flexibility (Harvey and Strand, 2002; Harvey et al., 1994, 1995, 1996, 2000, 2004; Tanaka et al., 1984; Weseloh, 1984). Harvey and Strand (2002) compared developmental strategies of a number of braconid and ichneumonid koinobiont parasitoids attacking hosts that differed in their approach. They found that wasps parasitizing earlier instars of exposed, foliar-feeding hosts favored a reduction in development time over an increase in body size, whereas the opposite trend occurred among parasitoids attacking concealed hosts. They also found a compromised strategy between development time and body size in some parasitoids attacking exposed hosts,

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such as with some noctuid larvae that switch from foliar-feeding to burrowing into soil during their development. However, based on the dearth of comprehensive studies available, more studies are required to determine the applicability of this model (Harvey et al., 2004).

Meteorus pulchricornis (Wesmael) [= *japonicus* Ashmead] is a solitary braconid endoparasitoid of numerous lepidopteran pests, from the gypsy moth (*Lymantria dispar* (L.)), to noctuids such as the cotton bollworm (*Helicoverpa armigera* (Hübner)) and (Wan et al., 2002) beet armyworm (*Spodoptera exigua* Hübner) (Ding and Su, 2002). It is widely distributed in the Palearctic Region. Strains from Europe have been reported as being biparental, but uniparental strains have been found in Asia (Fuester et al., 1993; Li, 1984). This species has been introduced into North America for the control of gypsy moth (Fuester et al., 1993) and accidentally introduced into New Zealand, where it attacks a range of Lepidoptera (Berry, 1997; Berry and Walker, 2004). However, there have been limited studies of its biology and most of these used the gypsy moth as host (Fusco, 1981; Fuester et al., 1993). Li (1984) undertook a preliminary study of the bionomics of the uniparental strain parasitizing *H. armigera* in southwestern China. As a parasitoid of the beet armyworm, *M. pulchricornis* has been recorded from Spain (Caballero et al., 1990) and China (He et al., 2002; Xu et al., 2001). However, little is known about the developmental interactions between this parasitoid and its host *S. exigua*. We conducted an experiment using this parasitoid–host system to test the hypothesis postulated by Harvey and Strand (2002) with regard to the compromised developmental strategy in koinobiont braconids and ichneumonids. We also wanted to document the development of this parasitoid in relation to its host, *S. exigua*, as a first step toward a better understanding of this less-known model system.

2. Materials and methods

2.1. Culture of the parasitoid and host

Wild stock of *M. pulchricornis* was originally collected in August 2002 as an asexual (thelytokous) population from *S. exigua* larvae on soybean in a suburb of Nanjing City, Jiangsu Province (32.0°N and 118.7°E). These were reared in an insectary using *S. exigua* as the host at 24 ± 1 °C and $60 \pm 10\%$ RH with a 14:10 h light–dark photoperiod. Host *S. exigua* were collected as larvae from cotton plants in Fen County (34.7°N, 116.5°E), Jiangsu Province, in July 1995, and maintained thereafter on an artificial diet (Shen and Wu, 1995). Host larvae were individually reared in 10×1.5 cm glass tubes, from hatching until pupation. Pupae were transferred in groups to cages ($23 \times 22.5 \times 32$ cm high) with 40-mesh nylon organza over wooden frames for adult eclosion and egg laying. We provided strips of paper as a substrate for egg deposition, and 10% sucrose solution as supplementary food for the moths. The *M. pulchricornis* were cultured in clear plastic contain-

ers (15 cm diameter \times 10 cm high) containing ≈ 40 L₃ or L₄ host larvae; three adult wasps were released into these for one day. Mature parasitoid larvae emerged from host larvae to pupate externally. Wasps used in the experiment were 4–6 days old (our previous observation showed that the wasp attained high daily oviposition at this age) and had not previously been exposed to host larvae.

2.2. Experiment

Spodoptera exigua larvae undergo five instars (designated L₁–L₅) before pupating. The mean weight and age of host larvae on the day that each instar-cohort was exposed are shown in Table 1. A cohort of 20 larvae of each instar (which had molted within 5 h) was individually weighed to 0.01 mg on a microbalance (LAC114, Lavrock, Changshu) and then transferred into a clear plastic container (11 cm in diameter and 6 cm in height) with a 3 cm hole in the lid covered by nylon organza for ventilation, and another hole on the side (1 cm) for introducing wasps. A fresh cotton leaf was spread on the bottom of the container, which was lined with 1% agar to keep the leaf fresh. A 4–6-day-old wasp was released into the container, which contained 10% honey solution as a supplementary food source. The host larvae were removed after 8 h exposure and reared singly in glass tubes on artificial diet until the parasitoid larvae emerged and pupated.

The host larvae reared in glass tubes were checked twice a day (8:00 and 20:00 h). Time of molting was recorded to determine the development time of each instar in days. Host larvae that died midway between instars were dissected to check if they died as a result of parasitism. Parasitoid larval egression from hosts was recorded, cocoons were individually weighed, and wasp eclosion recorded.

Parasitoid mortality was measured from larval egression to adult eclosion. Development time of the parasitoid was measured from oviposition to adult eclosion, in days. Eclosed adult parasitoids were killed in 70% alcohol and the length of the right hind tibia measured under a stereomicroscope as a standard measure of size (Godfray, 1994).

2.3. Statistical analysis

Parasitoid mortality data were compared using logistic regression to determine if the data were non-linear, and χ^2 to determine if the data varied significantly with host age at parasitism. Susceptibility rates of host instars to parasitism, transformed by arcsine square root, were tested by ANOVA and Tukey's multiple comparison test. As the experimental design included multiple observations of the body sizes of offspring parasitoids for each host instar, the linear regression was first tested for departure from linearity before fitting the linear model (Zar, 1996). Development times, cocoon weights, and hind tibia length of the parasitoids were compared using ANOVA and Tukey's multiple comparison tests. Differences in development

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