# Convergent development of a parasitoid wasp on three host species with differing mass and growth potential

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## Abstract

Koinobiont parasitoids develop in hosts that continue feeding and growing during the course of parasitism. Here, we compared development of a solitary koinobiont endoparasitoid, *Meteorus pulchricornis* Westmael (Hymenoptera: Braconidae), in second (L2) and fourth (L4) instars of three host species that are closely related (Lepidoptera: Noctuidae) but which exhibit large variation in growth potential. Two hosts, *Mamestra brassicae* L. and *Spodoptera littoralis* Boisduval, may reach 1 g or more when the caterpillars are fully mature, whereas *Spodoptera exigua* Hübner is much smaller with mature caterpillars rarely exceeding 200 mg. Parasitoid survival (to pupation) in the two host instars was much higher on the larger hosts than on *S. exigua*. However, other fitness correlates in *M. pulchricornis* were very similar in the three host species. Development time was fairly uniform in L2 and L4 hosts of the three host species, whereas wasps were larger in L4 than in L2 hosts. However, *M. pulchricornis* developmentally arrested each of the hosts differently. The mass of dying L2 and L4 hosts after parasitoid larval egression (i.e., when they emerge from the dying caterpillar) varied significantly, with *S. littoralis* being by far the largest and *S. exigua* the smallest. These results reveal that *M. pulchricornis* is able to adjust its own development in response to species-specific differences in host resources.

## Introduction

All organisms need food to survive and reproduce. In many holometabolous insects, different stages consume different kinds of food. For example, the caterpillars of most butterfly and moth species feed on plant tissues—leaves and shoots—prior to pupation, whereas the adult insects consume sugar-rich sources such as nectar. Most insect herbivores and predators must feed on a large amount of resources to complete their development; hence, they attack large plants or many prey, respectively, which effectively represent super-abundant resources. In studying resource-related constraints on growth and development, parasitoid wasps are generally under much larger constraints than herbivores or predators in terms of the quality and quantity of their resources (Mackauer & Sequeira, 1993; Godfray, 1994; Brodeur & Boivin, 2004; Harvey, 2005). Unlike other insect consumers, parasitoids are dependent upon the finite resources contained in a single host, that is, often not much larger than the adult female parasitoid that attacked it (Harvey, 2005). For this reason, parasitoids are strongly selected to optimize the acquisition, utilization, and allocation of these resources to fitness functions such as reproduction and survival (Slansky, 1986; Jervis et al., 2008).

Adult size, development time, and survival are the three best-studied fitness correlates in parasitoids (Harvey, 2005). These parameters often vary in accordance with host traits such as size or instar parasitized, host species, nutritional status (e.g., diet), and the presence of other competitors such as other parasitoids (both con- or

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heterospecific) or pathogens (Harvey, 2005). Parasitoids have been broken down into two groups based on strategies they exhibit in exploiting host resources ('dichotomous hypothesis'; Mayhew & Blackburn, 1999). Idiobiont parasitoids attack non-growing host stages, such as eggs or pupae, or hosts that have been permanently paralyzed prior to oviposition (Askew & Shaw, 1986). For idiobionts, the host represents a static resource because no new resources are added to it during parasitism; host quality is therefore based on the host's previous nutritional and developmental history (Vinson, 1988). Consequently, parasitoid size is often positively correlated with host size at oviposition, at least in solitary parasitoids (Arthur & Wylie, 1959; Sandlan, 1982; Otto & Mackauer, 1998; Harvey, 2008). Development often takes longer to complete in large hosts simply because they take longer to consume than small hosts (Mackauer & Sequeira, 1993).

In contrast, a separate group of parasitoids, collectively called 'koinobionts', attack hosts that continue feeding, growing, and defending themselves during the parasitism phase (Askew & Shaw, 1986). Hosts parasitized by koinobionts represent potentially dynamic resources where hosts may be many times larger when killed by the parasitoid than when they were parasitized (Mackauer & Sequeira, 1993). Consequently, the relationship between host size at parasitism and parasitoid fitness correlates is often more difficult to predict with koinobionts than with idiobionts. Some koinobionts attack and develop in tiny, early instar hosts (e.g., L1 or L2 instars) that grow too slowly for the host to acquire sufficient resources (and mass) for the parasitoid to maximize body mass and minimize development time (Harvey et al., 2004). In this case, the optimal phenotype is determined by a trade-off in these parameters, whereby there is less variation in the more important fitness correlate (Mackauer & Sequeira, 1993). In habitats where development time is correlated with precocious mortality, such as when hosts feed from exposed locations on the food plant, for example, selection favors a reduction in this parameter (Harvey & Strand, 2002). Alternatively, in habitats where survival is high, such as when hosts feed from concealed locations, selection often favors an increase in body mass at the expense of increased development time (Harvey & Strand, 2002).

Most koinobiont parasitoids exhibit high degrees of specialization because their eggs and larvae develop in a chemically hostile internal host milieu, where they are susceptible to immune cells such as circulating granulocytes and hemocytes (Strand & Pech, 1995; Lavine & Strand, 2002). For this reason, different parasitoid species (or occasionally genera) are restricted to attacking hosts in the same family that exhibit phylogenetically conserved immune responses. Thus, microgastrine species such as *Cotesia marginiventris* (Cresson) and many *Microplitis* species only parasitize larval hosts in the moth family Noctuidae (Harvey et al., 2014). In other cases, host specialization may become extreme. For example, *Cotesia rubecula* (Marshall) only attacks a single species of host, caterpillars of the cabbage butterfly *Pieris rapae* (L.). However, some koinobionts exhibit remarkably broad host ranges that transcend phylogenetic constraints. The solitary asexually reproducing parasitoid *Meteorus pulchricornis* Westmael (Hymenoptera: Braconidae) is exceptional in this regard. It is known to attack caterpillar hosts in up to 12 families of Lepidoptera, including groups that are not closely related phylogenetically (Suzuki & Tanaka, 2007).

Many koinobiont parasitoids regulate the growth of hosts to optimize offspring fitness (Vinson & Iwantsch, 1980; Pennacchio & Strand, 2006). Regulation is achieved by biochemical factors injected by the female parasitoid into the host during the oviposition sequence (Lawrence, 1986, 1990) and/or by manipulation of the host by the parasitoid eggs or larvae (Dahlman, 1990; Strand & Wong, 1991; Falabella et al., 2000; Beckage & Gelman, 2004). Host regulation is aimed at stabilizing host size-related variation in resource availability to the parasitoid larvae, and, in solitary species, often involves a significant reduction in the growth of parasitized hosts compared with healthy cohorts (Jones & Lewis, 1971; Vinson, 1972; Harvey et al., 1999, 2004, 2010).

This study examines development of *M. pulchricornis* in two instars of three host species that also differ profoundly in their growth potential. The three species are closely related and occur in the same family (Lepidoptera: Noctuidae). *Mamestra brassicae* L. and *Spodoptera littoralis* Boisduval are large moths whose mature larvae may also exceed 1 g prior to pupation (Harvey et al., 2014). By contrast, *S. exigua* is much smaller than the other two species and their larvae rarely exceed 200 mg at the same stage (Greenberg et al., 2001). Here, parasitoids developed in small (L2) and large (L4) instars of the three host species and survival, egg-to-adult development time, and adult body mass were compared. The terminal mass of dying larvae in the three hosts was also compared to determine whether differences in this parameter translated into effects on parasitoid development. To compare interspecific differences in the growth potential of the three noctuids, masses of unparasitized pupae were obtained. We hypothesize that, although there are large differences in the growth potential of the three host species, development of the parasitoid will be convergent in the

three hosts on the basis of host regulation by *M. pulchricornis*. Moreover, we expect that selection will favor rapid development over body mass in L2 hosts on the basis of the exposed feeding profiles of the three hosts in nature, as predicted by Harvey & Strand (2002).

## Materials and methods

### Insects

All cultures and experiments were conducted at 23 ± 2 °C with a L16:D8h photoperiod. The cabbage moth, *M. brassicae*, is considered to be a major pest of collard crops across much of Eurasia although it is a generalist herbivore and feeds on many herbaceous plants in nature. The species is univoltine. Female moths typically lay batches of eggs on plants in early to mid-summer and the caterpillars disperse at hatching and feed in loose assemblages on the natal plant or on neighboring plants. The larvae complete five instars and at maturity abandon the food plant and burrow into the soil where they pupate. The pupae overwinter in the soil and adult moths emerge late the following spring. *Mamestra brassicae* were originally collected in cabbage fields in Wageningen and were supplied by the Department of Entomology, Wageningen University (WU), The Netherlands. Male and female moths were placed in groups of ca. 10–15 into plastic flasks containing a vermiculite base and 20% (wt/vol) sugar solution absorbed into cotton wool in a small plastic vial. Blotting paper was placed around the inside of the flask and as a lid secured by an elastic band. The females lay batches of eggs directly onto the paper. Newly hatched larvae were placed in plastic boxes (25 × 10 × 10 cm) containing artificial diet especially made for the Noctuidae (for the recipe see Shorey & Hale, 1965). New plants were added as necessary. Pre-pupae were collected from the cages and placed in plastic boxes (25 × 10 × 10 cm) containing a layer of vermiculite into which they pupate.

The southern beet armyworm, *S. exigua*, is native to warm regions of Eurasia and it is also a major pest of several crops in different parts of the world. The culture of this noctuid species was supplied by the Department of Virology, WU. The congeneric species *S. littoralis* is native to northern Africa and the Mediterranean countries and feeds on many plants in nature including important crops. The culture of this herbivore was supplied by the Department of Ecology, Neuchâtel University, Switzerland. Both *Spodoptera* species exhibit similar developmental programs as *M. brassicae* except that they have continual life cycles in the warm countries where they are native. Both species were reared according to the criteria described for *M. brassicae* (above).

*Meteorus pulchricornis* was originally obtained from a culture maintained at Nagoya University, Japan, and had been collected from agricultural fields near the university. It has been reared on *M. brassicae* at the Netherlands Institute of Ecology (NIOO) for over 3 years. This parasitoid is a widespread Palearctic species with asexual strains found primarily in Asia and sexual populations in Europe. It typically parasitizes several host instars. At egression the parasitoids produce strong threads which they anchor to the under surface of a leaf. The cocoons are constructed at the end of a thread and dangle from the leaf. This provides protection against predators like ants (Shirai & Maeto, 2009), but not against hyperparasitoids (Harvey et al., 2011).

### Experimental protocol

*Pupal mass of* Mamestra brassicae, Spodoptera exigua, *and* S. littoralis *(= control).* Eggs of the three herbivores were collected on blotting paper from separate rearings (by species). Upon hatching, the neonate larvae were placed into five separate plastic boxes (for each herbivore species, hence 15 boxes for each species) containing artificial diet. The larvae were allowed to feed and develop on diet until pupation; diet was refreshed as necessary and boxes were cleaned at least twice to remove feces. Late in the final (= fifth) instar vermiculite was added to the boxes as the larvae use this as a pupal medium. Fresh pupae were weighed on a Mettler microbalance (accuracy 1 μg).

*Survival, egg-to-adult development time, and adult mass of* Meteorus pulchricornis *in larvae of* Mamestra brassicae, Spodoptera exigua, *and* S. littoralis. Neonate larvae of the three herbivore hosts were reared separately in large plastic boxes in groups of ca. 100 containing artificial diet. One day after molting to L2, larvae were individually presented to individual female parasitoids in vials at the end of a finely tipped artist's paint brush. Females were allowed to sting the larvae once and these larvae were then reared in groups of 50–70 in plastic boxes. Fresh parasitoid pupae were collected and placed in large Petri dishes (18 cm diameter) until adult eclosion. Development time was determined as the number of days between parasitism and adult eclosion. Newly emerged wasps were also weighed on a Mettler microbalance (accuracy 1 μg). Survival was measured as the number of parasitized larvae that produced adult parasitoids.

*Maximum larval mass of parasitized* Mamestra brassicae, Spodoptera exigua, *and* S. littoralis. At egression, dying L2 and L4 caterpillars of the three herbivore species were collected and weighed individually on the Mettler

microbalance (accuracy 1 μg). This enables us to compare this parameter as it relates to host species and instar.

### Statistical analysis

Pupal masses of *M. brassicae*, *S. exigua*, and *S. littoralis* were compared via a one-way ANOVA. Survival data of the parasitoid in the three hosts was compared via a $\chi^2$ test with a binomial test used to compare instars. All development data were analyzed by means of General Linear Model ANOVAs with (1) host species and instar as factors, as well as the interactive effect between host and instar, or (2) final host mass and instar as factors, as well as the interactive effect between host and instar. All statistics were calculated in Minitab v.16 (Minitab, Coventry, UK).

## Results

### Pupal mass of *Mamestra brassicae*, *Spodoptera exigua*, and *S. littoralis* (= control)

There was highly significant variation in the pupal mass of the three host species ($F_{2,70} = 261.17$, P<0.0001). *Mamestra brassicae* was the largest in terms of pupal mass, with *S. littoralis* about 25% smaller. By far the smallest species was *S. exigua*, with a pupal mass only about 25% that of *M. brassicae* (Figure 1).

### Survival, egg-to-adult development time, and adult mass of *Meteorus pulchricornis* in larvae of *Mamestra brassicae*, *Spodoptera exigua*, and *S. littoralis*

Survival of *M. pulchricornis* to eclosion varied significantly with treatment ($\chi^2 = 4.31$, d.f. = 5, P<0.001). More specifically, it varied between the host species (Wald = 11.47, d.f. = 2, P<0.001), but not with instar parasitized within host species (Wald = 1.58, d.f. = 1, P = 0.21). Parasitoid

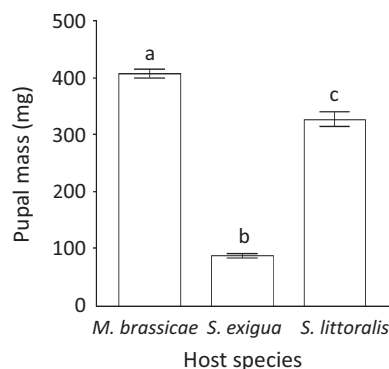survival was also higher in *M. brassicae* and *S. littoralis* than in *S. exigua* but was approximately similar in both host instars (Figure 2A). Egg-to-adult development time did not vary significantly with either host species parasitized ($F_{2,121} = 1.18$, P = 0.31) or instar ($F_{1,121} = 0.44$, P = 0.51), nor was the interactive effect between these parameters significant, although there was a trend ($F_{2,121} = 2.65$, P = 0.08). Development time was ca. 15 days in the different host species and was similar in both L2 and L4 hosts (Figure 2B). Adult body mass also did not vary significantly with host species ($F_{2,121} = 0.64$, P = 0.53), but did so with instar ($F_{1,121} = 116.89$, P<0.0001). Adult parasitoids were typically some 0.5 g heavier when developing in L4 than in L2 hosts (Figure 2C). However, as with development time, there was uniformity in this parameter across the three host species.
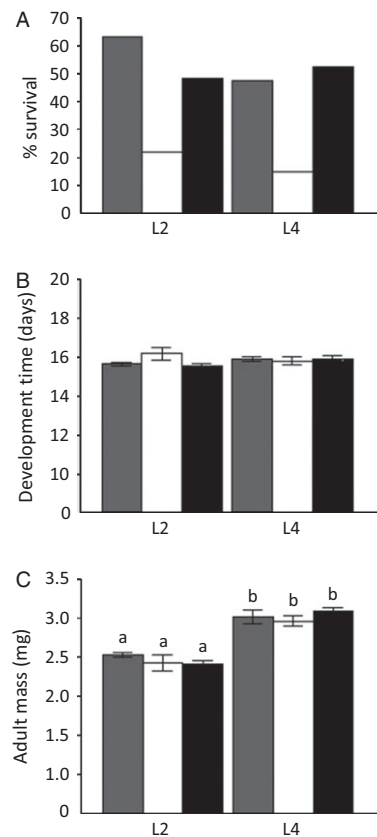


**Figure 1** Mean (± SE) pupal masses of *Mamestra brassicae* (n = 37), *Spodoptera exigua* (n = 16), and *Spodoptera littoralis* (n = 20). Bars with different letters are significantly different (Tukey–Kramer tests: P<0.05).



**Figure 2** (A) Survival and mean (± SE) (B) egg-to-adult development time (days) and (C) body mass (mg) of *Meteorus pulchricornis* on L2 and L4 instars of *Mamestra brassicae* (gray bars), *Spodoptera exigua* (white bars), and *Spodoptera littoralis* (black bars). Bars with different letters are significantly different (Tukey–Kramer tests: P<0.05). Sample sizes: (L2, L4) *M. brassicae* = 38, 19; *S. exigua* = 13, 9; *S. littoralis* = 34, 21.

**Maximum larval mass of parasitized *Mamestra brassicae*, *Spodoptera exigua*, and *S. littoralis***

The terminal mass of dying host larvae varied significantly with host species ($F_{2,66} = 13.82$, P<0.0001) and instar parasitized ($F_{1,66} = 31.35$, P<0.0001). Furthermore, there was a significant host*instar interaction on terminal mass ($F_{2,66} = 9.44$, P<0.0001). In partial contrast with controls, the development of L2 and L4 *S. littoralis* caterpillars was arrested at a larger mass than the other two hosts (Figure 3). In L4 larvae, the difference in mass was exceptional. *Spodoptera exigua* were developmentally arrested when they were smaller than the other two species.

## Discussion

In this study, we found that there was remarkable similarity in host quality (= development time and adult body mass) of *M. pulchricornis* developing in three host species that nevertheless exhibited significant variation in growth potential both in unparasitized and parasitized cohorts. However, some differences in quality were observed in progeny emerging from hosts parasitized as L2 or L4. Parasitoids typically took 15 days to complete their life cycles in both instars of the three hosts, but were about 0.5 mg (or 15–20%) larger when developing in the larger host instar. Host suitability in terms of parasitoid survival, however, was much lower in *S. exigua* than in the two larger hosts, *M. brassicae* and *S. littoralis*, with less than 20% of parasitized caterpillars producing adult wasps in the smallest host species. However, larval parasitoid survival never exceeded 62% in any of the host species or instars. This could be because *M. pulchricornis* is an extreme generalist, being able to develop in up to 12 families in the Lepidoptera (Suzuki & Tanaka, 2006). Thus, the parasitoid may trade-off extreme generalism where it can parasitize a wide range of hosts in its habitat with reduced adaptation
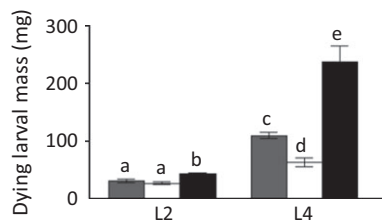


**Figure 3** Mean (± SE) body mass (mg) of dying L2 and L4 *Mamestra brassicae* (gray bars), *Spodoptera exigua* (white bars), and *Spodoptera littoralis* (black bars) larvae immediately following larval parasitoid egression. Bars with different letters are significantly different (Tukey–Kramer tests: P<0.05). Sample sizes: (L2, L4) *M. brassicae* = 4, 10; *S. exigua* = 13, 6; *S. littoralis* = 20, 20.

to optimally exploit many of these hosts. Specialist parasitoids are involved in intimate co-evolution with one or a few species of closely related hosts and are under intense selection to optimally exploit and utilize these hosts (Godfray, 1994). By contrast, selection for host exploitation and utilization in *M. pulchricornis* may be much more diffuse in any given host species, owing to its broad host range.

Other studies have also reported host species related effects on the development of both koinobiont and idiobiont parasitoids (Harvey, 2005). In koinobionts, larger host species are often (but not always) of higher quality, at least in terms of parasitoid size (Mackauer & Sequeira, 1993; Godfray, 1994; Harvey, 2005). However, effects on development time and survival are often much less clear-cut (Godfray, 1994; Visser, 1994). Larger hosts may possess stronger immune defences (Strand & Pech, 1995) or grow too large for the immature parasitoids to consume and assimilate (Beckage & Templeton, 1985; Harvey, 1996).

Host instar-related patterns in development in koinobionts may also vary quite widely from one parasitoid association with another. In larger host instars, initial host resources are sufficient for the parasitoid to optimally synchronize development by minimizing development time and maximizing adult size (Reznik et al., 1992; Harvey, 2005). However, when developing in nutritionally deficient early host instars, these two fitness correlates must be trade-off against one another, because the host grows too slowly to achieve minimal development time and maximal size. In this case, the trait that most influences offspring fitness will be the main target of selection. In some parasitoids development time is negatively correlated with host instar, whereas adult size is fairly constant (Gunasena et al., 1989; Harvey et al., 2000; Harvey & Strand, 2002). However, in others an almost opposite pattern is observed, whereby development time is fairly constant across host instars, but parasitoid size increases linearly with instar at parasitism (Harvey & Strand, 2002). Intermediate patterns are also sometimes reported (Smilowitz & Iwantsch, 1973; Malcicka & Harvey, 2014).

Harvey & Strand (2002) examined host size-related variations in koinobiont development and found that there was a strong correlation in the importance of development time or size with the feeding profile of the host species. Parasitoids attacking exposed-feeding hosts, such as caterpillars on leaf tissues of plants, tended to favor rapid development time over increased body size, whereas the opposite pattern was found for parasitoids attacking hosts that feed in concealed locations, such as leaf miners. The authors suggested that these differences may be attributable to the susceptibility of parasitized hosts to predators such as other insects or birds. If the host dies before the parasitoid can complete its development, so does the

parasitoid (Fritz, 1982). The 'slow-growth-high-mortality' hypothesis predicts that the longer an insect takes to complete the larval stage of its life cycle, the more it is prone to predation and thus selection under these conditions should aim to reduce development time, irrespective of effects on growth and size (Clancy & Price, 1987; Benrey & Denno, 1997; Williams, 1999; Fordyce & Shapiro, 2003). The results of Harvey & Strand (2002) lend support to this hypothesis in parasitoids.

Most koinobionts are endoparasitoids, and therefore they must abrogate or circumvent the host's immune defences, and this entails the evolution of regulatory strategies that target a very conservative number of closely related host species (Strand & Pech, 1995). However, *M. pulchricornis* is exceptional amongst koinobionts in that it exhibits an extremely broad host range that includes at least 12 families in the Lepidoptera (Suzuki & Tanaka, 2007). This parasitoid possesses extremely potent venom that has clearly played an important role in enabling *M. pulchricornis* to quite dramatically expand its host range (Suzuki & Tanaka, 2006). In addition to dealing with the host's immune defences, many koinobionts must manipulate host growth to optimize the amount of resources available to their progeny. Host growth regulation has long been considered to be an important weapon in the arsenal of koinobiont parasitoids. Many koinobionts significantly reduce host growth compared with the growth of healthy (unparasitized) individuals. However, *M. pulchricornis* is fairly unique amongst koinobionts in that its hosts include species that are physiologically and morphologically very different. For instance, Harvey et al. (2010) compared development of *M. pulchricornis* in L2 instars of a micro-lepidopteran (*Plutella xylostella* L.) and a macro-lepidopteran (*Mythimna separata* Walker) host. Larvae of *P. xylostella* only grow to about 10 mg whereas larvae of *M. separata* may exceed 1 g just prior to pupation. The authors found that, although *M. separata* was the higher quality host and produced significantly larger parasitoids than *P. xylostella*, the parasitoid manipulated host growth by reducing the size of the large host by >95% compared with controls, while stimulating growth of the small host by up to 30%. In this way, it reduces size-related constraints on resource allocation to the parasitoid progeny, thus streamlining host quality in the two species to some degree.

In summary, this study has reported strong similarity in two important fitness-related traits of the parasitoid *M. pulchricornis* developing in three host species, which vary in growth potential both during parasitism and in healthy (unparasitized) hosts. This is likely due to adjustments in the feeding behavior of the parasitoid larvae in which they consume proportionally more resources in the smaller host species (*S. exigua*) as well as the fact that the host is not consumed piecemeal, but instead significant host resources are left behind by the mature parasitoid larva. Both factors have probably played a profoundly important role in enabling *M. pulchricornis* to optimize size and development time in the three host species. However, given that *M. pulchricornis* survived poorly in the smallest host species (*S. exigua*) studied here, clearly other factors influencing host suitability are unrelated to host size.

## Acknowledgements

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