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# Trade-offs between developmental parameters of two endoparasitoids developing in different instars of the same host species

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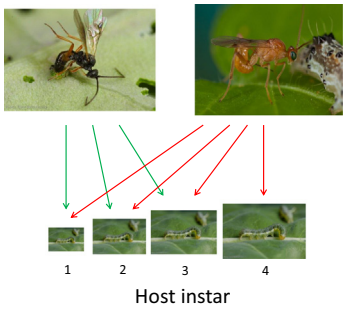
## HIGHLIGHTS

- This study compares fitness-related traits in two koinobiont endoparasitoids.
- *Meteorus pulchricornis* is approximately twice the size of *Microplitis mediator*.
- Both parasitoids developed in different larval instars of *Mamestra brassicae*.
- Development time was more important for fitness than body size.
- Trade-offs in these traits were more apparent in *M. pulchricornis*.

## GRAPHICAL ABSTRACT

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## ABSTRACT

Trade-offs amongst life history traits is a major theme in evolutionary biology. Parasitoid wasps are important biological control agents and make excellent organisms to examine trade-offs in fitness related traits such as size, development rate and survival. Here, we examined trait-related trade-offs in 2 solitary endoparasitoids developing in different stages (or instars) of the same caterpillar host, the cabbage moth *Mamestra brassicae*. *Microplitis mediator* is a small specialist parasitoid that attacks first (L1) to third (L3) instars of *M. brassicae*; *Meteorus pulchricornis* is a larger highly generalized parasitoid that attacks L1–L4 instars of the same host species. When developing in early host instars (e.g. L1–L2), both parasitoids differently traded-off size against development time. In *M. mediator*, adult body mass was smaller in wasps developing in L1 than in L2 and L3 hosts, whereas development time was unaffected by instar. By contrast, adult body mass in *M. pulchricornis* was smaller and development time longer when developing in L1 and L2 than in L3 and L4 instars. Periodic starvation of *M. brassicae* caterpillars parasitized by *M. pulchricornis* further reduced adult mass and extended development time of wasps in L2 (but not L4) hosts. Maximum egg load in *M. pulchricornis* (but not *M. mediator*) was correlated with adult female body size. Our results imply that rapid development time is more important than body size for fitness in both species, although in *M. pulchricornis* both development time and adult size are traded off in determining the optimal phenotype. Developing a better understanding of association-specific patterns of development in parasitoids can assist in the optimization of mass rearing of these insects for biological control.


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## 1. Introduction

One of the most enduring areas of evolutionary biology has been to identify and quantify suites of traits that influence the fitness of organisms in their natural environment (Stearns, 1989; Abrams and Rowe, 1996). These traits include body mass, structure and morphology, development rate, reproductive biology, fecundity and other parameters (Roff, 2002). The evolution of life history traits in a species is influenced by a number of environmental factors as well as its own phylogenetic history. The ideal organism, if it indeed existed, would optimize every trait that plays an important role in determining its fitness. Such a hypothetical species would produce many offspring at frequent intervals, would enjoy a long lifespan, develop rapidly and reach sexual maturity early in life, and be well protected against its natural enemies such as predators and pathogens. However, given metabolic limitations on all of these functions, no such organism exists. Instead, the optimal phenotype in any species is determined by trade-offs amongst traits in such a way that fitness is generally maximized. In this scenario, when traits are costly to maintain, those traits that more importantly influence fitness will be selected for at the expense of others that are less important. Among the most important life-history trade-offs so far described are between early and later reproduction and/or between reproduction and survival (Lessells, 1991; Vollrath and Parker, 1992).

Parasitoid wasps have long been considered as excellent organisms to study trade-offs in various life-history traits. Parasitoids are insect natural enemies whose eggs and larvae develop in or on the body of other arthropods, whereas the adults are free-living (Godfray, 1994). One of the main reasons they are so well studied is because of their importance in biological control programs against a wide range of serious insect pests (Hajek, 2004). At the same time, the more we know about the bionomics of parasitoids, the more effective we will be in mass rearing them for inoculative or inundative releases in agro-ecosystems. Parasitoids are unique, at least compared with other organisms, such as predators, in that they depend on ostensibly finite resources contained in a single host individual for their entire immature development. The host in turn is often not much larger than the parasitoid, even when it is destroyed, and thus parasitoids are under severe selection to optimize the exploitation and allocation of these limited resources to different, and potentially competing, fitness functions.

It has long been known that the quality and quantity of host resources strongly affects parasitoid fitness (Godfray, 1994). Host quality is defined as variation in host-related traits, such as size, nutritional status and intrinsic competition that affect the dynamic properties of parasitoid growth, body size development rate and survival (Mackauer and Sequeira, 1993; Harvey et al., 2013). In parasitoids adult body size is often positively correlated with demographic parameters such as longevity and fecundity, and therefore host quality represents a major constraint upon parasitoid fitness (King, 1989; Mackauer and Sequeira, 1993; Godfray, 1994; Harvey, 2005). Although the effect of development time on parasitoid fitness is poorly understood, an increased development rate can be beneficial early in the season when populations are growing (Godfray, 1994), or else reduces the risk of predation and/or pathogenic infection when these are high (the 'slow-growth-high-mortality-hypothesis' *sensu* Clancy and Price, 1987; Benrey and Denno, 1997; Williams, 1999). Given that both size and development time may importantly affect parasitoid fitness it is often possible to determine which of these parameters is more important by examining the development of parasitoids in hosts of differing size (Harvey and Strand, 2002).

Based on differing host utilization strategies, parasitoids have been divided into two groups, 'idiobionts' and 'koinobionts' (Harvey, 2005). Idiobionts are primarily ectoparasitoids which utilize venom in order to paralyze the host, or they attack sessile (non-feeding) host stages such as eggs or pupae (Harvey, 2005). By contrast, koinobionts are primarily endoparasioids which attack hosts that continue feeding and growing through much of the course of parasitism (Pennacchio and Strand, 2006). For idiobionts, the host represents a largely static resource that does not attain additional mass during parasitism (Mackauer and Sequeira, 1993; Otto and Mackauer, 1998). Hosts parasitized by koinobionts, on the other hand, represent potentially dynamic resources that may differ greatly in mass between parasitism and host death (Sequeira and Mackauer, 1992a,b; Harvey et al., 1994, 1999, 2004; Pennacchio and Strand, 2006). Many koinobionts attack and develop in small, nutritionally suboptimal early host instars that are only a fraction of the size of the ovipositing female parasitoid. In these circumstances, the host may grow too slowly to obtain sufficient resources for the parasitoid progeny to maximize body size and minimize development time. Consequently, the parasitoid offspring may have to regulate their own developmental program by trading off rapid development time against small adult size or *vice versa*.

Mackauer and Sequeira (1993) proposed three different patterns of host usage by parasitoids, based on the empirical literature. Two of the three models describe host-related nutritional constraints on koinobiont development. The first koinobiont model assumes that body size is more important than development time in determining parasitoid fitness. Consequently, parasitoids developing in low quality early host instars will delay their development and not destroy the host until it reaches a size in which the parasitoid can maximize its own body size. Alternatively, parasitoids attacking large, high quality hosts are assumed to grow at a constant rate and do not need to exhibit a lag phase: host resources are sufficient to optimize both adult size and development time. This pattern of development has been described in several species of primary koinobiont endoparasitoids (Harvey et al., 1994, 2000) and even a primary hyperparasitoid (Harvey et al., 2012). In the second model, parasitoid growth and development are assumed to be resource and time-limited. Under such conditions, parasitoids are also expected to initially delay development in small, low quality hosts, but are also assumed to exhibit a compensatory increase in growth rate during late stages to balance fitness gains from increased size against losses incurred by delayed development. This pattern has been particularly well-described in solitary endoparasitoids of aphid hosts (Sequeira and Mackauer, 1992a,b). Importantly, in both models, parasitoid fitness is host size-dependent, and is determined by a trade-off between size and development time (Mackauer and Sequeira, 1993).

This study compares and contrasts development patterns in two solitary koinobiont endoparasitoids sharing the same host species. *Microplitis mediator* Haliday (Hymenoptera: Braconidae) is a specialist parasitoid that parasitizes first (hereafter L1) to third (L3) larval instars of the cabbage moth, *Mamestra brassicae* Linnaeus (Lepidoptera: Noctuidae) Fuester et al., 1993. *Meteorus pulchicornis* Wesmael (Hymenoptera: Braconidae) is a generalist parasitoid that is known to attack hosts in at least 12 families of the Lepidoptera (Suzuki and Tanaka, 2007; Harvey et al., 2010). Adult females are approximately twice the size of adult *M. mediator* females and are capable of attacking L1–L4 instars of *M. brassicae*. Both parasitoids are important biological control agents of various noctuid pests and have been introduced widely to control both natural and novel hosts (e.g. Arthur and Mason, 1986; Li et al., 2004; Suzuki and Tanaka, 2007; Chhagan et al., 2008).

The aims of this paper are: (1) to compare development time and adult fresh body mass of *M. mediator* and *M. pulchicornis* developing in different instars of the cabbage moth, *M. brassicae*, (2) to determine if maximum egg loads (an indirect measure of fecundity