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THE DEVELOPMENTAL STRATEGIES OF ENDOPARASITOID WASPS VARY WITH HOST FEEDING ECOLOGY

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Abstract. 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. For insect herbivores, resolution of this trade-off is thought to be strongly influenced by feeding ecology and mortality risks. In contrast, how these factors might affect the developmental strategies of third trophic level organisms, like parasitoid wasps, is less understood. To address this question, we compared the development of larval endoparasitoids in the families Ichneumonidae and Braconidae that parasitize larval stage herbivores in the order Lepidoptera. The campoplegine ichneumonid *Venturia canescens* parasitized concealed hosts and exhibited a developmental strategy that favored progeny size over development time. In contrast, the closely related ichneumonid *Campoletis sonorensis* parasitized exposed hosts and exhibited the opposite strategy of favoring rapid development time over size. The microgastrine braconid *Microplitis croceipes* attacks partially concealed hosts and showed evidence of a trade-off between maximizing body size and minimizing development times. These results suggested that parasitoids attacking apparent, foliar-feeding hosts may favor rapid development time over size while parasitoids that attack concealed hosts favor size over development time. A broader survey of the literature supported the trends found in our experimental studies. The braconids and ichneumonids examined in this study also exhibit distinct differences in larval feeding and pupation behavior. These developmental traits did not appear to affect the size–development time continuum. However, these traits may affect the size range of hosts that larval endoparasitoids can successfully exploit.

Key words: *Campoletis sonorensis*; *development, insect*; *herbivore, insect*; *insects*; *life history*; *Microplitis croceipes*; *parasitoid*; *Venturia canescens*.

INTRODUCTION

The evolution of life history traits is influenced by both environmental factors and phylogenetic history. As a consequence, trait evolution almost always involves trade-offs between competing fitness functions (Stearns 1989, Lessells 1991, Abrams and Rowe 1996). Among the most important trade-offs is whether to grow larger at the cost of longer development time, or to develop more rapidly at the cost of reduced size. Studies from diverse taxa indicate that size is a primary target for selection, and that animals often allocate resources in ways that maximize this parameter. However, accelerated development at the cost of reduced size can be favored under conditions of high predation risks or limiting resources (Cole 1954, Schaffer 1974, Hirshfield and Tinkle 1975, Charlesworth 1980, Curio 1989). The slow growth–high mortality hypothesis (SG–HM), as originally conceived for insect herbivores (Clancy and Price 1987), similarly predicts that re-

duced plant quality or allelochemicals will increase development time and mortality risks from natural enemies (Moran and Hamilton 1980, reviewed by Williams 1999). Evidence for mortality increasing with development time derives from several studies on insect herbivores that develop in exposed locations (Price et al. 1980, Grossmueller and Lederhouse 1985, Leather 1985, Benrey and Denno 1997). However, prolonged development times appear to have lower costs for species that feed in concealed sites, because risks of predation and parasitism are lower (Clancy and Price 1987, Craig et al. 1990, Johnson and Gould 1992).

The abundance and mortality risks faced by insect herbivores have long been thought to impact the evolution of fecundity in natural enemies (e.g., balanced mortality hypothesis) (Price 1973, 1974, 1980). In contrast, how host ecology might affect the development of third trophic level organisms is much less understood (Strand 2000). Parasitoid wasps are of particular interest in this regard, because all resources for development derive from feeding on one host individual. Parasitoids usually lay their eggs in (endoparasitoids) or on (ectoparasitoids) the bodies of insect herbivores, and their offspring develop by consuming host tissues or hemolymph. Most parasitoids develop in only a narrow range of host species and are only able to attack a particular life stage (egg, larva, pupa, or adult). En-

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doparasitoids that attack larval stage hosts are also referred to as koinobionts, because hosts continue to grow after being parasitized (Askew and Shaw 1986). Because of this interaction, hosts of koinobionts represent an open resource that can either be consumed rapidly by the developing parasitoid larva or that can increase in mass before being consumed to yield a larger parasitoid. Adult size has usually been considered the primary target for selection in parasitoids and that offspring should develop in ways that maximize this trait (Waage and Godfray 1985, King 1989, Mackauer and Sequeira 1993, Visser 1994, Mackauer et al. 1997). Yet, if the host dies before the parasitoid completes development, then the parasitoid also obviously dies. This intuitively suggests that selection should favor developmental strategies that maximize progeny survival to adulthood first and other traits secondarily. It also suggests that while increased size may be favored over development time in parasitoids that face low mortality risks, rapid development time at the expense of size may be favored in parasitoids whose hosts confront high risks of predation.

Among the largest taxa of parasitoid wasps is the monophyletic superfamily Ichneumonoidea, which itself is divided into the families Ichneumonidae and Braconidae (Whitfield 1998, Quicke et al. 2000). The ichneumonid subfamily Campopleginae and braconid subfamily Microgastrinae are comprised exclusively of koinobiont endoparasitoids that attack larval stage herbivores in the order Lepidoptera (moths and butterflies). These parasitoids are very similar in size and commonly have overlapping host ranges. Yet, they also differ in two key developmental traits. Campoplegine ichneumonids obligately consume most or all host tissues and usually pupate after the host is consumed, while microgastrine braconids usually feed only on host hemolymph and emerge from the still living host to pupate externally (Gauld and Bolton 1988, Harvey et al. 2000).

In this study we examined the development of selected campoplegines and microgastrines in relation to host ecology and wasp feeding behavior. In the first part of this study, we measured development times, adult size, and host consumption by *Venturia canescens* Gravenhorst (Ichneumonoidea: Ichneumonidae, Campopleginae), *Campoletis sonorensis* Cameron (Ichneumonoidea: Ichneumonidae, Campopleginae), and *Microplitis croceipes* (Ichneumonoidea: Braconidae, Microgastrinae). We then conducted a survey to determine whether the broader literature supported the trends found in our experimental studies. Our results indicated that the developmental strategies of ichneumonoid koinobionts vary with the feeding ecology of their hosts. Larval feeding and pupation behavior of the parasitoid did not affect developmental strategies, but these traits could affect the size range of hosts that endoparasitoids can successfully parasitize.

METHODS

Biology of hosts and parasitoids

All hosts and parasitoids were reared at $27^{\circ} \pm 2^{\circ}\text{C}$, $65 \pm 5\%$ relative humidity, and a 16:8 h light:dark photoperiod. Each parasitoid used in the study was also solitary (i.e., a single offspring develops per host). *Venturia canescens* was obtained from a culture maintained for several years at Wageningen University, The Netherlands. It is a cosmopolitanly distributed parasitoid of Lepidoptera in the family Pyralidae. Host larvae feed almost exclusively in stored grains, nuts, and fruit (Harvey 1995). Most populations of *V. canescens* are comprised of asexual (thelytokous) individuals that obligately produce only female offspring. A female wasp locates concealed hosts by probing the substrate with its ovipositor. Upon contacting a host, the female pierces its cuticle and oviposits into the hemocoel. The parasitoid egresses from the host at the end of its larval development to spin a cocoon within the concealed, silken gallery constructed by the host. Adult emergence generally occurs 7–8 d later. For this study, *V. canescens* was reared on larvae of the Indian meal moth, *Plodia interpunctella* Hubner (Lepidoptera: Pyralidae), as outlined by Harvey and Thompson (1995). *P. interpunctella* was originally obtained from a culture maintained at Colorado State University, Fort Collins, Colorado, USA. Host larvae were reared in glass jars on diet consisting of a 5:1:1 mixture of cornmeal, yeast, and glycerol. Approximately 50 moths were added to jars after eclosion, and they were allowed to oviposit directly onto the diet.

Campoletis sonorensis was obtained from a culture maintained for many years at Texas A&M University, College Station, Texas, USA. It is a Nearctic, sexually reproducing, parasitoid of ~30 macrolepidoptera in the family Noctuidae (Lindgren 1970). Hosts are all foliar feeders that develop in exposed locations. Female wasps locate hosts with their antennae and then rapidly oviposit into the host hemocoel. Unlike *V. canescens*, however, the mature parasitoid larva emerges and pupates on the host's food plant before the host has constructed a cocoon. Adult wasps emerge 5–6 d later. *C. sonorensis* was reared in the current study on larvae of the soybean looper, *Pseudoplusia includens* Walker (Lepidoptera: Noctuidae). Cultures of *P. includens* were originally obtained from Clemson University, Clemson, South Carolina, USA. Host larvae were reared in 30-mL plastic cups on artificial diet (Strand 1990). Moths were held in 4-L glass jars and fed a 20% sucrose solution. Female moths oviposited directly onto cotton netting used to cover the jars, which netting was secured by elastic bands. *C. sonorensis* was maintained in large Plexiglass boxes and a fed a 20% sucrose solution. Several adult female wasps were added to large Petri dishes (20 cm diameter) containing ~50 second–third stadium *P. includens* larvae. After several hours exposure to hosts, parasitoids were returned to

culture and parasitized hosts were isolated and reared in cups as described a few sentences earlier.

Microplitis croceipes was obtained from a culture maintained for several years at the University of Kentucky. Like *C. sonorensis*, it is also a Nearctic, sexually reproducing, parasitoid of noctuid Lepidoptera in the genera *Heliothis* and *Helicoverpa* (Lewis 1970, Powell and Elzen 1989). Females oviposit into the hemocoel of foliage feeding host larvae. However, toward the end of development of the parasitoid larva, the host leaves its host plant and burrows into the soil to form a pupal cell. The mature *M. croceipes* larva then emerges in this concealed location from the still living host by chewing a hole through the cuticle. The parasitoid larva spins a cocoon beside the host and the adult wasp emerges 5–6 d later. Here, *M. croceipes* was reared on larvae of the tobacco budworm, *Heliothis virescens* Fabricius (Lepidoptera: Noctuidae), which were also supplied by the University of Kentucky. Hosts and parasitoids were reared using the same methods described for *C. sonorensis* and *P. includens*.

All parasitoid females used in this study were mated and <10 d old before being presented with hosts. Individual wasps were allowed to parasitize up to several hosts for the duration of the experiment.

Determination of parasitoid size and development times

P. interpunctella larvae undergo five or six instars (designated L_1 – L_5 or L_6) before pupating (Harvey 1995). Last stadium larvae of *P. interpunctella* attain maximal larval masses between 20 and 35 mg prior to pupation (Harvey 1995). For this study, L_2 – L_5 hosts, weighing between 300 μ g and 35 mg, were presented individually to *V. canescens* in small plastic Petri dishes (4 cm diameter). Hosts were parasitized singly to assure that none were superparasitized. Hosts were then weighed on a Cahn 29 electrobalance (accuracy ± 1 μ g; ThermoCahn, Madison, Wisconsin, USA) and reared in plastic vials (8 \times 3 cm) containing excess diet. Newly emerged adult *V. canescens* were killed by freezing and weighed on the Cahn electrobalance to determine their fresh body mass. Egg-to-adult development times were also recorded. After parasitoid emergence, both the host and parasitoid cocoons were carefully opened and the remaining head capsule and adjoining tissues of *P. interpunctella* larvae were weighed to compare the relationship between host size at parasitism and terminal host mass.

P. includens typically completes five instars before pupation and attains a maximum larval mass of 250–320 mg (Strand 1990). Different instars of *P. includens* were determined by head capsule dimensions and fresh mass. L_1 – L_5 hosts, weighing between 100 μ g and 80 mg, were presented individually to mated *C. sonorensis* females in 4-cm Petri dishes. After being parasitized once, hosts were immediately weighed and reared singly in Petri dishes containing excess diet that was

changed daily. At eclosion, adult wasp sizes and development times were recorded and the remaining host carcass was isolated and weighed. *H. virescens* complete five instars during development and attains a maximum mass of 400–500 mg before pupation (King and Hartley 1985). *H. virescens* was parasitized by *M. croceipes* females as described in the preceding section. Female wasps were allowed to parasitize L_1 – L_5 hosts that weighed from 100 μ g to 350 mg. After parasitism, hosts were weighed and then transferred to plastic cups containing excess diet. Immediately following larval parasitoid egression, host larvae were killed by freezing and weighed. Adult parasitoid masses and egg-to-adult development times were also recorded at eclosion.

Preliminary analysis of the data obtained for each parasitoid–host system indicated that offspring size and final host sizes increased nonlinearly with initial host size at oviposition. As a result, initial host size data were log transformed. We used analysis of covariance (ANCOVA) to detect sex-differential effects of host size and development time. The relative importance of adult size or development time for parasitoid fitness was determined by parasitizing hosts that differed in their initial size and comparing the variation in size and development time of the resulting progeny. Evidence that size was favored over development time would be if offspring size was similar across all host sizes, but development times were significantly longer in small vs. large hosts. Evidence that development time was favored over size would be if development times were similar among host sizes but parasitoid size was significantly smaller in small vs. large hosts. Evidence for a trade-off between size and development time would be if progeny size significantly increased and development times significantly decreased with host size (Mackauer and Sequeira 1993, Harvey et al. 2000).

Development of other ichneumonids and braconids

Comparative data on development of koinobiont ichneumonids and braconids were obtained by surveying the literature. Only studies on solitary species of parasitoids were included. A total of 33 parasitoid–host associations were identified that contained information on parasitoid size and development time in relation to host size (or instar) and feeding behavior. The relative importance of size or development time for fitness of each parasitoid species was made by comparing the variation in these parameters in relation to host size as described in the preceding paragraph. Comparisons of species in different taxa often requires special statistical approaches since differences could be confounded by phylogenetic differences (Felsenstein 1985, Harvey and Pagel 1990). However, this does not apply here as ichneumonids and braconids form a monophyletic assemblage and share a common ancestor (Whitfield 1998). Therefore, interactions between parasitoid fam-

TABLE 1. Development characteristics of the parasitoids *Venturia canescens*, *Campoletis sonorensis*, and *Microplitis croceipes* in their respective host species.

Parasitoid species (Family)	Host species (Family)	<i>N</i>	Max. mass of nonparasitized hosts (mg)†	Size range of parasitized host (mg)	Size range of adult parasitoids (mg)	Max. parasit- ized host mass/ max. mass of unparasitized host‡
<i>V. canescens</i> (Ichneumonidae)	<i>P. interpunctella</i> (Pyralidae)	57	26.7 ± 1.2	0.3–34.3	4.1–7.2	100
<i>C. sonorensis</i> (Ichneumonidae)	<i>P. includens</i> (Noctuidae)	80	279.37 ± 5.33	0.1–66.0	2.6–6.9	23.6
<i>M. croceipes</i> (Braconidae)	<i>H. virescens</i> (Noctuidae)	69	414.9 ± 19.2	0.11–352.9	4.4–7.2	85.1

† Mass data are mean ± 1 SE. Sample size for all controls (unparasitized larvae) = 10.

‡ This figure describes the mass ratio of the body mass of the largest host successfully parasitized (producing an adult wasp) against the mean maximum mass of controls.

ily (Ichneumonidae, Braconidae), host feeding location (exposed or concealed), and parasitoid developmental strategy (size, development time, or a trade-off between these traits) were examined using conventional *G* tests.

RESULTS

As previously discussed, most koinobionts encounter larval stage hosts of different instars that vary greatly in size. If oviposition occurs in small hosts, progeny can either consume the host rapidly, at the potential cost of reduced size, or it can delay consumption of the host (i.e., exhibit a lag phase) which ultimately results in a larger host and a bigger parasitoid, but at the cost of longer development times. The outcomes of experiments with *V. canescens*, *C. sonorensis*, and *M. croceipes* are summarized in Table 1 and Figs. 1–4.

Venturia canescens maximizes size at the cost of increased development time in *Plodia interpunctella*

V. canescens developed successfully in L_2 – L_5 *P. interpunctella* that ranged from 330 µg to 34.3 mg at oviposition (Table 1). Females failed to locate and oviposit in L_1 hosts weighing <200 µg. Females occasionally detected and attempted to parasitize L_1 hosts by jabbing their ovipositor at them, but hosts were never stung due to their small size. Parasitoids that emerged from hosts weighed 4.12–7.24 mg (mean 5.6 ± 0.09 mg) and their size was unaffected by host size at oviposition ($F_{1,55} = 305$, $P = 0.09$, $r^2 = 5.30$) (Fig. 1a). This indicated that *V. canescens* progeny attain a similar adult size regardless of a host's initial size. In contrast, development time from egg to adult emergence decreased significantly with host size at oviposition ($F_{1,55} = 77.08$, $P < 0.001$, $r^2 = 58.40$) (Fig. 1b). Development times for *V. canescens* ranged from 19 to 26 d (mean 20.8 ± 0.24 d) with offspring from hosts parasitized as second instars taking 5–7 d longer to develop than wasps from hosts parasitized as fifth instars.

Hosts parasitized by *V. canescens* continued to feed and grow until the parasitoid larva shifted from hemolymph feeding to consumption of tissues. Con-

sumption of host tissues always occurred after the parasitoid larva molted to its final instar (Harvey 1995). *V. canescens* consumed the entire host, leaving uneaten only the host's head capsule and cuticle. Initial host mass varied positively with the terminal mass of the host carcass ($F_{1,32} = 20.26$, $P < 0.001$, $r^2 = 38.50$) (Fig. 1c). Dividing the mass of the adult parasitoid by the combined final mass of the host and parasitoid yielded an estimate of the proportion of host resources used by *V. canescens*. The proportion of host resources consumed by *V. canescens* decreased significantly with initial host size ($F_{1,31} = 11.66$, $P = 0.002$, $r^2 = 27.40$). However, this trend is unlikely of great biological significance as *V. canescens* consumed >95% of the host irrespective of its initial size at parasitism (Fig. 1d). Based on these results, we defined the threshold for small and large hosts as ±15 mg. We found no difference in the percentage of *V. canescens* (~75%) that survived to adulthood in these two size classes of hosts (Yates-corrected $\chi^2 = 0.03$, $df = 1$, $P > 0.05$) (Fig. 4).

Campoletis sonorensis minimizes development time at the cost of size in *Pseudoplusia includens*

The mass of hosts successfully parasitized by *C. sonorensis* ranged from 96 µg to 66 mg (Table 1). *C. sonorensis* oviposited into *P. includens* larvae up to 78 mg in size but the progeny always died in these very large hosts before pupating. The effect of offspring sex on adult parasitoid size and development time was examined using ANCOVA, because no significant differences were found in the regression lines for male and female wasps (size: $t = 1.21$, $df = 66$, $P > 0.05$; development time: $t = 0.26$, $df = 66$, $P > 0.05$). Adult parasitoid size covaried significantly with host size ($F = 15.96$, $df = 1$, 77, $P < 0.001$) and offspring sex ($F = 6.45$, $df = 1$, 77, $P = 0.01$) with females on average weighing more (4.5 ± 0.14 mg) than males (3.9 ± 0.14 mg) (Fig. 2a). In contrast, wasp development time was unaffected by initial host size ($F = 2.16$, $df = 1$, 77, $P = 0.15$) and did not covary with offspring sex ($F = 0.16$, $df = 1$, 77, $P = 0.69$) (Fig. 2b). Development

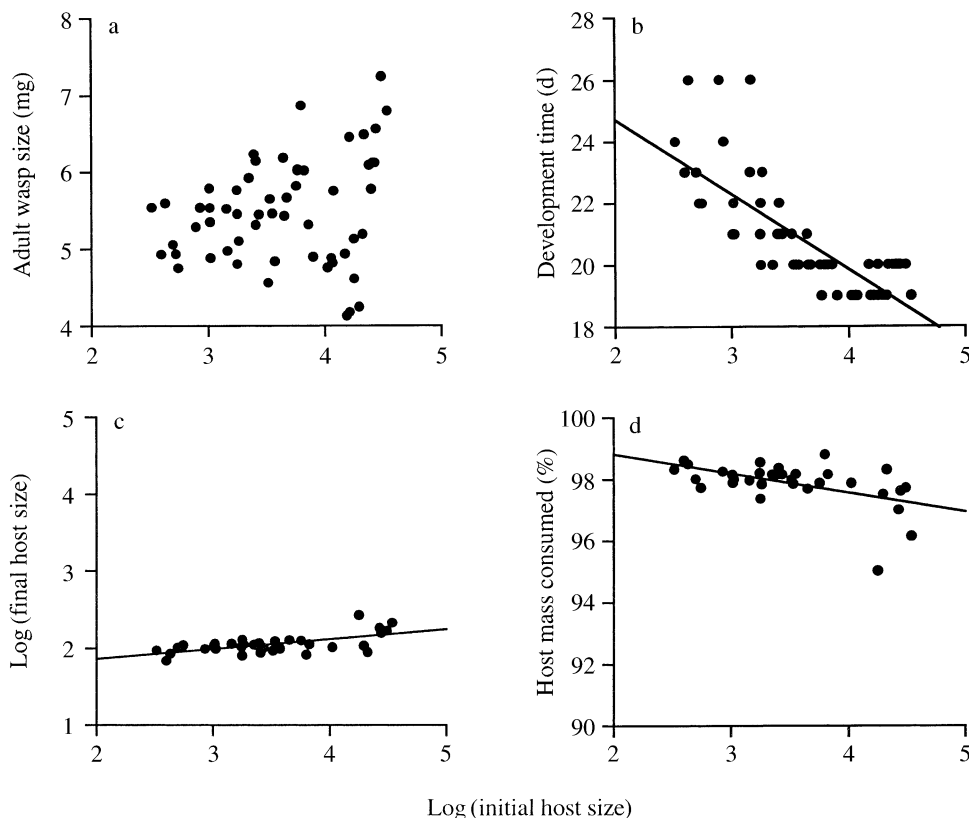


FIG. 1. Relationships between the size of *Plodia interpunctella* larvae and developmental traits in *Venturia canescens*. (a) Relationship between host size at oviposition and adult female size at eclosion. The regression equation is: wasp size = $0.27(\log \text{ host size}) + 4.50$, $n = 57$ parasitoid individuals. (b) Relationship between host size at oviposition and egg-to-adult development time. The regression equation is: development time = $29.55 - 2.41(\log \text{ host size})$, $n = 57$ parasitoid individuals. (c) Relationship between initial host size and final host size at parasitoid emergence. The regression equation is: $\log \text{ final host size} = 0.13(\log \text{ initial host size}) + 1.60$, $n = 34$ parasitoid individuals. (d) Relationship between initial host size and the percentage of host mass consumed by parasitoid offspring, i.e., parasitoid mass/(final host mass + parasitoid mass). The regression equation is: percentage consumed = $100.05 - 0.62(\log \text{ initial host size})$, $n = 34$ parasitoid individuals.

time in *C. sonorensis* varied from 13 to 20 d (female mean = 14.9 ± 0.22 d, male mean = 15.1 ± 0.27 d).

The largest hosts parasitized by *C. sonorensis* (30 mg at oviposition) gained little, if any, mass after parasitism. In contrast, smaller hosts continued to feed and grow, albeit at a reduced rate compared with non-parasitized hosts, up to 24 h before parasitoid pupation. Final host size varied positively with initial host size ($F = 20.71$, $df = 1, 28$, $P < 0.001$, $r^2 = 42.50$) (Fig. 2c), but overall the final masses attained by hosts were very similar (2.8–3.2 mg). *C. sonorensis* consumed most of the host before pupating adjacent to the host carcass. The proportion of host resources used by *C. sonorensis* decreased with host size at oviposition ($F = 12.39$, $df = 1, 29$, $P < 0.001$, $r^2 = 29.90$) (Fig. 2d). Using a threshold ± 30 mg for large and small hosts, parasitoid larvae consumed $>90\%$ of hosts that were small at oviposition, and $\sim 80\%$ of hosts that were large. Correspondingly, more *C. sonorensis* survived to adulthood in small hosts than large (pooled sex data: Yates-corrected $\chi^2 = 4.02$, $df = 1$, $P < 0.05$) (Fig. 4).

Microplitis croceipes exhibits a trade-off in fitness between size and development time in *Heliothis virescens*

Of the three parasitoid species studied here, *M. croceipes* successfully parasitized the widest range of host sizes. The smallest host to produce an adult wasp was a first instar weighing $107 \mu\text{g}$ at oviposition and the largest was a fifth instar weighing 351 mg. Plotting wasp size against initial host size revealed significant differences in the slopes of the regression lines for males and females ($t = 2.05$, $df = 61$, $P < 0.05$), but we detected no differences between the sexes in development time as a function of initial host size ($t = 0.39$, $df = 61$, $P > 0.05$). We therefore used ANCOVA for the development time data and separate regression analyses for male and female wasps to analyze the relationship between host and offspring size. Adult parasitoid size increased slightly but significantly with host size for male wasps ($F = 11.85$, $df = 1, 42$, $P < 0.01$, $r^2 = 22.00$; Fig. 3a), but not females ($F = 0.17$,

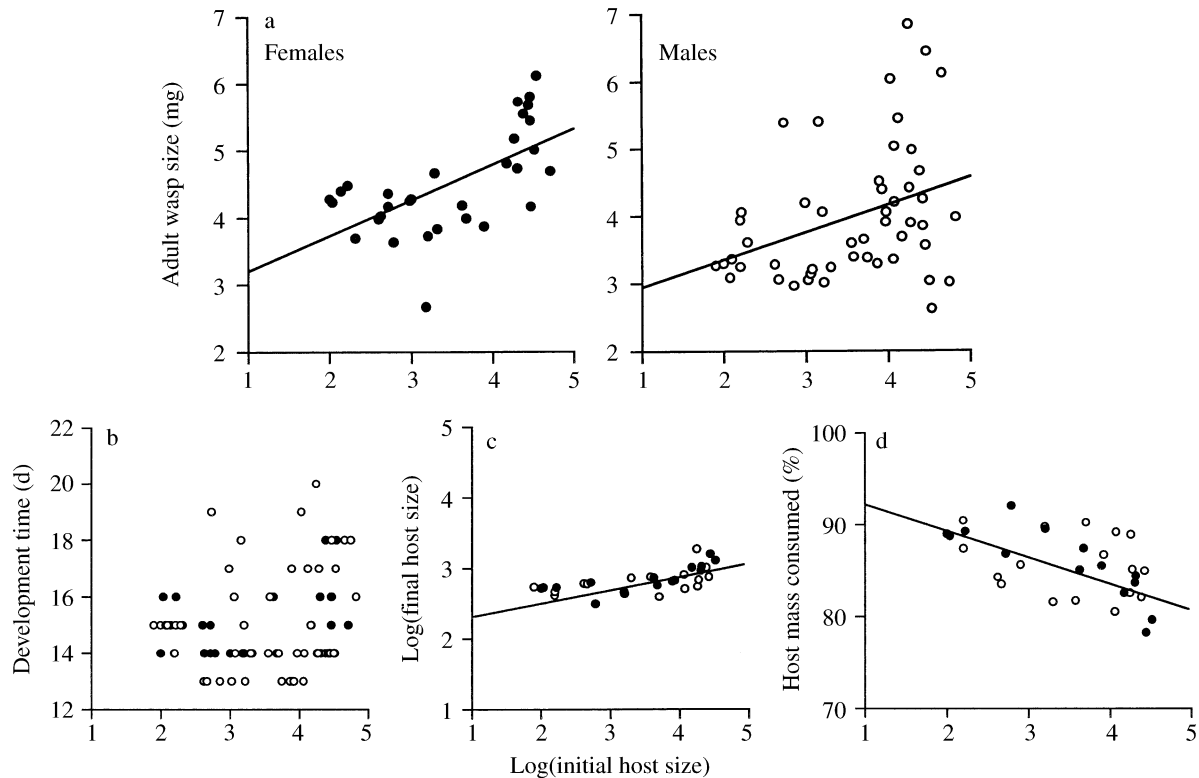


FIG. 2. Relationships between the size of *Pseudoplusia includens* larvae and developmental traits in *Campoletis sonorensis*. (a) Relationship between host size at oviposition and adult female (solid circles) and male (open circles) size at eclosion. Host size similarly affected parasitoid size in both sexes, although females were larger: female wasp size = $0.53(\log \text{ host size}) + 2.67$, $n = 31$ parasitoid individuals; male wasp size = $0.41(\log \text{ host size}) + 2.54$, $n = 49$ parasitoid individuals. (b) Relationship between host size at oviposition and adult female (solid circles) and male (open circles) egg-to-adult development time: female development time = $0.24(\log \text{ host size}) + 14.12$, $n = 31$ parasitoid individuals; male development time = $0.43(\log \text{ host size}) + 13.55$, $n = 49$ parasitoid individuals. (c) Relationship between initial host size and final host size at parasitoid emergence. Hosts contained either female (solid circles) or male (open circles) wasp offspring. The pooled regression equation is $\log \text{ final host size} = 0.14(\log \text{ initial host size}) + 2.35$, $n = 31$ parasitoid individuals. (d) Relationship between initial host size and the percentage of host mass consumed by parasitoid offspring, i.e., parasitoid mass/(final host mass + parasitoid mass). Hosts contained either female (closed circles) or male (open circles) offspring. The pooled regression equation is: percentage consumed = $93.82 - 2.33(\log \text{ initial host size})$, $n = 31$ parasitoid individuals.

$df = 1, 22$, $P = 0.69$, $r^2 = 0.80$; Fig. 3a). However, *M. croceipes* laid fewer fertilized (=female) eggs in small hosts than large, which may account for this discrepancy. The average size of adult female (5.6 ± 0.11 mg) and male (5.4 ± 0.06 mg) offspring did not significantly differ. Total development time covaried significantly with host size ($F = 6.92$, $df = 1, 65$, $P < 0.05$, $r^2 = 6.10$) and offspring sex ($F = 6.50$, $df = 1, 65$, $P < 0.05$). Development time decreased slightly but significantly with initial host size, and on average female wasps took longer to develop (mean = 17.1 ± 0.31 d) than males (mean = 16.3 ± 0.27 d).

Hosts weighing up to 100 mg at oviposition continued to feed and grow during parasitism, although the rate of growth declined with host size. Large hosts on the other hand ceased feeding within hours of parasitism and usually lost considerable mass before emergence of *M. croceipes*. Despite these trends, the larger the host was at oviposition, the higher its final mass

($F = 253.23$, $df = 1, 60$, $P < 0.001$, $r^2 = 79.90$) (Fig. 3c). Regardless of size at oviposition, however, parasitized *H. virescens* always burrowed into the substrate to form a pupal cell before the parasitoid offspring emerged and spun a cocoon. There was a highly significant relationship between final host size and the percentage of host mass consumed by the parasitoid larva ($F = 272.47$, $df = 1, 60$, $P < 0.001$, $r^2 = 82.0$) (Fig. 3d). Yet, regardless of host size, *M. croceipes* consumed only a small proportion (3–12%) of available host resources, because of its habit of feeding only on hemolymph. Since *M. croceipes* was able to parasitize much larger hosts than the other two parasitoid species, the size threshold between “large” and “small” hosts was also deemed to be considerably higher. We designated this threshold as 100 mg since this was the approximate division between the average mass of fourth and fifth instar hosts. Parasitoid survival to adulthood did not significantly differ between large and

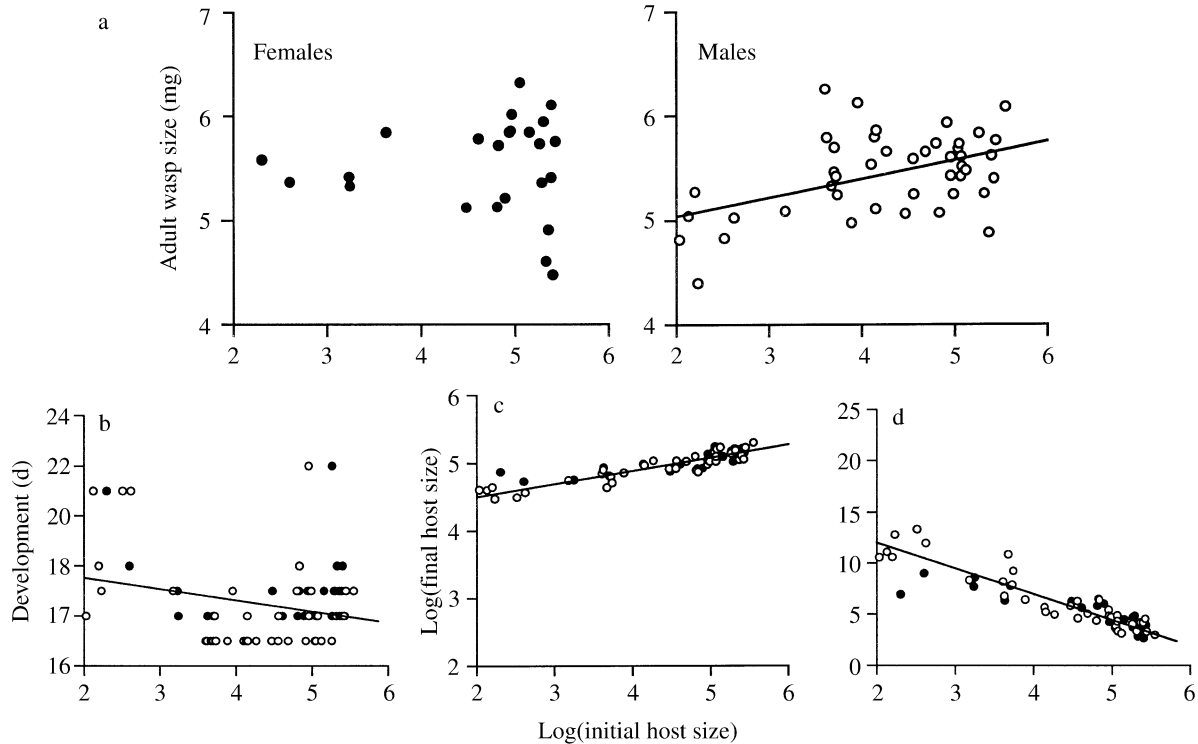


FIG. 3. Relationships between the size of *Heliothis virescens* larvae and developmental traits in *Microplitis croceipes*. (a) Relationship between host size at oviposition and adult female (solid circles) and male (open circles) size at eclosion. Female wasp size = $0.05(\log \text{ host size}) + 5.36$, $n = 25$ parasitoid individuals; male wasp size = $0.18(\log \text{ host size}) + 4.68$, $n = 44$ parasitoid individuals. (b) Relationship between host size at oviposition and adult female (solid circles) and male (open circles) egg-to-adult development time. Host size affected female and male development time similarly. Development time = $18.52 - 0.43(\log \text{ host size})$, $n = 69$ parasitoid individuals. (c) Relationship between initial host size and final host size at parasitoid emergence. Hosts contained either female (solid circles) or male (open circles) wasp offspring. The pooled regression equation is: $\log \text{ final host size} = 0.18(\log \text{ initial host size}) + 4.20$, $n = 61$ parasitoid individuals. (d) Relationship between initial host size and the percentage of host mass consumed by parasitoid offspring (parasitoid mass/final host mass + parasitoid mass). Hosts contained either female (closed circles) or male (open circles) offspring. The pooled regression equation is: $\text{percentage consumed} = 16.04 - 2.29(\log \text{ initial host size})$, $n = 62$ parasitoid individuals.

small hosts (pooled sex data: Yates-corrected $\chi^2 = 2.25$, $df = 1$, $P > 0.05$) (Fig. 4).

Developmental strategies of other ichneumonid and braconid koinobionts

Our survey of the literature identified data for 12 ichneumonid- and 21 braconid-host associations that contained data on parasitoid size and development times in hosts of different size (or instar). Table 2 presents whether the host developed in an exposed or concealed site, and whether the parasitoid exhibited a developmental strategy that favored size, development time, or a trade-off between these fitness traits. Hosts were classified as exposed if they fed on exposed foliage or in concealed locations like stems, seeds, or fruit. Using these associations, we found that parasitoid family (p), host feeding location (h), and developmental strategy (d) were not independent ($G_T = 45.0$, $df = 7$, $P < 0.05$). The interactions between developmental strategy and host feeding location ($G_{hd} = 80.1$, $df = 2$, $P < 0.05$), as well as parasitoid family and

host feeding location ($G_{ph} = 26.6$, $df = 1$, $P < 0.05$) were highly significant. This indicated that the developmental strategies of ichneumonid and braconid koinobionts differed with host feeding site. For the parasitoids that attacked exposed herbivores, 15 clearly favored short development time over size. Nine others exhibited a trade-off strategy whereby progeny from small, early instar, hosts took longer to develop and were smaller than progeny from large hosts. In contrast, seven of the eight parasitoids that attacked concealed hosts favored size over development time (Table 2). Although the feeding behavior of campoplegine ichneumonids (tissue) and microgastroid braconids (hemolymph) differ, we found no significant interaction between parasitoid family and developmental strategy ($G_{pd} = 5.2$, $df = 2$, $P > 0.05$). However, differences in the feeding of parasitoid larvae could influence the size range of hosts these parasitoids attack. As previously noted, the microgastroid *M. croceipes* successfully parasitized a much wider range of host sizes than *V. canescens* or *C. sonorensis* (see Figs. 1–3). We were

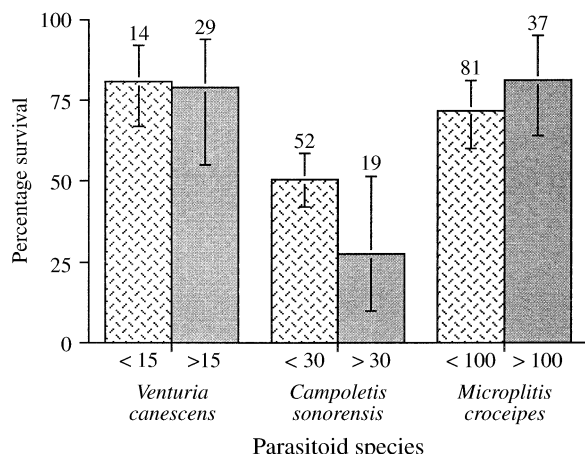


FIG. 4. Percentage survival (mean and 95% confidence interval) to adult stage for *Venturia canescens* ($n = 71$ parasitoid individuals), *Campoletis sonorensis* ($n = 181$ parasitoid individuals), and *Microplitis croceipes* ($n = 118$ parasitoid individuals) in large (shaded bars) and (basket-weave bars) hosts of their respective host species. Numbers above the histogram bars are numbers of successfully emerged parasitoids within the size ranges specified. The threshold between the two size categories (in mg) was determined on the basis of host growth potential and the size range of hosts habitually attacked by each parasitoid species.

unable to analyze this trend among the species presented in Table 2, because in many of these studies only host instars (rather than initial host size) were reported. However, our own studies (Harvey et al. 1999, 2000) suggest that hemolymph feeding braconids parasitize a much larger size range of hosts than tissue feeding ichneumonids.

Based on the experimental and comparative data presented here, we developed simple graphical models to illustrate the development of koinobiont parasitoids that attack exposed and concealed hosts (Fig. 5). In these models, we assumed that parasitoids can oviposit in hosts of different initial size (small–large) and/or instar (x -axis). Parasitoid development time is plotted below the x -axis while offspring size is plotted along the y -axis. The growth phase of parasitoid larvae is illustrated as a continuously increasing exponential curve with a sharp cutoff. All studies in the literature we are aware of indicate that parasitoid growth conforms to this function (Mackauer and Sequeira 1993, Harvey 1995, Harvey et al. 2000). Parasitoids of concealed hosts, like *V. canescens*, maximize size at the expense of development time (Fig. 5a). Progeny size is similar across the range of host sizes that are parasitized, but development times are longer in small hosts than in large hosts. This is because progeny delay consumption of available host resources in small and medium hosts until their host achieves a larger mass. In contrast, parasitoids of exposed hosts, like *C. sonorensis*, develop at a constant rate that is independent of initial host size (Fig. 5b). This results in uniformly

rapid development times but progeny from small hosts are on average smaller than those from large hosts. Endoparasitoids, like *M. croceipes*, exhibit a trade-off between development time and size as evidenced by development times being longer and progeny being smaller in small hosts vs. large hosts (Fig. 5c).

DISCUSSION

Body size has often been considered the most important determinant of life history variation in both vertebrates and invertebrates (Calder 1984, King 1989, Stearns 1989). Yet, the intimate relationship that exists between third trophic level organisms, like parasitoids, and their insect hosts suggest several reasons why body size may not always be the primary target for selection. Among the most important of these are the mortality risks faced by insect herbivores, which if parasitized, confer a similar risk on a developing parasitoid (Price 1980, Blackburn 1991). Focusing on ichneumonoids that parasitize larval Lepidoptera, our results indicate that developmental strategies differ between wasps that parasitize exposed and concealed hosts.

If size is the primary target for selection, we would assume that koinobionts laid in host larvae of suboptimal size should delay their development until the host attains an optimal size or quality value. Our results with *Venturia canescens* conform well to this assumption since offspring always exhibit a lag phase in development when laid in smaller hosts. This results in adult wasps of similar size but development times that are always longer in small hosts than large hosts. In contrast, the closely related campoplegine *Campoletis sonorensis* exhibited exactly the opposite strategy of minimizing development time at the cost of size. Intermediate between these extremes was the microgastriine braconid *Microplitis croceipes*, which showed evidence of a trade-off between size and development time. The most obvious difference between these parasitoid–host associations was the apparency of the host larvae. *V. canescens* exclusively parasitizes well-concealed pyralid larvae, *C. sonorensis* parasitizes noctuid larvae that feed on exposed foliage, and *M. croceipes* parasitizes noctuid larvae of intermediate apparency that feed on exposed foliage but that burrow into the soil before parasitoid emergence. The influence of host apparency on developmental strategies of ichneumonoids is also supported by our survey of the literature. Ichneumonoids and braconids that attacked external, foliar feeding hosts either favored short development time over size, or exhibited a trade-off between these traits. In contrast, species that attacked concealed hosts almost always favored size over development time. Based on these results, we conclude that the importance of size and development time for fitness of koinobiont ichneumonoids varies with host feeding ecology, which in turn is likely correlated with mortality risks.

In developing the balanced mortality and slow growth–high mortality hypotheses, Price (1974) and

TABLE 2. The relationship between the feeding ecology of the host species and the developmental strategies of solitary koinobiont endoparasitoids in selected ichneumonid and braconid wasps.

Parasitoid species	Host species	Apparency	Favored strategy	Reference
Ichneumonidae				
<i>Venturia canescens</i>	<i>Plodia interpunctella</i>	concealed	size	this study
<i>Venturia canescens</i>	<i>Anagasta kuehniella</i>	concealed	size	Harvey and Vet (1997)
<i>Diadegma chrysostictos</i>	<i>Plodia interpunctella</i>	concealed	size	J. A. Harvey (<i>unpublished data</i>)
<i>Campoletis sonorensis</i>	<i>Pseudoplusia includens</i>	exposed	DT	this study
<i>Campoletis sonorensis</i>	<i>Heliothis virescens</i>	exposed	DT	Gunasena et al. (1989)
<i>Campoletis flavicincta</i>	<i>Spodoptera frugiperda</i>	exposed	DT	Patel and Habib (1987)
<i>Hyposoter exiguae</i>	<i>Heliothis virescens</i>	exposed	Comp	Campbell and Duffey (1979)
<i>Hyposoter exiguae</i>	<i>Trichoplusia ni</i>	exposed	Comp	Jowyk and Smilowitz (1978)
<i>Hyposoter exiguae</i>	<i>Manduca sexta</i>	exposed	DT	Beckage and Templeton (1985)
<i>Hyposoter fugitivus</i>	<i>Manduca sexta</i>	exposed	DT	Beckage and Templeton (1985)
<i>Trathala flavoorbitalis</i>	<i>Leucinodes orbonalis</i>	concealed	Comp	Sandanayake and Edirisinghe (1992)
<i>Tranosema rostrale</i>	<i>Choristoneura fumiferana</i>	exposed	DT	Cusson et al. (1998)
Braconidae				
<i>Cotesia rubecula</i>	<i>Pieris rapae</i>	exposed	DT	Harvey et al. (1999)
<i>Cotesia urabae</i>	<i>Uraba lugens</i>	exposed	Comp	Allen and Keller (1991)
<i>Cotesia marginiventris</i>	<i>Heliothis virescens</i>	exposed	Dtime	Bolling and Pitre (1970)
<i>Cotesia medicaginis</i>	<i>Colias eurytheme</i>	exposed	Dtime	Allen (1958)
<i>Dolichogenidea eucalypti</i>	<i>Uraba lugens</i>	exposed	Comp (?)	Allen and Keller (1991)
<i>Apanteles carpatus</i>	<i>Tineola bisselliella</i>	concealed	size	Harvey et al. (2000)
<i>Apanteles galleriae</i>	<i>Galleria mellonella</i>	concealed	size	Wani et al. (1994)
<i>Microplitis demolitor</i>	<i>Pseudoplusia includens</i>	exposed	DT	Harvey et al. (2000)
<i>Microplitis demolitor</i>	<i>Heliothis virescens</i>	exposed	DT	Strand et al. (1988)
<i>Microplitis mediator</i>	<i>Pseudoplusia includens</i>	exposed	DT	J. A. Harvey (<i>unpublished data</i>)
<i>Microplitis mediator</i>	<i>Leucania separata</i>	exposed	DT	Tanaka et al. (1984)
<i>Microplitis croceipes</i>	<i>Heliothis virescens</i>	exposed†	Comp	this study
<i>Microplitis rufiventris</i>	<i>Spodoptera littoralis</i>	exposed	DT	Hegazi et al. (1988)
<i>Ephedrus californicus</i>	<i>Acyrtosiphon pisum</i>	exposed	Comp	Sequeira and Mackauer (1993)
<i>Aphidius sonchi</i>	<i>Hyperomyzus lactucae</i>	exposed	DT	Liu (1985)
<i>Aphidius ervi</i>	<i>Acyrtosiphon pisum</i>	exposed	DT	Sequeira and Mackauer (1992a,b)
<i>Opius dissitus</i>	<i>Liriomyza sativae</i>	concealed	size	Pettit and Wieslebach (1993)
<i>Dacnusa sibirica</i>	<i>Liriomyza sativae</i>	concealed	size	Croft and Copland (1995)
<i>Meterous trachynotus</i>	<i>Choristoneura fumiferana</i>	exposed	Comp	Hebert and Cloutier (1990)
<i>Cardiochiles nigriceps</i>	<i>Heliothis virescens</i>	exposed	Comp	Pennachio et al. (1994)
<i>Cardiochiles diaphaniae</i>	<i>Diaphania hyalinata</i>	exposed	Comp	Smith et al. (1994)

Note: Size, development time (DT), and compromise between these traits (Comp) are defined as favored strategies on the basis of variation estimates in these parameters across a range of host sizes or stages at parasitism.

† *H. virescens* parasitized by *M. croceipes* feed in exposed locations but burrow into a concealed location prior to parasitoid emergence.

Clancy and Price (1987) similarly stressed the importance of herbivore ecology in assessing mortality risks. Experimental data supporting this assumption include mortality schedules, which are known to vary among herbivores that feed in exposed and concealed locations (Cornell 1990, Denno and Benrey 1997, Williams 1999). Studies of parasitoid species loads also underscore the importance of host feeding niche for host mortality and intraguild competition among natural enemies. In their survey of the literature, Hawkins and Lawton (1987) and Hawkins (1988) determined that external foliar feeders, leaf rollers, and leaf miners had much higher parasitoid species loads than galler, borer, and root feeding species. Blackburn (1991) also amassed data from the literature on 474 species of parasitoids from diverse taxa in an effort to identify correlations between life history traits and ecological variables. While the phylogenetic relationships among the species in this large data set were often unclear, it is interesting to note that one of the few significant re-

lationships detected was that species attacking exposed hosts exhibited shorter development times than those attacking concealed hosts. Correlations clearly do not indicate causality, but collectively these studies support our own conclusion that host feeding ecology strongly affects mortality risks and the developmental strategies of parasitoids.

Relatively few studies have attempted to directly measure the mortality risks faced by parasitoids and other third trophic level organisms in the field. Nonetheless, several lines of evidence indicate that parasitoids often experience high mortality risks. First, it is well known that parasitoids are susceptible to many of the same pathogens that infect their hosts (Brooks 1993). Parasitoids are also known to experience high levels of intraguild predation via hyperparasitoids, other primary parasitoids (via multiparasitism), and generalist predators (Rosenheim et al. 1995, Rosenheim 1998, Brodeur 2000). These risks appear to be especially high for koinobionts, which are almost always

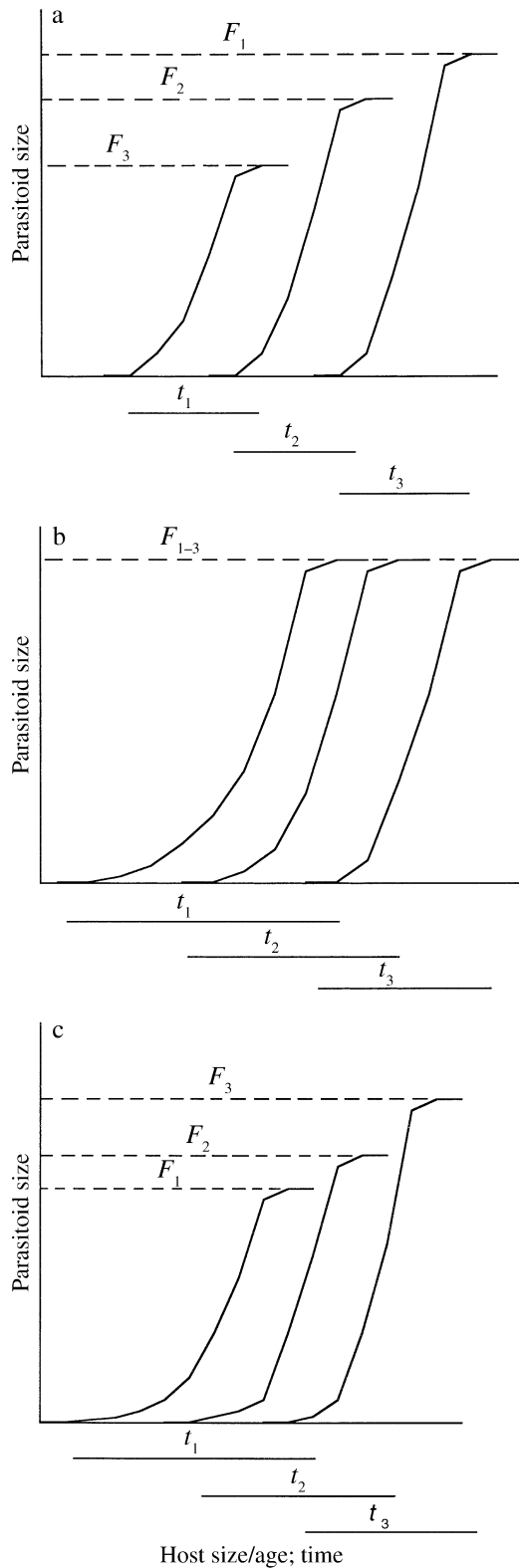


FIG. 5. Graphical models illustrating the developmental strategies of koinobiont endoparasitoids that parasitize larval stage hosts of varying initial size (small, medium, and large). (a) Parasitoids attacking exposed foliar-feeding hosts exhibit uniform development times (t_1 – t_3) in hosts of different initial

competitively inferior to idiobionts like ectoparasitoids and most hyperparasitoids (Varley 1947, Askew 1975, Shaw 1994, Stiling and Rossi 1994). Focal observation and cage studies similarly suggest that both immature and adult parasitoids that exist in exposed locations experience heavy predation (Rees and Onsager 1982, Ferguson and Stiling 1996, Heimpel et al. 1997). Finally, adaptations in addition to rapid development time indirectly suggest that parasitoids have evolved under selection pressures exerted by risks of predation. For example, koinobionts often induce changes in the feeding activity, microhabitat preferences, and defensive behavior of hosts that decrease their likelihood of being encountered by predators or other parasitoids (Brodeur and McNeil 1992, Adamo 1997).

We originally thought that differences in feeding and pupation might result in differences in whether campoplegine ichneumonids and microgastroid braconids favor large size or rapid development time. Our results do not indicate this to be the case, but we do note that tissue and hemolymph feeding may affect the size range of hosts that larval endoparasitoids can attack. The suitable range of host sizes attacked by *C. sonorensis* was considerably narrower than was demonstrated by *M. croceipes*. The latter species successfully parasitized hosts weighing up to 350 mg, or >80% of the growth potential of healthy host larvae, whereas *C. sonorensis* could only exploit hosts growing up to ~60 mg, or <25% of their growth potential. The narrower size range of hosts parasitized by tissue feeding campoplegines likely reflects the requirement that these parasitoids must consume most host tissues to successfully pupate (Harvey et al. 2000, Strand 2000). In contrast, hemolymph feeding and external pupation greatly reduce the risks offspring face when developing in hosts larger than themselves since consumption of the host is not required for survival. One consequence of this dichotomy is that hemolymph feeding has potentially facilitated host range shifts toward larger species and to the evolution of gregariousness by microgastroids (Strand 2000). Another is that differences in host feeding behavior could affect competitive interactions between campoplegines and microgastroid braconids since the host ranges of wasps in these taxa overlap greatly in nature (Lindgren 1970, Jones and Lewis 1971, Gauld 1988, Gauld and Bolton 1988).

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size but offspring size (F_1 – F_3) is reduced in small vs. large hosts. Fitness as measured by development time, therefore, is favored over size. (b) Parasitoids attacking concealed hosts (e.g., root-feeding or gall-forming insects) attain a similar size in hosts of different initial size, but development times are longer in small hosts vs. large hosts. Here, fitness as measured by size is favored over development time. (c) Parasitoids exhibiting a trade-off between development time and size. Development time decreases while offspring size increases with initial host size. This strategy suggests that the two measures of fitness are balanced in determining the optimal phenotype.

In reviewing the literature, Abrams and Rowe (1996) describe how the development of many organisms is affected by predation risks. For example, Martin (1995) reported that North American land birds nesting in the open suffer higher risks of early predation and exhibit shorter development times between egg hatch and fledging than birds that nest in concealed tree cavities. Vollrath and Parker (1992) in turn found that the degree of sexual size dimorphism among spider families is correlated with the higher risk of predation suffered by males when compared to females. The importance of mortality risks and other host factors for parasitoid development is still often ignored despite Salt (1941) over half a century ago stating: "It is evident that, far from being a purely passive victim, obliterated without trace, the host is often able to impress its mark, and a very real mark at that, on the insect parasitoid that destroys it." Our results reaffirm Salt's observation by underscoring the importance of host feeding ecology when interpreting the fitness value of different developmental strategies. Future studies will undoubtedly shed light on other features of host biology affecting the life-history evolution of parasitoids and other third trophic level organisms.

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