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Developmental interactions between the solitary endoparasitoid *Venturia canescens* (Hymenoptera: Ichneumonidae), and two of its hosts, *Plodia interpunctella* and *Corcyra cephalonica* (Lepidoptera: Pyralidae)

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Ichneumonidae, *Venturia canescens*, koinobiont, parasitoid, development, Pyralidae, *Corcyra cephalonica*, *Plodia interpunctella*

Abstract. Developmental interactions between the solitary koinobiont endoparasitoid *Venturia canescens*, and two of its hosts, the pyralid moths *Plodia interpunctella* and *Corcyra cephalonica*, were investigated. Wasps reared from second (L2) through fifth (L5) instars of *Corcyra* were larger than those from the corresponding stages of *Plodia*, but took longer to complete development and generally suffered higher mortality. Starved L5 *Plodia* of a given mass produced significantly larger wasps than starved L5 *Corcyra*. Adult wasp size was positively correlated with the number of ovulated eggs in *Venturia* emerging from both hosts; thus, the larger wasps that emerged from *Corcyra* had higher egg complements than the smaller wasps from *Plodia*. The final size of parasitized L2–L4 *Corcyra* was influenced by *Venturia*, with all three instars significantly smaller than unparasitized larvae.

For *Venturia*, developmental flexibility and host regulation are important adaptive mechanisms that allow the parasitoid to develop in a wide range of host instars. However, for koinobiont parasitoids differences in the biology of the host species strongly influence their development and fitness.

INTRODUCTION

The growth and development of insect parasitoids is often markedly influenced by the host species from which they develop. Host-related variations in certain fitness correlates such as size and survivorship have been observed in many associations (Lewis & Vinson, 1971; Legner & Thompson, 1977; Rotheray et al., 1984; Moratorio, 1987; Janssen, 1989). Salt (1940) showed that the size of emerging adult *Trichogramma evanescens* varies with host species. Similarly, Corrigan & Lashomb (1990) found that the eulophid wasp *Edovum puttleri* was larger and produced more oocytes when reared from eggs of *Leptinotarsa texana* than *L. decemlineata*. Therefore host quality, as affected by host species, can influence the biology of parasitoids.

Most studies on host species suitability, however, have been undertaken using idiobiont parasitoids, which attack non-growing or paralysed hosts (Haeselbarth, 1979; Askew & Shaw, 1986). Therefore, host resources are static during the interaction, and parasitoid size is often a function of host species size (for example, Salt, 1940; Arthur & Wylie, 1959; Rotheray et al., 1984). Another group of parasitoids, termed koinobionts, attack hosts that continue to feed and grow during parasitism (Haeselbarth, 1979; Askew & Shaw, 1986). In koinobiont-host associations the amount of resources for parasitoid growth and development are not fixed and parasitoid development depends largely upon feeding rate and capacity for growth during the interaction (Mackauer, 1986; Godfray, 1994). Therefore, it

may be expected that host instar and species affect koinobionts differently from idiobionts, because the amount of host resources available is not predictable at oviposition.

Venturia canescens (Gravenhorst) (Hymenoptera: Ichneumonidae) is a parthenogenetic koinobiont endoparasitoid of several pyralid moth larvae which infest flour mills and granaries (Salt, 1975). Harvey et al. (1994) showed that the growth of *Venturia* is delayed in early instar *Plodia interpunctella*, with accelerated development occurring only after the host has completed its final larval moult. Although in the laboratory *Venturia* is commonly reared on *Plodia* and a similar host, *Anagasta kuehniella*, Salt (1964, 1975) found that it will also parasitize other hosts which vary considerably in their rate of development and growth potential. Therefore, an investigation was undertaken to determine the effects of host species and instar or fitness related traits in *Venturia*. Few studies have simultaneously investigated the influence of instar and species on koinobiont development. We examine the development of *Venturia* from L2–L5 instars of *Plodia interpunctella* (Hübner) and *Corcyra cephalonica* Stainton (Lepidoptera: Pyralidae). When reared at the same temperature, *Corcyra* develops more slowly than *Plodia*, but attains a much greater mass at pupation. This study reports the influence of host species and instar on the development of *Venturia*, with particular reference to adult size, development rate and mortality.

METHODS

Insect cultures

All insects were reared at 25 ± 1°C with a 16 hour photoperiod. *Plodia* was reared in clear glass jars on a 10 : 1 : 1 mixture of finely milled wheat bran, yeast, and glycerol. We controlled the number of hosts by adding a set number of eggs to jars containing a measured amount of food (approximately 300 eggs per 25 g). This allowed *Plodia* to develop with excess food throughout larval life. Under our experimental conditions adult moths begin to emerge about 4 weeks after oviposition.

Corcyra was reared in larger jars on a 6 : 4 : 4 : 1 mixture of finely milled wheat bran, cornmeal, yeast and glycerol. Each jar contained 500–750 g of food medium, and between 50 and 75 adult moths were added soon after eclosion. As with *Plodia*, the amount of food available per host was not a limiting factor in development. The egg-to-adult development time of *Corcyra* was approximately 6 weeks, although there was considerable variablility.

Irrespective of host species, the parent wasps were reared from *Plodia* alone. This is because the original culture had been reared on *Plodia* for many generations and we wanted to determine if this affected the parasitoid's ability to utilize resources from the source host (*Plodia*) and from the factitious host (*Corcyra*).

Venturia was cultured in clear plastic boxes (17.5 × 11 × 5 cm). Approximately two hundred 21 day old *Plodia* from culture were placed into each box with 10 adult wasps every 4 days. Some of the containers were left until wasps eclosed, with these being fed diluted honey ad libitum and used to re-stock the culture. In order to segregate wasps according to age for experiments, host pupae in other containers were removed 18 days after parasitism, and placed singly into glass vials. Upon eclosion a drop of pure honey was smeared on the inside lid of the vial. *Venturia* produces alecithal (= hydropic) eggs which are laid singly into hosts. Following a successful oviposition, the wasp preens and produces a new egg at the tip of the ovipositor via a characteristic flexing or cocking of the abdomen, so that it is easy to determine when an egg has been laid.

Parasitoid mortality, development time, and adult size

L2–L5 *Plodia* and *Corcyra* larvae were isolated from cultures according to head capsule dimensions (Tables 1, 2) and were individually presented to parasitoids. Wasps were allowed to oviposit once in each host that were then transferred to glass vials containing approximately one gram of their respective food media. Parasitized hosts were monitored daily for the emergence of adult wasps or moths. Following eclosion, parasitoids were killed by freezing, and then placed into an oven 100°C for 3 days in order to obtain

dry mass data. Wasps were subsequently weighed on a Cahn 29 electrobalance and hind tibia measurements made to within 0.05 mm using a calibrated stereomicroscope. Development time was recorded as the number of days from oviposition to parasitoid eclosion.

Encapsulation was recorded when a parasitized host produced an adult moth instead of a wasp. If neither wasp nor moth had emerged within 50 (*Plodia*) or 70 (*Corcyra*) days of oviposition, dead host larvae or pupae were removed from vials and dissected in order to determine at what stage the parasitoid had died within the host.

TABLE 1. Range of head capsule widths and corresponding age for L2–L5 instars of *Corcyra*.

Instar	n	Head capsule width (mm)	Larval age (d)*
2	10	0.50–0.60	12
3	10	0.70–0.85	18
4	10	1.00–1.20	24
5	10	1.40–1.50	32

* Days after oviposition

TABLE 2. Range of head capsule widths and corresponding age for L2–L5 instars of *Plodia*.

Instar	n	Head capsule width (mm)	Larval age (d)*
2	10	0.28–0.33	10
3	10	0.40–0.45	13
4	10	0.60–0.70	16
5	10	0.85–1.15	21

* Days after oviposition

Relationship between adult wasp size and egg load

When deprived of hosts, *Venturia* attains a full egg complement between 4 and 6 days after eclosion (Harvey et al., 1994). In order to test the relationship between adult wasp size and egg complement, a number of 5-day old wasps reared from both host species were killed by freezing, placed on a dampened slide and dissected by grasping the metasoma with forceps and pulling the ovipositor distally with another pair of forceps. This enabled the paired lateral oviducts to be removed. Ovulated eggs were counted by cutting the oviducts at the calyx gland just below the ovaries, and teasing them carefully into the suspension. Adult wasp size was determined by measuring hind tibia lengths under a calibrated stereomicroscope (to within 0.05 mm).

Relationship between non-growing L5 host size and parasitoid size

In order to determine if the size of adult wasps is affected by host size in final instar *Corcyra* and *Plodia*, a number of L5 hosts from each species of a range of sizes were taken from cultures, weighed to within 0.1 mg on a Cahn 29 electrobalance and singly parasitized by *Venturia*. Some L5 *Corcyra* and *Plodia* may not have completed their growth at the time of parasitism, so all parasitized larvae, irrespective of size or species were starved by placing the larvae singly in vials without food after parasitism. Eclosing wasps were killed by freezing, and their hind tibia measured under a stereomicroscope.

Head capsule widths of parasitized L2–L4 *Corcyra* and unparasitized larvae

In a previous study, we showed that the growth of L2 and L3 *Plodia* is reduced in parasitized hosts compared with unparasitized larvae, but that hosts parasitized as L4 grew as large as healthy larvae (Harvey et al., 1994). In order to determine the influence of parasitism on the growth of *Corcyra*, a number of L2, L3 and L4 hosts were taken from cultures, parasitized singly by *Venturia* and placed in vials with approximately 2 g of food medium. A separate group of unparasitized L2 hosts were isolated from cultures and similarly placed in vials with approximately 2 g of food medium. Upon eclosion of parasitoids (from L2–L4 hosts) or adult moths the *Corcyra* cocoon was carefully cut open and the final larval head capsule at time of death or pupation was removed and measured under a stereomicroscope.

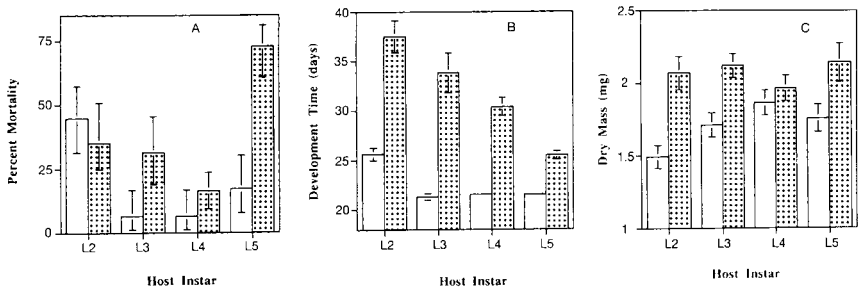

Fig. 1. A – Percentage mortality of *Venturia* from hosts parasitized as L2–L5 *Corcyra* (stippled bars) and *Plodia* (open bars). Lines represent confidence intervals (± 95%). Sample sizes are – *Corcyra*: L2 = 58, L3 = 51, L4 = 80, L5 = 172; *Plodia*: L2 = 67, L3 = 47, L4 = 47, L5 = 53. B – The egg-to-adult development time in days of *Venturia* emerging from hosts parasitized as L2–L5 larval *Corcyra* (stippled bars) and *Plodia* (open bars). Line bars represent confidence intervals (± 95%). Sample sizes as in Fig. 1A. C – The size of newly eclosed adult *Venturia* as defined by dry mass in mg, emerging from hosts parasitized as second (L2) through fifth (L5) larval instars of *Corcyra* (stippled bars) and *Plodia* (open bars). Lines represent confidence intervals (± 95%). Sample sizes are – *Corcyra*: L2 = 38, L3 = 35, L4 = 67, L5 = 47; *Plodia*: L2 = 37, L3 = 44, L4 = 44, L5 = 44.

RESULTS

Parasitoid mortality, development time and adult size

In a preliminary experiment to establish if *Venturia* had successfully oviposited into *Corcyra* after abdomen cocking and to determine the fate of parasitoid eggs, forty-one parasitized L5 *Corcyra* larvae were dissected 5 days after parasitism. Six hosts were found to contain healthy first-instar wasp, while a further 30 contained heavily melanized parasitoid eggs or first-instar larvae, indicating that they had been encapsulated. No parasitoids were found in the remaining 5 hosts, but parasitoid eggs and early-instar larvae are tiny relative to the size of the host and are difficult to detect in the dense haemolymph, so that it is possible that these hosts, too, had been parasitized.

Mortality was consistently higher in all but L2 instar *Corcyra* compared to *Plodia* instars. Percentage encapsulation was highest from L5 *Corcyra*, with 76 moths emerging from 172 parasitized hosts and a further 49 producing neither wasp nor moth. *Venturia* was able to develop with greater success in L2–L4 *Corcyra*, where mortality was less than 40%. *Plodia* suffered less than 20% mortality in L3–L5 hosts. However, this increased to 44% in L2 hosts, most of these larvae dying within 2 days of oviposition. A 3-way contingency table was used to analyse mortality data, with instar, host species and whether parasitoid development was successful or not (parasitoid mortality) as factors. The overall test of independence was rejected ($G = 214.53$, $df = 10$, $P < 0.01$; Fig. 1A) and there were significant interactions between host species and mortality ($G = 12.27$, $df = 1$, $P < 0.01$) and instar and mortality ($G = 16.77$, $df = 1$, $P < 0.001$).

A two-way ANOVA on development time, with host species and instar as factors, revealed a significant interaction between species and instar ($F = 33.0$, $df = 3, 348$, $P < 0.001$; Fig. 1B) showing that the effect of instar on development time varied with species.

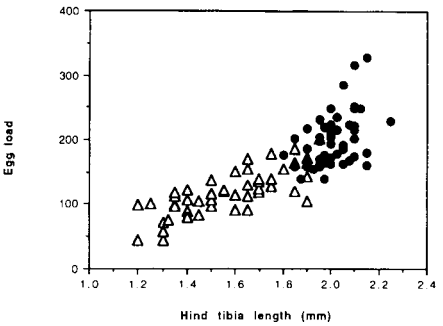

Fig. 2. The relationship between adult *Venturia* size, measured as hind tibia length, and the number of mature eggs carried in the lateral oviducts when five days old from *Corcyra* (circles) and *Plodia* (triangles).

Parasitoid development time also varied significantly with instar ($F = 92.02$, $df = 3, 348$, $P < 0.001$) and between hosts ($F = 746.41$, $df = 1, 348$, $P < 0.001$). The egg-to-adult development time of *Venturia* from *Plodia* was fairly uniform in L3–L5 instars, but wasps from L2 hosts took some 4 days longer to complete development to eclosion. However, parasitoid development time decreased steadily with host instar at parasitism from *Corcyra*, ranging from about 38 days (L2) down to 25 days (L5). In all instars, parasitoid development was longer from *Corcyra* than *Plodia* (Fig. 1B).

A two-way ANOVA on adult wasp size also revealed a significant interaction between species and instar ($F = 8.30$, $df = 3, 348$, $P < 0.001$; Fig. 1C). Parasitoid size also varied significantly with instar ($F = 4.03$, $df = 3, 348$, $P < 0.01$) and species ($F = 107.49$, $df = 1, 348$, $P < 0.001$). The size of adult wasps increased from L2–L4 *Plodia* instars but decreased marginally in L5 hosts. Conversely, *Corcyra* produced wasps were fairly uniform in size irrespective of instar at parasitism, and were also larger than parasitoids emerging from the same *Plodia* instars.

Relationship between adult size and egg load

The relationship between adult wasp size and egg load is shown in Fig. 2. There was a significant positive correlation between adult wasp size and egg load for *Venturia* from *Plodia* ($n = 50$, $r = 0.73$, $P < 0.001$) and *Corcyra* ($n = 50$, $r = 0.45$, $P < 0.01$; Fig. 2). The larger wasps that emerged from *Corcyra* stored more eggs than their smaller counterparts from *Plodia*.

Relationship between non-growing L5 host size and parasitoid size

A two-tailed t-test was performed to determine if a significant difference existed in the slopes of the 2 regression lines of parasitoid size for the *Plodia*/*Corcyra* starved data. The difference was not significant ($t = 0.216$, $n = 39$, $P > 0.05$). This enabled us to perform an ANCOVA to determine if parasitoid size (hind tibia length) varied significantly between host species of a given mass. Parasitoid size covaried significantly with host size ($F = 66.00$, $df = 1, 36$, $P < 0.001$) and host species ($F = 17.32$, $df = 1, 36$, $P < 0.001$). For a given host size at the onset of starvation, *Plodia*-produced wasps were significantly larger than *Corcyra*-produced wasps.

Head capsule widths of parasitized L2–L4 *Corcyra* and unparasitized (control) larvae

The head capsule sizes of *Corcyra* at the time of host death or pupation varied significantly between parasitized L2–L4 hosts and unparasitized (L2) controls (one-way ANOVA,

$F = 25.54$, $df = 3, 28$, $P < 0.001$; Table 3). Tukey's pairwise comparisons revealed that head capsule widths of parasitized L2, L3 and L4 hosts did not differ significantly, but for each parasitized instar, head capsules were much smaller than unparasitized (control) larvae. At the time of death, the head capsule width of *Corcyra* from parasitized L2–L4 hosts was fairly constant, and about 20–30% smaller than controls at pupation.

TABLE 3. Head capsule widths of various larval instars of *Corcyra cephalonica* at time of death when parasitized in different instars by *Venturia canescens*, compared with healthy (unparasitized) hosts at pupation.

Instar parasitized	Sample size	Head capsule width ($x \pm$ SE in mm)
L2	8	0.95±0.04*a*
L3	4	1.03±0.01*a*
L4	6	1.03±0.05*a*
Unparasitized	14	1.31±0.03*b*

Means with different letters differ significantly ($P < 0.05$; Tukey's pairwise comparisons).

DISCUSSION

Parasitoid mortality varied considerably between the 2 hosts (Fig. 1A). From *Plodia*, it was highest from L2 instars, probably due to the physical damage inflicted at oviposition, when the minute larva frequently became attached to the parasitoid ovipositor (Harvey et al., 1994). L2 *Corcyra* were larger and consequently mortality was reduced. However, over 70% of parasitoids failed to develop from L5 *Corcyra*, most of this being the consequence of encapsulation. Salt (1975) examined the host size-specific variations in encapsulation ability of *Corcyra* parasitized by *Venturia*, and found that older L5 larvae encapsulated significantly more parasitoid eggs than younger L5 larvae. He attributed this to the stronger haemocytic reaction of later instar hosts parasitized beyond a certain size threshold. *Plodia* are considerably smaller hosts and never exceeded this threshold, hence encapsulation was low in all instars. Final host size, as determined by head capsule widths, was much smaller in parasitized L2–L4 *Corcyra* than in unparasitized hosts (Table 3). This was presumably due to some form of host regulation by *Venturia* that effectively weakens the host immunological response by preventing hosts growing beyond a certain size (Vinson & Iwantsch, 1980; Gunasena et al., 1989).

The egg-to-adult development time of *Venturia* also varied with host species (Fig. 1B) and was consistently greater from all *Corcyra* instars. Parasitoid development occurred more rapidly from L3–L5 *Plodia* instars, probably in response to rapid host development after parasitism (Harvey et al., 1994). *Venturia*, in common with many larval endoparasitoids, delays destructive feeding until the host is a final instar, ensuring enough resources are available for its own development. The development of *Venturia* is extended in poorly nourished L3 *Plodia* because these hosts take longer than well-fed hosts to reach their final instar (Harvey et al., 1995). Similarly, the slower growth rate of *Corcyra* was reflected in the increased development time of *Venturia* from pre-L5 instars.

The size of emerging parasitoids was consistently greater in all *Corcyra* instars (Fig. 1C). When both hosts were provided with excess food, the growth potential of *Corcyra* was much greater than that of *Plodia*, with post-feeding wandering *Corcyra* larvae often twice as large (mass, fresh weight) as the corresponding stage *Plodia* larvae (unpublished

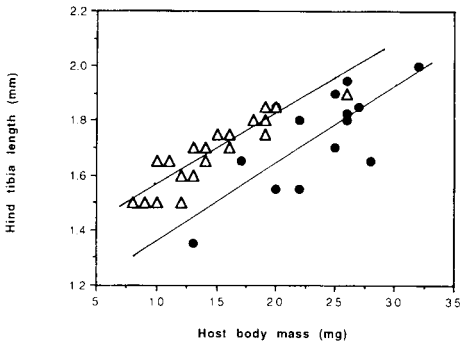

Fig. 3. Relationship between adult *Venturia* size, measured as hind tibia length, emerging from different sizes (body mass, mg) of starved L5 *Corcyra* (circles) and *Plodia* (triangles).

observations). Hence, when *Venturia* commence destructive feeding, potentially more resources are available from *Corcyra* than *Plodia*, accounting for the differences in size of eclosing wasps. However, parasitoid development proceeded faster on *Plodia* presumably because they are smaller and therefore consumed in less time than *Corcyra* (Godfray, 1994).

Within starved, final instars of each host species, parasitoid size was strongly correlated with host weight (Fig. 3). However, for a given host size, *Plodia* produced much larger wasps than *Corcyra*, showing that *Venturia* appears to be able to convert host tissue more effectively from *Plodia*. The reduced suitability of *Corcyra* may be due to differences in nutritional quality rather than quantity. Sandlan (1982), investigating interspecific patterns of host suitability for the pupal idiobiont wasp *Coccygomimus* (= *Pimpla*) *turionellae*, also found that factors other than host weight affected parasitoid development. He suggested that differences in relative amounts of various nutrients amongst host species affected the growth of the parasitoid. This could be a major factor for *Venturia*, because the parent wasp were derived from stock reared for many generations on *Plodia* alone. Legner & Thompson (1977) also found that the development of the braconid *Chelonus* near *curvimaculatus* was influenced by the host from which the parent female wasp was reared.

Host size may affect the reproductive success of *Venturia* in a number of ways. Size was positively correlated with ovulated egg complement in wasps emerging from both hosts (Fig. 2). However, estimating fecundity by counting eggs is not necessarily an accurate measure of reproductive potential for *Venturia*, because it is synovigenic (Flanders, 1950) and is able to mature several times as many eggs as can be stored in its oviducts at a given time when conditions are favourable (unpublished observations). Size may also influence longevity, mobility and colonizing ability (Sandlan, 1982; Godfray, 1994; Harvey et al., 1994).

We have shown that *Venturia* uses a different developmental strategy in *Plodia* compared with *Corcyra*. The stage at which host development was arrested was different, perhaps in response to the size differences between the two hosts. For koinobionts, which attack nutritionally unsuitable early host instars, parasitoid development is often dependent upon the host attaining a critical size, which in the case of starved *Plodia* is 6–8 mg, during the host's final (5th) instar (Harvey et al., 1995). Different hosts are expected to exhibit species-specific growth and development patterns, where the critical size threshold may occur earlier in a larger host of *Venturia*, *Corcyra*, compared to *Plodia*. Beckage & Templeton (1985) similarly observed that interactions between the ichneumonid

koinobiont *Hyposoter exiguae* and various host species are characterized by host developmental arrest, which varies with the species of host in accordance with the nutritional requirements of the parasitoid.

At the other extreme, there appears to be a maximum host size that is capable of supporting the development of *Venturia*. Late L5 *Corcyra* were only marginally suitable for parasitoid development because wasps frequently became encapsulated after parasitism, although others appeared to develop normally and eclosed as healthy adult wasps. However, dissections of some L5 *Corcyra* that died producing neither wasp nor moth revealed that the parasitoids had developed normally to their final instar, but perished within the confines of the host integument. As suggested by Salt (1964), the parasitoid may have been unable to consume all host tissue, or became ensheathed within the larval cuticle.

As the suitability of a host should primarily depend upon its ability to support parasitoid development, we suggest that *Corcyra* is less suitable than *Plodia* as a host because *Venturia* suffer higher mortality from them, particularly from final instars. This is particularly important since it is likely that later instars are easier to find for a wasp that predominantly locates hosts through probe searching (Rogers, 1971). The larvae of lepidopterous pests of stored products spend most of their development concealed in the food medium, and larger, later instars are more likely to be encountered. Thus, the persistence of the parasitoid may be severely affected if the most accessible stage is largely invulnerable to parasitism.

Few studies have investigated instar-dependent variations in parasitoid growth and development for koinobionts attacking different host species that vary considerably in growth rate and potential. We have shown that interspecific host differences in size and growth rate have profound effects upon the growth and development of *Venturia*. Further studies are needed to determine the efficacy of *Venturia* parasitizing both hosts under natural conditions, where environmental heterogeneity may influence and perhaps alter suitability.

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