

Nutritional ecology of the interaction between larvae of the gregarious ectoparasitoid, *Muscidifurax raptorellus* (Hymenoptera: Pteromalidae), and their pupal host, *Musca domestica* (Diptera: Muscidae)

JEFFREY A. HARVEY, LOUISE E. M. VET, NANQING JIANG* and RIETA GOLS

Department of Entomology, Wageningen Agricultural University, The Netherlands, and *Department of Biology, Beijing Normal University, Beijing, China

Abstract. In this study we examined the relationship between clutch size and parasitoid development of *Muscidifurax raptorellus* (Hymenoptera: Pteromalidae), a gregarious idiobiont attacking pupae of the housefly, *Musca domestica* (Diptera: Muscidae). Host quality was controlled in the experiments by presenting female parasitoids with hosts of similar size and age. This is the first study to monitor the development of a gregarious idiobiont parasitoid throughout the course of parasitism. Most female wasps laid clutches of one to four eggs per host, although some hosts contained eight or more parasitoid larvae. In both sexes, parasitoids completed development more rapidly, but emerging adult wasp size decreased as parasitoid load increased. Furthermore, the size variability of eclosing parasitoid siblings of the same sex increased with clutch size. Irrespective of clutch size, parasitoids began feeding and growing rapidly soon after eclosion from the egg and this continued until pupation. However, parasitoids in hosts containing five or more parasitoid larvae pupated one day earlier than hosts containing one to four larvae. The results are discussed in relation to adaptive patterns of host utilization by gregarious idiobiont and koinobiont parasitoids.

Key words. Development, parasitism, host quality, idiobiont, *Musca domestica*, *Muscidifurax raptorellus*.

Introduction

In the study of host–parasitoid interactions, many workers have examined the mechanisms of parasitoid growth and development and the reciprocal effects of parasitism on host growth (Hebert & Cloutier, 1990; Strand & Dover, 1991; Harvey *et al.*, 1994; Croft & Copland, 1995; reviewed by Vinson & Iwantsch, 1980a,b). It is clear that parasitoids and their hosts profoundly influence one another's development. However, most of these studies have paid little attention to the adaptive significance of these mechanisms. Host-related constraints on parasitoid growth and development may also be

considered within an evolutionary context, by examining the fitness value of developmental characteristics and patterns of host utilization by parasitoids (Mackauer & Sequeira, 1993; Godfray, 1994).

An important macroevolutionary division occurs in the parasitic Hymenoptera, between parasitoids that develop in non-growing or paralysed hosts (termed 'idiobionts') and parasitoids developing in hosts that continue feeding and growing, at least during the early phases of parasitism (termed 'koinobionts'; Askew & Shaw, 1986). Because idiobionts attack hosts which contain a fixed resource complement, large hosts are assumed to be of higher quality than small hosts because they contain more resources for the developing parasitoid larva (host quality is defined as the state or condition of the host that influences the dynamic processes of parasitoid growth, development and survival). For many solitary and gregarious idiobiont species, host size determines the size (and/or mass)

Correspondence: Dr. J. A. Harvey, Department of Entomology, University of Wisconsin-Madison, Room 739, Russell Laboratories, 1630 Linden Drive, Madison, WI 53706, U.S.A.

of the emerging parasitoid adult(s) (Salt, 1940; Arthur & Wylie, 1959; Heaversedge, 1967; Rivers & Denlinger, 1995). In parasitoids, fecundity is usually positively correlated with adult female size, thus host quality represents an important constraint upon parasitoid fitness (Godfray, 1994). By contrast, for koinobionts, parasitoid growth and development are not only functionally dependent on host size at oviposition, but on the host's potential for growth after parasitism (Mackauer, 1986). Studies with koinobionts have shown that larval parasitoid growth, adult size, survival and development time are influenced by variations in host size, age, stage of development and rate of development, that are in turn influenced by variations in host condition and diet (Sequeira & Mackauer, 1992a,b; Harvey *et al.*, 1994, 1995; reviewed by Mackauer & Sequeira, 1993, and Godfray, 1994).

A better understanding of the effects of host stage or size on parasitoid development can be obtained by examining the dynamics of host and parasitoid growth throughout the association. This provides a direct measure of host quality because it reflects the degree of nutritional integration between host and parasitoid throughout the course of parasitism. Furthermore, it can also reveal the extent to which the parasitoid alters host growth in order to improve its quality for parasitoid development (=host regulation; Vinson & Iwantsch, 1980b). Using growth trajectories, Sequeira & Mackauer (1992a) and Harvey *et al.* (1994) plotted the development of the solitary koinobionts *Aphidius ervi* (Hymenoptera: Braconidae) and *Venturia canescens* (Hymenoptera: Ichneumonidae), respectively, from four instars of their hosts. Both studies revealed that emerging parasitoid adult size (dry body mass) was not a linear function of host size (dry body mass) at oviposition. Although in both parasitoids there was a linear increase in adult wasp size to the penultimate host instar, in the final host instar parasitoid body size did not increase. Sequeira & Mackauer (1992a) argued that, in associations where the functional relationship between host size and quality is non-linear, constraints upon the larval growth rate may play an important role in the evolution of adaptive developmental responses of insect parasitoids.

Comparing empirical data, Mackauer & Sequeira (1993) suggested that parasitoid life-history strategies may have evolved in response to host quality constraints and described these strategies using three graphical models. One of the models describes the predicted development pattern of idiobionts, whereas the other two describe koinobiont development. However, as pointed out by the authors, detailed studies on the dynamics of parasitoid development under different constraints have been made on very few species, most of them solitary koinobionts. Thus, the models of Mackauer & Sequeira (1993) are based on an extremely limited data set. Notably, few studies have examined the growth and development of idiobionts, in particular pupal parasitoids.

Optimal clutch size models, developed to explain the evolution of clutch size variability, have predicted that differences in this life-history parameter may be influenced by several factors. These include the amount and quality of host resources, or a limitation in time or eggs available to the foraging adult female parasitoid (Iwasa *et al.*, 1984; Parker &

Courtney, 1984; Waage & Godfray, 1985). Furthermore, several studies have reported that, in gregarious koinobiont parasitoids, the rate of host food consumption increased with a corresponding increase in parasitoid load, compensating for the greater nutritional demands of the parasitoids (reviewed by Slansky, 1986). However, once some threshold of parasitoid burden is exceeded, then adult parasitoid body weight and survival may decrease (Slansky, 1978). For idiobiont parasitoids, increased parasitoid density is not offset by a compensatory increase in host food consumption, because the host represents a static resource. Therefore, idiobionts are under a different set of constraints with respect to clutch size variability because host quality is largely pre-determined at parasitism, whereas for koinobionts it will be influenced by host feeding rate and capacity for growth after parasitism (= future host quality). However, rigorous experimental testing of host quality for gregarious idiobionts, particularly as it applies to the evolution of clutch size variability, is lacking.

The present study examines developmental interactions between the gregarious idiobiont pupal ectoparasitoid, *Muscidifurax raptorellus* (Kogan & Legner) (Hymenoptera: Pteromalidae) and its host, the housefly *Musca domestica* (L.) (Diptera: Muscidae). A considerable amount of information has been gathered on the genetic basis of gregarious parasitism in the *Muscidifurax* complex (e.g. Legner, 1987, 1988, 1989a,b). However, little information is available on the development of the parasitoid. Using non-linear regression equations, we compare the growth trajectories of parasitoids in standard-sized and aged hosts containing different numbers of parasitoid larvae. We then compare the egg-to-adult development time and adult size of parasitoids eclosing from host pupae containing different numbers of parasitoid larvae. We show that, for *M. raptorellus* (and possibly other gregarious idiobiont parasitoids), variations in clutch size strongly influence resource availability, with concomitant effects on parasitoid growth, adult size and rate of development. Moreover, the growth of individual parasitoid larvae is affected by scramble competition with other parasitoids, as related to nutritional stress resulting from crowding. The development of *M. raptorellus* is discussed in relation to the evolution of life-history strategies and patterns of host utilization in parasitoids.

Materials and Methods

Culturing of M. domestica and M. raptorellus

Hosts and parasitoids used in experiments were maintained at 25°C and LD 12:12 h. Adult house flies were maintained in steel cages (40 × 23 × 25 cm) at a density of approximately 100 flies per cage. They were fed a 2:2:1 mixture of sugar, powdered milk and yeast. Water was constantly supplied in a small Petri dish. Flies oviposited into a mixture consisting of 15 g of powdered milk and one litre of water absorbed into paper towel. Eggs were removed daily from the cages, and larvae were reared in 1-kg jars on the following diet: (a) a mixture of 265 g yeast, 265 g powdered milk and 1500 ml water; (b) 54 g agar and 1500 ml water, mixed and boiled.

(a) and (b) were mixed and left for approximately 30 min before being poured into the jars. Eggs were added to the food medium, which was then covered by a 10-cm layer of fine sawdust. Pupae were isolated from the medium after 4–5 days using sieves, and eclosing adult flies were transferred to other cages for culturing.

Muscidifurax raptorellus were reared in small glass vials (1 cm diam.) containing approximately fifty pupae of *M. domestica*. Several male and female parasitoids were placed in the vials with the host pupae, and sealed with a plug of cotton wool; newly-emerged parasitoids were transferred to separate vials containing fresh host pupae.

Experimental protocol

Host pupae were selected for experiments according to age and size. All pupae were 1–2 days old and of uniform mean size for all treatments (between 5.8 and 6.2 mm long, measured on a calibrated microscope at 1.2 \times). *Muscidifurax raptorellus* is a synovigenic, host-feeding parasitoid (Flanders, 1950) and proteins from host haemolymph are a necessary prerequisite for prolonged egg maturation after eclosion (see Jarvis & Kidd, 1986, for a review). As the ovaries of newly-emerged parasitoids contain few fully-developed eggs (J. A. Harvey, unpublished data), we allowed parasitoids to host-feed and mature further eggs prior to the commencement of the experiment.

Influence of clutch size and sex on the development time and adult size of *M. raptorellus*

Several newly-eclosed adult male and female *M. raptorellus* were placed in plastic vials (3 cm diam.) containing ten *M. domestica* pupae for 3 days. Honey was smeared on the inside of the vial. After 3 days, the mated female parasitoids were placed individually in small Petri-dishes (8 \times 3 cm) containing ten 1- or 2-day-old *M. domestica* pupae. After 24-h exposure to parasitoids, host pupae were placed individually in plastic vials until parasitoid eclosion. Vials were checked several times daily (until 17.00 h) for parasitoid emergence; eclosing wasps were killed by freezing, sexed, and oven-dried for 3 days at 100°C before being weighed individually on a Cahn 33 electronic microbalance (accuracy 1 μ g).

Size variability of adult *M. raptorellus* as a function of clutch size

In order to compare the variability in the size of *M. raptorellus* emerging from each host pupa, the dry mass of the smallest wasp was determined as a percentage of the largest wasp (of the same sex). For each clutch size (1–2, 3–4 or 5+ wasps per host) we obtained a mean value from the data; from this we calculated the coefficient of variation (CV) using the equation:

$$CV = SD/\bar{X} \times 100$$

where SD = standard deviation of the mean, and \bar{X} = mean.

This enabled us to ascertain if scramble competition for limited host resources, as influenced by clutch size, affects parasitoid performance at the level of the individual.

Growth of male *M. raptorellus* and weight of parasitized hosts

Several unmated adult *M. raptorellus* were taken from culture at eclosion and placed in plastic vials (3 cm diam.) with ten housefly pupae for 3 days. Honey was smeared on the inside of the vial. After 3 days, the unmated female parasitoids were placed individually in small Petri dishes (8 \times 3 cm) containing ten 1- or 2-day-old *M. domestica* pupae. Host pupae were exposed to parasitoids for 24 h; after this time the pupae were placed in separate Petri dishes that were dated and labelled. To obtain comparable dry mass data, the method described in Mackauer (1986), Sequeira & Mackauer (1992a) and Harvey *et al.* (1994) was followed. Beginning on the third day after exposure to parasitoids, host pupae were randomly selected from Petri dishes and carefully dissected on pre-weighed aluminium trays in order to isolate parasitoid larvae from the host. Both host and parasitoid(s) were then dried in an oven at 100°C for 3 days to obtain comparable dry mass data. Due to the variability in clutch size per host, parasitoid larvae were grouped according to the following clutch-size categories: 1–2 parasitoids per host, 3–4 parasitoids per host, and 5 or more parasitoids per host. All *M. raptorellus* in hosts with less than 5 parasitoids per host were weighed individually to within 1 μ g on a Cahn 33 electronic microbalance. *Muscidifurax raptorellus* in hosts containing more than five parasitoids per host were weighed in groups and the mean weight obtained by dividing the weight by the number of parasitoids. Hosts were also weighed on the microbalance, in order to determine the change in their dry body mass with time.

Results

Influence of clutch size and sex on the development time and adult size of *M. raptorellus*

Figure 1 shows the percentage distribution of clutch sizes that were laid by adult female *M. raptorellus* in this study. Most female wasps laid clutches of 1–3 eggs per host, with few hosts receiving clutches of more than five eggs.

The egg-to-adult development time of male and female *M. raptorellus* can be seen in Fig. 2a. Parasitoid development time varied significantly with clutch size (two-way ANOVA, $F = 4.87$, d.f. = 2, 130, $P < 0.01$) and sex ($F = 12.32$, d.f. = 1, 130, $P < 0.001$). However, there was no significant interactive effect of clutch and sex on development time ($F = 0.13$, d.f. = 2, 130, $P > 0.05$). Development time decreased with clutch size, and was consistently greater in female than in male parasitoids (Fig. 1a). Whereas female *M. raptorellus* took 15–

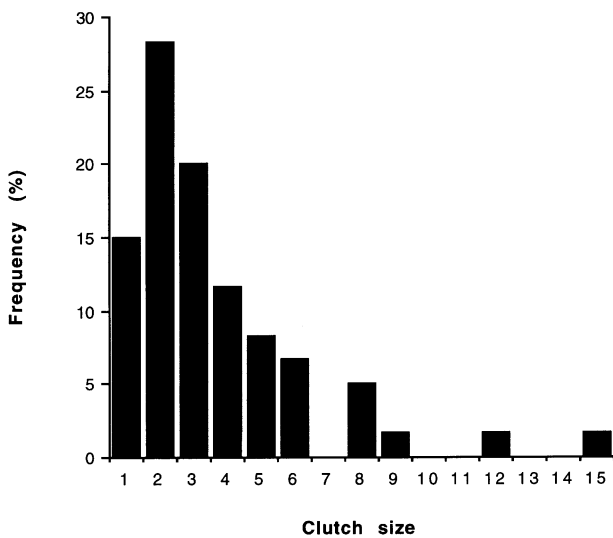


Fig. 1. Frequency distribution (%) of clutch sizes laid by *Muscidifurax raptorellus* in *Musca domestica* pupae. $n = 60$.

16 days to complete development irrespective of clutch size, male parasitoids emerged in under 15 days from hosts containing clutch sizes of three or more.

Adult parasitoid size (dry mass) varied significantly with clutch (two-way ANOVA, $F = 21.08$, d.f. = 2, 130, $P < 0.0001$) and sex ($F = 28.47$, d.f. = 1, 130, $P < 0.0001$; Fig. 2b). There was also a significant interactive effect between clutch size and sex on parasitoid size ($F = 5.09$, d.f. = 2, 130, $P < 0.01$). The size of both male and female parasitoids decreased with clutch size (Fig. 2b), although in female wasps the decrease was only apparent in heavily parasitized hosts, compared with male parasitoids.

Size variability of adult M. raptorellus as a function of clutch size

Preliminary analysis revealed that the size-variability of emerged parasitoids did not vary with sex in any of the three clutch size treatments (one-way ANOVA's, $P > 0.05$). We therefore combined the data for male and female wasps. The coefficient of variation (CV) in adult parasitoid size for *M. raptorellus* is shown in Fig. 3. In hosts containing two parasitoids, the CV for adult size was only 10%, but this increased to 27% in hosts containing five parasitoids or more. Thus, the relative variability in size between the smallest and largest wasp of the same sex emerging from parasitized host pupae increased with clutch size.

Growth of M. raptorellus and weight of parasitized hosts

The dry weight of parasitized *M. domestica* pupae is shown in Fig. 4. Host dry weight during the early phases of parasitism was fairly constant at 4–5 mg per host, irrespective of clutch

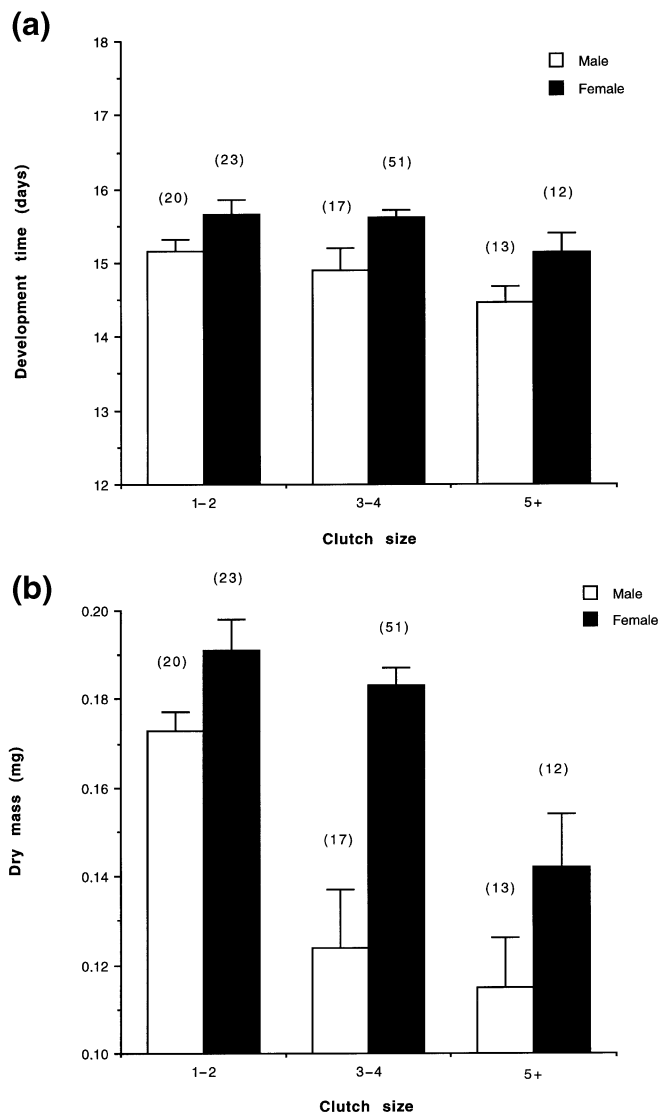


Fig. 2. (a) Mean development time, in days, of *M. raptorellus* emerging from hosts containing different numbers of parasitoid larvae. Data from hosts containing more than five parasitoids were pooled. Line bars represent standard error of the mean. Sample sizes are as indicated above each bar in the figure. (b) Mean adult parasitoid size (dry mass in mg) of *M. raptorellus* emerging from hosts containing different numbers of parasitoid larvae. Data from hosts containing more than five parasitoids were pooled. Line bars represent standard error of the mean. Sample sizes are as indicated above each bar in the figure.

size. However, heavily parasitized host individuals lost dry mass more rapidly than lightly parasitized hosts (Fig. 4). In many host pupae containing more than five parasitoids per host, all host tissues were consumed by the seventh day after parasitism.

Adult female *M. raptorellus* laid anhydrotic (= yolk-rich) eggs which hatched about 48 h after oviposition (J. A. Harvey, unpublished data). Parasitoid larvae began feeding on all host tissues soon after eclosion from the egg, and developed rapidly. As shown in other studies with different parasitoids (e.g.

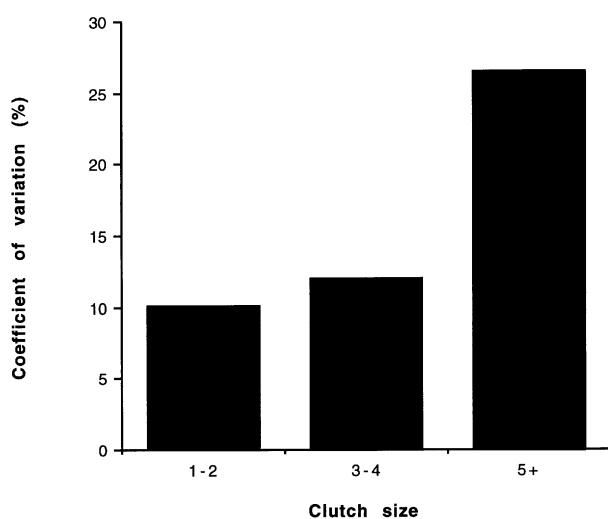


Fig. 3. Coefficient of variation (CV) of the mean size of the smallest parasitoid as percentage dry mass of the largest parasitoid of the same sex emerging from hosts containing different numbers of parasitoid larvae. Sample sizes: 2 parasitoids, $n = 14$; 3–4 parasitoids, $n = 20$; 5 + parasitoids, $n = 21$.

Table 1. Estimates of parameters a and b derived from the growth and pupation equation, describing the development of *Muscidifurax raptorellus* from host pupae containing different numbers of parasitoids. Max. DM = day on which maximum parasitoid dry mass was reached.

Clutch size	Growth parameters				Max. DM
	a		b		
	Mean	SE	Mean	SE	
<i>Logarithmic growth phase</i>					
1–2	–4.01	0.26	0.61	0.05	7
3–4	–3.74	0.22	0.55	0.04	7
≥ 5	–4.21	0.50	0.77	0.08	6
<i>Pupation phase</i>					
1–2	–0.95	0.12	0.05	0.01	
3–4	–0.99	0.09	–0.05	0.01	
≥ 5	–0.96	0.12	–0.08	0.02	

Sequeira & Mackauer, 1992a; Harvey *et al.*, 1994), the development of *M. raptorellus* was characterized by an exponential increase in dry mass during the growth phase, followed by an abrupt ‘cut-off’ at pupation. From pupation until adult emergence, there was a further decreasing exponential loss in parasitoid dry mass. Calow (1981) and Sibly & Calow (1986) described both growth and pupation phases as a ‘J-curve’. We fitted a curvilinear function separately to the male parasitoid dry mass data for larval growth and pupation, using the following equation:

$$P = \exp(a + bt_p)$$

where P represents parasitoid dry mass (mg), t_p is the parasitoid

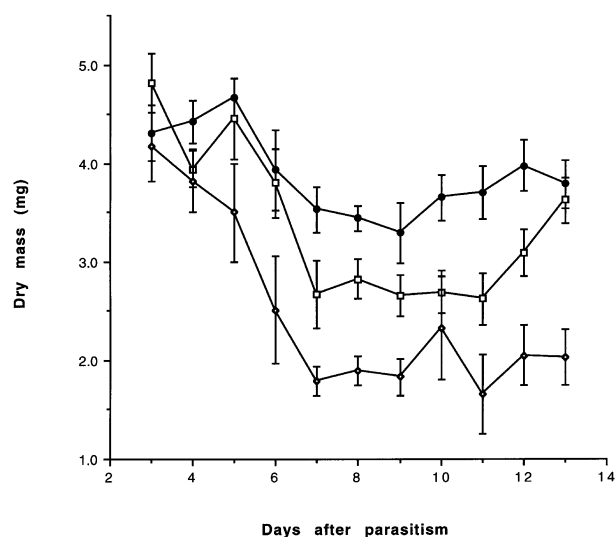


Fig. 4. Changes in mean host size (dry mass in mg) with time of *M. domestica* pupae containing different numbers of parasitoid larvae. Line bars represent standard error of the mean. Clutch sizes: ● = 1–2 parasitoids, □ = 3–4 parasitoids, ◇ = 5 + parasitoids. $n = 10$ for each treatment.

age in days from parasitism, and a and b are fitted parameters. The parameter values derived from the data fitted into the equation are shown in Table 1. The fitted parameters a and b are used to describe the pattern of the growth trajectory, which varies as the parasitoid develops and passes through its different instars. The fitted growth and pupation curves are shown in Fig. 5. Regardless of clutch size, *M. raptorellus* began to grow exponentially 3 days after parasitism, which is soon after eclosion from the parasitoid egg (Fig. 5a–c). Growth was most rapid during the early phases in hosts containing more than five parasitoids (Fig. 5c). The plotted growth trajectories predict that maximum parasitoid size is reached earlier in heavily than in lightly parasitized hosts. However, the plotted trajectory also predicts that parasitoids in heavily parasitized hosts do not grow as large as those in hosts containing fewer than five parasitoids (Fig. 5a–c).

Discussion

The growth and development of *M. raptorellus* was clearly affected by variations in clutch size, given that host size (= mass) was uniform. Parasitoids in heavily parasitized hosts (containing five or more parasitoid larvae) were smaller than those in lightly parasitized hosts with male wasps consistently smaller than female conspecifics. The pronounced reduction in male size also became apparent at lower clutch sizes than it did for female parasitoids, indicating that the effects of competition for limited host resources had a more deleterious effect on male parasitoids. However, parasitoid egg-to-adult development time decreased with clutch size, with males completing development more rapidly than females, irrespective of parasitoid number per host.

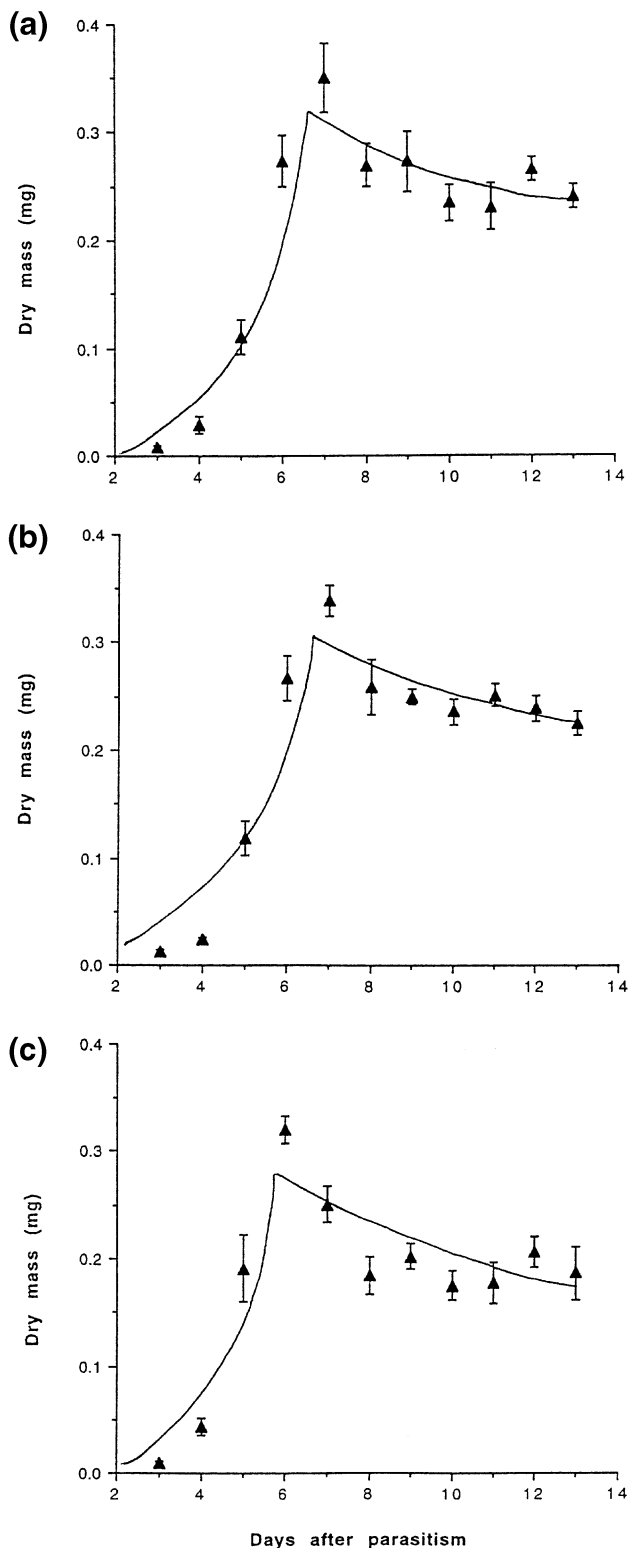


Fig. 5. The development of male *M. raptorellus* (▲) in hosts containing different numbers of parasitoid larvae. (a) = 1–2 parasitoids; (b) = 3–4 parasitoids; (c) = 5 + parasitoids. Line bars represent standard error of the mean. $n = 10$ for each treatment.

Differences in the size and development time of *M. raptorellus* can be explained by comparing parasitoid growth and host dry mass loss in response to clutch size variability. The observed growth patterns of *M. raptorellus* were largely invariant, irrespective of clutch size per host. Parasitoid larvae began exponential growth soon after eclosion from the egg, and continued to feed and grow rapidly until pupation. In hosts containing 1–4 parasitoids, maximum parasitoid size was not reached until 7 days after parasitism, compared with 6 days in hosts containing five parasitoids or more. Heavily parasitized hosts were consumed more rapidly than lightly parasitized hosts, such that on the sixth day after parasitism little or no host tissues remained. The remaining host dry mass consisted largely of the pupal cuticle, which the parasitoid larvae do not feed upon. Parasitoids deprived of host resources in heavily parasitized hosts were able partially to offset the reduction in size by pupating earlier, thus completing development to adult more rapidly than conspecific wasps in lightly parasitized hosts.

Differences in the clutch size of *M. raptorellus* clearly have fitness consequences for the parasitoid, even when host size and age (hence quality) were standardised. The relative variability in size between the largest emerged wasp and their smallest sibling increased with clutch size. In hosts with a high parasitoid burden this effect may be attributable to a scramble-type competition for limited host resources, which has also been recorded in other studies with gregarious parasitoids (e.g. Waage & Ng, 1984; Taylor, 1988; Vet *et al.*, 1993). However, the effects of larval competition may vary between gregarious idiobiont and koinobiont parasitoid species. Whereas idiobionts attack ostensibly 'fixed' resources (Vinson & Iwantsch, 1980b) many gregarious koinobionts stimulate host food consumption rate and/or utilization efficiency during parasitism (Slansky, 1978; Dushay & Beckage, 1993; Alleyne & Beckage, 1997). This allows the size of emerging parasitoids to be unaffected over a wide range of clutch sizes (Slansky, 1986). Changes in host development after parasitism may be mediated by factors injected into the host by the female wasp during the oviposition sequence, including polydnnaviruses and poison gland secretions (Vinson, 1988; Strand & Dover, 1991; Dushay & Beckage, 1993). Stimulation of host food consumption and growth thus allows koinobionts a much greater 'clutch size plasticity' than is available to idiobionts. Pupal parasitoids are largely constrained by host quality as determined by a host's previous nutritional history, whereas koinobionts can manipulate (to a certain degree) future host quality for their progeny and adjust their clutch size accordingly. Although resource quantity in pupal hosts is largely pre-determined at parasitism, host quality may decrease as hosts age, because of developmental changes which reduce the ability of the parasitoid to utilize specific nutrients (Sandlan, 1982; King, 1990). *Muscidifurax raptorellus* injects venom into its fly host pupae prior to oviposition or host-feeding activity which may induce developmental arrest that is sustained until host death (Rivers & Denlinger, 1995).

For idiobionts, the host represents a closed resource environment with parasitoid growth and development constrained by host quality as defined by available host biomass at oviposition. Parasitoid fitness is thus optimised by growing at the physiological limit, at least during the early phases of

parasitism. Our results, which support the predictions of a model for idiobiont development (e.g. Mackauer & Sequeira, 1993), show that the growth trajectory of *M. raptorellus* is largely inflexible, irrespective of clutch size. Immature parasitoids feeding and developing more slowly than sibling larvae suffered a reduction in size, and thus potentially fitness, through the effects of competition for limited host resources. However, smaller parasitoids developed more quickly to eclosion than their larger conspecifics, thus compensating at least partially. As pointed out by Roff (1981), adult size and development rate may have very different effects on fitness, thus parasitoid development is potentially optimised under different conditions (e.g. host size, clutch size) and is determined by a trade-off in these parameters.

Idiobiont and koinobiont life-history strategies are adaptive responses to the metabolic requirements of the immature parasitoid as mediated by available host biomass, growth potential and survival (Mackauer & Sequeira, 1993). Consequently, host-parasitoid associations are governed by a high degree of nutritional and physiological integration (Vinson & Iwantsch, 1980a,b; Thompson, 1990). The growth rate, development time and adult size of parasitoids are constrained by host quality, and are characteristic of each association. King (1987) and Mackauer & Sequeira (1993), discussing the metabolic processes that ultimately determine parasitoid fitness, argued that body size is the main target of selection because it is correlated with life-history and demographic traits (see also Jervis & Copland, 1996).

However, host quality is one of many factors that will determine oviposition decisions, including clutch size, by parasitoids (Kouame & Mackauer, 1991). Decision-making processes by female parasitoids have evolved in response to the competing demands of parental and progeny fitness. When encountering a host, *M. raptorellus* must decide whether to host-feed or oviposit, what sex ratio to allocate and what clutch size to lay in accordance with various host quality attributes, and the state of her ovaries and metabolic energy reserves (Jervis & Kidd, 1986). If she decides to oviposit, her clutch-size decisions will potentially be influenced by both resource allocation to her progeny and her physiological state, including the number of mature eggs she may mobilize for oviposition. A parasitoid mother may still increase her fitness under conditions of time-limitation if she lays larger clutches, thus increasing competition for host resources such that her progeny receive less than optimal quantities of food for their own development. However, a closer examination of the clutch size frequency laid by *M. raptorellus* reveals that the parasitoid usually laid 1–3 eggs per host, conditions which would yield large parasitoid offspring. This suggests that host quality and offspring size significantly influenced oviposition decisions by the parasitoid mother.

Thus far, very few studies have examined developmental interactions and the degree of nutritional integration throughout parasitism between idiobiont parasitoids and their hosts. Our data have shown that the development of *M. raptorellus* is influenced by variations in clutch size, and that the growth of individual larvae is increasingly affected when competing with siblings for resources in heavily parasitized hosts. We are

currently comparing the developmental responses of *M. raptorellus* in two host species of considerably different mass (*M. domestica* and *Calliphora vomitoria*) in order to determine whether qualitative and quantitative differences in host nutrition affect the performance of the parasitoid. Comparative studies investigating association-specific functional constraints in both koinobiont and idiobiont parasitoids may help explain the evolution of life-history strategies in the parasitic Hymenoptera.

Acknowledgments

We wish to thank Dr Mark Jervis and Antoon Loomans for reading early drafts of the manuscript and Hanneke van Heest, Leo Koopman, Andre Gidding and Frans van Aggelen for technical support. The senior author would like to gratefully acknowledge the Royal Society (U.K.) for financial support through the European Fellowship Exchange Programme.

References

- Alleyn, M. & Beckage, N.E. (1997) Parasitism-induced effects on host growth and metabolic efficiency in tobacco hornworm larvae parasitized by *Cotesia congregata*. *Journal of Insect Physiology*, **43**, 407–424.
- Arthur, A.P. & Wylie, H.G. (1959) Effects of host size on sex ratio, development time and size of *Pimpla turionellae* L. *Entomophaga*, **4**, 297–301.
- Askew, R.R. & Shaw, M.R. (1986) Parasitoid communities: their size, structure and development. *Insect Parasitoids: 13th Symposium of the Royal Entomological Society of London* (ed. by J. K. Waage and D. J. Greathead), pp. 225–264. Academic Press, London.
- Calow, P. (1981) *Invertebrate Biology. A Functional Approach*. Croom-Helm, London.
- Croft, P. & Copland, M.J.W. (1995) The effect of host instar on the size and sex ratio of the endoparasitoid *Dacnusa sibirica*. *Entomologia experimentalis et applicata*, **74**, 121–124.
- Dushay, M.S. & Beckage, N.E. (1993) Dose-dependent separation of *Cotesia congregata*-associated polydnavirus effects on *Manduca sexta* larval development and immunity. *Journal of Insect Physiology*, **39**, 1029–1040.
- Flanders, S.E. (1950) Regulation of ovulation and egg disposal in the parasitic Hymenoptera. *Canadian Entomologist*, **82**, 134–140.
- Godfray, H.C.J. (1994) *Parasitoids: Behavioral and Evolutionary Ecology*. Princeton University Press, Princeton, New Jersey.
- Harvey, J.A., Harvey, I.F. & Thompson, D.J. (1994) Flexible larval growth allows use of a range of host sizes by a parasitoid wasp. *Ecology*, **75**, 1420–1428.
- Harvey, J.A., Harvey, I.F. & Thompson, D.J. (1995) The effect of host nutrition on development of the solitary parasitoid wasp, *Venturia canescens*. *Entomologia experimentalis et applicata*, **75**, 213–220.
- Heaversedge, R.C. (1967) Variation in the size of insect parasites of puparia of *Glossina* spp. *Bulletin of Entomological Research*, **58**, 153–158.
- Hebert, C. & Cloutier, C. (1990) Host instar as a determinant of preference and suitability for two parasitoids attacking late instars of the spruce budworm (Lepidoptera: Tortricidae). *Annals of the Entomological Society of America*, **83**, 734–741.
- Iwasa, Y., Suzuki, Y. & Matsuda, H. (1994) Theory of oviposition strategy of parasitoids. I. Effect of mortality and limited egg number. *Theoretical Population Biology*, **26**, 205–227.

- Jervis, M.A. & Kidd, N.A.C. (1986) Host-feeding strategies in hymenopteran parasitoids. *Biological Reviews*, **61**, 395–434.
- Jervis, M.A. & Copland, M.J.W. (1996) The life cycle. *Insect Natural Enemies: Practical Approaches to their Study and Evaluation* (ed. by M. A. Jervis and N. A. C. Kidd), pp. 63–161. Chapman & Hall, London.
- King, B.H. (1987) Offspring sex ratios in parasitoid wasps. *Quarterly Review of Biology*, **62**, 367–396.
- King, B.H. (1990) Sex ratio manipulation by the parasitoid wasp *Spalangia cameroni* in response to host age: a test of the host-size model. *Evolutionary Ecology*, **4**, 149–156.
- Kouame, K.L. & Mackauer, M. (1991) Influence of aphid size, age, and behaviour on host choice by the parasitoid wasp *Ephedrus californicus*: a test of host-size models. *Oecologia*, **80**, 197–203.
- Legner, E.F. (1987) Inheritance of gregarious and solitary oviposition in *Muscidifurax raptorellus* Kogan and Legner (Hymenoptera: Pteromalidae). *Canadian Entomologist*, **119**, 791–808.
- Legner, E.F. (1988) *Muscidifurax raptorellus* (Hymenoptera: Pteromalidae) females exhibit post mating behaviour typical of the male genome. *Annals of the Entomological Society of America*, **81**, 524–527.
- Legner, E.F. (1989a) Wary genes and accretive inheritance in Hymenoptera. *Annals of the Entomological Society of America*, **82**, 245–249.
- Legner, E.F. (1989b) Paternal influences in males of *Muscidifurax raptorellus* (Hymenoptera: Pteromalidae). *Entomophaga*, **34**, 307–320.
- Mackauer, M. (1986) Growth and developmental interactions in some aphids and their hymenopterous parasites. *Journal of Insect Physiology*, **32**, 275–280.
- Mackauer, M. & Sequeira, R. (1993) Patterns of development in insect parasites. *Parasites and Pathogens of Insects, Vol 1* (ed. by N. E. Beckage, S. N. Thompson and B. A. Federici), pp. 1–23. Academic Press, New York.
- Parker, G.A. & Courtney, S.P. (1984) Models of clutch size in insect oviposition. *Theoretical Population Biology*, **26**, 27–48.
- Rivers, D.B. & Denlinger, D.L. (1995) Fecundity and development of the ectoparasitic wasp *Nasonia vitripennis* are dependent on host quality. *Entomologia experimentalis et applicata*, **76**, 15–24.
- Roff, D.A. (1981) On being the right size. *American Naturalist*, **118**, 405–422.
- Salt, G. (1940) Experimental studies in insect parasitism. VII. The effects of different hosts on the parasite *Trichogramma evanescens* Westw. *Proceedings of the Royal Entomological Society of London A*, **15**, 81–95.
- Sandlan, K.P. (1982) Host suitability and its effects on parasitoid biology in *Coccygomimus turionellae* (Hymenoptera: Ichneumonidae). *Annals of the Entomological Society of America*, **75**, 217–221.
- Sequeira, R. & Mackauer, M. (1992a) Nutritional ecology of an insect host–parasitoid association: the pea aphid–*Aphidius ervi* system. *Ecology*, **73**, 183–189.
- Sequeira, R. & Mackauer, M. (1992b) Covariance of adult size and development time in the parasitoid wasp, *Aphidius ervi* in relation to the size of its host, *Acyrthosiphon pisum*. *Evolutionary Ecology*, **6**, 34–44.
- Sibly, R.M. & Calow, P. (1986) *Physiological Ecology of Animals. An Evolutionary Approach*. Blackwell, Oxford.
- Slansky, F. Jr. (1978) Utilization of energy and nitrogen by larvae of the imported cabbageworm, *Pieris rapae*, as affected by parasitism by *Apanteles glomeratus*. *Environmental Entomology*, **7**, 179–185.
- Slansky, F. Jr. (1986) Nutritional ecology of endoparasitic insects and their hosts: an overview. *Journal of Insect Physiology*, **32**, 255–261.
- Strand, M.R. & Dover, B.A. (1991) Developmental disruption of *Pseudoplusia includens* and *Heliothis virescens* larvae by calyx fluid and venom of *Microplitis demolitor*. *Archives of Insect Biochemistry and Physiology*, **18**, 131–145.
- Taylor, A.D. (1988) Host effects on larval competition in the gregarious parasitoid *Bracon hebetor*. *Journal of Animal Ecology*, **57**, 163–172.
- Thompson, S.N. (1990) Physiological alterations during parasitism and their effects on host behaviour. *Parasitism and Host Behaviour* (ed. by C. J. Barnard and J. M. Behnke), pp. 64–94. Taylor & Francis, London.
- Vet, L.E.M., Datema, A., van Welzen, K., & Snellen, H. (1993) Clutch size in a larval-pupal endoparasitoid: 1. Variation across and within host species. *Oecologia*, **95**, 410–415.
- Vinson, S.B. (1988) Physiological studies of parasitoids reveal new approaches to the biological control of insect pests. *ISI Atlas of Science*, **1**, 25–32.
- Vinson, S.B. & Iwantsch, G.F. (1980a) Host suitability for insect parasitoids. *Annual Review of Entomology*, **25**, 397–419.
- Vinson, S.B. & Iwantsch, G.F. (1980b) Host regulation by insect parasitoids. *Quarterly Review of Biology*, **55**, 143–165.
- Waage, J.K. & Ng, S.M. (1984) The reproductive strategy of a parasitic wasp. I. Optimal progeny allocation in *Trichogramma evanescens*. *Journal of Animal Ecology*, **53**, 401–415.
- Waage, J.K. & Godfray, H.C.J. (1985) Reproductive strategies and population ecology of insect parasitoids. *Behavioural Ecology, Ecological Consequences of Adaptive Behaviour* (ed. by R. M. Sibly and R. H. Smith), pp. 449–470. Blackwell Scientific Publications, Oxford.

Accepted 24 October 1997