



Parasitization Site on the Host of the Parasitoid Wasp *Spalangia endius* (Hymenoptera: Pteromalidae)

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ABSTRACT *Spalangia endius* Walker, a parasitoid wasp, parasitizes both young and old *Musca domestica* L. pupae, but parasitization site differed with host age. With young hosts, a mother's first drill attempt was about equally likely to be on either half of the host; and host half did not affect the number of drill attempts, the proportion of those attempts that were successful, or the duration of the first successfully completed drill. In contrast, with old hosts, mothers tended to attempt drilling sooner and more often on the posterior versus anterior half of hosts; and a greater proportion of drills were successful on the posterior half. Offspring head width did not differ significantly between offspring oviposited on the posterior versus anterior half of hosts, regardless of host age. Once adult, most offspring chewed out through the anterior half of the host, regardless of host age.

KEY WORDS *Spalangia endius*, parasitization site, pteromalid, parasitoid wasp, house fly, host age

THE VALUE OF a host to a parasitoid varies depending on the host species, strain, stage of development, size, and whether it has already been parasitized (e.g., references in Godfray 1994). Here I examine whether host value also varies across a single host. I use the parasitoid wasp *Spalangia endius* Walker and a natural host, house fly pupae, *Musca domestica* L. (Diptera: Muscidae). I examine whether female *S. endius* preferentially drill the anterior or the posterior half of hosts and consequences of doing so in terms of drilling duration, drilling success, and offspring size. I test for preference and consequences in both young hosts and old hosts.

Musca domestica pupae are found in and on decaying organic matter or manure. A female *Spalangia* uses her ovipositor to drill through the puparium (outer shell) of a host. The anterior half of the puparium may be easier to drill because it has the weak cleavage lines that allow adult flies to emerge, or the posterior half may be easier because of its anal spiracles. The female deposits an egg on the host developing within or feeds on fluids exuding from wounds that she makes in the host. Within the puparium the parasitoid larva feeds by repeatedly biting through the host integument (Gerling and Legner 1968). The host's head and abdomen end may differ in nutritional quality, rate of sclerotization, and ease with which the integument can be pierced. Once adult, the parasitoid offspring exits the host by chewing through the puparium. Young hosts appear to be of greater value than old hosts to *Spalangia* both in terms of a female's ability to produce offspring and in terms of the future fitness of those offspring (King 1998, 2000).

Materials and Methods

General Methods. An *S. endius* colony was established from collections from a poultry house in Florida in March 1996 by C. Geden. Experiments were done ≈ 1 yr later, except the female video-experiment, which was done within 6 mo (less than eight generations) of the collection. The colony was maintained on *M. domestica*. Voucher specimens of *S. endius* are being deposited in the Insect Collection at the Illinois Natural History Survey.

I produced hosts by providing 800 mm³ of *M. domestica* eggs with 1,030 ml media at $\approx 25^{\circ}\text{C}$ (King 1988). "Young hosts" were 0–24 h old (from when the puparium turned red) when initially presented to parasitoids; "old hosts" were 3 d older. Female parasitoids had emerged within 2 d before use and had been observed to mate.

Means are presented with ± 1 SE or the range. I used alpha of 0.05 for comparisons of means. Two-tailed *P* values are presented; however, one-tailed tests do not change major conclusions. Mann–Whitney *U* tests were used in place of independent *t*-tests when assumptions of normality were strongly violated. Statistical analyses were with SPSS-PC (SPSS 1988).

Oviposition Restricted to One Half of the Host. In the first experiment, each female was presented with 10 young hosts for each of two successive days. Each mother was presented with just the anterior half of hosts or with just the posterior half. The hosts were presented in plastic vials (40 mm high by 36 mm top diameter by 27 mm bottom diameter) two-thirds full of sand. The hosts were half-buried, with the long axis of the host perpendicular to the surface of the sand. The surface of the sand was then wetted, which pre-

vented females from burrowing. After exposure to a female, five of the 10 hosts were placed in an empty vial for the parasitoid offspring to complete development. (The other five were dissected and parasitoid eggs inside were counted.) All adult offspring were counted, those that emerged as well as those that failed to emerge or emerged but then crawled back in. The head width of one offspring of each sex from each mother was measured. Because head widths of sisters and brothers were not correlated, they were analyzed separately.

The second experiment was identical to the first except that hosts were old rather than young. For each experiment, number of hosts parasitized (i.e., number with at least one egg) and parasitoid offspring sex ratio were analyzed by repeated measures analysis of variance (ANOVA), with days 1 and 2 as the repeated measures.

A control experiment demonstrated that differences among treatments in these two experiments were not confounded by differences in fly survivorship in the absence of parasitoids. Fly survivorship from pupa to adulthood was $99 \pm 0.30\%$, $n = 60$; and ANOVA revealed no effect of pupa age ($F = 1.000$; $df = 1, 36$; $P = 0.32$) nor of which half was buried ($F = 1.000$; $df = 1, 36$; $P = 0.32$) and no interaction ($F_{1,36} = 1.000$; $df = 1, 36$; $P = 0.32$). In addition, whether the fly pupa was buried did not affect its subsequent survivorship ($99 \pm 0.30\%$, $n = 60$ versus $99 \pm 0.61\%$, $n = 19$; $F = 2.09$; $df = 1, 57$; $P = 0.15$).

Videotapes of Drilling. To determine which half of hosts females drill into when given a choice, I videotaped each of 40 females for 3 h with one young host and one old host. The hosts were in a petri dish (35 mm diameter by 10 mm deep) secured to the dish with a small drop of water, parallel to each other, head to head, about a host length apart (≈ 2.5 wasp lengths) and dorsal side up. (*S. cameroni* Perkins often parasitizes the dorsal side [Gerling and Legner 1968]). I alternated which age of host was in the left position. Females had no prior experience with hosts or honey. Illumination was from fiber-optic gooseneck lights, which gave off no noticeable heat.

From these tapes, for each host age, I recorded which host half the female first antennated (King 1994) and which she first attempted to drill for at least 1 min. One minute was chosen to facilitate comparison with previous studies (King 1994, 1998) and to avoid confusion with ovipositor probing. For each half of each host age, I also recorded the number of drill attempts of >1 min, proportion of drill attempts that were successful, and the duration of the first successful drill. A drill was considered successful if the ovipositor was inserted all the way into the host at a site not already successfully drilled (King 1994). Not all females provided data on all measures.

Number of drill attempts on each half of each host age was analyzed by repeated measures ANOVA, followed by paired *t*-tests when the interaction was significant. Proportion of attempts that were successful was compared by independent tests rather than by repeated measures because there were few females

Table 1. Out of five old hosts, the number parasitized by mothers exposed to the anterior half of hosts versus mothers exposed to the posterior half

	Day 1 mean \pm SE (n)	Day 2 mean \pm SE (n)
Anterior	0.95 \pm 0.29 (20)	2.00 \pm 0.39 (21)
Posterior	1.57 \pm 0.27 (20)	3.05 \pm 0.32 (21)

Host half: $F = 5.35$; $df = 1, 39$; $P = 0.026$. Day: $F = 20.87$; $df = 1, 39$; $P < 0.001$.

Host half by day: $F = 0.59$; $df = 1, 39$; $P = 0.45$.

with data on all four host age–host half combinations; however, patterns were the same, regardless.

Results

Oviposition Restricted to One Half of the Host.

Young Hosts. The number of hosts parasitized did not differ significantly between mothers that oviposited on the anterior versus posterior halves of hosts ($F = 0.35$; $df = 1, 38$; $P = 0.56$) regardless of day (day: $F = 0.63$; $df = 1, 38$; $P = 0.43$; host half by day: $F = 0.40$; $df = 1, 38$; $P = 0.53$). The same was true for number of eggs per parasitized host (day 1: $U = 105.5$, $n_1 = 12$, $n_2 = 18$, $P = 0.81$; day 2: $t = 0.68$, $df = 32$, $P = 0.50$). Offspring sex ratio also did not differ significantly with host half ($F = 0.02$; $df = 1, 40$; $P = 0.88$) irrespective of day (day: $F = 0.75$; $df = 1, 40$; $P = 0.39$; host half by day: $F = 0.84$; $df = 1, 40$; $P = 0.36$). Offspring head width also did not differ significantly with host half for females ($t = 0.35$, $df = 48$, $P = 0.73$) or males ($t = 1.49$, $df = 31$, $P = 0.15$).

Most offspring chewed out through the anterior half of the puparium. Among mothers that oviposited on the anterior half of hosts, 99% of offspring (range, 83–100%) chewed out through the anterior. This was significantly greater than the 93% of offspring (range, 50–100%) that chewed out through the anterior among mothers that oviposited on the posterior half of hosts ($U = 241.0$, $n_a = 23$, $n_p = 27$, $P = 0.05$). Three of 57 mothers had an adult offspring that failed to chew its way out of its hosts; one had oviposited in anterior halves and two in posterior halves.

Old Hosts. The number of hosts parasitized was greater for mothers that oviposited in the posterior versus anterior halves of hosts (Table 1). The number of eggs per parasitized host did not differ significantly with host half on the first day of oviposition ($U = 88.5$, $n_1 = 11$, $n_2 = 17$, $P = 0.70$) or on the second day of oviposition ($U = 116.0$, $n_1 = 16$, $n_2 = 21$, $P = 0.07$). Offspring sex ratio did not differ significantly with host half ($F = 0.08$; $df = 1, 33$; $P = 0.78$) regardless of day (day: $F = 2.32$; $df = 1, 33$; $P = 0.14$; host half by day: $F = 0.85$; $df = 1, 33$; $P = 0.36$). Offspring head width also did not differ significantly with host half for females ($U = 221.0$, $n_a = 22$, $n_p = 25$, $P = 0.25$) or males ($t = 0.77$, $df = 30$, $P = 0.45$).

Most offspring chewed out through the anterior half, but the proportion that chewed out through the anterior was not significantly greater for mothers that oviposited on anterior versus posterior halves (0.91,

Table 2. Number of drill attempts in the anterior versus the posterior half of the host when mothers were given one young host and one old host for 3 h

	Young hosts mean \pm SE (<i>n</i>)	Range	Old hosts mean \pm SE (<i>n</i>)	Range
Anterior	0.90 \pm 0.22 (39)	0–6	0.59 \pm 0.15 (39)	0–4
Posterior	0.97 \pm 0.21 (39)	0–5	1.74 \pm 0.32 (39)	0–8
t_{33}	0.23		3.42	
<i>P</i>	0.82		0.002	

0.50–1.00 versus 0.84, 0.50–1.00, $t = 1.33$, $df = 40$, $P = 0.19$). Four of 58 mothers had an adult offspring that failed to chew its way out; three had oviposited in anterior halves, and one in posterior halves.

Videotapes of Drilling. The first antennation of a host was on the anterior as often as on the posterior half for both young hosts (15 versus 23; $\chi^2 = 1.68$, $P > 0.10$) and old hosts (21 versus 17; $\chi^2 = 0.42$, $P > 0.50$). The first drill attempt was on the anterior as often as on the posterior half for young hosts (17 versus 13; $\chi^2 = 0.53$, $P > 0.10$) but was less often on the anterior than on the posterior for old hosts (8 versus 17; $\chi^2 = 10.24$, $P < 0.005$). The effect of host half on number of drill attempts depended on host age ($F = 5.87$; $df = 1, 38$; $P = 0.02$): females made as many attempts in the anterior half as in the posterior half of young hosts; but made more attempts in the posterior half than in the anterior half of old hosts (Table 2).

For young hosts, drills were about equally successful on the posterior as on the anterior half (Table 3), and the duration of a female's first completed drill was not detectably shorter on the posterior versus anterior half (16.3 \pm 3.1 min, $n = 10$ versus 17.2 \pm 2.8 min, $n = 9$; $t = 0.22$, $df = 17$, $P = 0.83$). In contrast, for old hosts, drills were sometimes successful on the posterior half but never on the anterior half (Table 3). Thus, the five mothers that host fed on old hosts all did so on the posterior, and these feedings were all at the anal spiracles. Three of the four mothers that host fed on young hosts did so on the posterior, at the spiracles. Two females fed twice at the same site, reinserting the ovipositor in the interim; five females that reinserted the ovipositor did not then feed there again.

Discussion

The effect of host end on parasitization by *S. endius* mothers depended on host age. For old hosts, mothers

Table 3. The proportion of drill attempts that were successful in the anterior versus the posterior half of hosts when mothers were given one young host and one old host for 3 h

	Young hosts mean \pm SE (<i>n</i>)	Range	Old hosts mean \pm SE (<i>n</i>)	Range
Anterior	0.56 \pm 0.11 (17)	0–1	0.00 \pm 0.00 (14)	0–0
Posterior ^a	0.47 \pm 0.10 (18)	0–1	0.19 \pm 0.06 (19)	0–1
<i>P</i>	0.55 ^b		0.0034 ^c	

^a Posteriors of young versus old hosts: $U = 108.5$, $P = 0.05$.

^b $t_{33} = 0.61$.

^c $U = 70.0$.

attempted to drill first and more often on the posterior half. This appears to be adaptive given the greater success of drill attempts on the posterior half. For young hosts, mothers showed no preference for drilling either half, which is consistent with the success and duration of drills not differing between host halves. Mothers may detect which half is easier to drill during antennation. Antennation was not preferential with respect to host half for either young or old hosts.

Ease of drilling probably varies not only between the posterior versus anterior half of a host but also within each half. When a larva of the beetle *Aleochara bilineata* chews in through its host's puparium, it preferentially enters through the central abdominal area, an area in which the puparial ridges are relatively low (Royer et al. 1998). The puparium of *M. domestica* has visible rings around its width, which may differ in thickness or hardness. Also, the posterior half includes the anal spiracles at the tip; and females often, although not always, drilled at these spiracles, regardless of host age.

Published observations on within-host parasitization site exist for some ecologically similar confamilials of *S. endius* as well as for some more distantly related parasitoids. Unfortunately, often only anecdotal observations are available (e.g., Shaw and Huddleston 1991), or it is unclear whether differences in the size of different host sites have been controlled (e.g., Wylie 1971; Strand 1986; Olson 1998). Even in the absence of preference, i.e., even when parasitization site is random per unit area of host, a greater number of parasitizations are expected on larger body parts, e.g., abdomen versus head. Effects of host age on parasitization site have been explored infrequently as have consequences of site choice for both mother and offspring fitness.

In an Indiana strain of the solitary congener *S. cameroni*, females respond differently to young versus old *M. domestica* hosts (King 1994). When the first successful drill is within one-fifth of the end of a host, it tends to be at the posterior end if the host is old and at the anterior end if the host is young. When another solitary congener, *S. nigroaenea* Curtis (= *S. muscidarum*), parasitizes *Stomoxys calcitrans* (L.) hosts of unspecified age, females usually insert their ovipositors near the head end (Pinkus 1913). Consequences of parasitization site for offspring have not been explored in either species.

Wylie (1971) and Rivers and Denlinger (1994) both report that in the gregarious confamilial *Nasonia vitripennis* Walker, females oviposit more frequently in the thorax or abdomen than in the head. However, whether this is controlling for the difference in size of these body sections is not clear, so the preference may simply be a result of the thorax and abdomen being larger than the head. Clutch size does not differ between females restricted to ovipositing on the anterior versus posterior halves of hosts (Rivers and Denlinger 1994). Host age affects sting site in *Gyranusoidea tebygi* Noyes, a solitary endoparasitoid of mealybug larvae (Boavida et al. 1995).

In the *S. endius* studied here, an advantage to preferentially drilling the posterior half of old hosts is the ease of drilling for the mother. An advantage to her offspring in terms of size was not found. Oviposition site may be irrelevant to offspring if larvae wander on the host as has been demonstrated for *S. cameroni* (Gerling and Legner 1968, Wylie 1971). That parasitization site differs with host age in *S. endius* appears to be unrelated to host feeding. Host feeding was usually at the posterior regardless of host age, and young and old hosts were fed on with about equal frequency.

Among parasitoids in general, parasitizing particular parts of a host may affect not only ease of penetrating the host, but also nutritional value, risk of encapsulation, and ability of the mother to successfully envenomate the host (Godfray 1994). Successful envenomation may be necessary to subdue the host or to prevent the host from developing or rotting too quickly. In *N. vitripennis*, effects of envenomation differ with site, especially for younger hosts (Rivers and Denlinger 1994). Oviposition on the posterior rather than the anterior third of a host increases the offsprings' oxygen consumption, larval weight, and lipid content, but has no effect on development rate or later lipid content (Rivers and Denlinger 1994, Rivers and Yoder 1996). In parasitoids of active host stages, site may affect the survival of mothers and offspring by affecting the ability of the host to reach, injure, and kill them (Nakamura 1997), especially with older, larger hosts (e.g., Boavida et al. 1995, Brodeur et al. 1996).

Most *S. endius* offspring chewed out through the anterior half of hosts regardless of where the mother had oviposited. However, offspring in young hosts were especially likely to chew out through the anterior half of hosts when their mothers had oviposited there. Whether the part of the puparium that is easiest to chew corresponds to the part that is easiest to drill and whether which half of the puparium is tougher changes between these two events are not known. The end of the host from which parasitoid wasps emerge once they finish feeding appears to be quite variable among parasitoid wasps, with a fairly consistent exit site in some species but not in others (e.g., Shaw and Huddleston 1991, Liu and Stansly 1996 and references therein).

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