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Host Age Response in the Parasitoid Wasp *Spalangia cameroni* (Hymenoptera: Pteromalidae)

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Female Spalangia cameroni *produced more offspring from younger house fly pupae, both when given a choice of host ages and when not given a choice. Host age did not affect offspring survivorship. Offspring were larger when they had developed on younger hosts and the effect was independent of offspring sex. Having previously parasitized old hosts versus young hosts did not reduce a female's production of offspring in subsequent hosts. Females distinguished between young and old hosts both in the light and in the dark. Females did not distinguish between host ages prior to physical contact with the host but could distinguish by the time they first began exploring a host by tapping it with their antennae; thus, they could distinguish before drilling into a host.*

KEY WORDS: host age; parasitoid wasp; behavioral mechanism; fitness; Pteromalidae; *Spalangia*.

INTRODUCTION

The quality of the environment in which parents produce offspring may affect their own current and future offspring production as well as the future fitness of their offspring (e.g., Trimble and Wellington, 1979; van Alphen and Janssen, 1982; Pierce and Elgar, 1985). One important aspect of the environment is the quality and amount of food resources. In parasitoids, the quality and amount of food resources available to offspring may be affected by the age of the host on which a female leaves her offspring. Fitness effects of host age may be related not only to particular host developmental stages—egg, larval, pupal, and adult—but also the age within one or more of these stages (e.g., Rabinovich, 1970; Nechols and Kikuchi, 1985).

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In this paper, the effect of host age on parasitoid fitness and the mechanism by which adult parasitoids distinguish host ages are examined in *Spalangia cameroni* Perkins (Hymenoptera: Pteromalidae) parasitizing house fly pupae, *Musca domestica* L. (Diptera: Muscidae). *Spalangia cameroni* is a solitary parasitoid wasp, producing one offspring per host (Rueda and Axtell, 1985). To oviposit, a female must first drill through the puparium of the fly pupa. Females may kill hosts by mechanical injury during ovipositor insertion, by laying offspring, which then feed on the host, or by feeding on host fluids themselves. A female emerges as an adult with about 30 mature eggs (range, 13–40) but must host feed to produce additional eggs (Gerling and Legner, 1968; King and King, 1994).

Older hosts may provide less nutrition for host feeding and for offspring development. Older house fly pupae weigh less than younger ones (King, 1990). In addition, part of the biomass of older fly pupae has been converted to adult body parts that liquid feeders such as *S. cameroni* cannot ingest (Gerling and Legner, 1968). Even if females allocate the same amount of time and energy to parasitizing old hosts as to parasitizing young hosts, they probably will not be able to oviposit in as many old hosts as young hosts. Old hosts take longer for *S. cameroni* to drill into (e.g., 7 versus 23 min for 0- versus 3-day-old hosts), and drill attempts are more likely to be unsuccessful in older hosts (King, 1994).

Prior experience with old hosts versus young hosts also may affect future reproduction. Prior oviposition on older hosts may increase wear on the ovipositor from drilling and reduce energy available for subsequent reproduction. Alternatively, if females produce fewer offspring on older hosts and if eggs are limiting, prior oviposition on older hosts may leave the female with more eggs for subsequent reproduction. Older house fly pupae are darker than younger ones. Thus, females could potentially use color to distinguish host ages.

Here I use laboratory experiments with *S. cameroni* to test the predictions that (1) females will parasitize more young than old hosts, (2) offspring will be larger and have greater survivorship on younger hosts, and (3) having previously oviposited on old versus young hosts will affect a female's subsequent offspring production. I also examine whether female distinguish host age even in the absence of visual cues and at what time during host exploration they can distinguish host age. For example, can they distinguish prior to ovipositor insertion into a host?

METHODS

General Methods. The *S. cameroni* used in the second, third, and fifth experiments described below were from a colony that was established in 1985 with wasps that emerged from *Musca domestica* and *Stomoxys calcitrans* pupae collected in Indiana (King, 1991). The first and fourth experiments described below utilized a different colony of *S. cameroni* because the original was not available. This colony was established in 1995 from wasps obtained from C. Geden, who had established the original colony in 1992 from *M. domestica* from a poultry house in Florida. Wasp colonies were maintained at 23–28°C, 24 h L, using *M. domestica* as hosts.

Hosts were produced by providing 800 mm^3 of eggs with 1030 ml of fly larval medium (King, 1988). In the absence of any parasitoids, 2.5% of flies died prior to emergence [0.75 ± 0.23 (SE); range, 0–3 died of each set of 30 flies placed in a 1-oz plastic vial at 0 days of age; $n = 20$], similar to the 2% found by Morgan *et al.* (1979) and much less than the 32% found by Donaldson and Walter (1984). When initially presented to the wasps, 0-day-old hosts were 0–24 h old, timed from when the puparium became red. Host pupae were kept in an environmental chamber at 24–26°C. Old hosts were 3 days older than young hosts: hosts were either 0 and 3 days old or 1 and 4 days old, as specified below.

Newly emerged virgin wasps (less than 1 day old) were paired, and mating was observed. Then, within an hour of mating, each female was transferred to a 1-oz plastic vial (40 mm high × 36-mm top diameter × 27-mm bottom diameter), with a drop of honey on the side of the vial for food and experimental hosts on the bottom. Number and type of hosts presented are described in each experiment below.

Visual Cues Experiment. This experiment tested whether females produce more offspring from young hosts than from old hosts when presented with both simultaneously and whether they do so both in the presence and in the absence of visual cues. Each mated female was given 15 0-day-old hosts and 15 3-day-old hosts for 24 h. Thirty females were given hosts in the light, and 28 females were given hosts in complete darkness. Offspring production was analyzed by a multivariate analysis of variance (MANOVA), with light versus dark as the between-subjects effect and young hosts versus old hosts as the within-subject effect.

Host Ages 0–5 Experiment. This experiment examined the number, sex, and size of offspring produced by a female when she encountered only one host age class, either 0-, 1-, 2-, 3-, 4-, or 5-day-old pupae; $n = 31, 31, 31, 31, 28$, and 10 females for each of the six host age classes, respectively. Adult flies emerged from pupae more than 5 days old. Each female was presented with 30 hosts for 24 h.

Head width and head length of one randomly chosen offspring of each sex from each female were measured from a frontal view. Each measurement was made twice and averaged. Head size of offspring was analyzed by MANOVA, with host age as the between-subjects effect and offspring sex as the within-subject effect. Head width is positively correlated with other measures of body size in *S. cameroni* (King, 1988).

Survivorship Experiment. This experiment tested the effect of host age on offspring survivorship from egg to adult. In each of 31 replicates of this experiment, one female was given 20 1-day-old hosts and one female was given 20 4-day-old hosts for 24 h. For each female, 10 randomly chosen hosts were allowed to complete development so that emerged adult wasp offspring could be counted and their sex determined. The remaining 10 hosts were boiled to prevent their rupturing during dissection, and the parasitoid eggs within each host were counted. Survivorship was calculated for each female as the number of adult offspring divided by the number of eggs. Survivorship, number of hosts parasitized, and number of eggs per parasitized host were compared between young and old hosts.

Effect of Host Age on Subsequent Reproduction. This experiment examined the effect of exposure to young versus old hosts on a female's subsequent reproduction. In each of 31 replicates, on the first day, one female was given 30 1-day-old hosts and one female was given 30 4-day-old hosts; then, on the second day, each female was given 30 1-day-old hosts for 24 h. These treatments are abbreviated YY and OY, respectively.

The hosts from the first day were used to determine the effect of host age on offspring production, as in the experiments above. The hosts presented on the second day were used to examine whether experience with old versus young hosts on the first day affected subsequent offspring production. Offspring production across both days was compared to the number of eggs with which a female typically emerges (King and King, 1994) to determine whether eggs were likely to have been a limiting resource in this experiment.

Videotape Experiment. This experiment examined how soon during host encounter a female can distinguish between young and old hosts. Each *S. cameroni* female was videotaped for 3 h with one 1-day-old host and one 4-day-old host placed parallel to each other about one and one-half host lengths apart, which is equivalent to about two wasp lengths apart. Which age of host was in the left position was alternated. Each female had been pretreated for the previous 24 h with 14 young hosts and a drop of honey because preliminary observations indicated that this decreased subsequent time to oviposition. This experiment was designed only to test how soon females can distinguish young versus old hosts, not which age they prefer: because of the pretreatment with young hosts, any preference observed in this experiment could be a response to either host age or familiarity.

Forty females were videotaped with a Javelin color videocamera using a JVS s-VHS digital recorder with s-VHS tapes on extended play. Illumination was from fiber-optic gooseneck lights, which gave off no noticeable heat. Each female was videotaped in a 35-mm-diameter × 10-mm-deep plastic petri dish. A small drop of water was used to secure each host to the dish.

Data were collected from these tapes by observing the tapes on a 48-cm color monitor. Times were recorded to the nearest second from the video recorder. If a host moved, no data were used subsequent to its moving (5 of 40 females had a host move, but only 1 of these was prior to the start of the first drill). Females with a host that subsequently moved did not differ from the other females in duration until they first (1) made contact with a host [Mann–Whitney $U = 76.0$, $n_1 = 33$, $n_2 = 5$, two-tailed (2t) $P = 0.78$], (2) tapped a host with their antennae (Mann–Whitney $U = 72.0$, $n_1 = 33$, $n_2 = 5$, 2t $P = 0.65$), (3) probed a host with their abdomens (Mann–Whitney $U = 73.0$, $n_1 = 31$, $n_2 = 5$, 2t $P = 0.84$), or (4) started trying to drill a host (Mann–Whitney $U = 34.0$, $n_1 = 25$, $n_2 = 4$, 2t $P = 0.31$).

The following data were collected from these tapes.

(1) Which host the female first contacted, and when. First contact was often with just one antenna, although sometimes with two. The antennae were extended.
(2) Whether the female contacted both hosts prior to antennation of one. Antennation involved tapping the host with her antennae bent at their elbows at a $<90°$ angle, usually while she was on the host.
(3) Which host first received antennation and when.
(4) Which host the female first began probing with her abdomen and when. Abdominal probing involved pulling her abdomen forward and touching a host repeatedly in a small area with the distal tip of her abdomen.
(5) Which host the female first attempted to drill for at least 1 min, and when, and whether the drill was successful. A successful drill was completed when the ovipositor was completely inserted into the host, as indicated by the middle of the abdomen contacting the host and the angle between the ovipositor and the abdomen tip, going from V-shaped to nearly straight.
(6) Whether the female attempted to drill into both hosts.
(7) Duration at the first drill site: from the start of drilling to removing the ovipositor.

Within each behavior, the number of females choosing the young host first was compared to the number choosing the old host first. This was done sequentially until a significant difference was found.

Statistical Analyses. Host-age treatments were temporally blocked. However, in most cases, there was no block effect, in which case, to maximize power, the blocking effect was excluded in subsequent analyses (Zar, 1984, p. 152). Two-tailed P values are indicated by "2t," and one-tailed values by "1t," with the direction of the test based on the predictions made in the Introduction and using $\alpha = 0.05$. Conclusions regarding statistical significance are unaffected by switching to two-tailed tests throughout or by adjusting alpha to control error on an experimentwise basis using sequential Bonferroni tests (Rice, 1989).

RESULTS

Visual Cues Experiment. There was no interaction between the effect of host age and the effect of light. Females produced more offspring from young hosts than from old hosts, regardless of light conditions, and more in the dark than in the light, regardless of host age (Table I).

Host Ages 0–5 Experiment. Number of parasitoid offspring decreased with increasing host age (Fig. 1). Number of parasitoid offspring explained 63% of the variation in number of host deaths (= number of hosts from which no adult fly emerged) ($r^2 = 0.63$, df = 152, 2t $P < 0.001$, $Y = 0.84X + 5.91$).

There was no interaction between the effects of host age and offspring sex on head width (Table II). Head width decreased with increasing host age for both females and males (Fig. 2). Conclusions were the same for head length.

There was no significant interaction between the effects of host age and offspring sex on head shape (length/width), and head shape did not differ with host age (Table III). Both head size and head shape differed with sex (Tables II and III). Female heads were more elongated than male heads [mean and median were equal (range): females, 1.22 (0.83–1.29), versus males, 1.04

Table I. Offspring Production from 15 Young and 15 Old Hosts Presented Simultaneously When Oviposition Was in the Light Versus the Dark

	Light		Dark	
Hosts	Mean ± SE (range)	*n*	Mean ± SE (range)	*n*
Young	2.27 ± 0.38 (0–7)	30	3.34 ± 0.51 (0–10)	28
Old	0.90 ± 0.19 (0–3)	30	1.43 ± 0.34 (0–6)	28

MANOVA	Mean square	df	*F*	*P*
Between-subjects effect	21.58	1	5.18	0.027
Within cells	4.17	56		
Within-subject effect				
Host age	83.83	1	22.46	<0.0005
Light–dark by host age	3.24	1	0.87	0.36
Within cells	3.73	56		

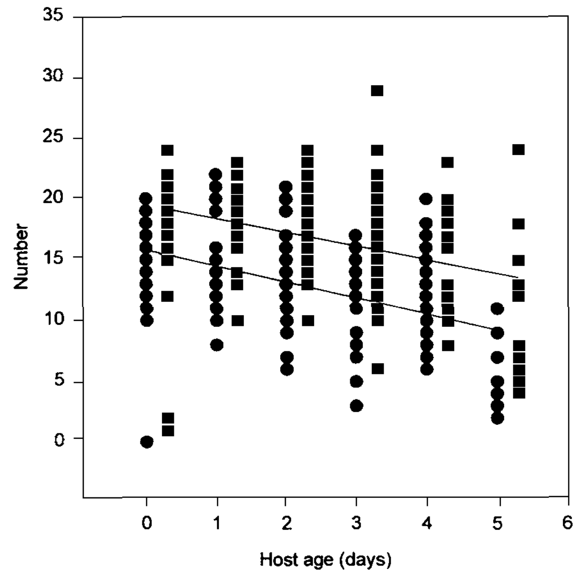

Fig. 1. Number of (●) parasitoid offspring produced and (■) dead hosts (= no adult fly emerged) versus host age when each female received 30 hosts of one age. Parasitoid offspring: $r^2 = 0.20$, df = 152, 1t $P < 0.001$, $Y = -1.31X + 15.83$. Dead hosts: $r^2 = 0.13$, df = 152, 2t $P < 0.001$, $Y = -1.12X + 19.18$.

(0.94–1.26)]. Females had longer heads than males, and males had wider heads than females.

Survivorship Experiment. Females oviposited in more young hosts than old hosts (Table IV). However, host age had no significant effect on number of eggs oviposited per parasitized host or on survivorship of parasitoid offspring (Table

Table II. Head Width of Offspring from Different Host Ages

MANOVA	Mean square	df	F	P
Between-subjects effect				
Host age	0.00136	5	5.12	<0.0005
Within cells	0.00027	141		
Within-subject effect				
Sex	0.06835	1	234.62	<0.0005
Sex by host age	0.00034	1	1.17	0.33
Within cells	0.00029	141		

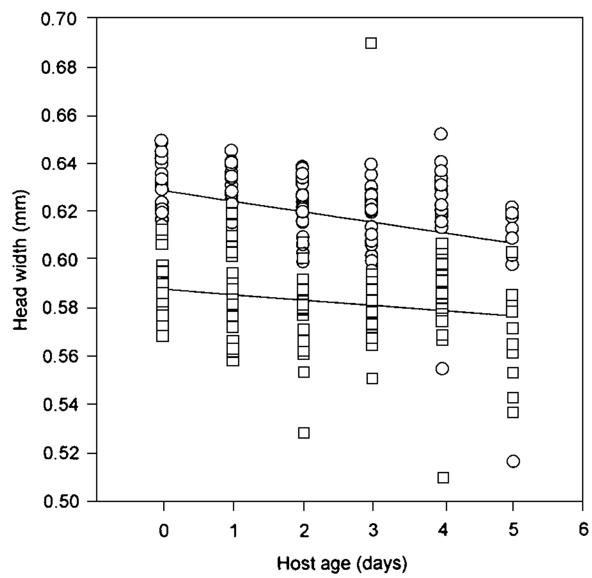

Fig. 2. Head width of female and male parasitoids versus host age. (□) Females: $r^2 = 0.04$, df = 148, 1t $P = 0.005$, $Y = -0.0024X + 0.59$. (○) Males: $r^2 = 0.15$, df = 148, 1t $P < 0.001$, $Y = -0.0045X + 0.63$.

IV). That the survivorship value for young hosts was greater than 1 (Table IV) was probably a result of sampling error with regard to which hosts were used to count eggs versus to count adult offspring: survivorship was not significantly greater than 1 (1t $P > 0.10$).

Effect of Host Age on Future Reproduction. As in the other experiments, offspring production was greater from young hosts than from old hosts on the

Table III. Head Shape of Offspring from Different Host Ages

MANOVA	Mean square	df	F	P
Between-subjects effect				
Host age	0.0015	5	1.12	0.35
Within cells	0.0013	141		
Within-subject effect				
Sex	1.85	1	961.20	<0.0005
Sex by host age	0.0012	1	0.61	0.70
Within cells	0.0019	141		

Table IV. Survivorship of Offspring from Young Versus Old Hosts

	Young hosts		Old hosts		
	Mean ± SE (range)	*n*	Mean ± SE (range)	*n*	
Number of hosts parasitized[a]	5.9 ± 0.3 (3–9)	31	3.5 ± 0.3 (0–8)	31	Independent $t = 5.02$ 1t $P < 0.001$
Number of eggs per parasitized host[b]	1.08 ± 0.03 (1–1.67)	31	1.06 ± 0.02 (1–1.33)	30	$U = 446.5$ 2t $P = 0.74$
Survivorship[c]	1.2 ± 0.1 (0.5–2.7)	30	1.0 ± 0.1 (0.0–3.0)	30	Paired $t = 0.84$ 1t $P = 0.20$

[a]For each mother, of the 10 dissected hosts, the number of hosts that contained at least one egg.
[b]For each mother, of the dissected hosts, the total number of eggs found across all hosts divided by the number of hosts that contained at least one egg.
[c]For each mother, the number of adult offspring emerging from the 10 undissected hosts divided by the total number of eggs found in the 10 dissected hosts.

first day [5.26 ± 0.54 (SE) (range, 0–11) versus 1.32 ± 0.32 (range, 0–5); $t = 6.27$, df = 60, 1t $P < 0.001$]. However, exposure to young versus old hosts did not significantly affect a female's subsequent offspring production in young hosts (YY, 3.23 ± 0.34, versus OY, 4.23 ± 0.44; $t = 1.80$, df = 60, 2t $P = 0.08$).

Across both days of the experiment, offspring production was 8.48 ± 0.75 (range, 1–16) for females that received young hosts both days and 5.55 ± 0.60 (range, 0–15) for females that received old hosts the first day and young hosts the second day.

Videotape Experiment. Older hosts in this experiment were not smaller than young hosts in external width (paired $t = 0.17$, df = 23, 1t $P = 0.44$).

Females did not appear to distinguish between young and old hosts prior to host contract. The number of females that contacted young hosts first was not significantly different from the number that contacted old hosts first (Table V). Females did distinguish host age sometime during or after first contact, i.e., by the time they first antenna tapped a host. Significantly more females antennae tapped young hosts first than antenna tapped old hosts first (Table V).

Of the 38 females that contacted a host, 28 contacted both hosts at least once before any antennation of a host. For 35 of the 37 females that stepped onto a host, the first host that received antennation was the first host on which the female had stepped.

About half of females drilled successfully on their first attempt of more than 1 min, 12 of the 21 females for which success could be determined: 10 of

Table V. Of 40 Females,[a] the Number Responding First to Young Versus Old Host and the Interval[b] Between Behaviors When Each Female Was Presented with One Young and One Old Host

Young host		Old host
	Placement of ♀ in host arena	
18 ♀'s		20 ♀'s[c]
0.32 min		0.24 min
0–144.33 min		0–5.23 min
	First physical contact	
28 ♀'s		10 ♀'s[d]
2.06 min		0.50 min
0–35.07 min		0.07–4.52 min
	First antenna tapping	
27 ♀'s		9 ♀'s
1.46 min		1.50 min
0.18–90.52 min		0.53–10.20 min
	First abdominal probing	
20 ♀'s		9 ♀'s
2.92 min		15.43 min
0.27–75.40 min		0.23–54.38 min
	First drill attempt of 1 min or more	

[a]Sums across young and old hosts are less than 40 because not all ♀'s completed all behaviors.
[b]Median and range are reported because of broad and nonnormal distributions.
[c]$\chi^2 = 0.11$, df = 1, $P > 0.50$.
[d]$\chi^2 = 8.53$, df = 1, $P < 0.005$.

15 females whose first attempt was on a young host and 2 of 6 whose first attempt was on an old host. Females that drilled successfully spent longer at the drill site (from start of drilling to leaving that site) than unsuccessful drillers [15 ± 1.6 min (range, 8–25 min) versus 5 ± 0.7 min (range, 3–6 min); t = 4.36, df = 16, 2t $P < 0.001$]. Only one female appeared to host feed after her first drill attempt, on a young host. Eighteen females made drill attempts only on one host during the 3 h of observation; 11 made drill attempts on both hosts.

DISCUSSION

Female *S. cameroni* produced more offspring from young hosts than from old hosts when given a choice of host ages and when not given a choice. Both the Florida strain and the Indiana strain of *S. cameroni* produced more offspring from young hosts than from old hosts, although the Florida strain produced fewer offspring overall than the Indiana strain.

The greater offspring production from younger hosts when females were given only one host age did not result from females with younger hosts beginning to drill sooner. Duration until the first successful drill is independent of host age when only one host age is present [(King, 1994): paired $t = 1.32$, df = 16, 2t $P = 0.21$].

Offspring survivorship was unaffected by host age, but offspring were larger when they developed in younger hosts. The effect of host age on size did not differ between daughters and sons. How the increased size of *S. cameroni* offspring from younger hosts will affect their subsequent fitness will depend on environmental conditions. Larger females have greater reproductive success under conditions of high, but not moderate or low, host density (King and King, 1994). Larger males may live longer when they lack access to carbohydrates (King and King, 1994); however, they also have higher wing loading (weight per wing area) (King and Lee, 1994). Higher wing loading may potentially decrease dispersal ability (e.g., Epting and Casey, 1973; Kammer and Heinrich, 1978; Ruohomäki, 1992), but this has not been well studied in such small organisms.

Whether a female oviposited in young or old hosts did not significantly affect her subsequent offspring production. The pattern, although nonsignificant (2t $P = 0.08$), was for females that had oviposited on old hosts to produce more offspring the next day than females that had oviposited on young hosts. It seems unlikely that females that oviposited on younger hosts both days had used up their egg supply by the end of the second day. There is no evidence that females are either egg-limited or handling time-limited, at least in the short term. Females typically emerge with 30 mature eggs (King and King, 1994), yet no female produced more than 30 offspring in any of the experiments. In addition, if all time was available for drilling and oviposition, females could easily have oviposited in all 0-day-old and in all 3-day-old hosts [based on durations of behaviors of King (1994)]. However, additional time may be required for other activities such as egg maturation, rest, and grooming.

The absence of a decrease in reproduction after oviposition in older hosts suggests that oviposition on older hosts did not damage the ovipositor or reduce the energy available for subsequent reproduction. However, females oviposited in only 0 to 5 (mean = 1.3) old hosts. Whether offspring production would have been reduced if there had been more ovipositions in older hosts remains to be determined.

S. cameroni females oviposited more offspring in younger hosts both in the light and in the dark, i.e., both in the presence and in the absence of visual cues. Likewise, *S. cameroni* females distinguish host size both in the light and in the dark (King, 1994). The lack of reliance on visual cues may be related to *S. cameroni* parasitizing hosts that are often buried (Rueda and Axtell, 1985).

S. cameroni's assessment of host age may occur in initial contact: females did not distinguish between young and old hosts at first contact; however, they did distinguish by the first antennation of a host. Thus, females were able to assess host age even prior to inserting their ovipositor into a host. In some parasitoid wasps, females distinguish among hosts on the basis of differences in external dimensions (Sandlan, 1979; Schmidt and Smith, 1985; Takagi, 1986; but see Wylie, 1967). However, *S. cameroni* females do not appear to use external host dimensions in distinguishing hosts of different external size (King, 1994); nor do they seem to use external dimensions in distinguishing among host ages, as external dimensions do not differ with host age (King, 1990; this study). Whether females use textural or chemical cues has not been examined. The mechanisms by which other parasitoids distinguish different host ages and host sizes have not been well studied (reviewed by Waage, 1986).

A decrease in offspring production with increasing host age, as in the present study, was not found in another study with *S. cameroni* under different conditions. *S. cameroni*'s offspring production was unaffected by host age when hosts were unburied and increased with host age when hosts were buried under used fly medium when pairs of *S. cameroni* females, one of the same Indiana strain as used here, were given 50 hosts either 0 or 3 days old at 70–75% relative humidity on a 12 h light: 12 h dark photoperiod (King, 1997). The difference between studies may be related to differences in host mortality: in the present study mortality in the absence of parasitoids was 2.5%, whereas in the study by King (1997) mortality was 3–4% for 3-day-old pupae and 6 and 12% for 0-day-old pupae when unburied and buried, respectively (King, unpublished). The greater mortality in King (1997) may have resulted from the higher moisture levels to which pupae were exposed.

The decrease in offspring production with increasing host age in the present study was fairly steady, whereas when *S. cameroni* parasitizes stable fly pupae, offspring production is reduced only in the oldest hosts, about 6 days old (Moon *et al.*, 1982). In some other pteromalids, offspring production is generally lowest for 3- to 5-day-old house fly pupae and highest for 0-, 1-, or 2-day-old pupae [*S. nigroaenea*, *S. endius*, *Nasonia vitripennis*, *M. zaraptor* (Wylie, 1963; Markwick, 1974; Coats, 1976; Morgan *et al.*, 1979; Siafacas, 1980; Petersen and Matthews, 1984), but not *Pachycrepoides vindemiae* and *S. gemina* (Markwick, 1974; Morgan *et al.*, 1991)].

In *S. cameroni*, there was no effect of host age on offspring survivorship, whereas in some other pteromalids, offspring survivorship decreases with age of the house fly pupa [*S. endius*, *M. zaraptor*, *N. vitripennis* (Markwick, 1974; Wylie, 1963); but see the nonlinear relationship in *S. endius* (Morgan *et al.*, 1979)].

The negative effect of host age on the head size of *S. cameroni* in the present study contrasts with no significant effect of host age on parasitoid weight in a previous study (King, 1990). However, weight may not have been measured precisely enough. In the present study there was only a 2% difference in male head width between 0- and 3-day-old hosts, yet previously weight had been measured to the nearest 0.01 mg, which is almost 5% of the male weight (King, 1990). As in *S. cameroni*, in the gregarious *N. vitripennis*, offspring are smaller from older hosts, despite fewer offspring developing on older hosts (Wylie, 1963).

I have suggested that host age may affect *S. cameroni*'s fitness through differences in the amount and quality of food and in maternal handling cost. Under natural conditions, other potential differences between young and old hosts that might affect a female's fitness, or that of her offspring, include the amount of intraspecific and interspecific competition (van Alphen and Thunnissen, 1983; references given by Waage, 1986) and the prevalence of predators and hyperparasitoids.

Effects of host age on parasitoid fitness have been found not only for pupal parasitoids, but also for egg and larval parasitoids (references given by Waage, 1986; Godfray, 1994). Host age usage sometimes, but not always, matches up with measures of host suitability.

S. cameroni is sometimes sold commercially for the control of pest flies, including house flies (Hunter, 1994). Results here indicate that even 5-day-old hosts can be used to produce wasps but suggest that, under conditions of low fly pupa mortality as here, the number and size of wasps will be greater with younger hosts.

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