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SPERM DEPLETION AND MATING BEHAVIOR IN THE PARASITOID WASP *SPALANGIA CAMERONI* (HYMENOPTERA: PTEROMALIDAE)Bethia H. King<sup>1,2</sup>

## ABSTRACT

Mating behavior was examined in the parasitoid wasp *Spalangia cameroni*. Males attempted copulation with both virgins and already mated females. Males attempted copulation regardless of whether they still had sperm. Already mated females rejected attempts to mate again but virgin females would mate with males regardless of whether or not they had sperm left. Males mated with 12–52 females before exhausting their sperm supplies. Males that had mated only once daily exhausted their sperm supplies in their late thirties (days old), if ever; and males that had mated four times daily exhausted their's at 7–13 days. Males produced as many as 438 daughters from their first four matings. Fifty-seven percent (17 of 30) of females that had mated with virgin males exhibited a decrease in proportion of daughters with age, presumably as a result of sperm depletion. Whether or not a female depleted her sperm supplies was not related to her size or the total number of daughters that she had produced.

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In many insects, females store sperm. In arrhenotokous insects such as wasps, whether a female releases sperm to fertilize an egg generally determines whether the female produces a daughter or a son. Unfertilized eggs develop into sons; fertilized eggs into daughters. Thus, daughter production requires mating and may be limited by sperm availability. Here I examine mating behavior and male and female sperm depletion in the parasitoid wasp *Spalangia cameroni* Perkins (Hymenoptera: Pteromalidae).

*Spalangia cameroni* parasitizes the pupal stage of certain fly species (Rueda and Axtell 1985). *Spalangia cameroni* is a solitary species, meaning only one offspring completes development per host. Mating in *S. cameroni* may occur both at, and away from, the natal site (Myint and Walter 1990) and with no aversion to siblings (King and King 1995). Male *S. cameroni* emerge as adults with their full complement of sperm. They apparently do not produce sperm as adults (Gerling and Legner 1968); thus there is a potential for males to exhaust their sperm supplies by mating multiply. Females may also exhaust their sperm supplies, particularly if they mate with males that have already mated.

Sperm depletion in both sexes was assayed by recording the proportion of female offspring. For females, sperm depletion was assayed directly; for males it was assayed by following their mates. This allowed me to estimate

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how many females a male can inseminate. Although male parasitoid wasps are thought to be able to inseminate a large number of females, this has been quantified for relatively few species.

Information on the mating behavior of *S. cameroni* is relevant to sperm depletion. Whether females become sperm depleted will depend on whether they mate with sperm-depleted males and on whether males and/or females mate multiply. Details of mating behavior also may be useful in species discrimination and in determining evolutionary relationships among taxa (e.g., van den Assem 1974; references in Godfray 1994, p. 275).

### MATERIALS AND METHODS

The *S. cameroni* (and *S. endius* Walker, see below) used in this study were from a colony established in 1985 with wasps that emerged from *Musca domestica* L. and *Stomoxys calcitrans* (L.) pupae collected in Indiana (King 1990). The wasp colony was maintained at 23–28°C under continuous light, using *M. domestica* as hosts (King 1988). The colony was less than two years old at the time of data collection. Hosts were produced by rearing 800 mm<sup>3</sup> of eggs in 1030 ml of fly larval medium (King 1988).

**Mating behavior.** Descriptions of *Spalangia*'s mating behavior are based on observations of newly emerged (less than one day old) pairs of one virgin female with one virgin male, except where noted otherwise.

**Sperm depletion in males: daily mating experiment.** I tested whether males would exhaust their sperm supplies if they mated daily for life. Six males were tested, and their size and the size of the hosts from which they emerged are presented in Table 1. Each male was allowed to mate once daily (except for one male, male 4, which due to a shortage of virgin females, was not mated on his sixteenth day). Copulations were observed. In this and the next experiment, between matings, males were kept individually in 1 oz. plastic cups with wet honey. Each female mate was given 14 hosts for each of two days—the first set of hosts within 8 hours of mating and the second set the next day or the day after next.

**Sperm depletion in males: four-times-daily mating experiment.** I examined the effects of daily multiple mating on male sperm supplies. Each of four males copulated with four females daily for life. The females were presented to the males at 0900, 1100, 1300, and 1500. These 2-hour intervals should provide ample time for additional sperm to become available for insemination because within 5–10 minutes of ejaculation, sperm move from the

Table 1. Results of Daily Mating Experiment: males' head width (mm), width (mm) of the host from which he emerged, longevity, and number of mates that produced only sons from both their first and second days of hosts.

Male ID	Head Width	Host Width	Days Alive	Mates That Produced Only Sons
1	0.54	2.90	34	10th–34th, except 16th, 20th and 23rd
2	0.61	2.75	38	36th–38th
3	0.62	2.35	11	none
4	0.61	2.75	40	1st and 36th–40th
5	0.61	2.35	38	37th, 38th
6	0.61	2.75	40	39th, 40th

anterior to the posterior half of the seminal vesicles where they remain until copulation (Gerling and Legner 1968). Unfortunately, it was not feasible to give all the mated females hosts daily for life. Instead, the first and fourth females of every third day were given hosts. Of these, the first and tenth day females, i.e., his first, fourth, thirty-seventh, and fortieth mates, were given 14 hosts daily until the females died; the others were only given hosts for their first two days. For two males in this experiment, all four mates of the first day of mating were given 14 hosts daily for life.

**Sperm depletion in females experiment.** To test for sperm depletion in females, I examined the relationship between maternal age and proportion of female offspring for 31 females. Fifteen of the females had developed on small hosts (about 15 mm<sup>3</sup>) and 16 on large hosts (about 24 mm<sup>3</sup>) (King 1988). Since wasp size is positively correlated with host size (King 1988), this allowed me to examine the effect of female size on sperm depletion. Each female was mated with a virgin male prior to being given 14 hosts daily for life (King 1988). The relationship between maternal age and proportion of female offspring was analyzed by Pearson product moment correlation (Zar 1984), excluding one female that produced only sons during her life. I looked at the relationship for all females combined as well as females individually, because lumping all females together sometimes obscures trends (Rotary and Gerling 1973).

## RESULTS

**Mating behavior: newly emerged virgin pairs.** When a male detected a female, he walked rapidly towards her, sometimes fanning his wings briefly (less than 3 s). She moved away as he approached. If he caught up to her, he mounted her, usually from the rear. He placed his fore tarsi on her mesoscutum (the middle section of the thorax) and his hind legs on the sides of her abdomen. He then began tapping her head with his antennae, and the sides of her thorax with his middle legs. Both of his antennae moved up and down in synchrony. The tapping by *S. cameroni* males was not continuous, but rather was punctuated with pauses. The female raised her abdomen and exposed her genital aperture after about 6 s (mean = 5.7, s.e. = 0.31, n = 20). Her antennae usually remained extended out away from her head throughout mating. The male backed up, curled his abdomen below hers and inserted his aedeagus into her genital aperture. In this position, he tapped her thorax with his antennae and her abdomen with his middle legs.

After a copulation of about 5 s duration (mean = 5.0, s.e. = 0.15, n = 21), the male withdrew his aedeagus and moved forward on the female to his previous position. He resumed tapping her head with his antennae and her thorax with his middle legs. The female began to slowly lower her abdomen, closing her genital aperture. When it was almost completely closed, she began walking and stroking her hind legs up and over her abdomen, as if trying to dislodge the male. The male continued tapping her with his antennae and middle legs even as he backed off of her. The interval from mounting to dismounting was about 2 min (mean = 2.3, s.e. = 0.10, n = 21).

**Mating behavior: miscellaneous observations.** Males mated repeatedly and with no apparent lag time. They readily mounted, courted, and tried to copulate with virgin or previously mated females, even with females they had just successfully mated. However, when already mated females were mounted by males, the females began walking and stroking their hind legs up and over their abdomens and did not open their genital aperture. Ovipositing in hosts did not result in renewed receptivity for four females

Table 2. Results of Four-Times-Daily Mating Experiment: males' head width (mm), width (mm) of the host from which he emerged, longevity, the mate and day on which he is last known to have produced daughters, and the lifetime number of daughters produced by his first, fourth, thirty-seventh, and fortieth mates combined, and the percent daughters from those females individually.

Male ID	Head Width	Host Width	Days Alive	Last Mate and Day of Successful Insemination	# Daughters Combined	% Daughters from Mate			
						1	4	37	40
1	0.58	2.35	50	52nd mate on 13th day	269	38	80	32	23
2	0.60	2.65	23	28th mate on 7th day	211	89	25	0	0
3	0.60	2.75	14	37th mate on 10th day	336	79	83	9	0
4	0.60	2.85	23	28th mate on 7th day	230	78	70	0	0

that were each given 14 hosts daily for 10 days and then exposed to a male. Virgin females were receptive regardless of age (at least up to 10 days old) and prior exposure to hosts. They would mate with virgin males, with males that just mated, or with males that had mated up to 52 times (Tables 1 and 2). Virgin females always opened their genital apertures once they had been mounted and courted.

Tapping by a male seemed to be the stimulus that caused a virgin female to open her genital aperture. Old males within a few days of death in the Sperm Depletion in Males Experiments had difficulty lining up with the female's genital aperture to insert the aedeagus. After a few seconds, the female's aperture would start to close. The male then would move forward and tap her; she would reopen and he would continue to try to copulate. This sequence might be repeated several times before he successfully copulated or her aperture closed completely. Once a female's aperture closed completely, it did not reopen, even if a male had never succeeded in inserting his aedeagus into her genital aperture.

When two *S. cameroni* males were placed with one virgin conspecific female, there was little male-male interaction. One occasionally tapped the other with his antennae, and then one or both moved away. When a male came upon an already mounted female, he sometimes tried to mount too. In only two of 54 matings observed did the second male, not the first, insert his aedeagus; and in one case the first male and then the second inserted before the female's genital aperture closed.

Interspecific mating with *S. endius* is absent or at least less common than with conspecifics. No interspecific mating was observed between *S. cameroni* and *S. endius*. *S. cameroni* males did not mount *S. endius* females ( $n = 7$ ), and *S. endius* males did not mount *S. cameroni* females ( $n = 4$ ).

**Sperm depletion in males: daily mating experiment.** Of the males that lived 30 days or more, all but the smallest male were able to produce daughters except in the few days prior to death (Table 1). The decrease in proportion of female offspring accelerated rapidly in the latter part of life for most males (Figure 1). However, male one first began failing to produce daughters with his tenth mate, long before his death 24 days later. His failure to produce daughters was not continual: after his 10th to 15th mates produced no daughters, his 16<sup>th</sup>, 20<sup>th</sup>, and 23<sup>rd</sup> mates produced daughters (Table

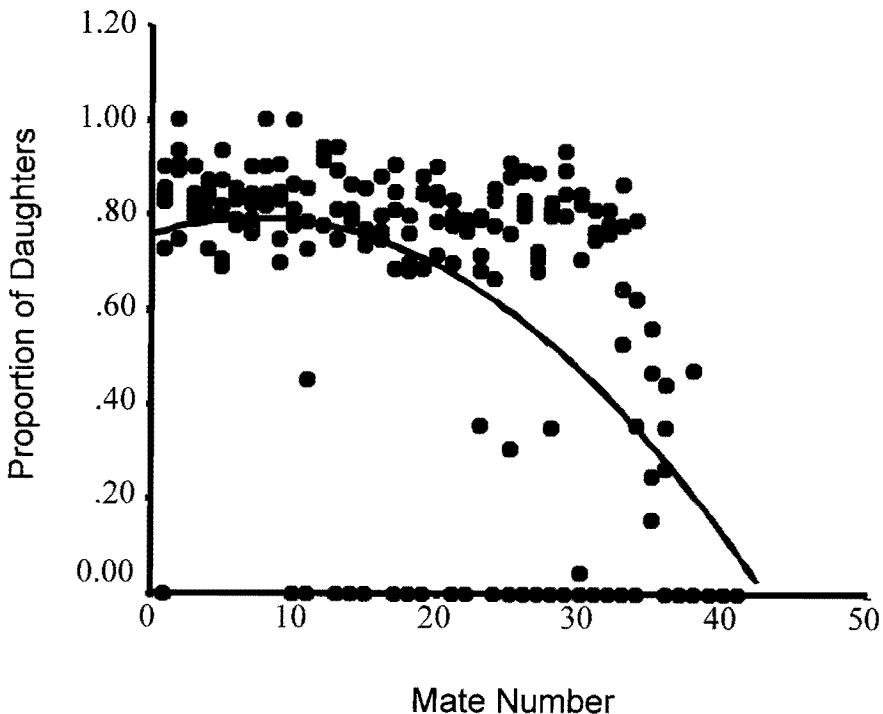


Figure 1. The change in proportion of daughters with sequential mates for males that mated once daily.

1). During the last days of life, males seemed to have difficulty in walking and did not approach or mount females as readily. Difficulty in walking and in inserting the aedeagus did not preclude successful insemination by males, as evidenced by their mates producing daughters. Males in this experiment successfully inseminated 11–38 females in their lifetimes (mean = 28, s.e. = 5.1).

#### **Sperm depletion in males: four-times-daily mating experiment.**

Sperm depletion occurred well before death (Table 2). Males # 2, 3, and 4 stopped successfully inseminating their mates at approximately the same time that they began having difficulty inserting their aedeagus; male # 1 stopped successfully inseminating his mates about two weeks before he exhibited difficulty. Males in this experiment successfully inseminated an estimated 28–52 females (mean = 36, s.e. = 11.3). The actual number of females inseminated is unknown because not all females in this experiment were tested for insemination (via host presentation).

Among females that produced at least some daughters, there was no difference in offspring sex ratios between 0900 h mates and 1500 h mates ( $G = 0.71$ ,  $P = 0.40$ ). Thus, generally, 1500 h mates appear not to be at any disadvantage in terms of amount of sperm received, despite the fact that they

Table 3. Results of Four-Times-Daily Mating Experiment: Lifetime percent and number of daughters produced by mates 1 to 4 of male 4 and male 5.

Mate	Male 4		Male 5	
	% Daughters	# Daughters	% Daughters	# Daughters
1	89	183	78	130
2	23	27	89	149
3	22	25	47	59
4	25	28	70	100

were the fourth mate of the day. For both males whose all four first day mates were given hosts daily for life, all four mates produced at least some daughters (Table 3).

**Sperm depletion in females experiment.** Females produced an average of 93 daughters over their lifetime (s.e. = 10, range: 0–191, n = 31). There was a significant negative correlation between maternal age and proportion of female offspring for the 30 females combined (Figure 2), and on an individual basis, for 57% (17 of 30) of the females examined. For only 3% (1 of 30) was there a significant positive correlation. The significant negative relationship held for equal proportions of females from small versus large hosts (7 of 15 versus 10 of 15;  $G = 1.23$ ,  $P = 0.27$ ).

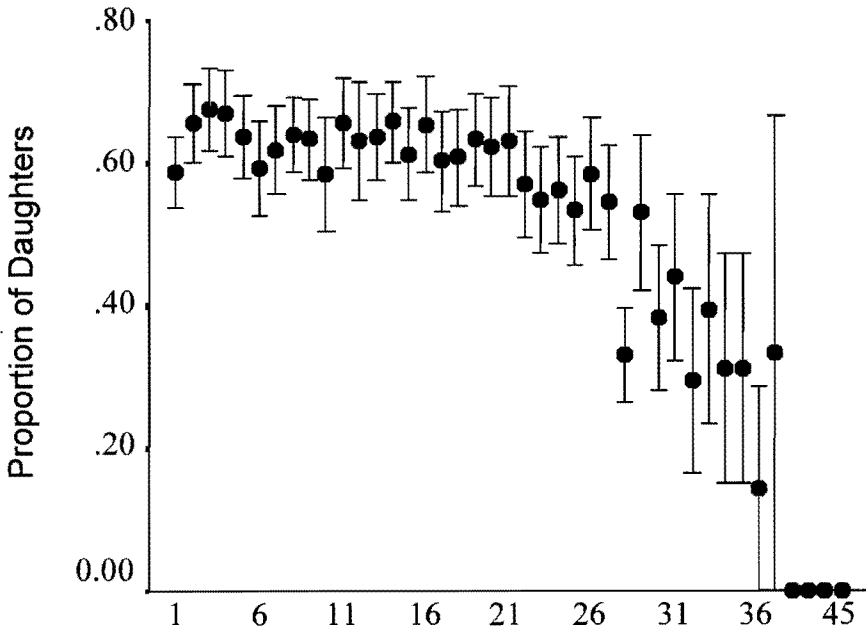


Figure 2. The change in mean  $\pm$  s.e. proportion of daughters with maternal age.

Table 4. Results of Sperm Depletion in Females Experiment: Mean  $\pm$  s.e. number of daughters, proportion of daughters, and head width (mm) of females that depleted their sperm supplies versus females that did not ( $t$  = statistic from t-test comparing sperm depleted and not sperm depleted females;  $P$  = significance of t-test).

Status	N	Number of Daughters	Proportion of Daughters	Head Width
Sperm Depleted	17	98.9 $\pm$ 13.76	0.59 $\pm$ 0.067	0.59 $\pm$ 0.003
Not Sperm Depleted	13	92.3 $\pm$ 14.25 $t$ = 0.33 $P$ = 0.37	0.62 $\pm$ 0.084 $t$ = 0.33 $P$ = 0.37	0.59 $\pm$ 0.003 $t$ = 0.52 $P$ = 0.30

Comparing mothers that exhibited a negative relationship between maternal age and proportion of female offspring (sperm depleted) to mothers that exhibited no significant relationship or a positive relationship (not sperm depleted), there was no significant difference in either number of daughters or proportion of female offspring (Table 4). Females that exhibited sperm depletion also did not differ in size from females that did not (Table 4).

## DISCUSSION

**Mating behavior.** Complete mating by *S. cameroni* from mount to dismount took about 2 min, which is longer than in another well-studied pteromalid, *Nasonia vitripennis* Walker, for which "a complete mating sequence takes about 35 s" (van den Assem 1986, p. 141), "1 min to go through a full mating" (van den Assem 1986, p. 155). However, copulation (coitus) took less time in *S. cameroni* than in two other pteromalids: about 5 s in *S. cameroni* versus about 15 s in *N. vitripennis* (van den Assem 1986) and 40–52 s in *Muscidifurax* (van den Assem and Povel 1973).

Male *S. cameroni* appeared to be more active than females during courtship as may generally be true of parasitoid wasps (van den Assem 1986). Mating in *S. cameroni* was similar to that reported for other pteromalids in terms of mounting of the male onto the female from the rear, followed by stimulation of the female by male leg and antennal tapping both before and after copulation, and female raising the abdomen to expose the genital aperture (reviewed in van den Assem 1986).

*Spalangia* are in the subfamily Spalangiinae. The cue that male *S. cameroni* used to move back on the female to copulate differed from that reported for some species in the subfamily Pteromalinae (reviewed in van den Assem 1986). In Pteromalinae species such as *Muscidifurax* and *N. vitripennis*, the female draws her antennae against her head as she raises her abdomen, and the male backs up in response to the position of her antennae (van den Assem and Povel 1973, van den Assem 1974). This is necessary because of the male's frontal position during courtship: in *N. vitripennis*, the male's fore tarsi are on the female's head and his middle and hind legs on her thorax. In contrast, *S. cameroni* males placed their fore tarsi on the female's mesoscutum, and *S. cameroni* females kept their antennae extended as they opened their genital aperture. Thus, an *S. cameroni* male, like an *S. endius* (van den Assem 1986), can use the raising of the female's abdomen as the cue



to move back to copulate because his abdomen is on top of hers and thus is raised by hers.

*Spalangia cameroni* males were polygamous but females did not appear to be, or certainly not to the degree that males were, as seems to be true in most parasitoid wasps (Ridley 1993). Among parasitoid wasps, female monogamy is especially prevalent in species that are solitary like *S. cameroni*, but is relatively uncommon among insects other than Hymenoptera (Ridley 1993). *Spalangia cameroni* males readily attempted to mate with previously mated females, as also occurs in *N. vitripennis* and probably most parasitoid wasp species (van den Assem 1986), but in contrast to the pteromalids *Cecidostiba semifascia* (Walker) (van den Assem 1986) and mated *S. endius* males (personal observation). Female *S. cameroni* mated even when the male lacked sperm, as also occurs in other parasitoid wasp species (references in Godfray 1994). Post mating loss of receptivity in female *S. cameroni* did not require successful insemination. This contrasts with some other insects (reviewed in Ringo 1996), but is consistent with another pteromalid, *N. vitripennis* (van den Assem 1986).

**Sperm depletion in males.** The failure of *S. cameroni* males to transfer sperm successfully during copulation in the few days prior to their death in the Daily Mating Experiment and well before death in the Four-Times-Daily Mating Experiment may have occurred because of depletion of sperm supplies and/or because of a mechanical inability to transfer sperm through the aedeagus into the female's spermatheca. Failure to inseminate a female was sometimes temporary even when there should have been ample time for males to move sperm from the anterior to the posterior half of the seminal vesicles to make it available for insemination (Gerling and Legner 1968). Decreased proportion of female offspring with increasing male age or number of matings has been demonstrated in a number of species of parasitoid wasps besides *S. cameroni*, including *N. vitripennis* (reviewed in King 1987).

The number of females each male successfully inseminated was on the order of 11–52 females. If there is extreme variation in the number of mates per male in nature, males may encounter that many females in a lifetime. In a study of a poultry house in Indiana, at peak host density in the fall, the number of females in a single sample, a pupal trap 14 cm high by 11.4 cm diameter, reached 44 with 17 males present, though the average among traps with more than one wasp was 18.5 females (s.e. = 5.9, n = 6) with 9.5 males (s.e. = 2.4, n = 6) present (King unpublished). Males began to consistently fail to inseminate females when they were 20 to 30 days old in the Daily Mating Experiment versus when they were about ten days old in the Four-Times-Daily Mating Experiment. In the solitary pteromalid *Anisopteromalus calandrae* (Howard), males can inseminate at least 2–23 females (Garcia Saez 1988); and in the gregarious pteromalid *N. vitripennis*, small males can inseminate about 15 females and large males about 30 females (van den Assem 1986). *Diglyphus begini* (Ashmead) (Eulophidae) males can inseminate at least as many as 30 females (Heinz 1991), and *Goniozus nephantidis* males (Muesebeck) (Bethyridae) can inseminate at least 12 females and perhaps more (Hardy and Cook 1995).

A male *S. cameroni* could produce on the order of 100 daughters from an early mating, and as many as 438 daughters from his first day of four mates when his mates are given hosts for life (Male 5, Table 3). There was no difference in proportion of female offspring produced in a day by a male's first mate of a day and his fourth mate, six hours later. However, when presented with ten females simultaneously for a day, males inseminate an average of nine of the females, range 5–10, with these females producing a mean of 64% daughters on their first day of oviposition (King and King 1994). These fe-

males do not all seem to be getting a full complement of sperm given that first mates, that is females that mate with virgin males, produce about 75% daughters (King 1994, 1996) ( $64\% \pm 2\%$ ,  $n = 38$  versus  $75\% \pm 2\%$ ,  $n = 114$ ;  $t = 5.5$ ,  $1tP < 0.001$ ). In another solitary pteromalid, *A. calandrae*, males produce about 600–1000 daughters when allowed to inseminate 10 females sequentially in 12 hours (Garcia Saez 1988). In the gregarious pteromalid, *N. vitripennis*, males produce about 500 daughters just from their first mate (van den Assem 1986). Being small does not preclude a male successfully inseminating females (male #1 of Table 1).

**Sperm depletion in females.** The negative relationship between maternal age and proportion of female offspring suggests that female *S. cameroni* experience sperm depletion, and that sperm supplies were depleted for about half of the females examined, despite all females having mated with virgin males. That females may sometimes encounter enough hosts that they deplete sperm in their natural habitat seems likely given that host density from a single sample, a pupal trap 14 cm high by 11.4 cm diameter, reached into the hundreds in a study of a poultry house in Indiana. (King 1990). A negative relationship between maternal age and proportion of female offspring was also found for *S. cameroni* by Legner and Gerling (1967). In contrast, Moon et al. (1982) found no significant relationship. However, Moon et al. kept their wasps at higher temperatures. The reproductive longevity of their *S. cameroni* was only about 11 days versus about 30 days for the *S. cameroni* of Legner and Gerling (1967) and this study. Thus, the wasps may not have lived long enough for sperm depletion to occur.

As in the present study, for most species of parasitoid wasps that have been examined, females produce lesser proportions of female offspring later in life than they do early in life, probably as a result of sperm depletion (e.g., references in King 1987, Perez-Lachaud and Hardy 1999). Whereas about 50% of *S. cameroni* females exhibited sperm depletion, in a laboratory study of another parasitoid, the bethylid *Cephalonomia hyalinipennis* Ashmead, almost 80% did (Perez-Lachaud and Hardy 1999). However, *C. hyalinipennis* females receive only about 46 sperm during mating with virgin males, whereas *S. cameroni* females receive at least double that (see Number of Daughters, Table 4).

Both small and large *S. cameroni* females exhibited decreases in proportion of female offspring with maternal age. In *Aphytis melinus* DeBach (Aphelinidae), a negative relationship between proportion of female offspring and maternal age exists only for large females. In contrast to *S. cameroni* (King and King 1994), however, small *A. melinus* females do not live as long as large females (Abdelrahman 1974). Thus small *A. melinus* females may never become sperm limited, whereas large females may live sufficiently long to outlast their sperm supplies unless they remate.

The cause of the observed variation in the relationship between proportion of female offspring and maternal age among female *S. cameroni* is not clear. In *C. hyalinipennis*, females that produce more daughters are more likely to become sperm depleted. However, this was not the case in *S. cameroni*. Lifetime production of daughters did not differ between mothers that exhibited sperm depletion and mothers that did not. Thus, there was no evidence that mothers that became sperm depleted had received less sperm. Small females might be expected to have smaller spermathecal capsules and thus less sperm storage capabilities. Yet head widths were not smaller for the mothers that exhibited sperm depletion.

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