

Breeding Strategies in Females of the Parasitoid Wasp *Spalangia endius*: Effects of Mating Status and Size

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*Does the mating status or body size of a female parasitoid wasp affect her host size choice or propensity to burrow? In *Spalangia endius*, using smaller hosts appears to reduce a female's cost of parasitization but not her son's fitness. However, virgin females, which produce only sons, did not preferentially parasitize smaller hosts. Mated females also showed no host size preference. Mated females burrowed more than virgins in the presence of hosts, although not in their absence. Burrowing may reduce a mated female's harassment from males, and not burrowing may increase a virgin female's chance of mating because males avoid burrowing. Mating did not increase female longevity. Greater female size increased the offspring production of mated females burrowing for hosts but not in the absence of burrowing and not in virgin females. A female's size had no significant effect on whether her first drill attempt was on a large or a small host or on the duration of her successful drills.*

KEY WORDS: breeding strategies; arrhenotoky; virgin; host size; body size; parasitoid.

INTRODUCTION

The evolution of behaviors is often described in terms of costs and benefits. Individuals are expected to behave in ways which maximize net benefits. However, the behavior that yields the greatest net benefit may vary among individuals because of differences in benefits and/or costs of a behavior

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among individuals. For example, virgin and mated females may behave differently because of differences in benefits and costs of mating. In many animals, virgin females need to mate to produce offspring, and mated females do not. However, in arrhenotokous wasps, bees, and ants, virgin females can produce male offspring, whereas mated females can produce both sons and daughters. The study reported here uses an arrhenotokous parasitoid wasp, *Spalangia endius* Walker (Hymenoptera: Pteromalidae), to examine how a female's mating status and body size affect her resource use, specifically her use of different host sizes and substrate depths.

Spalangia endius females burrow through decaying organic matter or manure to parasitize pupae of certain fly species (Rueda and Axtell, 1985a). These fly pupae are of variable size (King, 1990) and are located at variable depths (Rueda and Axtell, 1985a). A female drills through the puparium of a host with her ovipositor, then deposits an egg on the host pupa within or feeds on fluids from wounds that she makes in the host. One offspring is produced per host. An adult female ecloses with some eggs but must host-feed to produce additional eggs (Gerling and Legner, 1968). As adults, females are generally larger than males (Napoleon and King, 1999). It is possible that some *S. endius* females remain virgin or become sperm-depleted in nature. Sperm-depleted females are functionally equivalent to virgins, producing only sons. In the congener *S. cameroni* Perkins many females leave the natal site without having mated (Myint and Walter, 1990). In *Bracon hebetor* Say in the laboratory about 10% of females do not mate even in the presence of males (Guertin *et al.*, 1996). Virgin or sperm-depleted females have been found at oviposition sites in nature in *B. hebetor* and some other parasitoid species (reviewed by Godfray, 1994).

An arrhenotokous female's mating status may affect the relative benefit of choosing large versus small hosts (Nishimura, 1997). In *S. endius*, the fitness of daughters, but not sons, appears to be affected by host size (Napoleon and King, 1999). Thus, large hosts may benefit mated females when they produce daughters but are of no greater value than small hosts for virgin females since they produce only sons. However, large hosts may be more costly to parasitize (e.g., Kouamé and Mackauer, 1991). In the case of pupal hosts, the puparium may take more time or energy to drill through (e.g., King, 1994). Given a higher cost of large hosts without a compensatory benefit, virgin females are expected to prefer small hosts. Whether mated females prefer large or small hosts should depend on the relative benefit of large hosts (in terms of the incremental fitness of daughters) versus the added cost of parasitizing large hosts.

A female's mating status may affect not only the benefit and cost of different host sizes but also the benefit and cost of different host microhabitats. Searching for hosts in microhabitats used by males may benefit virgin

females via the opportunity to mate. Mating may be advantageous to virgins by allowing the production of daughters: sex ratio theory predicts an advantage to being able to produce particular ratios of daughters to sons, provided population size is finite (Verner, 1965). Searching for hosts in microhabitats used by males may cost mated females via harassment (e.g., McLain and Pratt, 1999), particularly if females are monogamous as is generally true of *S. endius* (unpublished data). In *S. cameroni*, males have been caught in traps placed above the substrate (Myint and Walter, 1990). Assuming that males are not also found down in the substrate, it might be advantageous for virgin females also to stay on or above the substrate but for mated females to burrow out of reach and in search of hosts.

The present study tests the predictions that virgin females prefer small hosts to large hosts and burrow less than mated females. Assumptions that led to these predictions are also tested: that large hosts are more costly than small hosts to parasitize, that males are usually on or above the substrate surface, and that mating does not nutritionally benefit a female, as measured by the effect of mating on longevity. Finally, whether the ability to parasitize hosts increases with female size is tested. Large size will have a more positive effect on the fitness of mated than of virgin females if (1) mated females parasitize more large hosts, and parasitizing large hosts is easier for larger females, or (2) mated females burrow more than virgin females, and larger females can better push their way through the substrate than smaller females.

METHODS

General Methods

Experiments were performed within a year of establishing a *S. endius* colony from wasps collected at Zephyr Hills, Florida. Wasps were reared on a natural host, *Musca domestica* L. (Diptera: Muscidae). Different host sizes were produced by varying the number of fly eggs per container of medium [a mixture of Purina fly larvae medium, fishmeal, vermiculite and water (King, 1988)]. After all hosts had been removed, the host medium was used in the two burrowing experiments below. Large hosts were about 1.5 times the volume of small hosts. Large hosts were used in all experiments unless specified otherwise. Hosts were less than 1 day old (from when the puparium turned red) when initially presented to the wasps. Females referred to as "mated" were less than 2 days old (unless otherwise noted) and had been observed to mate with a newly emerged virgin male.

To keep the statistical power high, specific hypotheses were examined, and with directional tests (i.e., not analyses of variance) when warranted by

predictions made in the introduction. Two-tailed P values are indicated by “ $2tP$ ”; one-tailed values, by “ $1tP$.” Means \pm standard errors are presented.

Offspring Production Experiment

This experiment was to determine (1) whether virgin mothers produce more offspring from small hosts than from large hosts, (2) whether mated mothers produce more offspring from large hosts or from small hosts, and (3) whether female size positively affects offspring production. Female head width was variable (0.57 ± 0.002 mm; range, 0.52 to 0.62 mm) and did not differ with mating status ($t = 0.55$, $df = 59$, $2tP = 0.58$). Head width is positively correlated with other measures of body size in *S. endius* (Napoleon and King, 1999). Each female was presented with 10 small and 10 large hosts for 1 day in a 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. The two host sizes were separated by a ridge of used host medium, across which females freely walked.

Videotape Experiment

This experiment was to determine whether (1) large hosts are more difficult to drill than small hosts (as measured by speed and success of drills), (2) virgin females first try to drill small hosts rather than large hosts, (3) mated females show a host-size drilling preference, (4) larger females are faster or more successful at drilling, and (5) larger females are more likely than small females to try drilling large hosts first.

Each of 39 females was videotaped for 3 h with one small host and one large host placed parallel to each other about 1.5 wasp lengths apart in a 35-mm-diameter \times 10-mm-deep petri dish. A small drop of water was used to secure each host to the dish. The relative position of the small versus the large host was alternated between females. Females had no prior experience with hosts or honey.

During videotaping, illumination was from fiber-optic lights, which gave off no noticeable heat. The following data were collected from these videotapes.

- (1) When the female first began antennating a host
- (2) When, and which host, the female first attempted to drill for at least 1 min and whether the drill was successful [that is, whether the female was able to insert her ovipositor fully through the host puparium (King, 1994)]

- (3) The total number of drill attempts and the number that was successful
- (4) Duration at the first drill site from the start of drilling to success

Drill success was estimated as the proportion of drills that were successful among drills for which success could be determined.

Burrowing-Without-Hosts Experiment

This experiment was to determine whether the propensity to burrow differs between virgin and mated females and between mated females and mated males. Each wasp was placed in a glass vial 7 cm high and 2 cm in diameter, filled three-fourths full of used host medium and plugged with cotton. Mated wasps had mated within the 3 min prior to placement in the vial. After 30 min in the vial, wasp position was recorded, i.e., whether a wasp was in the deeper half of the medium, in the upper half of the medium, or between the media and the cotton. Vertical spatial distribution patterns in the laboratory are predictive of distribution patterns in the field (Legner, 1977; versus Rueda and Axtell, 1985b; Guertin *et al.*, 1996). Using the chi-square test of independence, the observed distributions of wasps were compared to those expected if the wasps were distributed among sections of the test container in proportion to the relative volume of each section.

Burrowing-with-Hosts Experiment

This experiment was to determine whether mated females burrow more than virgin females, thus parasitizing more buried hosts and fewer unburied hosts, and whether larger females parasitize more hosts. Female head width was variable (mean = 0.55 mm; range, 0.46 to 0.61 mm; $n = 75$) and did not differ by mating status (Mann-Whitney $U = 778.0$; $n = 40$ or 41 ; $2tP = 0.69$).

Each female was placed in a black plastic vial, 3 cm in diameter and 4.6 cm deep. On the bottom of the vial were five hosts covered with 3 cm of used host medium (=buried hosts), and on top of the medium were five more hosts (=unburied hosts). Mated females had mated within 3 min of being placed in the vial. The vial was covered with a white cotton cloth secured with a rubber band.

After 2 days in the vial, whether the female was in the deeper half of the medium was recorded, and her head width was measured. Hosts were dissected to determine the number of hosts parasitized (i.e., with at least one egg) for each female for buried and for unburied hosts.

Longevity Experiment

This experiment was to determine the effect of mating status on longevity. Mating by males might reduce their longevity by using up re-sorbable nutrients in the sperm and seminal fluid, and those same nutrients might increase a female's longevity, at least in the absence of any other energy source. Wasps that had emerged within the last 24 h were isolated in test tubes plugged with cotton, which was moistened daily. Wasps were maintained at 29°C and longevity determined to the nearest day.

RESULTS

Offspring Production Experiment

No female produced offspring from all 20 hosts; the average offspring number was 12.8 ± 0.31 ($n = 76$). Virgins did not produce significantly more offspring from small hosts than from large hosts (6.4 ± 0.29 versus 6.1 ± 0.35 ; $t = 0.69$, $df = 37$, $1tP = 0.25$). Offspring production of mated females also did not differ for small versus large hosts (6.6 ± 0.27 versus 6.6 ± 0.32 ; $t = 0.22$, $df = 37$, $2tP = 0.83$). The total offspring production from small and large hosts combined was independent of the mother's mating status ($t = 1.18$, $df = 74$, $2tP = 0.24$). The mean proportion of sons produced by mated females was 0.15 ± 0.02 ($n = 38$; range, 0.00–0.67) and was independent of the mother's size (correlation of ranks = 0.16, $n = 30$, $2tP = 0.19$).

Offspring production did not increase with the female's size, regardless of whether the female was mated or virgin or was ovipositing in large or small hosts (mated, large hosts, $r^2 = 0.026$, $df = 28$, $1tP = 0.20$; mated, small hosts, $r^2 = 0.0082$, $df = 28$, $1tP = 0.32$; virgin, large hosts, $r^2 = 0.0087$, $df = 29$, $1tP = 0.31$; virgin, small hosts, $r^2 = 0.066$, $df = 29$, $1tP = 0.087$).

Videotape Experiment

Mated females did not differ significantly from virgin females in (1) duration until they first began exploring hosts with their antennae (22 ± 10.1 versus 20 ± 6.9 s; $t = 0.14$, $df = 36$, $2tP = 0.89$), (2) duration until their first drill attempt (48 ± 8.6 versus 67 ± 9.4 s; $t = 1.52$, $df = 30$, $2tP = 0.14$), or (3) number of total drill attempts (4.2 ± 0.72 versus 2.9 ± 0.63 ; $t = 1.32$, $df = 37$, $2tP = 0.20$).

Host size did not influence which host a female drilled first for either virgin or mated females: 56% of virgins drilled the small host first ($\chi^2 = 0.25$,

$P > 0.50$), and 50% of mated females drilled the small host first ($\chi^2 = 0.00$, $P = 1.00$). Likewise, drill attempts were not more often on small hosts than on large hosts for virgin females ($62 \pm 11\%$ on small hosts; $t = 1.14$, $df = 15$, $1tP > 0.20$) or mated females ($54 \pm 9\%$ on small hosts; $t = 0.50$, $df = 17$, $2tP > 0.50$).

Drills took about one and a half times longer on large hosts than on small hosts (mated and virgin females combined: 1241 ± 153 versus 790 ± 77 s; $t = 2.75$, $df = 26$, $1tP = 0.006$). However, the proportion of drills that were successful was not significantly lower for large hosts than for small hosts (0.33 ± 0.084 versus 0.38 ± 0.084 ; $t = 0.44$, $df = 47$, $1tP = 0.33$).

Females that tried to drill the large host first were not significantly larger than females that tried the small host first (mated and virgin females combined, head width— 0.554 ± 0.006 versus 0.557 ± 0.005 mm; $t = 0.32$, $df = 31$, $2tP = 0.75$). Drill duration did not greatly decrease with increasing female size for drills into large hosts or drills into small hosts (mated and virgin females combined: $r^2 = 0.076$, $df = 10$, $2tP = 0.38$; $r^2 = 0.095$, $df = 13$, $1tP = 0.13$). Likewise, greater female size did not result in a large increase in drilling success for large hosts or for small hosts (mated and virgin females combined: $r^2 = 0.10$, $df = 20$, $1tP = 0.08$; $r^2 = 0.019$, $df = 23$, $2tP = 0.51$).

Burrowing-Without-Hosts Experiment

Mated and virgin females did not differ from each other in vertical distribution (Table I) ($G = 0.55$, $df = 2$, $P > 0.90$). Mated females did differ from mated males ($G = 16.65$, $df = 2$, $P < 0.001$): females were found in all three parts of the vial, whereas males were not found in the deeper half of the medium. The distribution of the females was not significantly different from random, whereas the males' distribution was (Table I).

Table I. Wasp Distribution [Number and (Proportion)] in the Absence of Hosts

	Virgin females	Mated females	Mated males	Expected if random ^a
Above medium	13 (0.34)	14 (0.37)	14 (0.67)	0.25
Upper one-half of medium	10 (0.26)	12 (0.32)	7 (0.33)	0.38
Deeper one-half of medium	15 (0.39)	12 (0.32)	0 (0.00)	0.38
Compared to expected				
χ^2	2.60	2.84	22.56	
P	>0.10	>0.05	<0.001	

^aExpected based on vial volume.

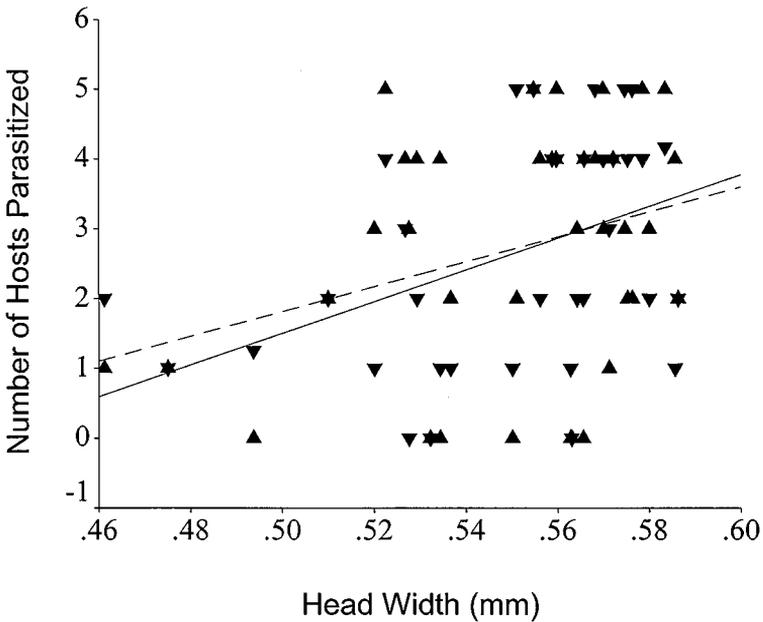


Fig. 1. Number of hosts parasitized versus mated mother's head width. (▼, —) Buried hosts: $r^2 = 0.18$, $df = 36$, $1tP = 0.0043$; $y = 22.7x - 9.9$. (▲, ---) Unburied hosts: $r^2 = 0.09$, $df = 36$, $1tP = 0.030$; $y = 17.8x - 7.1$.

Burrowing-with-Hosts Experiment

Twenty-six of 35 mated females were in the deeper half of the medium, versus only 15 of 31 virgin females ($\chi^2 = 4.69$, $P = 0.03$). Mated females parasitized more buried hosts than did virgins [2.6 ± 0.26 ($n = 38$) versus 1.9 ± 0.24 ($n = 38$); $t = 1.94$, $1tP = 0.028$] and did not parasitize significantly fewer unburied hosts than virgins [2.7 ± 0.28 ($n = 38$) versus 2.3 ± 0.26 ($n = 38$); $t = 1.10$, $2tP = 0.27$]. The number of hosts that were parasitized by mated females increased with the mother's head width (Fig. 1). The number of hosts that were parasitized by virgins was not significantly related to the mother's head width (buried hosts, $r^2 = 0.015$, $df = 35$, $1tP = 0.23$; unburied hosts, $r^2 = 0.015$, $df = 35$, $2tP = 0.46$).

Longevity Experiment

The longevity of mated males was not less than that of virgin males [10.59 ± 0.085 ($n = 40$) versus 10.07 ± 0.25 ($n = 38$)]. Likewise, the longevity of mated females was not greater than that of virgin females (8.92 ± 0.22 versus 9.28 ± 0.24 ; $t = 1.07$, $df = 77$, $2tP = 0.29$).

DISCUSSION

Cost of Drilling and Host Size Preference

Virgin *S. endius* females exhibited no strong preference for small hosts despite the apparently greater cost of drilling large versus small hosts and the absence of any apparent fitness advantage to developing on large hosts for sons (Napoleon and King, 1999). There was no significant preference either in terms of which host size they first tried to drill or in terms of the host size from which they produced more offspring. Mated females likewise showed no host size preference. *S. endius* females also lack a host age drilling preference (King, 2000).

Why did virgin females, whose sons' fitness seems to be unaffected by host size (Napoleon and King, 1999), not avoid large hosts because they take longer to drill? One explanation is that even if some females remain virgin for life, most probably do not (Godfray, 1994), in which case, selection for virgin-specific oviposition behaviors may be weak. In some other parasitoid wasp species, virgin females exhibit the same movements that mated females perform during the act of fertilization, despite virgins' inability to fertilize their eggs (reviewed by Godfray, 1994, p. 203). Behaviors associated with the act of fertilization have not been identified in *S. endius*. An alternative explanation for virgins not avoiding large hosts is that the greater time and energy necessary to drill large hosts may not represent a true cost, e.g., if time and energy to drill are not limiting.

Host size preference of virgin females has been examined in only two other parasitoid wasp species (Nishimura, 1997; Honek *et al.*, 1998). The pattern of preference is not consistent between these species, or with *S. endius*, and data on how host size affects male fitness are lacking for these species. Host size preference in parasitoid wasps has more commonly been examined for mated females (reviewed by Godfray, 1994).

The relative costs of parasitizing large hosts has not been well studied among pupal parasitoids but has been documented for some larval parasitoids. For larval parasitoids, a higher cost of parasitizing larger hosts appears to be related to greater active defense by larger hosts, e.g., thrashing and biting (e.g., Brodeur *et al.*, 1996; Chau and Mackauer, 1997).

Effect of Mating Status and Body Size on Fitness

Mating had a positive effect on *S. endius*'s offspring production in one experiment but no effect in another. Among parasitoid wasps in general, no significant difference in offspring production between mated and virgin females (Sandlan, 1979; Collins and Grafius, 1986; Hall and Fischer, 1988;

King, 1988; Hooker and Barrows, 1989; Heinz and Parrella, 1990; Petitt and Wietlisbach, 1993; Doury and Rojas-Rousse, 1994; Ramadan *et al.*, 1995; Guertin *et al.*, 1996; Fauvergue *et al.*, 1998) and mated females producing more offspring (Nong and Sailer, 1986; references cited by Godfray and Hardy, 1993; Michaud, 1994; Edwards and Hoy, 1998) have been reported with about equal frequency. Reports of virgin females producing more offspring are fewer (references cited by Godfray, 1994; Carpenter, 1995; Nishimura, 1997). Among arrhenotokous nonhymenopterans, no significant difference between virgin and mated female's offspring production has been reported for a thrips (Nakao, 1993) and some mites (Wheatley, 1990; Enkegaard *et al.*, 1997); however, in many other mites, mated females produce more offspring than virgins do (Bonato and Gutierrez, 1999, and references therein).

Mating had no significant effect on adult longevity for either females or males in *S. endius*. This, and the absence of a positive effect of mating on offspring production in the absence of burrowing, suggests that females do not obtain a substantial nutritional contribution from males during mating. Lack of nutritional contributions seems to be typical of parasitoid wasps (reviewed by Godfray, 1994, p. 276; but see Alcock and Gwynne, 1987; Jervis, 1998), in contrast to some other arthropod groups (reviewed by Vahed, 1998; Elgar, 1998).

Greater female size increased offspring production of mated females burrowing for hosts, but not in the absence of burrowing and not in virgin females. Greater body size had little or no effect on the speed or success of drilling.

Substrate Depth

That male *S. endius* were more often on or above the host medium than were females is consistent with the few other parasitoid wasps studied, e.g., *S. cameroni* (Myint and Walter, 1990) and *B. hebetor* (Guertin *et al.*, 1996). Given that *S. endius* males were not found in the deeper half of the host medium, mated females may be able to avoid mating harassment by burrowing, and virgin females may be able to increase their chances of mating by not burrowing. Mated females were deeper than virgin females only when hosts were present. One possibility is that in the absence of hosts, mated females did not remain below surface after exploring for hosts but, rather, returned to the surface to travel to a new site in search of hosts. In *B. hebetor*, virgin females more often stay on the surface of the host media; and when they do burrow, do not go as deep as mated females, at least when hosts are present (Guertin *et al.*, 1996).

Selection on virgin females to stay in microhabitats frequented by males may be weaker among arrhenotokous species than among nonarrhenotokous sexual species. In arrhenotokous species, staying may cost a virgin female in lost opportunities to oviposit sons, whereas there may be no such cost in regular diploid sexual species because virgin females cannot produce any offspring, not even sons. At present there are data on too few arrhenotokous species to evaluate this hypothesis.

Virgin females in arrhenotokous species have been described as “constrained” in the sense of being able to produce only sons (Godfray, 1990). They may also be constrained by their choice of microhabitat. However, in *S. endius*, the degree of constraint may be slight because some hosts are found on the surface of the substrate (King, personal observation), where males are.

Although the term “alternative breeding strategy” has been used primarily for males (e.g., Krebs and Davies, 1993), the difference in propensity to burrow between mated and virgin females can also be thought of as an alternative strategy. In contrast to many male alternative breeding strategies, the strategy switch in *S. endius* females is associated with mating status rather than body size.

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REFERENCES

- Alcock, J., and Gwynne, D. T. (1987). Courtship feeding and mate choice in thynnine wasps (Hymenoptera: Tiphiiidae). *Aust. J. Zool.* **35**: 451–456.
- Bonato, O., and Gutierrez, J. (1999). Effect of mating status on the fecundity and longevity of four spider mite species (Acari: Tetranychidae). *Exp. Appl. Acarol.* **23**: 623–632.
- Brodeur, J., Geervliet, J. B. F., and Vet, L. E. M. (1996). The role of host species, age and defensive behaviour on ovipositional decisions in a solitary specialist and gregarious generalist parasitoid (*Cotesia* species). *Entomol. Exp. Appl.* **81**: 125–132.
- Carpenter, J. E. (1995). *Ichneumon promissorius* (Erichson) (Hymenoptera: Ichneumonidae): Factors affecting fecundity, oviposition, and longevity. *J. Entomol. Sci.* **30**: 279–286.
- Chau, A., and Mackauer, M. (1997). Dropping of pea aphids from feeding site—A consequence of parasitism by the wasp, *Monoctonus paulensis*. *Entomol. Exp. Appl.* **83**: 247–252.
- Collins, R. D., and Grafius, E. (1986). Biology and life cycle of *Anaphes sordidatus*, a mymarid egg parasitoid of the carrot weevil. *Environ. Entomol.* **15**: 100–105.
- Doury, G., and Rojas-Rousse, D. R. (1994). Reproductive potential in the parasitoid *Eupelmus orientalis* (Hymenoptera: Eupelmidae). *Bull. Entomol. Res.* **84**: 199–206.

- Edwards, O. R., and Hoy, M. A. (1998). Biology of *Ageniaspis citricola* (Hymenoptera: Encyrtidae), a parasitoid of the leafminer *Phyllocnistis citrella* (Lepidoptera: Gracillariidae). *Ann. Entomol. Soc. Am.* **91**: 654–660.
- Elgar, M. A. (1998). Sperm competition and sexual selection in spiders and other arachnids. In Birkhead, T. R., and Møller, A. P. (eds.), *Sperm Competition and Sexual Selection*, Academic Press, San Diego, pp. 55–90.
- Enkegaard, A., Sardar, M. A., and Brodsgaard, H. F. (1997). The predatory mite *Hypoaspis miles*—Biological and demographic characteristics on two prey species, the mushroom scarid fly, *Lycoriella solani*, and the mould mite, *Tyrophagus putrescentiae*. *Entomol. Exp. Appl.* **82**: 135–146.
- Fauvergue, X., Hopper, K. R., Antolin, M. F., and Kazmer, D. J. (1998). Does time until mating affect progeny sex ratio—A manipulative experiment with the parasitoid wasp *Aphelinus asychis*. *J. Evol. Biol.* **11**: 611–622.
- Gerling, D., and Legner, E. F. (1968). Developmental history and reproduction of *Spalangia cameroni*, parasite of synanthropic flies. *Ann. Entomol. Soc. Am.* **61**: 1436–1443.
- Godfray, H. C. J. (1990). The causes and consequences of constrained sex allocation in haplodiploid animals. *J. Evol. Biol.* **3**: 3–17.
- Godfray, H. C. J. (1994). *Parasitoids*, Princeton University Press, Princeton, NJ.
- Godfray, H. C. J., and Hardy, I. C. W. (1993). Sex ratio and virginity in haplodiploid insects. In Wrensch, D. L., and Ebbert, M. (eds.), *Evolution and Diversity of Sex Ratio in Insects and Mites*, Chapman and Hall, New York, pp. 402–417.
- Guertin, D. S., Ode, P. J., and Strand, M. R. (1996). Host-searching and mating in an outbreeding parasitoid wasp. *Ecol. Entomol.* **21**: 27–33.
- Hall, R. D., and Fischer, F. J. (1988). Laboratory studies on the biology of *Spalangia nigra* (Hym: Pteromalidae). *Entomophaga* **33**: 495–504.
- Heinz, K. M., and Parrella, M. P. (1990). Holarctic distribution of the leafminer parasitoid *Diglyphus begini* (Hymenoptera: Eulophidae) and notes on its life history attacking *Liriomyza trifolii* (Diptera: Agromyzidae) in chrysanthemum. *Ann. Entomol. Soc. Am.* **83**: 916–924.
- Honek, A., Jarosik, V., Lapchin, L., and Rabasse, J. M. (1998). Host choice and offspring sex allocation in the aphid parasitoid *Aphelinus abdominalis* (Hymenoptera: Aphelinidae). *J. Agr. Entomol.* **15**: 209–221.
- Hooker, M. E., and Barrows, E. M. (1989). Clutch sizes and sex ratios in *Pediobius foveolatus* (Hymenoptera: Eulophidae), primary parasites of *Epilachna varivestis* (Coleoptera: Coccinellidae). *Ann. Entomol. Soc. Am.* **82**: 460–465.
- Jervis, M. (1998). Functional and evolutionary aspects of mouthpart structure in parasitoid wasps. *Biol. J. Linn. Soc.* **63**: 461–493.
- King, B. H. (1988). Sex-ratio manipulation in response to host size by the parasitoid wasp *Spalangia cameroni*: A laboratory study. *Evolution* **42**: 1190–1198.
- King, B. H. (1990). Interspecific differences in host (Diptera: Muscidae) size and species usage among parasitoid wasps (Hymenoptera: Pteromalidae) in a poultry house. *Environ. Entomol.* **19**: 1519–1522.
- King, B. H. (1994). How do female parasitoid wasps assess host size during sex-ratio manipulation? *Anim. Behav.* **48**: 511–518.
- King, B. H. (2000). Sex ratio and oviposition responses to host age and the fitness consequences to mother and offspring in the parasitoid wasp *Spalangia endius*. *Behav. Ecol. Sociobiol.* **48**: 316–320.
- Kouamé, K. L., and Mackauer, M. (1991). Influence of aphid size, age and behaviour on host choice by the parasitoid wasp *Ephedrus californicus*: A test size of host-size models. *Oecologia* **88**: 197–203.
- Krebs, J. R., and Davies, N. B. (1993). *An Introduction to Behavioural Ecology*, 3rd ed., Blackwell Scientific, London.
- Legner, E. F. (1977). Temperature, humidity and depth of habitat influencing host destruction and fecundity of muscoid fly parasites. *Entomophaga* **22**: 199–206.
- McLain, D. K., and Pratt, A. E. (1999). The cost of sexual harassment on the fecundity of a host-specific, seed-eating insect (*Neocoryphus bicrucis*). *Behav. Ecol. Sociobiol.* **46**: 164–170.

- Michaud, J. P. (1994). Differences in foraging behaviour between virgin and mated aphid parasitoids (Hymenoptera: Aphidiidae). *Can. J. Zool.* **72**: 1597–1602.
- Myint, W. W., and Walter, G. H. (1990). Behaviour of *Spalangia cameroni* males and sex ratio theory. *Oikos* **59**: 163–174.
- Nakao, S. (1993). Effects of temperature and photoperiod on wing form determination and reproduction of *Thrips nigropilosus*. *Appl. Entomol. Zool.* **28**: 463–472.
- Napoleon, M. E., and King, B. H. (1999). Offspring sex ratio response to host size in the parasitoid wasp *Spalangia endius*. *Behav. Ecol. Sociobiol.* **46**: 325–332.
- Nishimura, K. (1997). Host selection by virgin and inseminated females of the parasitic wasp, *Dinarmus basalis* (Pteromalidae, Hymenoptera). *Funct. Ecol.* **11**: 336–341.
- Nong, L., and Sailer, R. I. (1986). Arrhenotokous reproduction of *Pediobus foveolatus* (Hymenoptera: Eulophidae). *Ann. Entomol. Soc. Am.* **79**: 737–741.
- Petitt, F. L., and Wietlisbach, D. O. (1993). Effects of host instar and size on parasitization efficiency and life history parameters of *Opius dissitus*. *Entomol. Exp. Appl.* **66**: 227–236.
- Ramadan, M. M., Wong, T. T. Y., and Messing, R. H. (1995). Reproductive biology of *Biosteres vandenboschi* (Hymenoptera, Braconidae), a parasitoid of early-instar oriental fruit fly. *Ann. Entomol. Soc. Am.* **88**: 189–195.
- Rueda, L. M., and Axtell, R. C. (1985a). Guide to common species of pupal parasites (Hymenoptera: Pteromalidae) of the house fly and other muscoid flies associated with poultry and livestock manure. Technical Bulletin 278. North Carolina Agricultural Research Service, North Carolina State University, Raleigh.
- Rueda, L. M., and Axtell, R. C. (1985b). Effect of depth of house fly pupae in poultry manure on parasitism by six species of Pteromalidae (Hymenoptera). *J. Entomol. Sci.* **20**: 444–449.
- Sandlan, K. P. (1979). Sex ratio regulation in *Coccygomimus turionella* Linnaeus (Hymenoptera: Ichneumonidae) and its ecological implications. *Ecol. Entomol.* **4**: 365–378.
- Vahed, K. (1998). The function of nuptial feeding in insects—Review of empirical studies. *Biol. Rev.* **73**: 43–78.
- Verner, J. (1965). Selection for the sex ratio. *Am. Nat.* **99**: 419–421.
- Wheatley, J. A. C. (1990). *Biology of the Twospotted Spider Mite, Tetranychus urticae (Acari: Tetranychidae) on Several Genotypes of Soybean and Effects on a Predator mite, Phytoseiulus persimilis (Acari: Phytoseiidae)*, Ph.D. thesis, Louisiana State University and Agricultural and Mechanical College, Baton Rouge.