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Sex ratio manipulation in response to host size in the parasitoid wasp Spalangia cameroni: is it adaptive?

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manipulation

Many species of parasitoid wasps produce a greater proportion of sons in small than in large hosts. As described by the host size model, natural selection is becoming a standard explanation for the evolution of this phenomenon. We examined a critical assumption of the host size model, that host size has a more positive effect on female than on male reproductive success. In laboratory experiments with the parasitoid wasp Spalangia cameroni, females that developed on larger hosts contained more eggs at emergence. However, more eggs did not translate into more offspring, under either high or low host density, and regardless of whether a female had to burrow to reach hosts. The size of host on which a female developed also was unrelated to her longevity, regardless of the presence or absence of hosts. The size of host on which a male developed had no effect on his sperm production or ability to inseminate females, regardless of whether insemination ability was measured by the amount of sperm transferred to a female, by the proportion of a male's mates that produced any daughters, or by the proportion of daughters that a male's mates produced. Thus, despite data on multiple measures of fitness under a range of conditions, sex ratio manipulation in response to host size in S. cameroni does not appear to be adaptive and another explanation is needed.

Key words. -- sex ratio, sex allocation, host size, reproductive success, parasitoid wasps, body size, Pteromalidae, Hymenoptera

Examples of apparently adaptive behavioral traits lend credence to a basic premise of behavioral ecology that, in general, behavior is adaptive (e.g., Endler, 1986; Krebs and Davies, 1987). However, a danger arising from this premise is that counter-examples, behaviors for which adaptive explanations are not supported, tend to be explained away with reference to unmeasured variables and limitations in experimental protocols. Here we describe behavior that does not appear to be adaptive, offspring sex-ratio manipulation in the parasitoid wasp Spalangia cameroni (Hymenoptera: Pteromalidae).

This example is instructive because the behavior of S. cameroni is consistent with predictions of models for the adaptive evolution of sex-ratio behavior. Thus, uncritical application of the adaptationist program (Gould and Lewontin, 1979; Mayr, 1983) would lead to the conclusion that the sex-ratio behavior of S. cameroni is adaptive. However, as we show here, a critical assumption of these models is not met, despite experiments conducted under a wide range of environmental conditions and analysis of multiple measures of fitness. Although our data do not support an adaptive explanation, we do not reject the possibility that the sex-ratio behavior of S. cameroni may be adaptive. Our results serve as a reminder of the need to consider nonadaptive as well as adaptive hypotheses for behavioral evolution and the need to accept the tentative nature of scientific conclusions.

Maternal manipulation of offspring sex ratio (proportion of sons) in response to resource availability has been used to explain sex ratio patterns in a variety of taxa (e.g., wasps: Charnov et al., 1981; thrips: Crespi, 1988; mites: Young et al., 1986; mammals: Clutton-Brock and Iason, 1986; birds: Howe, 1977). That such behavior might be adaptive was first suggested for polygynous mammals by Trivers and Willard (1972) and was later formalized into mathematical evolutionary models, now referred to as host size or host quality models (Charnov, 1979; Charnov et al., 1981). The host size models were designed for solitary species of parasitoid wasps, i.e., species that produce only one offspring per host, although they are applicable to other organisms as well. The models predict that natural selection will result in mothers that oviposit a greater proportion of sons in small than in large hosts. A critical assumption is that host size has a more positive effect on female than on male reproductive success. One way that host size may have a greater effect on female than on male reproductive success is if host size is positively correlated with wasp size and if wasp size increases the reproductive success of females more than the reproductive success of males (Charnov et al., 1981).

Spalangia cameroni is a solitary species and one of the best studied organisms in terms of the host size models (King, 1988, 1990b, 1991a; Legner, 1969). As is probably the case for most parasitoid wasps (King, 1993), S. cameroni females oviposit a greater proportion of sons in small hosts than in large hosts (King, 1988, 1990b, 1991a). This pattern is found both in the laboratory and in the field for the host Musca domestica. Furthermore, host size has a positive effect on the size of both male and female S. cameroni in the laboratory (King, 1988), although not consistently in the field (King, 1991a). However, previous experiments revealed no effect of host size on either male or female reproductive success through an effect on wasp size (King, 1988; see also Discussion).

These earlier experiments were carried out under "relatively benign" conditions, with hosts presented daily, in abundance, and unburied (King, 1988). Host size may affect wasp reproductive success only under harsher ecological conditions. S. cameroni parasitizes pupae of flies associated with livestock manure (Rueda and Axtell, 1985). Female S. cameroni crawl as deep as 5 cm below the manure surface parasitizing these pupae (Rueda and Axtell, 1985). Females use their ovipositors to drill through the host shells and lay eggs on the pupae within. At emergence, each female contains about 20 or 30 mature eggs (Gerling and Legner, 1968; see also Results). In the absence of hosts, females resorb eggs. Host feeding, in

which females feed on fluids that exude from hosts following drilling, allows for continued egg production and increases longevity. In the field, females may sometimes experience a shortage of hosts for both feeding and oviposition because host availability varies temporally, and suitable hosts are sometimes scarce (King, 1990a). Through an effect on wasp size, host size may affect a female wasp's ability to burrow in search of hosts and to survive periods of food shortage.

Previous experiments with males revealed no effect of host size or wasp size on longevity in the presence of ample food or on ability to obtain a mate in the presence of another male (King, 1988). However, an effect on longevity may occur only when food is scarce, and the effect of a male's host and body size on his ability to inseminate females has not previously been investigated for *S. cameroni* (King, 1988). Although females mate only once, males will mate multiple times. By the time a male emerges from his host, sperm production is finished, and mature sperm have moved from the testes to the seminal vesicles for storage (Gerling and Legner, 1968). Possible effects of host size and body size on sperm production have not previously been examined in any parasitoid wasp.

Here we address the effects of host size and wasp size on previously ignored aspects of reproductive success of male and female *S. cameroni*. We examine the effects of both host size and wasp size, so that we can determine whether any effects of host size on reproductive success occur through effects on wasp size. We examine multiple measures of reproductive success in order to determine what, if any, aspects of reproductive success are affected by host size and under what environmental conditions. For females we examine: 1) the number of eggs at emergence; 2) longevity in the absence of hosts, honey, and water; 3) longevity in the presence of water only; 4) longevity and offspring production when few hosts are encountered; 5) longevity and offspring production when a female encounters many more hosts than she can parasitize; and 6) offspring production when a female must burrow for hosts. For males we examine: 1) longevity in the presence of water only; 2) seminal vesicle size, as a measure of sperm complement; 3) amount of sperm transferred to females; and 4) ability to inseminate multiple females.

METHODS

General methods

The *Spalangia cameroni* used in this study were from a colony established in 1985 with wasps that emerged from *Musca domestica* and *Stomoxys calcitrans* pupae collected in Indiana (King, 1991a). The wasps had been in culture for about 80 generations at the time of the experiments described herein. The wasp colony was maintained at 23-28°C, 24L, using *M. domestica* as hosts (King, 1988).

Experiments were done at 23-28°C, 24L using *M. domestica* that had pupated within 1 d of being presented to wasps as hosts. Large and small hosts were produced by manipulating the density of developing larvae (described in King, 1988). Females used in experiments had emerged less than 24 h prior to the start of experiments. Mated females had each been paired with a virgin male and observed to mate.

In all experiments, width and length of the hosts from which experimental wasps emerged were measured using an ocular micrometer on a dissecting microscope. Host volume was calculated using the equation for a prolate spheroid, $2/3\pi \times (\text{host width}/2)^2 \times (\text{host length})$ (Holdaway and Smith, 1932). Wasp size was measured by head width, which is positively correlated with other measures of body size in *S. cameroni* (King, 1988) but which is a more reliable indicator of size than is weight or abdomen width when females have access to food (Hurlbutt, 1987). The hosts used in our experiments were of comparable size to, or slightly smaller than, the hosts parasitized by *S. cameroni* in the field (Table 1).

Except where noted otherwise, in each experiment, we regressed wasp reproductive success on the volume of the host from which the wasp emerged and on the wasp's head width. Linear regression was used because visual inspection did not indicate any curvilinear relationships. When the

abscissa and ordinate were clearly in units of different powers (e.g., mm and mm³), the data were log-transformed (Harvey, 1982). However, log-transformation caused no more than a 1% difference in R², which is the percent of variation in the ordinate explained by the abscissa; thus, the nontransformed results are presented for simplicity.

In all experiments except those involving dissections, wasps were tested in pairs, a wasp from a small host and one from a large host. This was done to control for variation in laboratory conditions such as temperature and humidity. Wasps within each pair were the same age, mated with wasps of the same age, and received hosts that were matched in size and age. Therefore, in addition to regression analyses, we also examined the effect of host size on wasp reproductive success by using paired t-tests of wasps from small and large hosts. For simplicity, only the results of the regressions are reported except when one test showed a significant effect and the other did not.

Female reproductive success

Measures of female reproductive success are summarized in Table 1.

We determined the number of mature eggs for females less than 1 d old and from a range of host sizes (Table 1) by dissecting each female on a glass slide in a few drops of physiological saline (Gerling and Legner, 1968). Mature eggs are clearly distinguishable from undeveloped oocytes by size and coloration (Gerling and Legner, 1968; personal observation).

We determined longevity and offspring production of mated females under several conditions. Unless stated otherwise, we placed mated females individually in 4 dram glass shell vials with cotton plugs, checked them daily, and recorded their date of death. We determined longevity of females that were not given hosts, honey, or water and also longevity of females that were given water only. In the latter case, we placed a drop of water on the bottom of the vial and moistened the cotton daily.

We determined longevity and offspring production for females at low host densities by presenting females with two large young hosts every fourth day, along with honey ad libitum, and a drop of water every day that females did not receive hosts. We counted lifetime number of offspring for each female.

We determined offspring production for females at very high host densities by presenting each female with forty large young hosts every day for five days along with honey ad libitum. We chose forty hosts per day because the maximum number of eggs in a female at emergence was 40 (Table 2); and when given 40 hosts, females produced at most 26 offspring. Offspring production over the first five days was used to estimate reproductive success because in earlier experiments in which females received 14 hosts daily for life (King, 1988), reproductive success over the first five days was significantly correlated with lifetime reproductive success ($R = 0.79$, $n = 31$, $P < 0.001$).

We also determined offspring production for females that had to burrow for their hosts. We presented each female with hosts buried in a 1000 ml jar containing used host-rearing-media (to simulate poultry manure). We filled the jars to a depth of about 6 cm, and introduced hosts as mature larvae that were within one day of pupation. The hosts burrowed into the media and pupated at varying depths. We introduced twenty hosts on each of seven consecutive days. On the second day, we introduced a female to each jar. She had emerged, mated, and been given honey the previous day. A day after we introduced the last hosts, we removed all hosts from the media, along with the mother when we could find her (53 of 70 mothers). We counted the number of wasp offspring emerging from the hosts for each mother.

We determined whether a female's host size affects how quickly she mates, by pairing a female that had developed on a small host and a female that had developed on a large host each with a different virgin male in test tubes. We observed which pair mated first. We replicated this with a total of 49 pairs of females.

Male reproductive success

Measures of male reproductive success are summarized in Table 1.

We determined longevity of males that were given only water in the same way as for females except that virgin males were used instead of mated females. We determined seminal vesicle size for virgin males that had developed on a range of host sizes by dissecting males in physiological saline 6-24 h after emergence. Each male has a pair of two-chambered seminal vesicles (Gerling and Legner, 1968). Upon ejaculation, the posterior chamber empties and then refills from the anterior chamber. In virgin males, the seminal vesicles contain a male's lifetime complement of sperm. The size of the vesicles appears to reflect the amount of sperm that they contain (see Results). We measured the width and length of the anterior chambers of the seminal vesicles from the inside of the vesicle walls at 450X using an ocular micrometer (Figure 4 in Gerling and Legner, 1968). Because the anterior chamber cross sections are approximately elliptical, we estimated cross-sectional area as the area of an ellipse. When possible, we measured both of a male's seminal vesicles, in which case, we averaged size for further analyses. We compared the slopes and intercepts of the regressions of seminal vesicle area on head width for virgin versus mated males by t-tests (Zar, 1984).

We also estimated the amount of sperm that males transferred to females. Following insemination, females store sperm in a spermatheca. The sperm form a band that rotates around the perimeter of the spermatheca (as in *Pachycrepoideus vindemiae*: Fig. 1 and Fig. 3 in Nadel and Luck, 1985). We used the cross sectional area of the sperm band as an estimate of the amount of sperm that a male transferred to a female. We allowed virgin males to mate with virgin females 6-24 h after emergence, and then we dissected both 0-4 h after mating. We measured spermatheca length and width (from the inside of the spermathecal walls) and sperm band width at 1000X (oil immersion) using an ocular micrometer, and we used these measures to calculate the elliptical cross sectional sperm band area. We also measured the mated male's seminal vesicles (see above).

To determine insemination success, we placed males each in a vial with ten females for 24 h. Then we gave each female twenty hosts for 24 h. We estimated each male's reproductive success as the proportion of females that he inseminated (i.e., that produced any daughters) and as the percent of his mates' offspring that were daughters.

RESULTS

Effects of host size on reproductive success

Females that developed on larger hosts contained significantly more eggs at emergence than females from smaller hosts, with females from the largest hosts containing 1.2 times as many eggs as females from the smallest hosts (Table 2). However, females from larger hosts did not live longer or produce more offspring than females from smaller hosts in any of the experiments (Table 2). Also, females from larger hosts did not mate more quickly: they mated before females from small hosts only 62% of the time; which is not significantly more often than expected by chance ($X^2 = 2.47$, $df = 1$, $P > 0.10$, $n = 49$ pairs of mating pairs).

Whether males that develop on larger hosts live longer than males from smaller hosts when given only water is not clear: the regression was significant ($P = 0.05$), but the paired t-test was not ($P = 0.10$) (Table 2). However, among both virgin and mated males, males from larger hosts did not have significantly larger seminal vesicles than males from smaller hosts (Table 2) and did not transfer more sperm to their mate's spermatheca during mating (Table 2). Males from larger hosts also did not have greater mating success than males from smaller hosts, when mating success was measured as the proportion of females that a male successfully inseminated or the percent of offspring that were daughters (Table 2).

Effects of wasp size on reproductive success

Relative to smaller females, larger females contained significantly more eggs at emergence and produced more offspring at high host density, (Table 3). However, larger females did not produce more offspring than smaller females at low host density or when females had to burrow for hosts, and larger females did not live longer than smaller females in any of the

experiments (Table 3).

Relative to smaller males, larger males lived longer when given only water and had larger seminal vesicles, regardless of whether they had mated or not (Table 3). However, larger males did not transfer more sperm to their mate's spermatheca during mating and did not have greater mating success (Table 3).

For a given body size, mated males had smaller seminal vesicles than virgin males: the slope of the regression of seminal vesicle area on head width (Table 3) was the same for virgin and mated males ($t = 0.09$, $df = 98$, $P > 0.90$), but the intercept was slightly lower for mated males ($t = 3.59$, $df = 99$, $P < 0.001$).

DISCUSSION

There was little effect of host size on wasp reproductive success, as evidenced by few regressions being significant at alpha of 0.05, and low R^2 values even for statistically significant regressions (Table 2). There were no statistically significant relationships between the size of host on which a female wasp developed and her longevity, offspring production, or quickness to mate. Females did contain more eggs at emergence when they had developed on larger hosts; however, containing more eggs at emergence does not appear to translate into more offspring, regardless of host density and regardless of whether females have to burrow to reach hosts. Recall that the host size models assume that host size has a greater effect on the reproductive success of female wasps than male wasps. If there is no effect of host size on female reproductive success, the only way for this assumption to be met is if host size has a negative effect on male reproductive success. However, five of the six measures of male reproductive success exhibited positive (although usually nonsignificant) relationships with host size (Table 2).

The lack of significant positive effects of host volume on most aspects of *S. cameroni* reproductive success are probably not due simply to insufficient sample sizes. If this were the case, positive but nonsignificant effects of host volume on reproductive success would be expected. Of the seven measures of female reproductive success, only two, egg number and offspring production at high host density, showed positive relationships with host size, and the magnitudes of the effects were small (Table 2). For example, in terms of offspring production at high host density, host size had only a nonsignificant 1.08-fold effect. This contrasts with a 21-fold effect of host size on offspring production in the parasitoid wasp *Heterospilus prosopidis* (Jones, 1982). There are several ways that sex ratio manipulation in *S. cameroni* may be adaptive despite our results. One possibility is that, as is possible in any study of adaptation, we may not have measured that component of fitness that really matters in nature. We consider it noteworthy that there was no effect of host size on a female's offspring production, a measure of reproductive success that is affected by host size in the two other species that have been examined (Garcia-Saez, 1988; Jones, 1982). Another possibility is that host size may affect reproductive success of females only at host sizes larger than those included in our study. Our study did not include hosts as large as the largest ones parasitized by *S. cameroni* in the field, although our study did include most of the range of host sizes parasitized in the field (Table 1).

Alternatively sex ratio manipulation by *S. cameroni* may not be adaptive: host size may not have a greater effect on female than on male reproductive success. Rather, manipulation may represent a phylogenetic constraint: the trait may have been adaptive in ancestral species and may simply have been retained in *S. cameroni*. Without a better understanding of the phylogeny of *S. cameroni*, phylogenetic constraint cannot be ruled out. However, the fact that the congener *S. endius* does not manipulate sex ratio in response to host size (Donaldson and Walter, 1984) suggests that manipulation is mutable. Furthermore, genetic variation in other sex ratio manipulation traits has been demonstrated in the confamilials *Nasonia vitripennis* (e.g., Orzack and Parker, 1986) and *Muscidifurax*

raptor (Antolin, 1988).

Most parasitoid wasps that have been examined produce a greater proportion of sons in smaller hosts, as the host size model predicts (more than forty species from thirteen families: King, 1993). Yet for only a few of these species are there data on the model's assumption that host size has a greater effect on the reproductive success of females than of males. For Anisopteromalus calandrae and Heterospilus prosopidis the effect of host size on wasp reproductive success is greater for females than for males, as the model assumes (Garcia Saez de Nanclares, 1988; Jones, 1982). Thus, sex ratio manipulation in response to host size in these two species appears to be adaptive, as modeled by the host size model.

In contrast, for Muscidifurax raptor and S. cameroni the assumption is not supported. Traditional measures of reproductive success, such as offspring production, longevity, and mating success, are unaffected by host size in both female and male M. raptor (Seidl and King, in press). In S. cameroni there is a positive effect of host size on male but not female reproductive success (this study). Furthermore, host size differentially affects wasp development time for females versus males, but the direction of this effect differs between M. raptor and S. cameroni; and although statistically significant, the effect is less than the precision with which development time was measured (King, 1988; Seidl and King, in press). Thus, evidence that sex ratio manipulation in response to host size is adaptive in S. cameroni and M. raptor is lacking.

In the four species described above, the effect of host size on wasp reproductive success has been tested directly. Two additional studies have looked indirectly at effects of host size on wasp reproductive success: these studies demonstrated a positive effect of host size on wasp size and then examined the effect of wasp size on female versus male reproductive success. In both Lariophagus distinguendus and Diglyphus begini, wasp size affects both female and male reproductive success, and the investigators have concluded that females are more positively affected than males, supporting the host size model (van den Assem et al., 1989; Heinz, 1991).

Though an effect of host size on wasp reproductive success might logically proceed through an effect on wasp size, there are advantages to looking directly at the effect of host size on fitness when testing the model assumption. A positive effect of host size on wasp size and a greater effect of wasp size on female than male wasp fitness may not translate into support for the host size model assumption 1) if there is substantial noise in the relationship between host size and wasp size (as is the case for S. cameroni (King, 1988), 2) if the effect of host size on wasp size differs between the sexes, or 3) if the range of wasp sizes used in determining the relationship between wasp size and host size differs from the range of wasp sizes used to look at the effect of wasp size on wasp reproductive success. As an example of the latter, in S. cameroni, although both male and female wasps tend to be larger when they develop on larger hosts, occasionally dwarfs develop from large hosts; dwarfs are outliers in size, smaller even than wasps from the smallest hosts (King, 1988, 1991a). Showing that dwarfs differ from larger wasps in measures of reproductive success should not be taken as evidence that body size and reproductive success will be related in normal sized wasps (King, 1988).

Wasp size had significant positive effects on aspects of both female and male reproductive success in our study. Larger females produced more offspring than smaller females under very high host density (Table 3), although not under moderate (King, 1988) or low host density (Table 3). Larger S. cameroni males lived longer than smaller males when they received only water (Table 3), although not when they received honey (King, 1988). Larger males had larger seminal vesicles than smaller males but were not more successful at transferring sperm and inseminating females. In contrast to S. cameroni, in two other species of the same family, a male's size does affect his ability to successfully inseminate females (van den Assem et al., 1989; Grant et al., 1980). That a female's size affected her reproductive success only under high host density

conditions suggests that the relative effects of size on females versus males will depend on environmental conditions, as has been demonstrated for *D. begini* (Heinz, 1991).

Understanding why sex ratio manipulation in response to resource availability occurs is important because such manipulation is a common phenomenon, not only in parasitoid wasps (a large group in itself), but also in a range of other taxa (e.g., Clutton-Brock and Iason, 1986). Clearly we need to test further the effects of host size on reproductive success before the conclusion that size has a greater effect on female than male fitness among parasitoid wasps becomes dogma (Gauld and Bolton, 1988, p. 11; Southwood, 1988, p. 5). Our results also indicate that nonadaptive explanations for sex-ratio behavior deserve consideration.

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Table 1
 Range of host sizes parasitized by Spalangia cameroni in the field and host sizes and wasp sizes used in our experiments

	Host volume (mm ³)		Wasp head width (mm)	
	Mean ± s.e.	Range	Mean ± s.e.	Range
Field study (King, unpublished)*				
Females (n = 193, 54)		10.01 - 34.96		0.43 - 0.62
Males (n = 97, 46)		12.56 - 31.55		0.46 - 0.64
Laboratory Experiments with House Flies**				
Female Reproductive Success				
Egg Number	21.15 ± 0.53	5.90 - 29.50	0.56 ± 0.002	0.45 - 0.61
Longevity:				
Without Hosts, Honey, and Water	22.13 ± 0.90	11.08 - 34.22	0.57 ± 0.003	0.51 - 0.61
With Water Only	18.78 ± 0.87	6.96 - 31.34	0.57 ± 0.002	0.49 - 0.61
Offspring Production:				
Low Host Density	20.03 ± 0.65	8.88 - 32.71	0.48 ± 0.002	0.41 - 0.51
High Host Density	19.36 ± 1.16	7.21 - 31.34	0.57 ± 0.005	0.45 - 0.61
Burrowing for Hosts	20.07 ± 0.89	9.16 - 32.39	0.58 ± 0.001	0.54 - 0.60
Male Reproductive Success				
Longevity with Water Only	17.83 ± 0.86	8.60 - 31.10	0.62 ± 0.002	0.57 - 0.66
Seminal Vesicles				
Virgin Males	16.80 ± 0.88	7.04 - 27.74	0.61 ± 0.002	0.56 - 0.66
Mated Males	17.28 ± 0.84	8.51 - 29.28	0.60 ± 0.003	0.51 - 0.63
Sperm Transfer to Females	17.56 ± 0.77	8.51 - 29.28	0.60 ± 0.003	0.51 - 0.64
Proportion of Mates Inseminated and Offspring Sex Ratio	18.96 ± 1.33	8.41 - 29.50	0.60 ± 0.005	0.51 - 0.64

*Includes house flies and stable flies.

**Sample sizes as in Table 2.

Table 2

Reproductive success of female and male wasps and regressions of wasp reproductive success (Y) on host volume (mm³) (X)

	Mean ± SE	Range	R ²	N	P	Equation
Female Wasps:						
Egg number	30.2 ± 0.46	13 - 40	0.05	96	0.02	Y = 0.19X + 26.22
Longevity (days):						
Without Hosts, Honey, Water	4.68 ± 0.16	2 - 8	0.01	56	0.51	Y = -0.02X + 5.04
Water Only	10.32 ± 0.20	5 - 13	0.0004	68	0.86	Y = -0.005X + 10.41
Low Host Density	15.80 ± 0.62	8 - 33	0.01	86	0.32	Y = -0.10X + 17.88
Offspring Production:						
Low Host Density	7.64 ± 0.39	0 - 19	0.01	86	0.48	Y = -0.05X + 8.57
High Host Density	75.61 ± 1.88	40 - 89	0.03	33	0.19	Y = 0.22X + 71.4
Burrowing for Hosts	54.63 ± 0.89	0 - 84	0.004	70	0.60	Y = -0.12X + 56.99
Male Wasps:						
Longevity with Water Only (days)	10.4 ± 0.18	7 - 15	0.04	70	0.05*	Y = 0.041X + 9.70
Seminal Vesicle Size**						
Virgin Males	10.64 ± 0.15	8.32 - 13.20	0.01	54	0.21	Y = 0.019X + 10.31
Mated Males	9.61 ± 0.21	6.84 - 13.32	0.05	44	0.08	Y = 0.054X + 8.67
Quantity of Sperm Transferred***						
to Female	1.48 ± 0.09	0.49 - 3.46	0.03	53	0.12	Y = 0.019X + 1.16
Proportion of Mates Inseminated	0.90 ± 0.02	0.50 - 1.00	0.05	38	0.18	Y = -0.003X + 0.96
Offspring Sex Ratio	0.36 ± 0.02	0.17 - 0.76	0.03	38	0.32	Y = 0.002X + 0.31

Nonsignificant regression equations are included for heuristic purposes.

*Not significant by paired t-test: $t = 1.34$, $df = 33$, $P = 0.10$.

**Cross-sectional area of anterior chamber in mm² x 10⁻³.

***Cross-sectional area of sperm band in spermatheca in mm² x 10⁻³.

Table 3

Regressions of reproductive success of female and male wasps (Y)
on wasp head width (mm) (X)

	R ²	N	P	Equation
Female Wasps:				
Egg number	0.17	94	<0.001	Y = 78.18X - 13.82
Longevity:				
Without Hosts, Honey, Water	0.01	56	0.22	Y = 5.84X + 1.35
Water Only	0.002	68	0.35	Y = 3.39X + 8.38
Low Host Density	0.0002	86	0.89	Y = -5.59X + 18.49
Offspring Production:				
Low Host Density	0.002	86	0.35	Y = 10.26X + 2.71
High Host Density	0.39	31	0.0001	Y = 282.53X - 85.12
Burrowing for Hosts	0.04	53	0.18	Y = -173.17X + 156.58
Male Wasps:				
Longevity with Water Only	0.08	69	0.01	Y = 25.59X - 5.37
Seminal Vesicle Size**				
Virgin Males	0.22	54	0.0002	Y = 30.02X - 7.69
Mated Males	0.19	48	0.001	Y = 28.94X - 7.70
Quantity of Sperm Transferred to Female***				
Proportion of Mates Inseminated	0.00000	38	0.99	Y = -0.0055X + 0.90
Offspring Sex Ratio	0.0003	38	0.92	Y = -0.073X + 0.40

Nonsignificant regression equations are included for heuristic purposes.

**Cross-sectional area of anterior chamber in mm² x 10⁻³.

***Cross-sectional area of sperm band in spermatheca in mm² x 10⁻³.