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Offspring sex ratio response to host size in the parasitoid wasp Spalangia endius

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Abstract The host size model, an adaptive model for maternal manipulation of offspring sex ratio, was examined for the parasitoid wasp *Spalangia endius*. In a Florida strain, as the model predicts, daughters emerged from larger hosts than sons, but only when mothers received both small and large hosts simultaneously. The pattern appeared to result from the mother's ovipositional choice and not from differential mortality of the sexes during development. If sex ratio manipulation is adaptive in the Florida strain, it appears to be through a benefit to daughters of developing on large hosts, as the model suggests, rather than through a benefit to sons of developing on small hosts. Both female and male parasitoids were larger when they developed on larger hosts, but a parasitoid's host size had no effect on its wing loading or on the fluctuating asymmetry of its wings. For females, developing on a larger host 1) increased offspring production, except for the largest hosts, 2) increased longevity, and 3) lengthened development. For males, development on a larger host had no effect on any measure of male fitness -- mating success, longevity, or development duration. In contrast to the host size model and the Florida strain, a strain from India showed no difference in the size of hosts from which daughters versus sons emerged -- despite both female and male parasitoids being larger when they developed on larger hosts. These results together with previous studies of *Spalangia* reveal no consistent connection between host-size dependent sex ratio and host-size dependent parasitoid size among strains of *S. endius* or among species of *Spalangia*.

Introduction

Hymenopterans are haplodiploid: sons develop from unfertilized eggs and daughters from fertilized eggs. Thus, hymenopterans can control the sex ratio of their offspring by controlling fertilization. In hymenopteran parasitoids, the offspring develop on or in a host, which is usually an insect. In solitary species of parasitoids, by definition, one offspring develops on each host; thus, the parasitoid's size may increase with the size of its host. If being large increases a female's fitness while having little effect on a male's fitness, there will be selection for mothers to oviposit daughters on large hosts and sons on small hosts (Charnov et al. 1981). This adaptive explanation for the evolution of sex ratio manipulation in parasitoids is the host size model. The host size model is a variation of an earlier hypothesis for sex ratio manipulation in response to resource availability, the Triver's and Willard (1973) hypothesis, in which resource availability is measured by maternal condition and for polygynous mammals.

The host size model is tested here with the solitary parasitoid wasp Spalangia endius (Rueda and Axtell 1985). S. endius is of special interest because previous studies suggested that it does not manipulate sex ratio in response to host size, in contrast to the host size model and in contrast to most solitary parasitoid wasp species that have been tested (reviewed in King 1987, 1989, 1993; Godfray 1994). There was no relationship between offspring sex and host size either in laboratory experiments with S. endius from Southwell, England (Donaldson and Walter 1984) or in field collections of S. endius from Indiana, USA (King 1991b). In field collections, however, host size is potentially confounded with other variables, such as host age (King 1991). In contrast, in comparable studies of the congener S. cameroni, including a field study, sex ratio does change with host size, and in the direction that the host size model predicts (King 1988, 1990). For both species of Spalangia, differential mortality of the sexes has been ruled out (Donaldson and Walter 1984; King 1988, 1990, and see Results below). Thus, observed sex ratio patterns, as determined by counting emerged adult offspring, reflect the sex ratio at oviposition.

If there really is no manipulation of sex ratio in S. endius or if there is variation among strains of S. endius, this is of interest because variation among species or strains in whether or not they manipulate would facilitate use of the comparative approach (Harvey and Pagel 1991). Here we use a strain of S. endius from Florida and a strain from India to retest the host size model prediction that daughters emerge from larger hosts than sons when mothers receive two host size classes. For the Florida strain, we also examine whether daughters still emerge from larger hosts than sons when mothers receive only one host size class and whether differential mortality can be ruled out as an explanation for the relationship between parasitoid sex and host size.

We also expand on the previous studies of S. endius by looking in greater detail at the host size model assumption that host size has a greater effect on female than on male reproductive success. For both strains we test for a positive effect of host size on parasitoid size not only for females, as Donaldson and Walter (1984) did, but also for males. In addition, for the first time in this species, we also examine the effect of host size on more direct measures of fitness, using the Florida strain. Fitness measures that we examine are number of offspring, mating success, longevity, development duration, wing loading, and fluctuating asymmetry in wing dimensions.

Wing loading is weight per wing area (Starmer and Wolf 1989). Lower wing loading may decrease the cost of flight, which may make more energy available for reproduction and may improve ability to disperse in search of hosts or mates (Epting and Casey 1973; Kammer and Heinrich 1978; Ruohomäki 1992). Fluctuating asymmetry is "the deviation of a morphological character of an individual from perfect symmetry" when the deviation of the population has a mean of zero and is normally distributed (Mfller 1994). Fluctuating asymmetry is thought to reflect stress during development and has been negatively associated with fitness in a number of different organisms (reviewed in Mfller 1997). The effect of host size on a parasitoid's fluctuating asymmetry has not previously been examined. Because smaller hosts provide less energy for parasitoid development, we predicted that developing on a smaller host would increase fluctuating asymmetry.

Methods

General Methods

Except where noted otherwise, the Spalangia endius were a Florida strain obtained from C. Geden, who collected them from a poultry farm in Zephyr Hills, Florida in March 1996. Parasitoids from laboratory generations one to four were used in the experiments described here.

Parasitoids were propagated in plastic food storage containers with cloth covered "windows" for ventilation and were kept in an environmental chamber at about 27°C, 12L:12D. A natural host, the pupal stage of Musca domestica, was used as the host. Each container had honey smeared on the sides as a food source for the adult parasitoids. To generate parasitoids for experiments, petri dishes with variable numbers of hosts were placed with the parasitoids for parasitization for two days. Each host from which no adult M. domestica emerged was isolated in a glass test tube, which was checked daily for parasitoid emergence. Parasitoids used in experiments were newly emerged (less than 2 days old) and had no previous contact with other parasitoids (excluding mating). Mated females were generated just prior to use in experiments by pairing virgin females each with a virgin male and observing mating.

Small and large hosts were produced by manipulating the volume of host eggs per volume of host media following King (1988). All hosts used in experiments were less than two days old (from when the host pupa took on an ovoid shape and stopped movement), but age was matched to within the nearest day among treatments within each replicate.

Hosts were presented to females for 24 h periods in glass shell vials (7 cm high, 2 cm diameter) plugged with cotton or in plastic vials (40 mm high, 36 mm top diameter, 27 mm bottom diameter), with a drop of honey as food. Vial type has no significant effect on offspring production (Napoleon 1998).

Mean \pm standard error, range are presented. Nonparametric tests were employed when the assumptions of normality were not met.

Sex Ratio and Parasitoid Size

This experiment was designed to test the host size model prediction that daughters emerge from larger hosts than do sons. This experiment also provided data relevant to

the host size model assumption that developing on a larger host provides a greater gain in reproductive success for daughters than sons. Specifically, this experiment looked at the effect of host size on three potential indicators of parasitoid fitness, parasitoid size, a wing loading index, and fluctuating asymmetry of wing dimensions.

Thirty mated females were each presented with ten large and ten small hosts for 24 h for each of two days. Potentially parasitized hosts were removed and isolated. After parasitoids emerged and died, one male and one female offspring were randomly chosen from each mother. Each offspring's host length and width were measured using an ocular micrometer on a dissecting microscope. Then host volume was calculated with the equation for a prolate spheroid, $\frac{2}{3}\pi(\text{host width}/2)^2(\text{host length})$ (Holdaway and Smith 1932). The following measurements were taken from the offspring: head width and area; thorax area; and wing width, length, and area for both fore and hind, left and right, wings. Each body part was placed on double-sided sticky tape on a slide, projected onto a digitizing tablet with a microprojector, and measured using Sigma Scan 3.90 for DOS. Width and length were measured at the widest and longest parts, respectively. Areas were measured by tracing around the circumference of the body part.

Head width is often used as a measure of parasitoid size, but we used head area instead because it shows more variation. Conclusions are unaffected by using head width, the measure used in studies of *Spalangia* by Donaldson and Walter (1984), King (1991a), and King and Lee (1994). Head area was significantly positively correlated with all the other parasitoid measurements in males and with all the other parasitoid measurements except forewing length in females (Napoleon and King unpublished). Also, head size correlates significantly and positively with body weight in *S. cameroni* (King 1988).

A wing loading (weight per wing area) index was generated using the cubic square root of head area in place of weight (see Starmer and Wolf 1989 for a similar index). Wing loading has been calculated using either wing area or wing and thorax area (e.g., Starmer and Wolf 1989); the former is used here, but conclusions were the same when thorax area was included.

For each wing measurement, width, length, and area, for both fore and hind wings, we first tested whether the population mean of the left minus the right wing measurement was normally distributed with a mean of zero, i.e., whether the measurement exhibited fluctuating asymmetry. The wing measurements that met these criteria for both males and females were forewing width and length and hindwing width. Only these three wing measurements were used in subsequent analyses of fluctuating asymmetry. Conclusions were unaffected by looking just at wing length, the measure for which there is empirical support for an effect on flight performance, at least for a bird species (Swaddle 1997).

There was no correlation between a mother's daughter and son in host volume or head area; so to maximize statistical power, individual offspring, rather than mother, was used as the sampling unit (Zar 1984). Thus, whether the volume of the host from which offspring emerged was greater for daughters than for sons was tested with an independent t-test. ANCOVA (analyses of covariance) were used to examine the effects of host volume (covariate) and parasitoid sex (factor) on parasitoid size and

then on the parasitoid wing loading index. MANCOVA (multivariate analysis of covariance) was used to examine the effects of host volume and parasitoid sex on absolute fluctuating asymmetry of the three wing measurements. Conclusions were the same when analyses were restricted to the range of host volumes from which both daughters and sons emerged (to meet the ANCOVA assumption of independence of the covariate and factor).

For a second strain of *Spalangia endius*, which was from India, we again tested whether daughters emerged from larger hosts than did sons and whether both daughters and sons were larger when they developed on larger hosts. The India strain was obtained from C. Geden in *Musca domestica* pupae and had originally been collected from a poultry farm in Bangalore, India. Parasitoids from generations 114 to 116 were used in the experiments described here.

Differential Mortality

Differential mortality of daughters versus sons was examined by comparing offspring survivorship between mated mothers and virgin mothers. Mated mothers produce both daughters and sons; virgin mothers produce only sons. (About 10% of virgin females in an Australian colony of *S. endius* produce some daughters (Bandara and Walter 1993), but none have in our experience with the strain used here, $n > 100$ mothers (this study; King submitted).) If, for example, there is greater mortality of daughters than of sons, offspring of mated females will have lower survivorship than offspring of virgin females. Each of thirty replicates included four treatments, a virgin female or a mated female presented with either twenty small hosts or twenty large hosts. After 24 h, the hosts were removed. Ten were frozen and later dissected and the number of eggs per host determined. Parasitoids were allowed to complete development in the other ten hosts, and the number of adult offspring per host was determined. Offspring survivorship from egg to emergence as an adult was estimated for each mother as the number of adult offspring per host divided by the number of eggs per host. The effect of mating status on survivorship was examined within each host size class (small, large) rather than with a two-factor ANOVA (analysis of variance) because the assumption of normality was not met and because statistical power would be low for mating status due to host size being a random effect.

Development Duration

This experiment was designed to test for a difference between female and male parasitoids in the effect of host size on duration of parasitoid development from oviposition to emergence from the host as an adult. Each of four petri dishes of hosts of variable size was exposed to a colony container of parasitoids at about 29°C, for only 4 h to minimize differences among parasitoid eggs in when they were oviposited. The petri dish was then removed and development allowed to take place at about 22°C, with each potentially parasitized host isolated in a test tube plugged with cotton. Cooler temperature lengthens development (Shibles 1969), which we hoped would accentuate any differences in development duration. Accentuating differences was important because in previous studies of the congener *S. cameroni* and the confamilial *M. raptor*, statistically significant effects of host size on duration of development were

small, less than the precision of measurement, making them difficult to interpret (King 1988, 1990; Seidl and King 1993). The isolated hosts were checked daily for parasitoid emergence. Parasitoids were sexed and host volume was determined. ANCOVA assumptions were not well met, so the relationship between development duration and the parasitoid's host volume was analyzed within each parasitoid sex.

Longevity

This experiment was designed to test whether the host size on which a parasitoid had developed affected its adult longevity. Longevity was examined under the condition of no food (honey) because in earlier studies with *S. cameroni* there was some evidence of a significant effect for males without honey (King and King 1994), but no significant effect for males or females with honey (King 1988). Newly emerged parasitoids from small hosts and from large hosts were each isolated in test tubes plugged with moist cotton. Each day the cotton was rewet and parasitoid deaths were recorded. The effect of host size on longevity was examined within each parasitoid sex rather than with a two factor ANOVA because the assumption of normality was not met, and sample sizes were not uniform among cells. Female longevity was also examined in the offspring production experiment (below).

Male Mating Success

This experiment was designed to test whether a male's mating success increased with the size of the host on which he had developed. Male mating success was measured by number of daughters because production of daughters, but not sons, requires sperm. Males, which had developed on a range of host sizes, were each presented with seven virgin females for one hour in a glass shell vial plugged with cotton. Next each female was isolated with 10 large hosts for 24 h. The offspring were allowed to develop into adults, and the number of daughters was counted for each father. Number of daughters was regressed against the father's host volume.

Offspring Production

This experiment was designed to test whether offspring production increased with the size of the host on which the mother had developed. For each of five days, each of thirty females were presented with fifteen large hosts. Offspring production over a female's first five days is positively correlated with lifetime offspring production in *S. cameroni* (King 1988). Total number of adult offspring was regressed against the mother's host volume, using curvilinear regression analysis, as suggested by visual inspection of the data.

After the five days of hosts, the mothers were kept in vials plugged with moist cotton. Each day the cotton was rewet and parasitoid deaths were recorded. Longevity was regressed against the size of host on which the mother had developed.

Results Sex Ratio and Parasitoid Size In the Florida strain, daughters emerged from larger hosts than did sons ($18.7 \text{ mm}^3 \pm 1.19$, 7.3 - 30.6, $n = 28$ versus 11.1 ± 0.89 , 6.2 - 24.4, $n = 27$; $U = 144.0$, $2tP < 0.001$). For 20 of 26 mothers, daughters emerged from larger hosts than did sons; and for 6 mothers, daughters emerged from smaller hosts

than did sons (sign test, $1tP = 0.005$, $N = 26$). The absolute difference between the daughter's and the son's host size was of greater magnitude for the 20 mothers whose daughters emerged from larger hosts than for the 6 mothers whose daughters emerged from smaller hosts (10.3 ± 1.2 , $0.4 - 17.5$ versus 3.0 ± 1.0 , $0.5 - 6.6$; $t = t.91$, $df = 24$; $2tP < 0.001$).

Offspring sex ratio and clutch size did not differ between a mother's first versus second day of oviposition, and overall offspring sex ratio was female-biased: Number of sons per day was 1.8 ± 0.32 , range 0 - 14, with no significant difference between the first and second day of oviposition ($t = 0.16$, $df = 56$, $2tP = 0.89$). Number of daughters per day was 13.0 ± 0.46 , range 0 - 19, again with no significant difference between days ($t = 0.26$, $df = 56$, $2tP = 0.79$).

The head area of parasitoid offspring increased with increasing host volume ($F_{1,52} = 5.64$, $P = 0.02$, Fig. 1), and the rate of increase was independent of parasitoid sex ($F_{1,51} = 0.24$, $P = 0.63$). Females were larger than males ($F_{1,52} = 88.10$, $P < 0.001$, Fig. 1).

The wing loading index of parasitoid offspring was independent of host volume ($F_{1,29} = 0.89$, $P = 0.35$), and there was no significant interaction between offspring sex and host volume ($F_{1,28} = 0.97$, $P = 0.33$). Females had a higher wing loading index than males ($F_{1,29} = 24.71$, $P < 0.001$). Absolute fluctuating asymmetry of offspring wing measurements was independent of host volume ($F_{3,35} = 0.73$, $P = 0.54$) and offspring sex ($F_{3,35} = 0.22$, $P = 0.88$), and there was no significant interaction between offspring sex and host volume ($F_{3,34} = 1.86$, $P = 0.16$).

In contrast to the Florida strain, for the India strain there was no significant difference in the size of hosts that daughters versus sons emerged from ($15.4 \text{ mm}^3 \pm 0.85$, $6.8 - 23.4$, $n = 31$ versus $14.8 \text{ mm}^3 \pm 0.90$, $8.0 - 22.3$, $n = 31$; $t = 0.53$, $2tP = 0.60$). Of the 31 mothers, for 17 mothers, daughters' hosts were larger than sons' and for 13 the reverse (sign test $1tP = 0.29$). The maximum size of host from which parasitoids emerged in the India strain was less than for the Florida strain. However, this does not appear to explain the lack of difference in host size between parasitoid females and males in the India but not the Florida strain. When analysis of the Florida strain data is restricted to less than or equal to the maximum host size from which the India strain emerged, females still emerged from significantly larger hosts than did males ($t = 4.73$, $df = 47$, $1tP < 0.001$) and the difference in host size between females and males was still about 7 mm^3 .

As in the Florida strain, head area increased with increasing host volume in the India strain ($F_{1,59} = 14.43$, $P < 0.001$, Fig. 2), and the rate of increase was independent of parasitoid sex ($F_{1,58} = 0.47$, $P = 0.49$). Females were again larger than males ($F_{1,59} = 156.2$, $P < 0.001$).

Differential Mortality

For both small hosts and large hosts, there was no significant effect of maternal mating status on offspring survivorship (small hosts: $U = 424.5$, $2tP = 0.71$; large hosts: $t = 1.52$, $df = 47$, $2tP = 0.14$). Offspring sex ratio did not differ between mated mothers that received only large hosts and those that received only small hosts ($t = 0.77$, $df = 57$, $2tP = 0.45$).

Effects of Host Size on Parasitoid Fitness

Female *S. endius* took longer to develop on larger hosts, about 2 days longer; whereas male development duration was not influenced by host volume (Fig. 3).

Longevity did not differ significantly between males that developed on large versus small hosts (Mann-Whitney $U = 309.0$, $2tP = 0.79$). Males lived 7.4 ± 0.29 days, range 3 - 15 days, $n = 53$. However, in the absence of hosts, females that developed on large hosts lived longer than females that developed on small hosts (8.6 ± 0.34 days, 6 - 14, $n = 35$ versus 7.3 ± 0.25 days, 4 - 11, $n = 45$; $t = 3.20$, $df = 78$, $2tP = 0.002$). In contrast, in the offspring production experiment, in which females received hosts for their first five days, longevity was independent of the size of host on which the female had developed ($R^2 = 0.009$, $df = 28$, $2tP = 0.61$); mean longevity was 9.1 ± 0.43 days, range 5 - 13.

Male mating success, as measured by daughter production, was not significantly related to the size of host on which the male had developed ($R^2 = 0.022$, $df = 28$, $2tP = 0.43$). With seven mates, each male produced an average of 32.2 ± 2.25 daughters, range 0 - 51, $n = 30$.

There was a significant curvilinear relationship between a mother's host volume and her offspring production, with production increasing with increasing maternal host volume except at the largest host volumes (Fig. 4). Offspring sex ratio (proportion of sons) averaged 0.19 ± 0.012 , 0.04 - 0.38 and was not significantly related to the mother's host volume ($R^2 = 0.038$, $df = 28$, $2tP = 0.30$).

Discussion

In the Florida strain of *S. endius*, daughters emerged from larger hosts than sons when mothers received both small and large hosts simultaneously. This pattern appeared to result from the mother's ovipositional choice and not from differential mortality of the sexes during development (this study; King submitted). Thus, the Florida strain appears to meet the host size model prediction.

Whether the Florida strain meets the model's assumption of a greater effect of host size on female versus male fitness is less clear. Both female and male parasitoids were larger when they developed on larger hosts. However, how developing on a larger host affects a female's overall fitness is not simple to predict because different measures of fitness differed in the direction and pattern of their relationship with host size. Developing on a larger host increased a female's offspring production from small to medium size hosts, although offspring production did not increase with increasing host size for the largest hosts. Developing on a larger host had no effect on female longevity for females that received hosts for their first five days, but increased longevity for females without any exposure to hosts. Greater longevity may mean greater ability to survive until the female finds hosts. *Spalangia* females emerge from hosts with some eggs and can produce additional eggs throughout life (Gerling and Legner 1968). When no hosts are encountered, some eggs are resorbed. In *S. cameroni*, females from larger hosts have more eggs at emergence (King and King 1994). Thus, the greater longevity of female *S. endius* from larger hosts may result from such females having more eggs available for resorption.

On the other hand, developing on a larger host may be disadvantageous for females in terms of development duration. Females took longer to develop on larger hosts, about 10% longer from the largest versus the smallest hosts at about 22°C; the development effect may be less at warmer temperatures. Longer development is expected to decrease fitness if population size is increasing (Lewontin 1965; Caswell and Hastings 1980; Stearns 1992, p34-35), as may often be the case for Spalangia (King 1996). Longer development could also decrease fitness by increasing the length of exposure to larval mortality (Stearns 1992, p149; Giske et al. 1993).

Sex ratio manipulation in response to host size can be adaptive through an advantage to females of developing on larger hosts, as the original host size model (Charnov 1979; Charnov et al. 1981) and data on most other species suggest (reviewed in King 1993). It can also be adaptive via an advantage to males of developing on smaller hosts (King and King 1994; King and Lee 1994). However this does not appear to be the case for the Florida strain of S. endius because measures of male fitness -- daughter production, longevity, development duration, wing loading, and fluctuating asymmetry of wings -- were independent of host size.

The difference in host size between the sexes in the Florida strain of S. endius and the positive effect of host size on parasitoid size in the Florida and the India strain are consistent with data on most species of parasitoid wasp (King 1987, 1989, 1993; Lampson et al. 1996; Chow and Mackauer 1996), including the most comparable study of the congener S. cameroni (Table 1: Indiana (lab)). However, these results differ from results with the Southwell strain of S. endius (Donaldson and Walter 1984). Our finding that offspring sex ratio was unrelated to host size when females received only one host size is consistent with data on the Southwell strain.

The effects of host size on parasitoid fitness in the Florida S. endius were only partially consistent with S. cameroni data on the same host species (King 1988; King and King 1994). Like S. endius, S. cameroni males from smaller hosts do not inseminate more females or live longer (King 1988; King and King 1994), in contrast to some other parasitoid wasp species (e.g., van den Assem 1971; Jones 1982; Heinz 1991). In both S. endius and S. cameroni a female's host size has no effect on her wing loading (King and Lee 1994). In contrast, wing loading decreases with host size in male S. cameroni, but there was no effect of host size on a wing loading index in male S. endius. Effects of host size on wing loading have not been examined in other species. The positive effects of host size on longevity and offspring production in Florida S. endius females are consistent with most other parasitoid wasp species (references in King 1987, 1993; Lampson et al. 1996), but not with S. cameroni, which shows no effect (King 1988; King and King 1994).

In S. endius, host size had a positive effect on length of female but not male development. In contrast, there is no clear and consistent effect for either sex in S. cameroni and other sex ratio manipulating species that have been tested (reviewed in King 1993). In addition, the effect of host size on development duration in other parasitoid wasp species shows no consistent pattern with regards to the presence or absence of sex ratio manipulation (King 1993). Our ability to detect an effect of host size on development duration may have been greater in S. endius than in the other species due to our having lengthened development duration with cold (see Methods).

The differences between S. endius and S. cameroni in the effect of host size on various aspects of fitness suggest that selection on sex ratio manipulation differs between the two species. If sex ratio manipulation is adaptive in these species, evidence to date suggests that in S. endius it may be through a benefit to daughters of developing on large hosts; whereas in S. cameroni it may be through a benefit to sons of developing on small hosts (King 1988; King and King 1994; King and Lee 1994).

In the India strain of S. endius, daughters did not emerge from larger hosts than sons even though each mother received both small and large hosts simultaneously. Yet both female and male parasitoids were larger when they developed on larger hosts. The absence of a sex ratio effect in the India strain is not consistent with the Florida strain, the host size model, comparable S. cameroni studies (Table 1), and most other parasitoid wasps studied (references in King 1989, 1993). In contrast, the positive effect of host size on parasitoid size in the India strain is consistent with all of these (the Florida strain, the host size model, comparable S. cameroni studies, and most other parasitoid wasps studied), but contrasts with the lack of an effect in Donaldson and Walter's (1984) Southwell strain.

Our results together with previous studies reveal no consistent connection between host-size-dependent sex ratio and host-size-dependent parasitoid size among strains of S. endius or among species of Spalangia. Because experimental protocol was the same for both strains in our study, the differences between the Florida and India strains probably reflect genetic differences; and for these strains there also was no consistent association between sex ratio response to host size and effect of host size on parasitoid size. The strain differences may reflect the difference in their geographic origin or in their time in culture, although there is no evidence of time in culture affecting host-size dependent sex ratio in S. cameroni (King 1994). Strain differences in sex ratio response to parasitized versus unparasitized hosts have been found in the confamilial wasp Nasonia vitripennis (Orzack 1990; Parker and Orzack 1985). Whether phylogenetic analysis can explain sex ratio manipulation patterns among strains and species of Spalangia better than does the host size model, i.e., better than does adaptation, remains to be explored.

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Table 1. For *Spalangia* parasitizing the host species *Musca domestica*, host size effect on sex ratio (proportion of sons) when each mother received both small and large hosts and host size effect on parasitoid size.

Parasitoid Species	Sex Ratio	Parasitoid Size	Reference
<u>S. endius</u>			
Southwell (lab)	none	none for females males untested	Donaldson and Walter 1984
Indiana (field)	none		King 1991b
India (lab)	none	positive	this study
Florida (lab)	negative	positive	this study
<u>S. cameroni</u>			
Australia (lab)		none	Legner 1969 ¹
Indiana (lab)	negative	positive	King 1988, 1994 King and Lee 1994
Indiana (field)	negative	positive for males none for females ²	King 1991a
<u>S. nigra</u>			
California (lab)		none	Legner 1969 ¹

¹Hosts were long compared to the other studies

²P = 0.11, positive direction

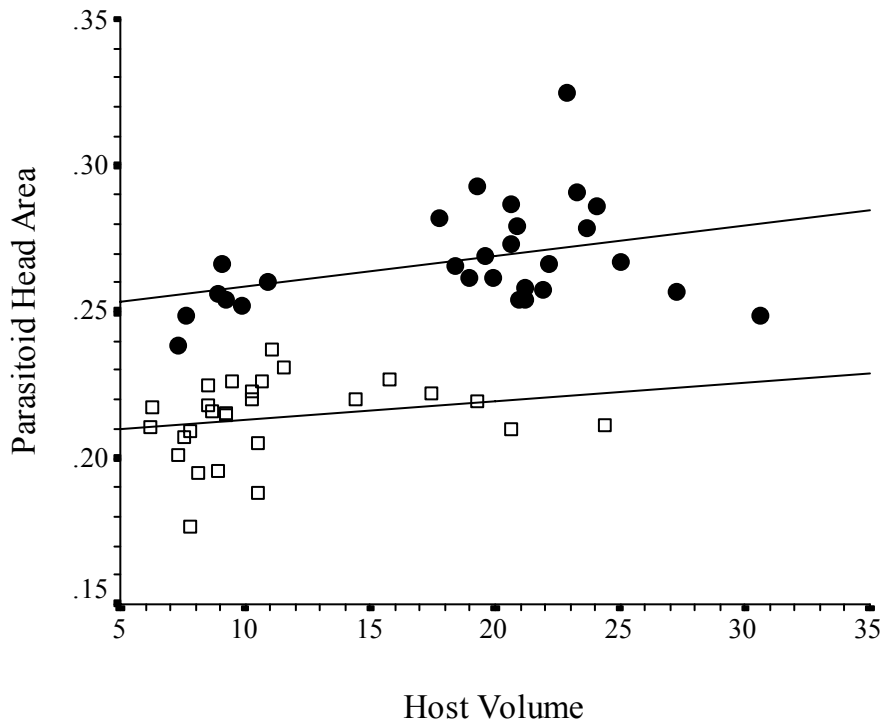


Fig. 1. The effect of host volume (mm³) on parasitoid head area (mm²) in the Florida strain. o = females, = males.

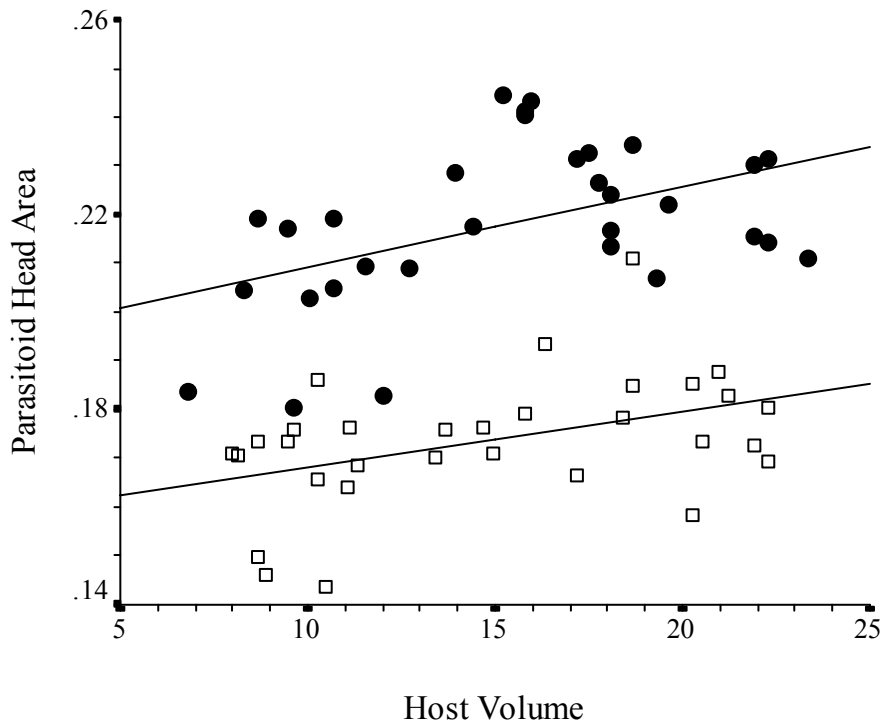


Fig. 2. The effect of host volume (mm³) on parasitoid head area in the India strain. o = females, = males.

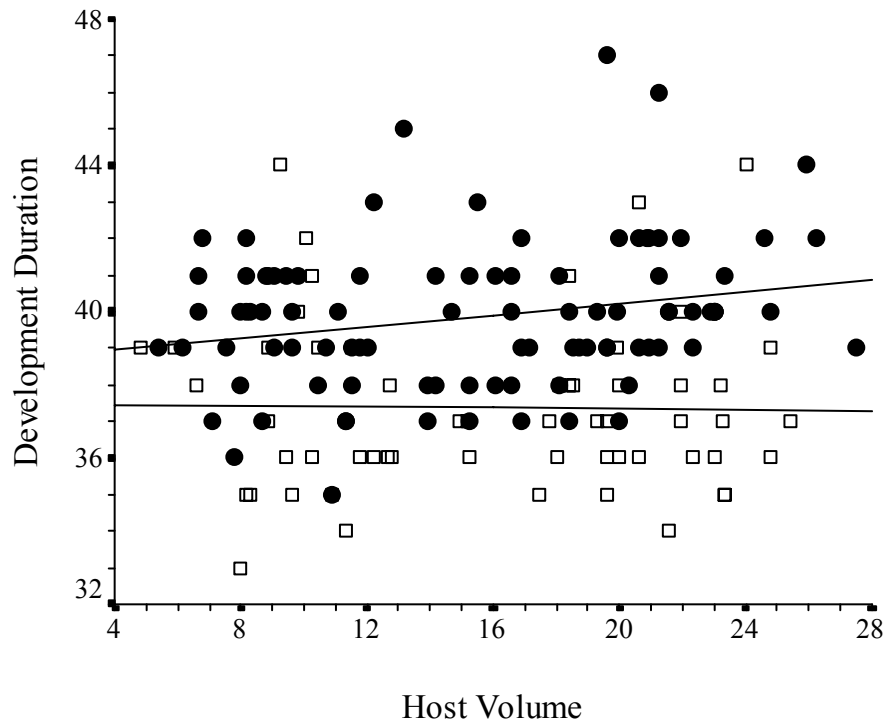


Fig. 3. The effect of host volume (mm^3) on parasitoid development duration (days); females (o): $R^2 = 0.052$, $y = 0.081x + 38.62$, $df = 92$, $2tP = 0.01$.; males (): Spearman rank correlation = 0.02, $n = 57$, $2tP = 0.87$. Note that the male line is nonsignificant and provided only for heuristic purposes.

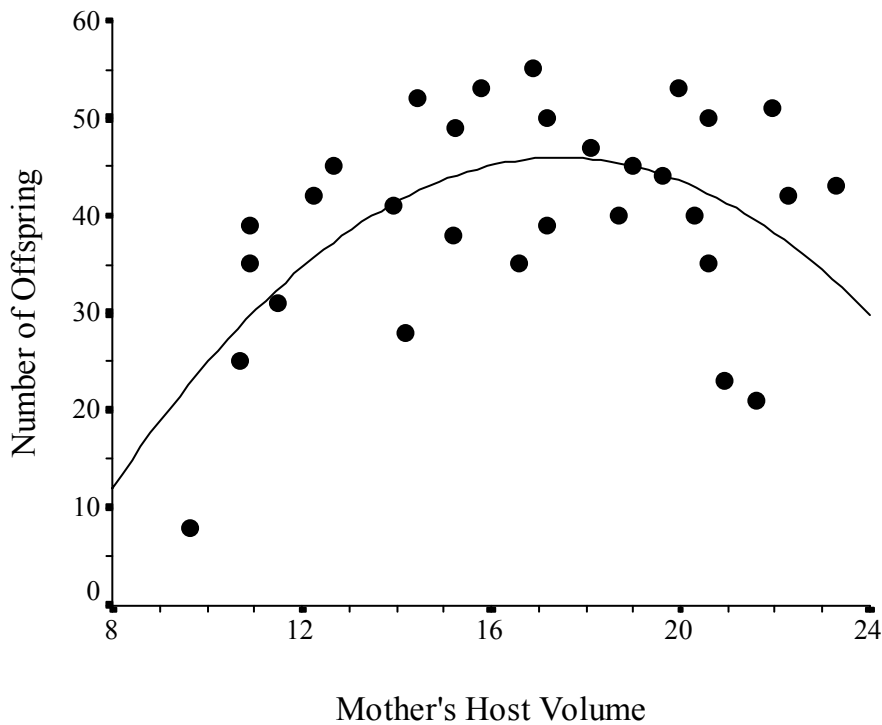


Fig. 4. The effect of maternal host volume (mm^3) on offspring production (total number of offspring produced in 5 days). $R^2 = 0.33$, $y = 13.19x - 0.38x^2 - 69.20$, $2tP < 0.01$.