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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 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. For females, developing on a larger host (1) increased offspring production, except for the largest hosts, (2) increased longevity, (3) lengthened development, and (4) had no effect on wing loading. For males, development on a larger host had no effect on any measure of male fitness – mating success, longevity, development duration, or wing loading. In contrast, a strain from India showed no difference in the size of hosts from which daughters versus sons emerged, although both female and male parasitoids were 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*.

Key words Sex ratio · Host size · Parasitoid wasp · Adaptation

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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, usually an insect. In solitary species of parasitoids, by definition, one offspring develops on each host; thus, parasitoid size may increase with host size. 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 called the host size model. It is a variation of an earlier hypothesis for sex ratio manipulation in response to resource availability, the Trivers 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* parasitizing *Musca domestica* pupae (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. 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 predicted by the host size model (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 in manipulation among species or strains would facilitate the use of the comparative approach (Harvey and Pagel 1991). Here we use a strain of *S. endius* from Florida and one 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 (Donaldson and Walter 1984), but also for males. In addition, for the first time in this species, we also examine, using the Florida strain, the effect of host size on more direct measures of fitness: number of offspring, mating success, longevity, development duration, and wing loading. 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 the ability to disperse in search of hosts or mates (Epting and Casey 1973; Kammer and Heinrich 1978; Ruohomäki 1992).

Methods

General methods

Except where noted otherwise, *S. endius* was a Florida strain obtained from C. Geden, collected 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, 12 L:12 D. A natural host, the pupal stage of *M. 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 2 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 each virgin female 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 2 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 ± SE and 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 for sons. Specifically, this experiment looked at the effect of host size on two potential indicators of parasitoid fitness, parasitoid size and a wing loading index.

On each of 2 successive days, each of 30 females was presented with 20 hosts, 10 small and 10 large. Potentially parasitized hosts were removed and isolated. After parasitoids emerged and died, one male and one female offspring were randomly chosen from each mother. Length and width of each offspring's host were measured using an ocular micrometer on a dissecting microscope. Then host volume was calculated with the equation for a prolate spheroid, $2/3\pi(\text{host width}/2)^2(\text{host length})$ (Holdaway and Smith 1932). The following measurements were taken from the offspring: head width and area; thorax area; 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 (M.E. Napoleon and B.H. King, unpublished data). In addition, 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.

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. Analyses of covariance (ANCOVAs) 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. 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 strain of *S. endius* 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 *M. 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 with $n > 100$ mothers (this study; B.H. King, unpublished data)] 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 20 small hosts or 20 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 10 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 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 adult emergence from the host. 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 in timing of oviposition among parasitoid eggs. 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 *Muscidifurax 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 parasitoid 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 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 analysis of variance 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 (see 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 as 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 1 h in a glass shell vial plugged with cotton. Next, each female was isolated with ten 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 5 days, each of 30 females was presented with 15 large hosts. Offspring production over a female's first 5 days is positively correlated with lifetime offspring production in *S. cameroni* (King 1988). The 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 5 days of exposure to 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 ± 1.19 mm^3, 7.3–30.6, $n = 28$ versus 11.1 ± 0.89, 6.2–24.4, $n = 27$; $U = 144.0$, two-tailed $P < 0.001$). For 20 of 26 mothers, daughters emerged from larger hosts than did sons; for the other 6 mothers, the reverse was the case (sign test, one-tailed $P = 0.005$, $n = 26$). 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, $df = 24$; two-tailed $P < 0.001$).

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 ($t = 0.16$, $df = 56$, two-tailed $P = 0.89$). Number of daughters per day was 13.0 ± 0.46, range 0–19, again with no significant difference between days ($t = 0.26$, $df = 56$, two-tailed $P = 0.79$).

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 ($F_{1,29} = 24.71$, $P < 0.001$).

In contrast to the Florida strain, for the India strain there was no significant difference in the size of hosts from which daughters versus sons emerged (15.4 ± 0.85 mm^3, 6.8–23.4, $n = 31$ versus 14.8 ± 0.90, 8.0–22.3, $n = 31$; $t = 0.53$, two-tailed $P = 0.60$). For 17 of the 31 mothers, daughters' hosts were larger than sons' and for 13, the reverse was found, and for 1 mother there was no difference (sign test one-tailed $P = 0.29$). 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 former 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 ($t = 4.73$, $df = 47$, one-tailed $P < 0.001$) 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 and large hosts, there was no significant effect of maternal mating status on offspring survivorship (small hosts: $U = 424.5$, two-tailed $P = 0.71$; large hosts: $t = 1.52$, $df = 47$, two-tailed $P = 0.14$). Offspring sex ratio did not differ between mated mothers that received only large hosts and those that received only small hosts ($t = 0.77$, $df = 57$, two-tailed $P = 0.45$).

Effects of host size on parasitoid fitness

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

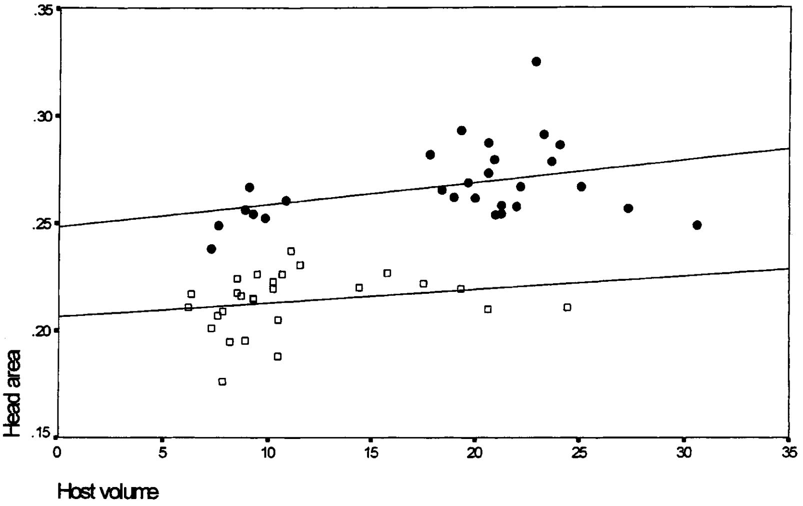

Fig. 1 Effect of host volume (mm^3) on parasitoid head area (mm^2) in the Florida strain (*circles* females, *squares* males)

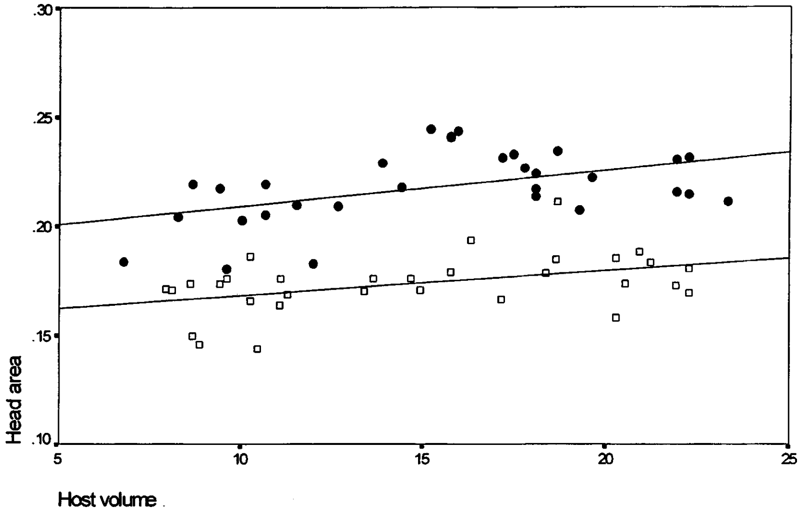

Fig. 2 Effect of host volume (mm^3) on parasitoid head area in the India strain (*circles* females, *squares* males)

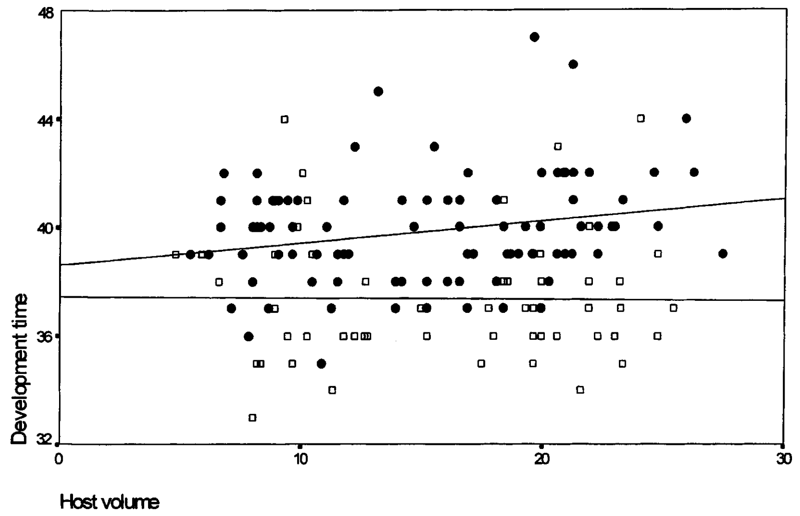

Fig. 3 Effect of host volume (mm^3) on parasitoid development duration (days). Females (*circles*): $R^2 = 0.052$, $y = 0.081x + 38.62$, $df = 92$, two-tailed $P = 0.01$. Males (*squares*): Spearman rank correlation = 0.02, $n = 57$, two-tailed $P = 0.87$. Note that the male line is nonsignificant and provided only for heuristic purposes

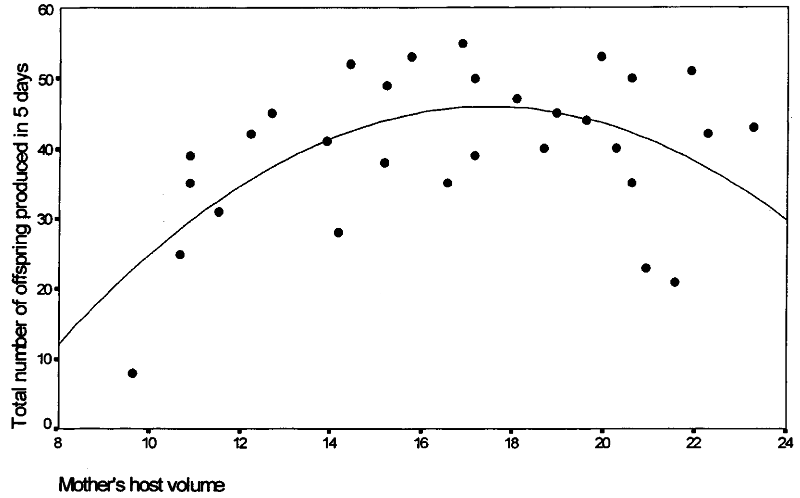

Fig. 4 Effect of maternal host volume (mm^3) on offspring production. $R^2 = 0.33$, $y = 13.19x - 0.38x^2 - 69.20$; two-tailed $P < 0.01$

Longevity did not differ significantly between males that developed on large versus small hosts (Mann-Whitney $U = 309.0$, two-tailed $P = 0.79$). 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, $n = 45$; $t = 3.20$, $df = 78$, two-tailed $P = 0.002$). In contrast, in the offspring production experiment, in which females received hosts for their first 5 days, longevity was independent of the size of host on which the female had developed ($R^2 = 0.009$, $df = 28$, two-tailed $P = 0.61$); 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 ($R^2 = 0.022$, $df = 28$, two-tailed $P = 0.43$). 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 ($R^2 = 0.038$, $df = 28$, two-tailed $P = 0.30$).

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; B.H. King, unpublished data). Thus, the Florida strain appears to meet the host size model prediction.

Whether the Florida strain meets the model 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, predicting how development on a larger host affects a female's overall fitness is not simple because different measures of fitness differed in the direction and pattern of their relationship with host size. As host size increased from small to medium, a female's offspring production increased, but ceased to do so on the largest hosts. Developing on a larger host had no effect on female longevity for females that received hosts for their first 5 days, but increased longevity for females without any exposure to hosts. Greater longevity may enable the female to survive until she 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 their 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 on 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, pp. 34–35), 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, p. 149; Giske et al. 1993).

Sex ratio manipulation in response to host size can be adaptive through an advantage to females 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, and wing loading – 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; Chow and Mackauer 1996; Lampson et al. 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 the 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).

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
S. endius			
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
S. cameroni			
Australia (lab)		None	Legner 1969[a]
Indiana (lab)	Negative	Positive	King 1988, 1994; King and Lee 1994
Indiana (field)	Negative	Positive for males; none for females (P = 0.11, positive direction)	King 1991a
S. nigra			
California (lab)		None	Legner 1969[a]

[a] Hosts were long compared to the other studies

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 because we 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 the 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 was also 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. There is some evidence against increasing culture duration causing a loss of sex ratio response. There is no evidence of time in culture affecting the host-size-dependent sex ratio in *S. cameroni* (King 1994). Two other parasitoid wasp species, one of which is also a Pteromalidae, exhibit host-size-dependent sex ratios despite more than 40 years in culture (Fujii and Khin Mar Wai 1990). (A literature survey to test for differences in culture time between species with versus without host-size-dependent sex ratios was not pursued because so many studies do not provide information on time in culture; e.g., see references in King 1989). In the confamilial *Nasonia vitripennis*, the sex ratio response to parasitized versus unparasitized hosts for recently cultured lines is similar to the response in 20-year-old strains (Orzack and Parker 1986, 1990). Whether phylogenetic analysis is better than the host size model (i.e., adaptation) in explaining sex ratio manipulation patterns among strains and species of *Spalangia* remains to be explored.

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