



Offspring Sex Ratio and Number in Response to Proportion of Host Sizes and Ages in the Parasitoid Wasp *Spalangia cameroni* (Hymenoptera: Pteromalidae)

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ABSTRACT In rearing parasitoids for biological control releases and in natural populations, female parasitoids may encounter variable distributions of host quality. Here I examine how the proportion of hosts that are small versus large or old versus young affects sex ratio and offspring production of the parasitoid wasp *Spalangia cameroni* Perkins parasitizing *Musca domestica* L. pupae. With increasing proportion of small hosts or old hosts, overall number of offspring did not significantly decrease and the overall proportion that were male (i.e., from small and large hosts combined) did not significantly increase. A greater proportion of sons from small versus large and from old versus young hosts was not restricted to the case of equal numbers of different host types. The proportion of sons produced from small hosts as well as the proportion of sons from large hosts decreased as the proportion of small hosts increased, and the proportion of sons produced from young hosts decreased as the proportion of old hosts increased. These results are relevant to recommendations for rearing *S. cameroni* for biological control releases and to testing evolutionary sex ratio theory, specifically a combined host-quality and local mate competition model.

KEY WORDS *Spalangia cameroni*, biological control, sex ratio, host size, host age

Spalangia cameroni PERKINS parasitizes the pupal stage of certain fly species found in manure or decaying organic matter and associated with humans (Butler et al. 1981, Mullens et al. 1986, Meyer et al. 1991). These fly hosts include some of the most important pests in livestock and poultry production in the United States and worldwide (Busvine 1980, Patterson and Rutz 1986). *Spalangia* is a common natural control agent and is raised and sold commercially for pest control, although applied control is still frequently with insecticides (Rutz and Scoles 1989).

S. cameroni is a solitary parasitoid, meaning it produces one offspring per host (Rueda and Axtell 1985). Older and smaller house fly (*Musca domestica* L.) hosts are lower quality hosts in that they provide less nutrition for offspring development (King 1988, 1990a, 1998), and possibly also for host feeding. Part of the biomass of older fly pupae has been converted to adult body parts that liquid feeders such as *S. cameroni* cannot ingest (Gerling and Legner 1968). Here I use laboratory experiments to examine how different proportions of host sizes or ages affect offspring sex ratio and number in *S. cameroni* parasitizing *M. domestica*.

The effects of host quality on parasitoid wasps have typically been examined by presenting females with equal numbers of two host types or just one type (e.g., references in King 1993, Godfray 1994). However, in

field conditions (King 1990b) and in production of parasitoids for release in biological control programs, females are likely to encounter different proportions of different host types, and this situation is examined here.

In most species of parasitoid wasp that have been examined, including *S. cameroni*, females oviposit a greater proportion of sons in the lower quality hosts when presented with equal numbers of high and low quality hosts (King 1988, 1990a, 1993). Do *S. cameroni* females still produce a greater proportion of sons in small than in large hosts and in old than in young hosts when the proportion of host types is other than half? Does sex ratio from a given type of host and overall sex ratio vary with the proportion of host types? Is production of parasitoid offspring affected by the proportion of host types?

Understanding the effects of host quality in parasitoid wasps is relevant to use of parasitoids in biological control and to understanding the evolution of sex ratios. Host types that result in greater production of parasitoid offspring and more female-biased sex ratios should be preferable when rearing parasitoids for biological control. More female-biased sex ratios may be more effective because adult females kill hosts both by oviposition, and in some species, including *S. cameroni*, also by feeding on host fluids themselves. The pattern of change in sex ratio with changing proportion of parasitized hosts that are low quality is also relevant to

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Table 1. Proportion of sons from small hosts and from large hosts for females presented with different proportions of small (versus large) hosts

Proportion small hosts	Proportion of sons from small hosts		Proportion of sons from large hosts		Sex ratio difference between host sizes		
	Mean \pm SEM	<i>n</i>	Mean \pm SEM	<i>n</i>	<i>t</i>	df	1-tailed <i>P</i>
0.00			0.25 \pm 0.038	22			
0.14	0.58 \pm 0.094	21	0.16 \pm 0.029	21	4.48	19	<0.001
0.29	0.38 \pm 0.068	22	0.21 \pm 0.036	22	2.40	21	0.013
0.43	0.34 \pm 0.049	21	0.17 \pm 0.039	21	3.49	20	0.001
0.57	0.29 \pm 0.036	22	0.25 \pm 0.052	22	0.62	21	0.27
0.71	0.30 \pm 0.025	22	0.14 \pm 0.034	22	3.51	21	0.001
0.86	0.28 \pm 0.030	22	0.056 \pm 0.031	21	5.72	20	<0.001
1.00	0.23 \pm 0.017	22					

n, number of females tested.

testing an adaptive sex ratio model, the combined host-quality and local mate competition model developed by Werren (1984) (See *Discussion*).

Materials and Methods

The North American strain of *S. cameroni* used in this study was from a colony established 9 yr before with wasps that emerged from *M. domestica* and *Stomoxys calcitrans* (L.) pupae collected in Indiana, U.S.A (King 1990b). Voucher specimens are in the insect collection at Purdue University's Department of Entomology. The wasp colony was maintained at 23–28°C, 24 L using *M. domestica* as hosts.

On their first day in an experiment, wasps were newly emerged (<1 d old) and had no previous contact with other wasps, aside from mating. Each female had mated with a virgin male <2 d old. Females were presented with hosts in plastic vials (40 mm high by 36 mm top diameter by 27 mm bottom diameter) for 24 h with a drop of honey on the side of the vial (to simulate a nectar source for females).

The host size experiment examined the effect of proportion of small versus large hosts. Hosts were young. The host age experiment examined the effect of proportion of old versus young hosts. Hosts were large. In both experiments, each female was presented with 28 hosts total. Each female received one of eight treatments: 0, 4, 8, 12, 16, 20, 24, and 28 small, or old, hosts, the other hosts being large or young, depending on the experiment. Sample sizes are in Tables 1 and 3.

Small hosts were about two-thirds the volume of large hosts and were produced by manipulating the amount of host eggs per media (King 1988, King 1996). Young hosts were <24 h old when presented to females (timed from the initiation of pupal tanning); old hosts were 3 d older. The pupal stage lasted about 5 d at experimental temperatures.

Overall offspring sex ratio (proportion of sons from both host types) as well as sex ratio from each host type and the difference in sex ratio between host types were each regressed against the proportion of small or old hosts presented to the female. The proportion of all hosts and hosts of each type from which offspring emerged were also regressed against the proportion of small or old hosts. Where assumptions of normality

and homoscedasticity were not met, transformations were unsuccessful, so analysis was by Spearman rank correlation. Because of its relevance to the combined host-quality and local mate competition model, I also regressed overall sex ratio and sex ratio from each host type not just against the proportion of small or old hosts that a female received but also against the proportion of small or old hosts among the hosts that she parasitized. However, only the former is presented since conclusions from the latter were identical. *P* values are 2-tailed except where noted.

Results

Host Size. Overall proportion of sons was not significantly related to the proportion of hosts that were small ($R^2 < 0.001$, $F = 0.019$; $df = 1, 173$; $P = 0.89$). However, the proportion of sons produced on small hosts and the proportion produced on large hosts both decreased as the proportion of small hosts increased ($r_s = -0.25$, $n = 152$, $P = 0.002$; $R^2 = 0.052$, $F = 8.20$; $df = 1, 149$; $P = 0.005$, $y = 0.24 - 0.15x$; Table 1). Sex ratio can change on each host type without overall sex ratio changing because the latter is not the average of the former since offspring number is not equal between host types. In addition, sex ratio from a given host type necessarily excludes the treatment in which females received only the other host type, whereas the overall sex ratio analysis includes these treatments.

Most females produced a greater proportion of sons from small than from large hosts regardless of the proportion of small hosts, with a significant difference in means by paired *t*-tests for all but the 57% small hosts treatment (Table 1). The difference in proportion of sons from small versus from large hosts was not significantly related to the proportion of small hosts ($r_s = -0.11$, $n = 128$, $P = 0.23$).

The proportion of all hosts (both small and large) that produced offspring did not change with increasing proportion of hosts that were small ($R^2 < 0.001$, $F = 0.068$; $df = 1, 174$; $P = 0.79$) nor did the proportion of small hosts that produced offspring ($r_s = -0.024$, $n = 154$, $P = 0.77$; Table 2). The proportion of large hosts that produced offspring increased with the proportion of small hosts ($r_s = 0.20$, $n = 154$, $P = 0.012$; Table 2).

Table 2. Proportion of hosts from which parasitoid offspring emerged among females presented with different proportions of small (versus large) hosts

Proportion of small hosts	Proportion of small hosts with offspring		Proportion of large hosts with offspring	
	Mean ± SEM	n	Mean ± SEM	n
0.00			0.50 ± 0.026	22
0.14	0.50 ± 0.052	22	0.43 ± 0.037	22
0.29	0.43 ± 0.048	22	0.48 ± 0.028	22
0.43	0.45 ± 0.038	22	0.49 ± 0.035	22
0.57	0.49 ± 0.040	22	0.48 ± 0.030	22
0.71	0.46 ± 0.028	22	0.57 ± 0.044	22
0.86	0.45 ± 0.030	22	0.61 ± 0.056	22
1.00	0.45 ± 0.019	22		

n, number of females tested.

Host Age. Overall proportion of sons did not significantly increase with the proportion of old hosts ($r_s = -0.13, n = 204, P = 0.08$). Sex ratio from old hosts also did not change significantly with the proportion of hosts that were old ($r_s = -0.13, n = 177, P = 0.098$; Table 3). However, the proportion of sons from young hosts decreased as the proportion of old hosts increased ($r_s = -0.39, n = 173, P < 0.001$; Table 3).

Most females produced a greater proportion of sons from old than from young hosts in all treatments except that with 14% old hosts. The difference in proportion of sons from old minus young hosts was statistically significant for some treatments (Table 3). The difference was greatest for females presented with the highest proportion of old hosts ($R^2 = 0.027, F = 4.04; df = 1, 144; P = 0.046$).

The proportion of all hosts (both old and young) that produced offspring was not significantly related to the proportion of old hosts ($R^2 < 0.001, F = 0.018; df = 1, 205; P = 0.89$) and averaged 0.51, range 0.00–0.82, $n = 207$. The proportion of old hosts and the proportion of young hosts that produced offspring also were not significantly related to the proportion of hosts that were old ($R^2 = 0.003, F = 0.61; df = 1, 179; P = 0.44; r_s = -0.029, n = 181, P = 0.69$).

Discussion

In terms of producing *S. cameroni* for augmentative biological control releases, rearing *S. cameroni* on

smaller *M. domestica* hosts does not appear to be disadvantageous. Overall proportion of sons did not increase with the proportion of small or old hosts. Similarly, original collections of this same strain of *S. cameroni* from a poultry house showed no significant change in overall sex ratio across dates differing in the distribution of available host sizes (King 1991). In the current study, using a greater proportion of small hosts also did not consistently decrease parasitoid production. In many other parasitoid wasp species, decreasing host size decreases not only the number but also the quality of offspring (references in Waage 1986, King 1987, Godfray 1994). Specifically, in most species, females that develop on smaller hosts produce fewer offspring. However, this does not appear to be true for *S. cameroni* (King 1988, King and King 1994, King and Lee 1994).

Rearing *S. cameroni* on older *M. domestica* hosts may have some disadvantages. Using a greater proportion of older hosts did not significantly decrease parasitoid production or increase the proportion of males produced in the current study. However, parasitoid production decreased with increasing host age in a previous study using a broader range of host ages (King 1998). In addition, female offspring that develop on older hosts are subsequently able to parasitize fewer hosts under conditions of high host density (King 1998).

In *S. cameroni* the proportion of sons produced from small hosts and the proportion from large hosts both decreased as the proportion of small hosts increased. Similarly, the proportion of sons from young hosts decreased as the proportion of old hosts increased. This host size pattern has also been reported for another parasitoid, *Lariophagus distinguendus* (Foerst.) (Hymenoptera: Pteromalidae) (Werren and Simbolotti 1989). Werren and Simbolotti (1989) interpret their results as support for an adaptive sex ratio model, a combined local mate competition - host quality model (Werren 1984). Like *S. cameroni*, *L. distinguendus* also produces a greater proportion of sons from smaller hosts as described by the original host quality model (Charnov et al. 1981).

S. cameroni exhibits host size-sex ratio patterns similar to *L. distinguendus* despite an apparent difference in a basic assumption of the combined local mate

Table 3. Proportion of sons from old hosts and from young hosts for females presented with different proportions of old (versus young) hosts

Proportion of old hosts	Proportion of sons from old hosts		Proportion of sons from young hosts		Sex ratio difference between host ages		
	Mean ± SEM	n	Mean ± SEM	n	t	df	1-tailed P
0.00			0.31 ± 0.036	25			
0.14	0.26 ± 0.064	25	0.27 ± 0.039	26	0.25	24	0.81 ^a
0.29	0.39 ± 0.052	26	0.24 ± 0.053	26	3.45	25	0.001
0.43	0.27 ± 0.028	24	0.18 ± 0.028	25	1.70	23	0.0515
0.57	0.35 ± 0.050	24	0.24 ± 0.054	24	3.13	23	0.003
0.71	0.28 ± 0.024	26	0.19 ± 0.053	24	1.67	23	0.0545
0.86	0.32 ± 0.053	26	0.11 ± 0.051	23	2.52	22	0.0095
1.00	0.22 ± 0.036	26					

n, number of females tested.

^a Two-tailed because means are in the opposite direction from that predicted.

competition - host quality model. As assumed by the model, a *L. distinguendus* female's reproductive success increases with the size of host on which she develops, at least in the laboratory (Charnov et al. 1981); whereas *S. cameroni*'s does not, even under a broad range of conditions (King and King 1994, King and Lee 1994). Perhaps the assumption of a positive effect of host size on female reproductive success is not critical to the model. This deserves theoretical exploration. In the original host quality model, it is the relative advantage of host quality for females versus males that matters. That is, the model works even if female reproductive success is unaffected by host quality, provided male reproductive success is negatively affected, as may be the case for *S. cameroni* (King and Lee 1994). *S. cameroni* appears to experience partial not full sibmating, but partial sibmating is sufficient for the predictions tested here (Werren 1984, Werren and Simbolotti 1989). A decrease in proportion of sons from each host type with increasing proportion of low quality hosts has not been tested for in other species of parasitoid wasps.

Previous studies have shown that *S. cameroni* produces a greater proportion of sons from small versus large and from old versus young hosts when given equal numbers of host types (King 1988, 1990a, 1994), a pattern consistent with most other species examined (King 1993). The current study demonstrates that this pattern is not restricted to the case in which females receive equal numbers of different host types.

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References Cited

- Busvine, J. R. 1980. Insects and hygiene, 3rd ed. Chapman & Hall, New York.
- Butler, J. F., R. L. Escher, and J. A. Hogsette. 1981. Natural parasite levels in house flies, stable flies, and horn flies in Florida, pp. 61-79. *In* Proceedings, Workshop on Status of Biological Control of Filth Flies. U.S. Dep. Agric.
- Charnov, E. L., R. L. Los-den Hartogh, W. T. Jones, and J. van den Assem. 1981. Sex ratio evolution in a variable environment. *Nature* 289: 27-33.
- Gerling, D., and E. F. Legner. 1968. Developmental history and reproduction of *Spalangia cameroni*, parasite of synanthropic flies. *Ann. Entomol. Soc. Am.* 61: 1436-1443.
- Godfray, H.C.J. 1994. Parasitoids. Princeton University Press, Princeton, NJ.
- King, B. H. 1987. Offspring sex ratios in parasitoid wasps. *Q. Rev. Biol.* 62: 367-396.
- King, B. H. 1988. Sex ratio manipulation in response to host size by the parasitoid wasp *Spalangia cameroni*: a laboratory study. *Evolution* 42: 1190-1198.
- King, B. H. 1990a. Sex ratio manipulation by the parasitoid wasp *Spalangia cameroni* in response to host age: a test of the host-size model. *Evol. Ecol.* 4: 149-156.
- King, B. H. 1990b. Interspecific differences in host (Diptera: Muscidae) size and species usage among parasitoid wasps (Hymenoptera: Pteromalidae) in a poultry house. *Environ. Entomol.* 19: 1519-1522.
- King, B. H. 1991. A field study of host size effects on sex ratio of the parasitoid wasp *Spalangia cameroni*. *Am. Midl. Nat.* 125: 10-17.
- King, B. H. 1993. Sex ratio manipulation by parasitoid wasps, pp. 418-441. *In* D. L. Wrensch and M. A. Mercedes (eds.), *Evolution and diversity of sex ratio in insects and mites*. Chapman & Hall, New York.
- King, B. H. 1994. How do female parasitoid wasps assess host size during sex-ratio manipulation. *Anim. Behav.* 48: 511-518.
- King, B. H. 1996. Fitness effects of sex ratio response to host quality and size in the parasitoid wasp *Spalangia cameroni*. *Behav. Ecol.* 7: 35-42.
- King, B. H. 1998. Host age response in the parasitoid wasp *Spalangia cameroni* (Hymenoptera: Pteromalidae). *J. Insect Behav.* 11: 103-117.
- King, B. H., and R. B. King. 1994. Sex ratio manipulation in response to host size in the parasitoid wasp *Spalangia-cameroni* - is it adaptive. *Behav. Ecol.* 5: 448-454.
- King, B. H., and H. E. Lee. 1994. Test of the adaptiveness of sex ratio manipulation in a parasitoid wasp. *Behav. Ecol. Sociobiol.* 35: 437-443.
- Meyer, J. A., T. A. Schultz, C. Collar, and B. A. Mullens. 1991. Relative abundance of stable fly and house fly (Diptera: Muscidae) pupal parasites (Hymenoptera: Pteromalidae; Coleoptera: Staphylinidae) on confinement dairies in California. *Environ. Entomol.* 20: 915-921.
- Mullens, B. A., J. A. Meyer, and J. D. Mandeville. 1986. Seasonal and diel activity of filth fly (*Musca domestica*) parasites (Hymenoptera: Pteromalidae) in caged-layer poultry manure in southern California. *Environ. Entomol.* 15: 56-60.
- Patterson, R. S., and D. A. Rutz. 1986. Biological control of muscoid flies. *Misc. Publ. Entomol. Soc. Am.* 61: 1-174.
- Rueda, L. M., and R. C. Axtell. 1985. , Guide to common species of pupal parasites (Hymenoptera: Pteromalidae) of the house fly and other muscoid flies associated with poultry and livestock manure. Technical Bulletin 278. North Carolina Agricultural Research Service, North Carolina State University, Raleigh.
- Rutz, D. A., and G. A. Scoles. 1989. Occurrence and seasonal abundance of parasitoids attacking muscoid flies (Diptera: Muscidae) in caged-layer poultry facilities in New York. *Environ. Entomol.* 18: 51-55.
- Waage, J. 1986. Family planning in parasitoids: adaptive patterns of progeny and sex allocation, pp. 63-95. *In* J. Waage and D. Greathead (eds.), *Insect parasitoids*. Academic, London.
- Werren, J. H. 1984. A model for sex ratio selection in parasitic wasps: local mate competition and host quality effects. *Neth. J. Zool.* 34: 81-96.
- Werren, J. H., and G. Simbolotti. 1989. Combined effects of host quality and local mate competition on sex allocation in *Lariophagus distinguendus*. *Evol. Ecol.* 3: 203-213.

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