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Abstract

The effect of conspecific females on offspring sex ratio was examined in the parasitoid wasp *Spalangia cameroni*. In the presence of a second female, females increased the proportion of sons they produced relative to when they were alone, as predicted by local mate competition theory. However, females did not seem to differentiate between two and more than two females: offspring sex ratios from groups of two, four, six, and ten females were not significantly different. The trace odor of another female was not a sufficient cue for females to increase the proportion of sons they produced. Results indicate that for species with large interfemale variation in offspring sex ratio, it is preferable to test how the presence of other females affects offspring sex ratio by looking for changes within individual females rather than by comparing different-sized groups of females.

Introduction

Variation in reproductive traits, e.g., the number, size, and sex ratio of offspring produced, is found both between and within species (references in Giesel 1976, Pianka 1988). In changing environments, selection may favor individuals with the ability to adjust reproductive traits in response to current environmental conditions (Cohen 1967). One condition which may influence the most advantageous offspring sex ratio is the number of other mothers present. Local mate competition (LMC) theory predicts a positive relationship between the number of mothers in a patch and the sex ratio of their offspring (defined here as proportion of sons) (Hamilton 1967). If just one mother produces offspring in a patch, she should produce only the number of sons needed to inseminate locally available females. Otherwise, her sons will be competing among themselves for mates. Producing fewer sons also will allow a mother to produce more daughters, and the more daughters a mother produces, the more mates there will be for her sons (Maynard Smith 1978, Taylor 1981). With more than one mother in a patch, a mother should produce an increased proportion of sons. When other mothers are present, the more sons a mother produces, the greater the probability that one of her sons, and not some other mother's son, will inseminate a given female. Also, the advantage of producing extra daughters is reduced because there is less probability that a mother's own sons will be the mates of any additional daughters she produces.

Hamilton (1979) derived the expected relationship between the number of mothers in a patch (n) and the expected offspring sex ratio (r) for haplodiploid organisms: $r = (n-1)(2n-1)/(n(4n-1))$. By this formula, as number of mothers present increases, sex ratio first increases rapidly and then asymptotically approaches a value of one half.

In this paper I test whether ovipositing females of the parasitoid wasp *Spalangia cameroni* Perkins (Hymenoptera: Pteromalidae) increase the proportion of sons they produce in response to the presence of other females as predicted by LMC theory. I also test whether the trace odor of another female provides the cue to increase offspring sex ratio.

Like most parasitoid wasps, *S. cameroni* has haplodiploid sex determination; unfertilized eggs develop into sons, fertilized eggs into daughters. Haplodiploid sex determination provides a mechanism by which females can potentially manipulate offspring sex ratio, and there is evidence that this mechanism is used. For example, in some species, including *S. cameroni*,

manipulation in response to relative host size has been demonstrated (King 1988).

LMC theory assumes that one or more mothers produce multiple offspring in a given patch, that offspring mate in their natal patch, and that daughters disperse after mating. For gregarious species of parasitoid wasps (multiple offspring complete development in a host), a patch can be a single host. For solitary species (only one offspring completes development in a host), a patch can occur only when hosts are clumped. *S. cameroni* is a solitary species. Hosts of *S. cameroni* are sometimes though not always, clumped (personal observation for the host *Musca domestica* L.). It is not known whether *S. cameroni* mate in their natal patches. Both females and males have the potential for dispersal: they have functional wings, in contrast to some species in which males have reduced wings (e.g., the gregarious species *Nasonia vitripennis* (Walker) in which mating takes place on or near the host from which the wasps emerge (Werren 1983)). However, when, relative to mating, dispersal occurs in *S. cameroni* is not known.

Material and methods

All experiments were conducted with laboratory populations of *Spalangia cameroni* and one of its natural host species, the house fly *Musca domestica*, at 23-25°C, 12L:12D. The *S. cameroni* colony was originated from wasps that emerged from *M. domestica* and *Stomoxys calcitrans* (L.) pupae collected from a poultry house in 1985 (Hurlbutt 1987). Methods for maintenance of the laboratory populations are presented elsewhere (Hurlbutt 1987, King 1988).

Hosts used in experiments were of relatively consistent size, mean width = 2.75 mm + 0.006 SE (produced following the procedure in King (1988) for large hosts). In all experiments, host pupae used were 0-30 hours old (timed from the initiation of pupal tanning) when presented to the wasps. Preliminary experiments had shown that about three times as many wasps are produced from 0-30 hour old host pupae as from 24-48 hour old pupae.

Only newly emerged wasps which had not been exposed to other wasps were used in experiments. Wasps were obtained by placing parasitized hosts individually in 1 oz clear plastic vials. The vials were new or had been washed with a soap, bleach, and water solution to remove wasp odors. Wasps were of unknown relatedness. Each female was allowed to mate in a 1 oz vial with a virgin male prior to being grouped with other females. Thus, increases in sex ratio with increasing number of females present would not result from 1) mating interference causing some females to remain unmated or 2) multiple mating by some males causing less sperm to be transferred by these males (see Hurlbutt 1987). Hosts were presented to females in 1 oz vials. A spot of honey was put on the vial wall as food for the females. Wasp offspring were counted and sexed about two months after parasitization, after they had all emerged and died.

Experiment One

Experiment one involved five treatments: one, two, four, six, and ten mated females per vial. Greater numbers of females were not used because at high numbers of females the increases in sex ratio predicted by LMC theory are small (see Discussion). Each vial of females was presented with twenty-eight hosts daily for six days. Treatments were each replicated seven to ten times. Offspring sex ratio was calculated separately for each replicate, and then the mean and standard deviation sex ratio were calculated across all replicates in a treatment. For each replicate, offspring sex ratio was calculated as the proportion of sons produced over the six day period. Except for the one-female treatment, the sex ratio for each replicate is an overall sex ratio, not a mean sex ratio across all females in the vial. A mean sex ratio could not be calculated for each replicate because offspring could not be assigned to individual females. An overall sex ratio weights a female's offspring sex ratio by the number of offspring she produces.

In *S. cameroni* there is a negative relationship between sex ratio and number of offspring produced (Hurlbutt 1987). Thus the overall sex ratio for each replicate is lower (more female-biased) than a replicate's mean sex ratio would be.

Experiment Two

In experiment two, the effect of changes in number of mothers present on offspring sex ratio were observed within rather than between mothers. Each replicate consisted of four females: two experimental females and two controls. The purpose of the controls was to control for any effect of maternal age on offspring sex ratio (Hurlbutt 1987). On days one to three, all four females were in separate vials and were each given thirty hosts daily. On days four and five, the two control females remained separate and continued to receive thirty hosts daily; the two experimental females were combined into a single vial and together were given thirty hosts daily. This experiment was replicated twenty times.

The change in sex ratio of emerged offspring from days 2-3 to days 4-5 was compared for the experimental versus the control females. LMC theory would predict a greater increase in sex ratio for the experimental females than for the controls. In experiment two, day one was considered a pretreatment, and the sex ratio on day one was not included in analyses. This was done to reduce maternal age effects on sex ratio. Earlier experiments had shown sex ratio on day one to be generally higher than on days 2-5 (unpublished observation).

Experiment Three

Experiment three was designed to test the effect of another female's odor on a female's offspring sex ratio. Vials used in this experiment were initially rinsed in a solution of fifty percent household bleach, in tap water, and then in seventy percent ethanol. Each replicate consisted of three females: an odor source female, an experimental female, and a control female. As in experiment two, the control female was a control for any effect of maternal age on offspring sex ratio. Each replicate lasted five days. On day one all three females were each put in a separate clean vial with honey streaked on the side. The experimental and control females were each given thirty hosts daily for days one to three. On day four, the odor source female was discarded and the experimental female was put in her vial; the control female was put in a clean vial. On days four and five, both females were each given thirty hosts daily. This experiment was replicated thirty-one times.

The change in sex ratio of emerged offspring from days 2-3 to days 4-5 was compared for the experimental versus the control females. In case the odor of the source female had worn off by day five, I also compared the change in sex ratio of emerged offspring from day three to day four (that is from the day before exposure to source female odor to the first day of exposure). If females respond to the odor of other females, LMC theory would predict a greater increase in sex ratio for the experimental females than for the controls.

Results

In experiment one, the mean offspring sex ratio for the one-female treatment (Tab. 1) was high relative to other experiments with *S. cameroni* in which isolated females have been presented with hosts (Hurlbutt 1987). This was because of an unusually high frequency of very male-biased sex ratios in the one-female treatment: three of the eight females produced offspring sex ratios of greater than 0.95. This contrasts with three of thirty-one females producing such high

sex ratios in another experiment involving isolated females (Hurlbutt 1987). The other five females in the one-female treatment produced sex ratios of less than 0.40.

Even disregarding the one-female treatment, experiment one provides no evidence that female *S. cameroni* increase their offspring sex ratios in response to the number of other females present (Tab. 2). A one-way analysis of variance shows no significant effect of number of mothers present on offspring sex ratio for groups of two, four, six, and ten mothers ($F = 1.78$, $p = 0.17$).

In experiments two and three, the problem of large interfemale variation in offspring sex ratio, which was observed in the one-female treatment of experiment one of this study and in King (1988), was eliminated by observing the effect of change in number of ovipositing females on offspring sex ratio within rather than between females.

In experiment two, as predicted by LMC theory, the increase in offspring sex ratio from days 2-3 to days 4-5 was greater for experimental females ($N = 1 \text{--D } 2$) than for controls ($N = 1 \text{--D } 1$) (Tab. 2). This was a result of experimental females decreasing the number of daughters they produced on days 4-5 relative to days 2-3 (paired t-test, $t = 2.95$, $p = 0.008$) and relative to control females (paired t-test, $t = 4.95$, $p < 0.001$).

In experiment three, the change in sex ratio of emerged offspring from days 2-3 to days 4-5 did not differ significantly between experimental females (exposed to trace odors of other females) and control females (paired t-test, $t = 0.72$, $p = 0.24$). Likewise, there was no significant difference between experimental and control females in change in sex ratio from day three to day four.

Discussion

In experiment one, the effect of number of females present on offspring sex ratio was examined between different-sized groups of females. In experiment two, the effect was examined within pairs of females--when two females were solitary versus when the same two females were together. In experiment three, the effect was examined within solitary females--when a female was not exposed to the odor of another female versus when she was. LMC theory is applicable to all three situations. However, results of experiment one suggest that for species with large interfemale variation in offspring sex ratio, like *S. cameroni*, it is better to test for an effect of other females on sex ratio by looking for sex ratio changes within individual females rather than by comparing different-sized groups of females.

It is not clear why, in experiment one, females in groups of two and larger did not produce an increased proportion of sons with increasing group size, as LMC theory would predict. Perhaps females rarely encounter more than two females in a patch, and so there has not been selection for females to respond differently to two versus more than two females.

In experiment two, the observed difference between experimental females ($N = 1 \text{--D } 2$) and controls ($N = 1 \text{--D } 1$) was eight percent. Hamilton's (1979) formula predicts a sex ratio increase of twenty-one percent. However, variables not considered in Hamilton's formula have since been shown to affect the expected magnitude of sex ratio and of sex ratio change, e.g., asynchronous female colonization of patches or some dispersal by males to mate in other patches after mating in the natal patch (Nunney and Luck 1988). With these additional considerations, the relationship between number of ovipositing females present and offspring sex ratio is still expected to be positive and asymptotic, but the increase in sex ratio with increasing numbers of mothers is expected to be smaller. Both asynchrony in female colonization and post-dispersal mating by males are plausible explanations for the smaller than expected sex ratio increase in *S. cameroni*. That male *S. cameroni* have wings strongly suggests that at least some of their mating

is away from their natal patch. Asynchronous colonization by female *S. cameroni* is likely given the asynchrony of flies in a patch reaching the stage which is susceptible to parasitization (personal observation).

A positive relationship between number of females present and offspring sex ratio has been shown for most species of parasitoid wasps examined, including gregarious species, facultatively gregarious species, and solitary species (Tab. 3). (In facultatively gregarious species, one to a few offspring complete development in a single host.) Among the solitary species which exhibit the expected positive relationship between number of mothers and offspring sex ratio, at least three of four (including *S. cameroni*) parasitize clumped hosts, and thus these species are expected to experience local mate competition (see Introduction): *Telenomus remus* Nixon and *Trichogramma japonicum* Ashmead parasitize lepidopteran egg masses (Gerling 1972; Clausen 1978). *Telenomus remus* males emerge about twenty-four hours before females and wait on the hosts for females to emerge (Schwartz and Gerling 1974).

Although LMC theory is also applicable to diploid organisms (e.g., Nunney and Luck 1988), most empirical studies of LMC theory have been with haplodiploid organisms. Among haplodiploid organisms, a positive relationship between sex ratio and number of mothers present has been found not only for parasitoid wasps, but also for fig wasps (Frank 1985, Herre 1985) and mites (references in Charnov 1982).

A positive relationship between number of females present and offspring sex ratio is not unequivocal evidence for LMC. An alternative explanation for such a relationship is greater mortality of daughters relative to sons in hosts parasitized by more than one female than in hosts parasitized by one female. This explanation can be ruled out for *S. cameroni*. The sex ratio of emerging offspring is the same from hosts artificially parasitized with three eggs as from hosts artificially parasitized with one egg Wylie (1971). A more negative effect of parasitization by multiple females on the survival of daughters than of sons has also been eliminated as an explanation for the observed positive relationships between number of mothers present and offspring sex ratio for *Nasonia vitripennis* (Walker 1967), *Trissolcus grandis* (Viktorov and Kochetova 1973), *Eupteromalus dubius* (Wylie 1976b), *Trichogramma evanescens* (Waage and Lane 1984), and *Telenomus remus* (van Welzen and Waage 1987).

Bracon hebetor Say, *Mellitobia* spp., and one strain of *Nasonia vitripennis*, all gregarious species, are the only reported parasitoid wasps which have not shown increases in offspring sex ratio as female number increases (Tab. 3). However, the study with *B. hebetor* used very high female numbers 50, 100, 150...400. From 50 to 400 females, the sex ratio is expected to increase by only 0.011 (see formula (Hamilton 1979) in Tab. 1). This small a change in sex ratio would not have been detectable.

S. cameroni is only the third reported species for which an effect of female odor on offspring sex ratio has been examined. Like *S. cameroni*, the gregarious parasitoid wasp *Nasonia vitripennis* (also in the family Pteromalidae) shows no effect of female odor on offspring sex ratio (Wylie 1976a). In contrast, the solitary species *Trissolcus grandis* Thoms (Scelionidae) does increase offspring sex ratio in response to trace odors of other females (Viktorov and Kochetova 1973). The results of the odor experiment with *S. cameroni* suggest that trace odors of another female are not the proximate cue for the greater offspring sex ratio of paired versus solitary females. Experiments comparing the number of eggs laid in hosts already parasitized by a conspecific to the number in unparasitized hosts suggest that females can detect parasitization by conspecifics (Wylie 1972). Detection may be 1) by a non-water-soluble marker applied to the outside of hosts by females at the time of oviposition, 2) by a venom females inject into hosts at the time of oviposition, or 3) by a change in the physical or chemical characteristics of

parasitized hosts. Any of these three evidences of parasitization may provide an *S. cameroni* female with a proximate cue for increasing sex ratio when another female has already oviposited in a patch.

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Tab. 1. Observed offspring sex ratio of *Spalangia cameroni* at different numbers of ovipositing females (n), compared to the sex ratio (r) predicted by LMC theory (Hamilton 1979):
 $r = (n-1)(2n-1)/(n(4n-1))$.

	Mean	SD in	Number of	
n	Sex Ratio	Sex Ratio	Sex Ratio	Treatment
	Predicted	Observed	Observed	Replicates
1	0.00	0.51	0.39	8
2	0.21	0.32	0.12	9
4	0.35	0.43	0.20	7
6	0.40	0.31	0.08	9
10	0.44	0.30	0.09	10

Tab. 2. Mean + SE offspring sex ratios of lone (N = 1) versus paired (N = 2) females of experiment two.

Experimental		Controls		
N	Females	N	Females	
Days 2-3	1	0.13 + 0.013	1	0.15 + 0.022
Days 4-5	2	0.25 + 0.019	1	0.19 + 0.017
Change***		0.12 + 0.019	0.04 + 0.014	

***significantly different by paired t-test, $t = 3.53$, $p = 0.001$

Tab. 3. The relationship between the number of female wasps present and offspring sex ratio for gregarious (G), facultatively gregarious (F), and solitary (S) species.

Solitary or Wasp Species	Relationship	Gregarious	Reference
<i>Muscidifurax zaraptor</i>	+ *	S	Wylie 1979
<i>Telenomus remus</i>	+ *1	S	Schwartz and Gerling 1974
	+	van Welzen and Waage 1987	
<i>Trichogramma japonicum</i>	+ *2	S	Kuno 1962
<i>Trissolcus grandis</i>	+	S 6	Viktorov 1968
<i>Trichogramma evanescens</i>	+ *3	F 7	Salt 1936
	+ *	Waage and Lane 1984	
<i>Trichogramma lutea</i>	+	F 8	Kfir 1982
<i>Bracon hebetor</i>	nd G	Reinert and King 1971	
<i>Dinarmus vagabundus</i>	+	G	Rojas-Rousse et al. 1983
<i>Eupteromalus dubius</i>	+ *4	G	Wylie 1976b
<i>Mellitobia</i> spp.	none	G	Wilhelm in Werren 1987
<i>Nasonia vitripennis</i>	+ *5	G	Velthuis et al. 1965
	+ Walker 1967		
	+ * Werren 1983		
3 strains	+	Orzack and Parker 1986	
1 strain	none	Orzack and Parker 1986	
<i>Pteromalus puparum</i>	+	G	Takagi 1985
<i>Tetrastichus hagenowii</i>	+	G	Narasimham 1984

Tab. 3, continued.

+ = positive, nd: nondirectional

*: statistically significant, $p < 0.05$

1 $G = 54.60$, $p < 0.001$ (1 female vs. 5 to 8 females)

2 $G = 11.09$, $p = 0.05$; $r_s = 1.00$, $p < 0.01$

3 $G = 142.12$, $p < 0.001$; $r_s = 1.00$, $p < 0.01$

4 $G = 242.88$, $p < 0.001$

5 $G = 151.23$, $p < 0.001$; $r_s = 1.00$, $p < 0.01$

6 Charnov 1982

7 1 to at least 6 offspring per host (Waage and Ng 1984)

8 1-5 offspring per host, average of 2.02