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Sex-ratios of the wasp *Nasonia vitripennis*
from self- versus conspicuously-parasitized hosts:
local mate competition versus host quality models

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Abstract

Sex ratio patterns in the parasitoid wasp *Nasonia vitripennis* are frequently cited in support of a major group of evolutionary sex ratio models referred to as local mate competition (LMC) models. It has been shown repeatedly that, as predicted by LMC models, females generally oviposit a greater proportion of sons in previously parasitized hosts than in unparasitized hosts. However, this sex ratio pattern is also a prediction of another group of sex ratio models, the host quality models. Here I test a prediction of LMC models that is not also a prediction of host quality models: a female should produce a greater proportion of sons when she parasitizes a host previously parasitized by a conspecific female than when she parasitizes a host previously parasitized by herself. Females made this predicted distinction between self- and conspicuously-parasitized hosts under some conditions. There was no evidence that a female recognizes a self-parasitized host when her exposure to the host is interrupted by exposure to an unparasitized host, or that a female can distinguish between hosts parasitized by sisters versus nonsisters.

Introduction

Sex ratio theory is considered by some to represent one of the most successful

groups of evolutionary models in terms of the match between major predictions and data (Bull and Charnov, 1988). Sex ratios (proportion of sons) have been especially well-studied in parasitoid wasps (recent reviews by Waage, 1986; King, 1987, in press). This is in part because in haplodiploids such as wasps a female can control her offspring sex ratio by controlling fertilization: sons develop from unfertilized eggs and daughters from fertilized eggs. Here I examine, in the parasitoid wasp Nasonia vitripennis, a sex ratio response that allows a distinction to be made between two major groups of evolutionary sex ratio models, local mate competition (LMC) models (first developed by Hamilton (1967, 1979)) and host quality models (Charnov, 1979; Charnov et al., 1981).

As the name implies, LMC models assume that mating is local. When only one female oviposits in a patch, all the male offspring emerging from that patch will be brothers. In this situation, selection is predicted to favor mothers that produce only enough sons to inseminate all locally available females. Any more sons than that will simply compete among themselves and thus waste resources which could have been used to produce additional daughters as mates for the sons (Maynard Smith, 1978; Taylor, 1981). In contrast, when multiple females oviposit in a patch, not all the males emerging from a patch will be brothers. In this situation, by producing an increased proportion of sons, a mother can increase the chance that one of her sons, and not another mother's son, will inseminate available females. Also, with multiple females in a patch, the advantage to a mother of producing additional daughters is reduced--the daughters now will provide mates not just for her sons but also for other mothers' sons.

The host quality models predict how mothers should manipulate sex ratio in response to host quality (Charnov, 1979; Charnov et al., 1981). The models predict that mothers should produce a greater proportion of sons under conditions that will result in smaller offspring. The assumption is that being small will be less disadvantageous to the reproductive success of males than of females. This prediction holds regardless of whether mating is local or panmictic (Werren, 1984a). The host quality models were designed for solitary species of parasitoids, i.e., species that produce only one offspring per host. However, the models can also be applied to gregarious species, i.e., species that produce multiple offspring per host (Waage, 1982; Werren, 1983). In gregarious species, one situation that is expected to result in smaller offspring is when a female oviposits in a host that has already been parasitized by another female. Thus, for gregarious species, the evolutionary advantage to ovipositing a greater proportion of sons in response to other females can be explained by LMC models and/or by host quality models (Waage, 1982; Werren, 1983).

Nasonia vitripennis is a small species of gregarious wasp which lays its eggs in the pupal stage of various fly species (Whiting, 1967). N. vitripennis seems to have the type of population structure that would lead to LMC: mating at the site of emergence, followed by female dispersal to new host patches for oviposition (a patch being one host or a clump of hosts). In addition, female N. vitripennis generally increase the proportion of sons that they produce both in response to the number of other females present (Wylie, 1965, 1966; Velthuis et al., 1965; Walker, 1967; Werren, 1983) and in response to a host having been previously parasitized by another female (Holmes, 1972; Werren, 1980; but see one strain of N. vitripennis,

Orzack and Parker, 1986). These sex ratio manipulation abilities of *N. vitripennis* have been interpreted primarily in terms of LMC models (e.g., Werren, 1980, 1983; Charnov, 1982; Krebs and Davies, 1987). However, host quality selection arguments may also apply (Werren, 1983) because when a *N. vitripennis* female oviposits in an already parasitized host, her offspring are smaller (Werren, 1983, 1984b).

Here I test a prediction that has the potential to distinguish between LMC and host quality effects. Under LMC but not host quality models, a female should oviposit a greater proportion of sons when she parasitizes a host previously parasitized by a conspecific female than when she parasitizes a host previously parasitized by herself. LMC models apply in this situation because the comparison is between hosts parasitized by two different females versus by one female. Host quality models are not expected to apply because all hosts are being exposed to parasitization twice; thus, all hosts are expected to have the same number and hence size of offspring. Here I test 1) whether a female distinguishes between self- and conspecifically-parasitized hosts under several different conditions, 2) whether the number of offspring from self- and conspecifically-parasitized hosts is the same, 3) whether a female can recognize a self-parasitized host when her exposure to the host is interrupted by exposure to an unparasitized host, and 4) whether a female can distinguish between hosts parasitized by sisters versus nonsisters. If females can distinguish between their own hosts and those of other females, they might also be able to distinguish between hosts of sisters and nonsisters.

Materials and methods

The results reported here are based on laboratory experiments with the scarlet eye strain of *N. vitripennis* (Saul et al., 1965) on the host *Sarcophaga bullata*. Wasps were maintained at 24-28°C. Mating of recently emerged virgin individuals occurred under controlled conditions: either pairs of males and females were left together for 24 h or mating was observed. After mating, females were given honey for 24 h, prior to being given any hosts. In some replicates each female was pretreated with an unparasitized host for 24 h prior to use in a treatment (indicated in Tables 1, 2).

A treatment consisted of a female initially being given an unparasitized host for a given time period. Then the host was removed, and, for a second time period of the same duration, the female was given a parasitized host, either the one she had previously parasitized (i.e., a self-parasitized host) or one parasitized by another female (i.e., a conspecifically-parasitized host). Number and sex of wasp offspring from each host were determined at the pupal stage. Hosts in which no wasps developed were excluded from analyses. Given my design, offspring from first and second parasitizations cannot be distinguished. However, first parasitizations should not differ systematically between treatments; thus any differences between treatments can be attributed to a difference in the second parasitizations.

Five experiments were performed. To determine whether the length of time that females were exposed to hosts affected the ability of females to distinguish self- and conspecifically-parasitized hosts, I did three experiments: females were given hosts for two 3 h periods separated by a 3 h interruption, for two 12 h periods, or for two 24 h periods. The effect of an intervening host on a female's ability to recognize a self-parasitized host was tested in two experiments: females were given hosts for two 3 h or two 24 h periods with exposure to an unparasitized host for 3 h inbetween.

Several of the experiments were replicated two or three times (Tables 1, 2). I do not compare absolute values of sex ratios and clutch sizes among replicates because of potential effects of differences among replicates in factors such as host age (Wylie, 1963), temperature (DeBach, 1943), humidity, and female pretreatment. Within a replicate all females were tested concurrently and hence were treated the same with regards to these factors.

In addition to testing whether females distinguish between self- and conspecifically-parasitized hosts, I also tested whether females oviposit a greater proportion of sons in hosts parasitized by nonsisters than in hosts parasitized by full-sisters. This was tested with 24 h parasitization periods: 24 h with an unparasitized host, followed by 24 h with a host that had been parasitized by a full-sister or by a nonsister for the previous 24 h.

In all treatments in which females were given conspecifically parasitized hosts, hosts were switched between pairs of females. Thus, clutch sizes and sex ratios from such pairs of hosts were not independent. To control for this lack of independence, offspring from such pairs of hosts were combined prior to analyses (with clutch size divided by two to obtain clutch size per host).

Mean sex ratios and clutch sizes were compared by t-tests using pooled variances when assumptions of normality and homoscedasticity were met and by Mann-Whitney U-tests when these assumptions were not met. Because t-tests are robust to deviation from these assumptions (Scheffé, 1959), I used $\alpha = 0.001$ for tests of these assumptions, whereas I used $\alpha = 0.05$ for comparisons of means. One-tailed tests were used to compare sex ratio means. (Two-tailed P values are given if the direction of difference is opposite to that predicted). Two-tailed tests were used to compare clutch size means. Alpha values were adjusted for multiple replicates within each experiment by the sequential Bonferroni technique (Rice, 1989). By this technique, within each experiment the significance of replicates is tested going from the replicate with the lowest P value to the replicate with the highest P value. The P value of each replicate is compared to its replicatewise α , which equals (experimentwise α)/(total # of replicates - # of replicates already tested).

Results

Under some conditions, the proportion of sons produced in response to conspecifically-parasitized hosts was greater than the proportion of sons produced in response to self-parasitized hosts. Specifically, a significant effect was found when the period of the first parasitization was 24 h with no time lag before a second 24 h parasitization period, as well as when the period of the first parasitization was 3 h with a 3 h interim with no host before the second 3 h parasitization period (Table 1). Females did not distinguish between self- and conspecifically-parasitized hosts when parasitization periods were 12 h (Table 1) or when given an unparasitized host during a 3 h interim between the treatment parasitization periods (Table 2). Though with 24 h parasitization periods females distinguished between their own hosts and those of other females, they did not distinguish between hosts parasitized by nonsisters and hosts parasitized by full-sisters (Table 1).

Number of emerging offspring differed significantly between self- and conspecifically-parasitized hosts only in one replicate of an experiment (3 h parasitization periods with a host for a 3 h interim between parasitizations, Table 2),

and in that experiment there was no significant sex ratio difference.

Discussion

The greater proportion of sons from self-parasitized than from conspecifically-parasitized hosts that was observed under some experimental conditions is best explained as resulting from maternal manipulation of offspring sex ratio. Differential mortality of the sexes is an unlikely explanation for the sex ratio pattern observed: 1) the number of emerging offspring did not differ significantly between treatments when sex ratio differed; 2) a sex ratio difference was observed even in the absence of crowding, i.e., even with relatively low numbers of offspring per host, as when the parasitization periods were each only 3 h (Table 1); and 3) survivorship for *N. vitripennis* on this host species is high (Werren, 1980).

The sex ratio difference between self-parasitized and conspecifically-parasitized hosts was in the direction predicted by LMC theory. The difference was 3-8 percentage points, which is a 14-33% increase (Table 1). Unfortunately, there are not yet sufficient data on the assumptions of LMC theory to make realistic quantitative predictions of the expected magnitude of sex ratio change. It is not clear why females did not distinguish between their own hosts and those of other females when the parasitization periods were 12 h. This result is difficult to explain given that females did make a distinction with 24 h parasitization periods and even with 3 h parasitization periods.

The greater proportion of sons from conspecifically-parasitized than from self-parasitized hosts is not consistent with host quality models. This is because the greater proportion of sons from conspecifically-parasitized hosts was not associated with more, and thus smaller, offspring per host (Table 1). Other evidence on *N. vitripennis* that is inconsistent with the host quality models is that among females parasitizing previously parasitized hosts, a female's proportion of sons decreases as her clutch size increases, but the size of her offspring does not vary with her clutch size (Werren, 1980, 1984b). How well this sex ratio result supports LMC theory is debated (Orzack, 1990).

Although there are data on *N. vitripennis* that are qualitatively consistent with LMC models but not host quality models, there are some features of sex ratios in *N. vitripennis* that current LMC models do not explain. For example, there is more variation in sex ratios than current LMC models predict (e.g., Orzack and Parker, 1986; Orzack, 1990). In addition, relative to the sex ratio response to unparasitized hosts, females increase the proportion of sons that they produce not only in response to conspecifically parasitized hosts, but also in response to hosts parasitized by other parasitoid wasp species (Wylie, 1973). This is predicted by host quality models; it is not predicted by LMC models unless females cannot distinguish between conspecifically-parasitized and allospecifically-parasitized hosts (King, 1987).

The difficulty of distinguishing LMC and host quality models in gregarious species is not restricted to *N. vitripennis*. In at least seven other gregarious species, females increase the proportion of sons that they produce in response to the presence of other females (Salt, 1936; Wylie, 1976; Kfir, 1982; Rojas-Rousse et al., 1983; Narasimham, 1984; Takagi, 1985; King and Skinner, 1991b). However, as discussed in the introduction, such a relationship can result from either LMC or host quality effects. Consistently female-biased sex ratios in some of these species (e.g.,

Narasimham, 1984; King and Skinner, 1991b) are predicted by LMC selection pressures but not by host quality selection pressures alone (Charnov et al., 1981). However, there are also other forces in addition to LMC that can lead to overall female-biased sex ratios (Fig. 2 of Bull and Charnov, 1988) and that might do so in combination with host quality effects. In contrast to most gregarious species examined, one species, Bracon hebetor, decreases proportion of sons in response to the presence of other mothers, a pattern not explainable by LMC models (Galloway and Grant, 1989). The pattern is predicted by host quality models if crowding and hence offspring size has a more negative effect on males than females (Galloway and Grant, 1989). This assumption needs to be tested more rigorously.

Testing for the ability to distinguish between self- and conspecifically-parasitized hosts may be useful in distinguishing between LMC and host quality selection pressures in other gregarious species besides N. vitripennis. A sex ratio distinction between self- and conspecifically-parasitized hosts suggests that LMC is important and host quality effects are not sufficient to explain the sex ratio behavior of a species. However, the lack of a sex ratio distinction by females does not necessarily indicate that LMC is not important. For example, if females do not normally parasitize previously parasitized hosts, selection to distinguish self- and conspecifically-parasitized hosts is not expected.

There have been few studies examining the ability of females to distinguish between self-parasitized and conspecifically-parasitized hosts. To my knowledge, sex ratio distinction between self- and conspecifically-parasitized hosts has been tested in only one species besides N. vitripennis, Trichogramma evanescens. T. evanescens is a gregarious species, and females increase sex ratio in response to the presence of other females (Salt, 1936; Waage and Lane, 1984). However, sex ratio does not differ either between parasitized and unparasitized hosts or between self- and conspecifically-parasitized hosts (van Dijken and Waage, 1987). T. evanescens females also do not distinguish between self- and conspecifically-parasitized hosts in their clutch size responses (van Dijken and Waage, 1987). Tendency to oviposit in self- versus conspecifically-parasitized hosts has been examined in two solitary species of parasitoid wasps: Asobara tabida avoids ovipositing in both types of hosts equally (van Alphen and Nell, 1982); Nemeritis canescens oviposits less in self- than conspecifically-parasitized hosts, provided only 0-24 h have elapsed since the initial parasitization (Hubbard et al., 1987).

The mechanism of distinction between conspecifically-parasitized and self-parasitized hosts remains to be determined. In N. vitripennis the distinction may be based on learned recognition of familiar hosts or on learned or inherent recognition of something present on a wasp's own eggs or in a wasp's own venom (King and Skinner, 1991a). (Females inject venom into a host prior to oviposition (Beard, 1964; Ratcliffe and King, 1967).) Some type of learned recognition seems most likely. There was no difference in sex ratio response to self- versus conspecifically-parasitized hosts when each female was exposed to an unparasitized host for 3 h between treatment parasitization periods. One explanation for this is that exposure to another host causes a female to forget her previous encounter. Also, there was no evidence of any sort of genetically based kin recognition mechanism (e.g., by means of a pheromone left during oviposition): females did not distinguish between hosts parasitized by nonsisters and hosts parasitized by full-sisters. Alternatively, the

failure to distinguish between sisters and nonsisters may be due to a high degree of genetic relatedness even among nonsisters in this inbred laboratory strain.

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TABLE 1. Offspring sex ratios (proportion of males) and clutch sizes from self- versus conspecifically-parasitized hosts. For each experiment, the experimentwise α is 0.05. When replicate-wise P values are = 0.10, the replicatewise critical value is given; this is the value which the P must be less than to give statistical significance while maintaining the experimentwise α at 0.05.

Type of Parasitized Host		Sex ratio		Number of Offspring
		n	Mean \pm s.e.	Mean \pm s.e.

3 hr parasitization periods with 3 hr interim				
conspecific	25	0.16 \pm 0.012	22.0 \pm 0.88	
self	44	0.13 \pm 0.014	23.6 \pm 0.93	
		U = 366.0	U = 406.0	
		P = 0.01	P = 0.07	
		alpha = 0.05	alpha = 0.05	
12 hr parasitization periods with no interim				
replicate 1:				
conspecific	16	0.26 \pm 0.021	34.1 \pm 2.27	
self	28	0.26 \pm 0.035	34.9 \pm 1.42	
		U = 177.0	t = 0.31	
		P = 0.13	P = 0.75	
replicate 2:				
conspecific	24	0.25 \pm 0.021	35.6 \pm 0.98	
self	42	0.24 \pm 0.026	36.3 \pm 1.16	
		U = 408.0	t = 0.37	
		P = 0.10	P = 0.71	
		alpha = 0.03		
24 hr parasitization periods with no interim				
replicate 1:				
conspecific	30	0.32 \pm 0.016	50.9 \pm 1.37	
self	56	0.24 \pm 0.010	51.3 \pm 1.49	
		U = 405.0	t = 0.16	
		P = 0.0001	P = 0.87	
		alpha = 0.02		
replicate 2:				
conspecific:				
sister	20	0.23 \pm 0.016	38.7 \pm 1.53	
nonsister	20	0.24 \pm 0.034	40.1 \pm 2.06	
		U = 165.5	t = 0.52	
		P = 0.35	P = 0.30	
self	29	0.18 \pm 0.020	39.3 \pm 1.41	
		U = 354.0 ^y	t = 0.02 ^y	
		P = 0.003	P = 0.98	
		alpha = 0.03		
replicate 3:				
conspecific	30	0.24 \pm 0.010	43.4 \pm 1.27	
self	56	0.21 \pm 0.010	44.0 \pm 1.00	
		t = 2.07	t = 0.36	
		P = 0.02	P = 0.72	
		alpha = 0.05		

* In these replicates each female received a pretreatment of an unparasitized host for 24 hours prior to use in the experiment
^y comparison of conspecific (sister and nonsister combined) versus self

TABLE 2. Offspring sex ratios (proportion of males) and clutch sizes from self- versus conspecifically-parasitized hosts when females were given an unparasitized host during a three hour interim between the treatment parasitization periods. For each experiment, the experimentwise α is 0.05. When replicate-wise P values are ≤ 0.10 , the replicatewise critical value is given; this is the value which the P must be less than to give statistical significance while maintaining the experimentwise α at 0.05.

Type of Parasitized		Sex ratio		Number Offspring	
Host	n	Mean \pm s.e.	Mean \pm s.e.	Mean \pm s.e.	
3 hr parasitization periods					
replicate 1:					
conspecific	6	0.13 \pm 0.015		16.9 \pm 4.03	
self	17	0.17 \pm 0.025		9.5 \pm 0.94	
		t = 0.79		t = 2.65	
		P = 0.44		P = 0.02	
				alpha = 0.03	
replicate 2:					
conspecific	15	0.16 \pm 0.025		9.4 \pm 1.94	
self	26	0.20 \pm 0.039		8.2 \pm 1.14	
		U = 192.5		U = 176.5	
		P = 0.95		P = 0.62	
24 hr parasitization periods					
replicate 1:					
conspecific	14	0.16 \pm 0.009		30.5 \pm 1.09	
self	29	0.16 \pm 0.013		27.7 \pm 1.39	
		t = 0.03		t = 1.34	
		P = 0.97		P = 0.19	
replicate 2:					
conspecific	15	0.21 \pm 0.014		35.8 \pm 0.96	
self	31	0.23 \pm 0.028		34.0 \pm 1.29	
		U = 203.5		t = 0.91	
		P = 0.25		P = 0.37	