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Effect of Host Density on Offspring Sex Ratios and Behavioral Interactions
Between Females in the Parasitoid
Wasp *Nasonia vitripennis* (Hymenoptera: Pteromalidae)

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Running head: Sex ratios in the Parasitoid Wasp *Nasonia vitripennis*

Pairs of females of the parasitoid wasp *Nasonia vitripennis* were videotaped with one or two hosts. The presence of an additional host decreased the number of interactions between females but had no measured effect on the nature of the interactions, i.e., on whether the interaction involved physical contact or occurred while one of the females was parasitizing a host. The number of hosts did not itself affect offspring sex ratios but did influence which other factors were correlated with sex ratio. When there was one host, the proportion of sons was more positively correlated with utilization of previously drilled holes than with female-female interactions; whereas when there were two hosts, the reverse was true. Parasitizing an already parasitized host appeared to affect a female's sex ratio beyond any effects of the physical presence of another female: when two hosts were present, the proportion of sons was greater from hosts parasitized by both females than from hosts parasitized by only one female. The observation that parasitizations in previously drilled holes and female-female interactions are correlated with sex ratios is consistent with previous studies; however, that these relationships are host density dependent is a new result and remains unexplained.

KEY WORDS: sex ratio, *Nasonia vitripennis*, local mate competition, parasitoid wasp, behavior

INTRODUCTION

Nasonia vitripennis (Hymenoptera: Pteromalidae) parasitizes the pupal stage of various fly species associated with bird nests, carrion, and refuse (see Whiting, 1967 for review of basic biology of *N. vitripennis*). The fly pupae may be aggregated or dispersed (Werren, 1983). Upon encountering a host, a female walks over it, tapping it with her antennae. To oviposit, she drills through the puparium (the hard shell around a fly pupa) with her

ovipositor and lays eggs on the pupa within. She may insert her ovipositor into a single host multiple times before moving on to another host. *N. vitripennis* is a gregarious species, meaning that multiple offspring develop from each host.

Nasonia vitripennis has been especially well-studied in relation to its offspring sex ratios (proportion of sons). Its dispersal pattern appears to lead to the population structure assumed by a group of sex ratio models referred to as local mate competition (LMC) theory (Hamilton, 1967). Females have full wings and fly, whereas males have reduced wings and do not fly. Thus, mating takes place locally at the site of emergence, followed by female dispersal to new oviposition sites. Under these conditions, LMC theory predicts that natural selection will favor females that produce a greater proportion of sons when ovipositing in the presence of other females than when ovipositing alone (e.g., Hamilton, 1967, 1979). LMC theory also predicts that females will produce a greater proportion of sons when ovipositing in previously parasitized hosts than when ovipositing in unparasitized hosts (Suzuki and Iwasa, 1980, Werren, 1980). *N. vitripennis* exhibits both of these sex ratio patterns (e.g., Holmes, 1972, Werren, 1980, 1983). Female *N. vitripennis* manipulate sex ratio by manipulating the ratio of fertilized eggs to unfertilized eggs; as in most parasitoid wasps, unfertilized eggs develop into males and fertilized eggs into females.

Here, we examine how host density affects the number and nature of interactions between females, the nature of parasitizations, and how these in turn are related to offspring sex ratios. We were especially interested in whether females increase their sex ratios (proportion of sons) 1) when they parasitize in previously drilled holes on hosts and 2) when they experience more interactions with other females. Understanding the proximal factors that affect a female's sex ratio is important because it may help us to understand constraints on adaptive sex ratio manipulation.

METHODS

Experiments were conducted with laboratory populations of *Nasonia vitripennis* and one of its natural host species, the flesh fly *Sarcophaga bullata*, at 24-28°C, 24L. Hosts were obtained commercially (from Grubco, Inc., Hamilton, Ohio). The experiments utilized two eye color strains of *N. vitripennis*, ScDr (scarlet eyes) and CB+ wildtype (Whiting, 1967). The eye color differences allowed us to distinguish both ovipositing females and their progeny.

Newly emerged virgin females were paired with newly emerged virgin males of the same strain and mating was observed (Skinner, 1985). Then males were removed, and each female was given honey for 24 h followed by honey and a host for 24 h prior to being videotaped. Females were then paired for videotaping, an ScDr female with a CB+ female, and given one of two treatments. In the one host treatment the paired females were given one host, and in the two host treatment, two hosts. The CB+ female was added to the host container first, immediately followed by the ScDr female. Each replicate consisted of a one host treatment and a two host treatment videotaped simultaneously. There were twenty-three replicates total.

Each host or pair of hosts was presented to females in a 1.5 cm diameter X 1 cm deep blue plastic cap. This arena size was chosen because it allowed us to achieve sufficient resolution to observe the females' behaviors with our videotaping system. The hosts were buried horizontally halfway in sand (collected from a limestone quarry) to prevent females from ovipositing in a position where their behaviors would not be observable (Skinner, 1985). Hosts are often partially buried in the field (Skinner, 1985; Werren, 1983). The sand provided sufficient contrast to make the wasps and hosts clearly visible without providing large amounts of glare.

Videotaping was with Javelin color video cameras with zoom lenses and JVC s-VHS digital recorders, using s-VHS tapes at extended play. Illumination was from fiber optic gooseneck lights, which gave off no noticeable heat. Videotaping allowed us to record more detail and to follow females for a longer time period than would have been possible by

direct observation. The behavior of each set of females was videotaped for 6 hours. This time period was chosen because 1) it is the maximum duration of a tape (on extended play), 2) in preliminary experiments it resulted in a variety of host parasitization situations (i.e., some hosts parasitized by just one female, some hosts parasitized by both females), and 3) longer periods would have compromised sample sizes.

After videotaping, the females were removed, and the hosts were isolated for development of offspring. After emergence, offspring were scored for eye color, sexed, and counted. There were no diapaused larvae. Offspring were assigned to their mothers on the basis of eye color. Mortality of *N. vitripennis* offspring in superparasitized *S. bullata* is low (Skinner, 1985) and does not appear to differ between the sexes (Holmes, 1970, 1972). Thus, the sex ratio of offspring when they emerge as adults is expected to provide a good estimate of the sex ratio at oviposition.

Data were collected from the videotapes by observing the tapes on a 19" color monitor with a JVC s-VHS digital recorder. Times were determined to the nearest second from the video recorder. All interactions that took place during the six hour period were recorded. An interaction was defined as occurring when one female clearly responded to the other; it involved contact and/or one female moving away from the other female or turning its head away. During an interaction, the initiator was defined as the wasp that most actively moved towards the other wasp first. The retreator was defined as the wasp that backed or moved away first, as long as the movement away was not clearly a continuation of movement before the interaction. The initiator was sometimes also the retreator. There was not always a clear initiator and retreator.

We use "parasitization" to include both drilling a host and time spent with the ovipositor in the host. We were not able to identify when an egg was being oviposited or the sex of egg, as has been observed for some other parasitoids (e.g., Suzuki et al., 1984). Each time that a female parasitized a host, we recorded:

- 1) which host she parasitized (for the two host treatment)
- 2) whether she was using a hole drilled by herself or another female during a previous parasitization (We were able to identify use of a previously drilled hole based on location and the very short time needed to insert the ovipositor in the hole.)
- 3) drill duration: from when drilling was initiated until the ovipositor was completely withdrawn from the host or until the ovipositor was completely inserted into the host, as indicated by the middle of the abdomen contacting the host and the angle between the ovipositor and abdomen tip going from v-shaped to nearly straight, whichever came first
- 4) within-puparium duration: from when the ovipositor was completely inserted into the host at the end of drilling (see #3 above) until it was withdrawn completely from the host
- 5) whether any interactions took place while the female was parasitizing, and if so, whether it resulted in the female pulling her ovipositor out of the host.

Not all information is available for all parasitization events because our view of the female's ovipositor was sometimes obstructed by the rest of the female's body.

Standard errors are presented throughout. Comparisons between treatments and between strains were by paired t-tests except when assumptions of normality were not met; in which case sign tests were used. Because t-tests are robust to deviation from the assumption of normality (Scheffé, 1959), we used $\alpha = 0.001$ for tests of this assumption, whereas we used $\alpha = 0.05$ for comparisons of means. $1t$ indicates a 1-tailed P-value, $2t$, a 2-tailed P value. Two-tailed P values are given if the direction of difference is opposite to that predicted or is not predicted. Paired tests were used to compare treatments because the one host treatment and two host treatment had been videotaped simultaneously in paired replicates to avoid differences between treatments being confounded with differences among taping days in environmental factors such as temperature, humidity, and host age. The relationships between sex ratios and behaviors were examined within treatments and wasp strains by correlations. Statistical analyses

were done using SPSS-PC version 3.1 (Norusis, 1988).

RESULTS

Interactions. There were significantly more interactions when there was one host than when there were two (mean \pm s.e.: 57.39 ± 6.405 versus 29.43 ± 5.883 ; $t = 4.70$, $df = 22$, $1t P < 0.001$). A smaller proportion of the interactions were on a host in the one host treatment (0.79 ± 0.049 versus 0.94 ± 0.014 ; sign test, $df = 22$, $1t P = .002$). Host density did not affect the proportion of interactions that took place while a female was parasitizing ($t = 0.55$, $df = 22$, $2-t P = 0.59$) or the proportion of interactions that involved physical contact between the females ($t = 1.25$, $df = 22$, $2-t P = 0.22$). On average, over a fourth of the interactions took place while a female was parasitizing; about half of the interactions involved physical contact. Females sometimes touched each other with their antennae; less often one would lunge at the other and even dislodge the other from a host.

There was no clear initiator in 5% of the interactions, no clear retreator in about 10% of the interactions. These values did not differ between treatments. Host density did not affect the proportion of interactions that were initiated by the ScDr female nor the proportion of interactions in which ScDr was the retreator; likewise for CB+ ($df = 22$, $P > 0.25$ for all comparisons). Combining treatments, CB+ was more likely than ScDr to be the initiator (0.54 ± 0.033 versus 0.40 ± 0.032 ; $t = 2.32$, $df = 22$, $2-t P = .03$), and ScDr was more likely than CB+ to be the retreator (0.50 ± 0.026 versus 0.38 ± 0.022 ; $t = 2.64$, $df = 22$, $2-t P = 0.02$).

Parasitizations. In the one host treatment, both ScDr and CB+ offspring emerged from the host in all 23 replicates. In all replicates of the one host treatment, the first female to parasitize the host also parasitized the host again after the second female; thus, no females encountered only an unparasitized host. In the two host treatment, offspring of both strains emerged from both hosts in 14 replicates; ScDr emerged from one host and CB+ from the other host in 5 replicates; both ScDr and CB+ emerged from one of the hosts and nothing from the other host in 2 replicates; both ScDr and CB+ offspring emerged from one of the hosts and ScDr only from the other host in 1 replicate; and CB+ emerged from one of the hosts and nothing from the other host in 1 replicate.

Both ScDr and CB+ females began drilling sooner in the two host treatment than in the one host treatment (Table I). For both strains, drill duration and within-puparium duration did not differ between treatments. There were significantly more parasitizations in the two host treatment than in the one host treatment for ScDr females but not for CB+ females.

For both strains, the proportion of parasitizations in previously drilled holes was similar in both treatments (Table II). However, of the parasitizations involving a previously drilled hole, a greater proportion were in another female's hole in the one host treatment than in the two host treatment (for ScDr: 0.41 ± 0.072 s.e. versus 0.21 ± 0.039 s.e., $t = 2.67$, $df = 22$, $P = 0.007$; for CB+: 0.31 ± 0.053 s.e. versus 0.19 ± 0.034 s.e., $t = 2.41$, $df = 22$, $P = 0.01$).

For both strains, a greater proportion of parasitizations involved interaction in the one host treatment than in the two host treatment (Table II). Of the parasitizations involving interaction, the proportion resulting in the female pulling her ovipositor out of the host did not differ between treatments (for ScDr: 0.40 ± 0.078 s.e. versus 0.42 ± 0.097 s.e., $t = 0.16$, $df = 16$, $2t P = 0.88$; for CB+: 0.29 ± 0.090 s.e. versus 0.37 ± 0.107 s.e., $t = 0.51$, $df = 12$, $2t P = 0.62$).

For ScDr in the one host treatment, when there was an interaction during parasitization, females drilled longer and within-puparium duration approached being significantly longer, although sample size is small (Table III). However, this did not occur in the two host treatment or in either

treatment for CB+ females.

Sex Ratio. Sex ratios did not differ between treatments for either strain (Table IV). Clutch size did not differ between treatments for CB+ but was greater in the two host treatment than in the one host treatment for ScDr.

In the one host treatment, for both strains, a female's sex ratio was negatively correlated with her mean within-puparium duration and positively correlated with the proportion of her parasitizations that were in a previously drilled hole (either hers or the other female's) (Table V a, b; Figure 1). Sex ratio was correlated with the proportion of a female's parasitizations that were in her own previously drilled hole for ScDr, although not for CB+ (Table V c). Sex ratio was not correlated with the proportion of a female's parasitizations that were in the previously drilled hole of the other female for either ScDr or CB+ (Table V d). However, per female, both strains had about five parasitizations in their own previously drilled holes versus only about two in other female's. Sex ratio was not correlated with the proportion of parasitizations involving interaction or with total number of interactions (Table V e, f).

By contrast, in the two host treatment, for both strains, a female's sex ratio was not correlated with her mean within-puparium duration (Table V a) or the proportion of her parasitizations that were in a previously drilled hole (Table V b-d). However, sex ratio was positively correlated with the proportion of parasitizations involving interaction and with the number of interactions (Table V e,f) (Figure 2).

If alphas for the correlations in Table V are adjusted by the sequential Bonferroni method (Rice, 1989), the only significant correlations are between interactions and ScDr sex ratios in the two host treatment.

Because of the contrasting results in the one host treatment versus the two host treatment, we also looked at partial correlations with sex ratio. For the one host treatment, when we controlled for the effect of proportion of parasitizations in a previously drilled hole, proportion of parasitizations involving interaction still was not related to sex ratio for either ScDr (partial correlation $r = 0.06$, $1t P = 0.40$) or CB+ (partial correlation $r = -0.13$, $2t P = 0.54$) and proportion of parasitizations in a previously drilled hole still was related to sex ratio for both ScDr (partial correlation $r = 0.42$, $1t P = 0.03$) and CB+ (partial correlation $r = 0.44$, $1t P = 0.02$). For the two host treatment, when we controlled for the effect of proportion of parasitizations involving interaction, proportion of parasitizations in a previously drilled hole became related to sex ratio for ScDr (partial correlation $r = 0.43$, $1t P = 0.03$) but still was not related to sex ratio for CB+ (partial correlation $r = 0.15$, $1t P = 0.25$). Proportion of parasitizations involving interaction still was related to sex ratio for ScDr (partial correlation $r = 0.77$, $1t P < 0.001$) and CB+ (partial correlation $r = 0.41$, $1t P = 0.03$).

In the two host treatment, in addition to looking at overall sex ratio from both hosts, we also looked at the sex ratio from just one host in each replicate. For ScDr, the pattern remained the same, proportion of parasitizations on that host that involved interaction was positively related to sex ratio on that host ($r = 0.63$, $n = 12$, $1t P = 0.01$), but proportion of parasitizations in a previously drilled hole was not related to sex ratio ($r = 0.05$, $n = 12$, $1t P = 0.44$). For CB+, neither proportion of parasitizations on that host that involved interaction nor proportion of parasitizations in a previously drilled hole was related to sex ratio ($r = 0.08$, $n = 9$, $1t P = 0.42$; $r = -0.30$, $n = 9$, $2t P = 0.44$).

In neither treatment, in neither strain, was a female's sex ratio positively correlated with the proportion of interactions involving contact, the proportion of interactions that the female initiated, or the proportion of interactions in which the female retreated (Table V g-i).

In the two host treatment, for both strains, the sex ratios were greater from replicates in which successfully parasitized hosts were parasitized by both strains than from replicates in which successfully parasitized hosts were parasitized by only one strain (ScDr: 0.53 ± 0.055 versus 0.29 ± 0.068 , $t = 2.26$, $df = 19$, $1t P = 0.02$; CB+: 0.25 ± 0.036 versus $0.11 \pm$

0.031, $t = 2.98$, $df = 20$, $1t P = 0.02$).

DISCUSSION

In our study, number of hosts influenced which factors were correlated with sex ratio. When there was only one host present, the proportion of sons that a female produced was positively correlated with the reuse of drill holes but not with interactions. This was reversed when there were two hosts.

That host density may influence the factors affecting sex ratios has not been suggested prior to this study. Why interactions were correlated with sex ratios when there were two hosts but not when there was one host is unclear. Likewise, why the proportion of parasitizations in a previously drilled hole was correlated with sex ratio when there was one host but not when there were two hosts is unclear.

That a female's sex ratio is correlated with the number of parasitizations in a previously drilled hole is consistent with earlier studies with *N. vitripennis*: Experiments by Wylie (1965, 1966) and by King and Skinner (1991) indicated that the sex ratio response to parasitized hosts relies on cues associated with the host pupa rather than with the puparium. Furthermore, the cues used in detecting that a host is parasitized appear to be localized, that is undetectable at the end opposite the parasitization site (King and Skinner, 1991).

A relationship between a female's sex ratio and interactions with other females is also consistent with earlier studies with *N. vitripennis*: Wylie (1966) demonstrated that females increase sex ratio in response to the presence of other females even when they do not encounter hosts parasitized by other females. Wylie (1966) had observed that females do not drill hosts during their first 24 hours after eclosion. When he exposed a host to one drilling female and three nondrilling females, a greater proportion of sons was produced than when a host was exposed to one drilling female.

Our results suggest that parasitizing an already parasitized host in the presence of another female affects a female's sex ratio beyond any effects of the physical presence of another female. When two hosts were present, the proportion of sons was greater from hosts parasitized by both females than from hosts parasitized by only one female. It has been well-demonstrated that encounters with parasitized hosts influence sex ratios in the absence of another female (e.g., Holmes, 1972).

In comparing sex ratios from hosts parasitized by a wild-type female with 1, 3, 7 or 15 stDR females, Orzack et al. (1991) concluded that "females adjust their sex ratios in response to the "host" environment (i.e., whether a particular host has been parasitized) and not in response to the "social" environment (i.e., the number of foundresses)." In contrast, our results suggest an effect of host environment on sex ratio when one host is present, but an effect of social environment (i.e., number of interactions between females) on sex ratio when two hosts are present.

The presence of a second host decreased the number of interactions between females but had no measurable effect on the nature of the interactions. Specifically, host density had no effect on the likelihood that interaction(s) occurred while one of the females was parasitizing a host or that interaction(s) involved physical contact.

Data on female-female interactions in this study suggest that CB+ is more aggressive than ScDr. CB+ was more likely than ScDr to be the initiator, and ScDr was more likely than CB+ to be the retreator during interactions. These strain differences in behavior suggest a genetic basis to female aggressiveness. Alternatively, the apparent strain differences might be due to CB+ being placed in the host arena first. This explanation seems unlikely because the wasps were placed in the arena in quick succession. The observation of a more male-biased sex ratio from ScDr than from CB+ in our study (Table IV) is consistent with findings of Orzack and Parker (1986) but contrasts with Werren (1980). Given the strain differences in aggressiveness and sex ratio, it is possible that the two strains might respond differently to members of their own strain than to each other. However, the two strains were consistent in the effects of

host density on the correlations between sex ratio and both interactions and parasitizations in previously drilled holes.

Although the number of hosts did not affect offspring sex ratios in this study, an earlier study with densities of fifty hosts and ten females found an effect of spatial distribution of hosts on sex ratio (Jones and Turner, 1987).

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superparasitized housefly pupae. Can. Entomol. 98: 645-653.

Table I. Mean \pm SE Number and Duration (s) of Oviposition Behaviors

Treatment	Number of parasitizations	Duration until drilling	Drill duration	Within-puparium duration
ScDr strain				
One host	6.17 \pm .575	4100.83 \pm 925.390	242.76 \pm 51.276	582.02 \pm 77.290
Two hosts	7.96 \pm .528	1477.74 \pm 347.658	198.33 \pm 20.467	790.74 \pm 86.168
	t = 2.54	t = 2.75	t = .77	t = 1.55
	df = 22	df = 22	df = 19	df = 11
	P = .01	P = .006	P = .45+	P = .15+
CB+ strain				
One host	6.78 \pm .569	2875.43 \pm 681.180	265.40 \pm 64.017	843.74 \pm 206.146
Two hosts	7.74 \pm .798	1257.35 \pm 362.126	207.97 \pm 37.197	691.43 \pm 79.392
	t = 1.02	t = 1.97	t = 0.84	t = 0.68
	df = 22	df = 22	df = 14	df = 11
	P = .16	P = .03	P = .42+	P = .51+

All comparisons were by 1-tailed t-tests except + was 2-tailed.

Table II. Proportion of Parasitizations
(mean \pm SE)

Strain	Involving interaction	In old location
ScDr strain		
One host	.51 \pm 0.051	.75 \pm 0.035
Two hosts	.28 \pm 0.046	.73 \pm 0.031
	t = 3.77	t = 0.48
	df = 22	df = 22
	P < .001	P = .32
CB+ strain		
One host	.39 \pm 0.066	.73 \pm 0.034
Two hosts	.22 \pm 0.044	.71 \pm 0.028
	t = 2.28	t = 0.41
	df = 22	df = 22
	P = .02	P = .34

All comparisons were by 1-tailed t-tests.

Table III. Oviposition Behavior (mean \pm SE)

	ScDr strain		CB+ strain	
	One host	Two hosts	One host	Two hosts
Drill duration (s)				
Interaction	668.96 \pm 233.044	246.18 \pm 92.135	184.840 \pm 96.704	154.72 \pm 45.063
No interaction	47.75 \pm 5.301	253.57 \pm 46.375	206.940 \pm 60.727	183.61 \pm 46.611
	t = 2.71	t = 0.06	Sign test	t = 0.51
	df = 5	df = 14	df = 9	df = 8
	P = .04	P = .95	P= .11+	P= .62
Time ovipositor in host (s)				
Interaction	960.21 \pm 176.065	896.39 \pm 109.801	693.79 \pm 151.995	519.89 \pm 50.755
No interaction	586.32 \pm 46.375	784.94 \pm 119.561	555.77 \pm 101.512	547.90 \pm 85.170
	t = 2.48	t = 0.68	t = 1.18	t= 0.25
	df = 5	df = 10	df = 9	df = 5
	P = .06	P = .51	P = .13	P= .81

(All comparisons were by 2-tailed t-tests except + were 1-tailed.)

Table IV. Sex Ratios and Clutch Sizes
(mean \pm SE)

Strain	Sex ratio	Clutch size
ScDr strain		
One host	.45 \pm 0.052	18.5 \pm 2.34
Two hosts	.49 \pm 0.049	26.6 \pm 3.20
	t = 0.52	t = 3.30
	df = 21	df = 22
	P = .61+	P = .002
CB+ strain		
One host	.26 \pm 0.026	18.0 \pm 1.52
Two hosts	.22 \pm 0.030	18.1 \pm 1.77
	t = 1.09	t = 0.05
	df = 22	df = 22
	P = .14	P = .48

All comparisons were by 1-tailed t-tests except + were 2-tailed.

Table V. Correlations of Sex Ratios (Proportion of Sons) with Behaviors

Oviposition behavior	One host			Two hosts		
	r	n	P	r	n	P
ScDr strain						
a) Within-puparium duration	-.49	14	.04	.06	18	.82+
b) Proportion of parasitizations in a previous location	.42	23	.02	-.29	22	.18+
c) Proportion of parasitizations in own previous location	.49	23	.01	-.36	22	.10+
d) Proportion of parasitizations in other female's location	-.30	23	.16+	.19	22	.19
e) Proportion of parasitizations involving interaction	.07	23	.37	.74	22	.001
f) Total number of interactions	.30	23	.08	.78	22	.001
g) Proportion of interactions involving contact	.25	23	.12	.10	22	.33
h) Proportion of interactions that the female initiated	.25	23	.13	-.09	22	.69+
i) Proportion of interactions in which the female retreated	.33	23	.06	.06	22	.40
Oviposition behavior	One host			Two hosts		
	r	n	P	r	n	P
CB+ strain						
a) Within-puparium duration	-.55	17	.01	-.25	18	.16
b) Proportion of parasitizations in a previous location	.43	23	.02	.07	23	.38
c) Proportion of parasitizations in own previous location	.14	23	.26	.002	23	.50
d) Proportion of parasitizations in other female's location	.20	23	.18	.08	23	.36
e) Proportion of parasitizations involving interaction	-.08	23	.70	.39	23	.03
f) Total number of interactions	.09	23	.34	.46	23	.01
g) Proportion of interactions involving contact	-.07	23	.75+	-.05	23	.82+
h) Proportion of interactions that the female initiated	-.17	23	.45+	-.07	23	.77+
i) Proportion of interactions in which the female retreated	-.28	23	.20+	-.12	23	.57+

All comparisons were by 1-tailed t-tests except + were 2-tailed tests.

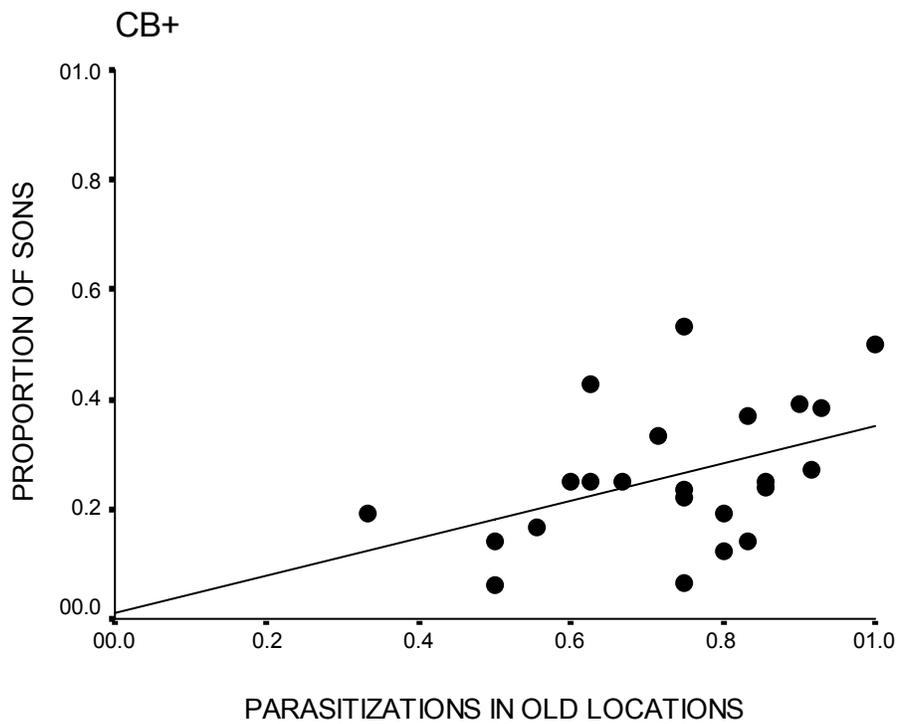
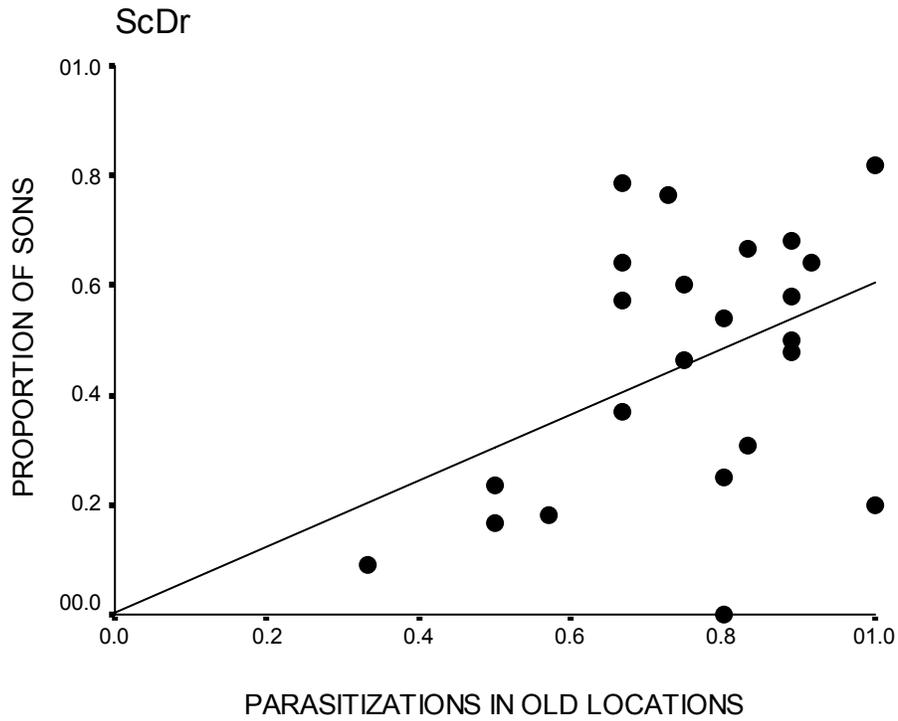


Figure 1. Correlation between a female's proportion of sons and the proportion of her parasitizations that were in a previous parasitization location for A) ScDr: $Y = .60X + .003$, $r = .42$, $n = 23$, $P = .02$; B) CB+: $Y = .34X + .013$, $r = .43$, $n = 23$, $P = .02$

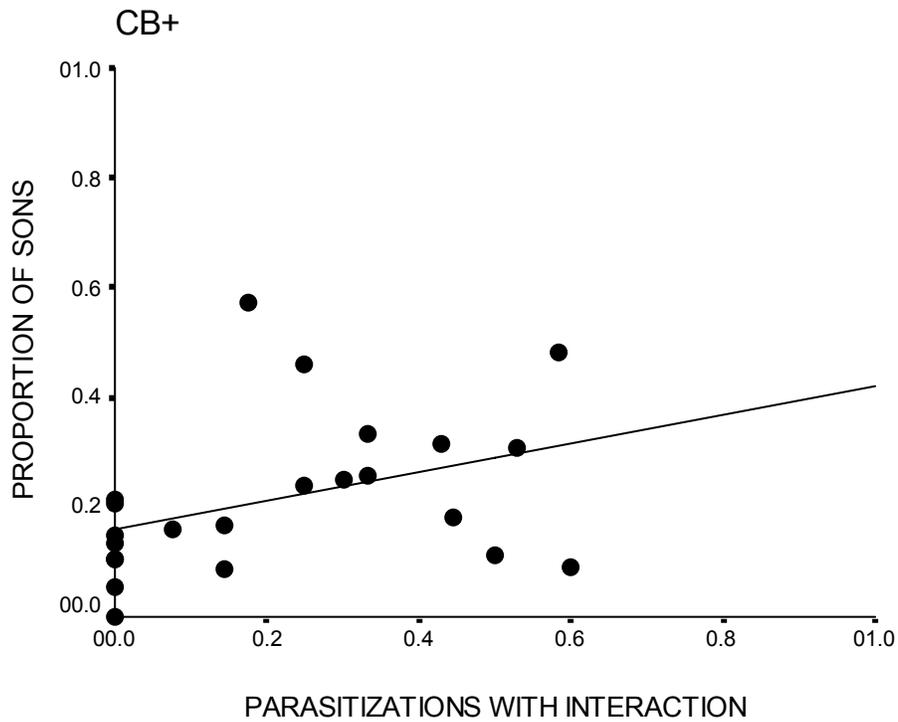
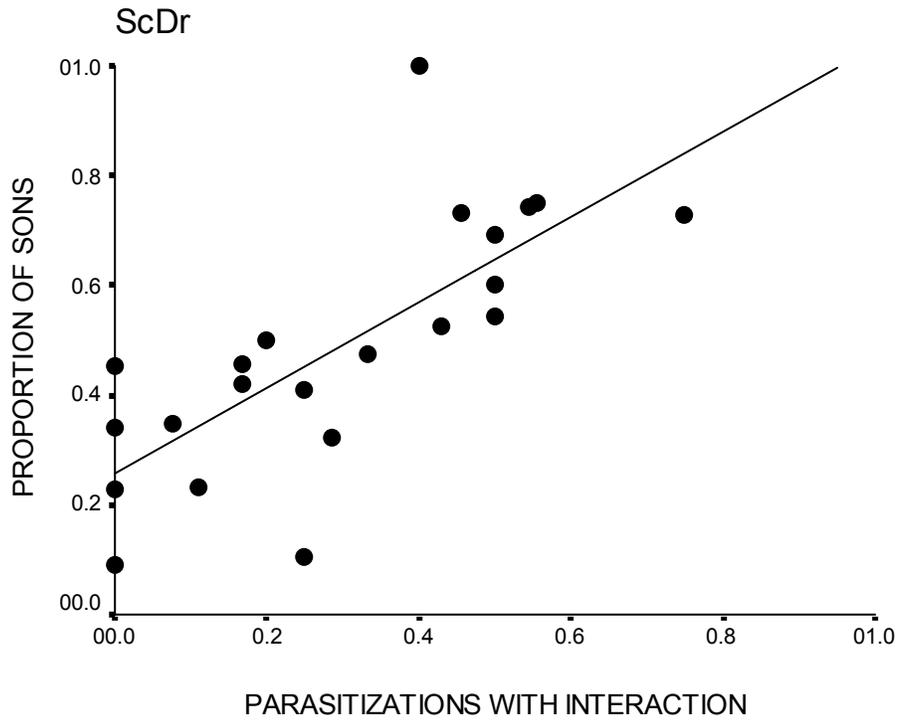


Figure 2. Correlation between a female's proportion of sons and the proportion of her parasitizations that involved interaction for A) ScDr: $Y = .78X + .26$, $r = .74$, $n = 22$, $P < .001$; B) CB+: $Y = .26X + .16$, $r = .39$, $n = 23$, $P = .03$