

SEXUAL COMPETITION FOR SPACE OF THE PARASITE
XENOS PALLIDUS BRUES IN
MALE *POLISTES ANNULARIS* (L.)
(STREPSIPTERA, STYLOPIDAE, AND
HYMENOPTERA, VESPIDAE)*

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INTRODUCTION

Xenos pallidus Brues is the only known stylopid parasite of *Polistes annularis* (L.) and is apparently restricted to this host (Bohart, 1941, and personal communication, 1979). *X. pallidus* within the host abdomen absorb nutrients directly from the blood. When mature the head and thorax is protruded between two of the wasp's abdominal segments. The female remains a permanent larvi-form parasite while the male metamorphoses to pupa and adult. The male emerges and flies in quest of a female for his lifespan of a few hours. Eggs hatch within the body of the female and the larvae crawl from her brood chamber onto the surface of the host. Eventually they find and bore into larvae of *P. annularis*. Two or more generations of parasites develop per season and apparently overwinter as adult females in queen *annularis*.

During the period 7 October-12 November 1979 I collected *P. annularis* on Newnan's Lake, near Gainesville, Florida. The colonies collected contained a total of 13372 queens and 11542 males. The queens were used for venom extraction and are not included in the following discussion, but my subjective impression while sexing the wasps was that the males were more often parasitized. Between 17 November and 23 November 1979, 1691 queen and 331 male *annularis* were collected at several other lakes near Gainesville. These queens were also used for venom extraction, and since only 3 of the males were parasitized by *pallidus*, only males from Newnan's Lake are used in the analysis which follows.

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METHODS

The *annularis* colonies collected were built over the water, primarily under branches of bald cypress, *Taxodium distichum*. Plastic bags were carefully slipped around the nests, and the bag was tied shut and placed in a cooler. The wasps were killed by freezing, and the parasitized males preserved in alcohol. The abdominal sclerites were separated with a dissecting needle while the wasps were examined at 20 \times to locate all exserted *pallidus*, including collapsed male puparia. Statistical analysis was performed using chi-square tests applied to contingency tables as described by Siegel (1956). Considerable lumping of data was necessary to perform the test in some categories.

RESULTS

Sex ratio of Polistes annularis:

Sex ratios of both wasp and parasite in this study are of course the ratios only at the time of collection in the life cycle of each. The ratio of male to female *annularis* at Newnan's Lake was 1.04:1 on 23 Oct. but decreased to 0.21:1 on 12 Nov. 1979 as the males died or left the nests at a greater rate than the females. Few of the wasps were foraging during the collection period. Therefore one would expect parasitized and unparasitized males to be otherwise equal with respect to predation pressure and energy consumption, and the parasitized individuals to die sooner. The per cent of parasitized males should decrease with time, but the data available for 4 dates show no clear trend. The per cent of males parasitized on 23 Oct. was 2.1, on 26 Oct. 8.4, on 5 Nov. 5.6, and on 12 Nov. 2.5, from 529, 309, 321, and 279 males collected on those days respectively.

Number of Xenos pallidus in individual male Polistes annularis:

Table 1 shows the number of male wasps with various combinations of male and female parasites. Only 1 host had as many as 6 female *pallidus*, while 6 had 6-8 males, possibly indicating that the male parasite extracts less nourishment from the host, because males are smaller. Bohart (1941) stated that males may decrease host survival due to evaporation of water from the empty puparia and invasion of fungi into the puparia. In the present study all but 6 of the 423 male *X. pallidus* had emerged. Fungus invasion did not appear to be a major cause of host mortality. Only a few of the puparia were slightly

moldy, and 3 of the male still in pupal cases had apparently died and become moldy. The average number of parasites per infested host was 2.1.

Table 2 compares the number of hosts observed with each parasite load to the number expected from a truncated negative binomial distribution obtained by modifying the method of Crofton (1971). This method predicts the number of hosts for each parasite load by referring to the pattern established with small parasite loads, in this case the number of hosts observed with 0–3 parasites. Table 2 shows an extremely close correspondence between observed and expected numbers of hosts until the parasite load reaches 9 and 10 per host. Thus 9 or more parasites probably kill the host relatively rapidly.

Sex ratio of *Xenos pallidus*:

The *Xenos* sex ratio was 423 males to 772 females or 1:1.83. This ratio probably results from the more rapid death rate of hosts carry-

Table 1. Number of male *Polistes annularis* with each combination of male and female *Xenos pallidus* parasites, collected at Newnan's Lake, Alachua Co., Florida, 7 Oct-12 Nov 1979.

Males per host	Females per host						Hosts	
	0	1	2	3	4	5		6
0	10973	246	56	15	3	4	1	325
1	55	55	24	13	6	2		155
2	9	13	11	5	2	3		43
3	6	5	7	4	2	2		26
4	1	2	3	1	2			9
5	1	2	2					5
6		1	1					2
7			1					1
8	1	1	1					3
Total Hosts	73	325	106	38	15	11	1	569

Table 2. Number of male *Polistes annularis* observed with 0 to 10 *Xenos pallidus* parasites compared with the number expected from a truncated negative binomial distribution, truncated at 3 parasites per host.

	Parasites per host										
	0	1	2	3	4	5	6	7	8	9	10 or more
Observed	10973	301	120	58	33	25	14	9	6	2	1
Expected	10972	302	118	60	34	21	13	9	6	4	8

ing male parasites. At first sight, this sex ratio seems contradicted by the higher maximum number of male parasites per host. I account for this discrepancy by postulating a short emergence season for the male *pallidus*. If, in a host with several male parasites, all the males emerged in rapid sequence before the host could die from the effects of desiccation, a situation would exist in which relatively fewer of the hosts that had carried males would be alive at any one time, but some of them could show high numbers of males per host. Other data from table 1 agree with this explanation of the sex ratio in that there were 325 hosts with just females and 244 with just males or with both males and females present. Antagonistic to this explanation is the probability that over 6 female *pallidus* kill the host outright so that we do not see these in the sample at all.

Location of *Xenos pallidus* in the host:

The *Xenos* exerted themselves under the edges of the sclerites of the second to the sixth abdominal segments posterior to the waist. The parasites showed a strong preference for a dorsal position on the abdomen, for several probable reasons. First, the parasite could force its way out more easily dorsally because the tergites separate when the wasp flexes its abdomen, while the sternites are compressed. Second, the tergites cover more of the surface of the abdomen than the sternites. Third, it would seem that natural selection would select for females to locate dorsally because they would be easier for males to fly to and mate with, especially if the female were located posteriorly. How mature stylopids penetrate the intersegmental membranes of the host has not been described.

No *pallidus* were located in segment 1 of the host in this study. However, Pierce (1909) did find one male protruding between the first and second tergites. As seen throughout the following discussion male *pallidus* are characteristically located more anteriorly than females. Only 1 female was found in segment 2 and only 1 male in segment 6. The maximum number of males under tergites 2, 3, 4, and 5 was 3, 4, 3, and 1 respectively, for males under sternites 2–5 the maximum numbers were 1, 2, 2, and 1 respectively. The maximum numbers of females under tergites 3, 4, 5, and 6 were 1, 3, 3, and 2 respectively, for females under sternites 3–6 the maximum numbers were 2, 2, 2, and 1 respectively.

Data on parasite position in the host was divided into 5 categories: (1) Only females in host, (2) Only males in host, (3) Equal numbers of both sexes in host, (4) Fewer males than females in host, and (5) More males than females in host. These categories had subcategories based on the sex combination of the parasites in each host.

Parasite position with only female *Xenos pallidus* in the host:

Table 3 shows that as the number of female parasites in a host changes, the location of the parasites under the tergites of the host significantly changes ($p < 0.001$). When only one female is present in a host, 90.8% of the dorsally located females had a preference for the fifth tergite. As the number of females in a host increases, the proportion under tergite 5 decreases, while the proportion under tergite 4, and possibly tergite 6, increases. Only 3 females were located under the third tergite in this category.

Table 3. Contingency table for correlation between number of female *Xenos pallidus* in male *Polistes annularis* and the tergite of the abdomen where the parasites were located. Parentheses indicate percentages of each row. $C = .41$, $X^2 = 78.4$, significant at $p < 0.001$, $DF = 6$, $N = 396$.

Number of females in host	Number of Abdominal Tergite			Total
	3 and 4	5	6	
1	12 (5.0)	217 (90.8)	10 (4.2)	239
2	18 (19.2)	69 (73.4)	7 (7.5)	94
3	10 (29.4)	23 (67.7)	1 (2.9)	34
4, 5, or 6	16 (55.2)	9 (31.0)	4 (13.8)	29
Total	56	318	22	396

Just 45 females in this category were located under the sternites, compared to 396 under the tergites. If females located ventrally are added to Table 3, the change in parasite location is still significant ($p < 0.001$). Most of the females (32/45) under the sternites were under the fifth sternite. As the number of females in a host increases, the proportion under sternite 5 increased similar to the proportion under tergite 4.

Thus intrasexual competition causes a tendency for the "losing" females to be shifted first to the fourth tergite, then others to the fifth sternite. One might expect the preferred fifth tergite position to be filled before the other positions were accepted. If we assume that 2 females fill the fifth tergite position, only 29 of 79 hosts with 2 or more

females show the filled condition. However, 72 of the 79 hosts had at least 1 female under the fifth tergite. Thus perhaps only 1 female under the fifth tergite fills that location so far as intrasexual competitive effect is concerned.

Parasite position with only male *Xenos pallidus* in the host:

Table 4 shows that the position of male parasites significantly changes as the number of parasites changes ($p < 0.02$). Most of the male *pallidus* present alone in a host prefer a location under the fourth tergite. Only 7 of the males were in the second segment, and only 6 in the fifth segment. Nine of the 14 males located under sternites were under sternite 4. The proportion of those under sternite 4 increases as the number of males per host increases. When 2 males are present in a wasp, one goes to the fourth tergite and the other to the third tergite. With 3 to 8 males present in a host the preferred location is the third tergite. Thus the males exhibit the same pattern of intrasexual competition as the females. The losing males are shifted from the preferred tergite 4 to the next anterior tergite and then to sternite 4. As in the females, only 1 parasite seemed to fill the preferred position, since only 1 of the 18 hosts with 2 or more males had 2 males under the fourth tergite, but 14 of the 18 had at least one male there.

Position of male relative to female *Xenos pallidus* in the host:

Clearly the male *pallidus* tends to extrude from the host more anteriorly than the female. This tendency is probably related to the fact that males are shorter than females. Ten adult females had a head-thorax length of about 1.5mm, an abdomen length of 6–7mm. Three of the females contained larvae. The 3 male pupae retaining puparium caps had a head-thorax length of 2mm, an abdomen length of 2.5–3mm. Comparing the total length of the *Xenos* to the abdomen of the host, it appears that both sexes of parasites usually brace themselves near the base of the second abdominal segment of the host to extrude the cephalothorax.

Position of *Xenos pallidus* in the host when the number of each sex is equal:

Not enough data were available to test the position of females in this category. The males did not show a significant change of position in the host as number of parasites per host increased ($p > 0.05$). However, the trends seemed to be for the males to prefer segment 3

Table 4. Contingency table for correlation between number of male *Xenos pallidus* in male *Polistes annularis* and the abdominal sclerite where the parasites were located. Parentheses indicate percentages of each row. $C = .29$, $X^2 = 10.1$, significant at $p < 0.02$, $DF = 3$, $N = 108$.

Number of males in host	Abdominal Tergite or Sternite		Total
	2 and 3	4 and 5	
1	19 (34.5)	36 (65.5)	55
2	9 (50.0)	9 (50.0)	18
3	10 (55.6)	8 (44.4)	18
4, 5, or 8	13 (76.5)	4 (23.5)	17
Total	51	57	108

Table 5. Contingency table for correlation between number of female *Xenos pallidus* in male *Polistes annularis* and the abdominal sclerite where the parasites were located when one male parasite was also present. Parentheses indicate percentages of each row. $C = .25$, $X^2 = 8.3$, significant at $p < 0.05$, $DF = 3$, $N = 121$.

Number of males (m) and females(f)	Abdominal Tergite or Sternite		Total
	4	5 and 6	
1m2f	6 (12.5)	42 (87.5)	48
1m3f	5 (12.8)	34 (87.2)	39
1m4f	8 (33.3)	16 (66.7)	24
1m5f	4 (40.0)	6 (60.0)	10
Total	23	98	121

and the females segment 5 in all subcategories. These data could mean that intersexual competition prevents the change in parasite position due to intrasexual competition that we saw above.

Position of *Xenos pallidus* in the host when the number of males was less than the number of females:

Table 5 indicates that an increasing number of females in hosts with one male caused a significant shift in position of the parasites (< 0.05). With an increasing number of females, the proportion in segment 5 decreases while the proportion in segment 4 increases. This is basically what we see in Table 3 where only female *pallidus* were present in a host, and suggests that mostly intrasexual competition is occurring. In this category, 2 or 3 females more often filled the preferred position at tergite 5 than when only females were present in a host, because 1 host had 3 females at tergite 5, 22 had 2, 17 had 1,

and 5 had 0 there. This filling effect may be due to intersexual competition, in which more females pile up at the preferred location before overcoming the effect of the male present.

Not enough data were available to test the effect on position of increasing number of males or when two or more males were present in a host in this category, but generally the females preferred segment 5 and the males segment 3 as before. When all the data for females in this category were lumped into three subcategories in which either 1, 2, or 3 males were present with the females, there was no significant change in the positions of females as number of males increased ($p > 0.05$). In other words, the data analyzed this way indicated either no intersexual competition, or that the intersexual competitive effect of 1 male was as strong as the effect of 3 males.

Position of *Xenos pallidus* in the host when the number of females was less than the number of males:

With one female present in a host, increasing number of males from 2 to 8 had no significant effect on position of the males ($p > 0.05$). This result is different from that of the preceding section where we saw more intrasexual competition between females in hosts with one male. In addition, with 2 females in a host with 3 to 8 males, no significant position changes in the males were observed ($p > 0.05$). These data seem to mean that the intersexual competitive effect on position is stronger than the intrasexual effect and the intersexual and intrasexual competitive effect of females is stronger than that of males.

There were not enough data to test female position in this category, but where one female was present with 2 to 8 males, 17 of 23 females were under the fifth tergite. Where two females were present with 3 to 8 males, 25 of 33 females were under the fifth tergite. In this category, males were rather scattered among segments 2–4. In summary, no intrasexual competition is seen in this category, but females seem to take their preferred position and suppress position changes of the males.

DISCUSSION

Notes on small collections of *pallidus* have been given by several investigators. Hubbard (1892) confined and studied a nest of Florida *P. annularis* for three weeks. He noted that parasitized hosts rarely left the nest, and states that the parasites extrude from the abdomen

before the wasp emerges from the pupa. Brues (1905) compared a nest of *annularis* taken in July with one collected in October in Texas. In the adult October wasps he found *X. pallidus* larvae as well as adults. Thus possibly in the present study non-extruded *Xenos* may have been missed. However, I dissected 49 male *P. annularis* whose abdomens looked abnormal, but no *X. pallidus* were found. Brues suggested that all the wasps carrying male *Xenos* die before the next spring since he saw none with male pupal cases in the spring. This would also mean the death of the female *pallidus* in the same wasp carrying males. If this is so, the effect on the populations of both host and parasite could be severe.

Pierce (1909) reported on two large colonies of Texan *annularis* taken in September and kept alive through October containing 1311 male and 242 female wasps. The males were 19.8% parasitized by *pallidus*, the females 2.9% parasitized. One male wasp carried 15 male *pallidus*, whereas the highest parasite load in the present study was 8 males with 2 females. Pierce states that several queen wasps with empty male *pallidus* puparia were found hibernating, but whether such queens could reproduce the next spring remains unproved. Pierce (1909) also states that male *pallidus* did not protrude from the host until several days after the host left its pupal cell, a contradiction with Hubbard (1892). The winged males left the host 10–17 days after the host became adult.

Pierce (1918) points out that in *Delphax* (Homoptera) the female strepsipteran is located more anteriorly in the host than the male probably because the female is smaller than the male, the reverse of the case in *pallidus*. Salt (1927) found no morphological change at all in a small series of *annularis* carrying *pallidus*, nor was any change except deformation of the abdomen noted in the present study.

According to Bohart (1941) only two strepsipterans are known to parasitize *Polistes* in North America, *pallidus* in *annularis* and *X. peckii* Kirby in several other species. The most extensive study of *X. peckii* was done by Schrader (1924). She found extreme differences in infestation rates, from 0 to 25%, in different localities in New England. The parasites extruded from the host after the wasps emerged from pupae, the males 5–10 days before the females. The sex ratio of larval *X. peckii* was 38 male: 37 female. Further work on both species of *Xenos* in North America, and comparison between them, is certain to provide much new information on the evolution of parasite/host interactions in a very interesting system.

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