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Regulating Factors of Ovarian Development in Paper Wasps of the Genus *Polistes*

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in Paper Wasps of the Genus
Polistes

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Abstract. Wasps of the genus *Polistes* were used to determine the effects of larval nutrition, position within the nest, and parasitism on ovarian development. *Polistes* nests were collected from Iowa, Minnesota, and Utah during the summer of 1994. The wasps were reared out, and dissected, and their ovaries examined. The total number of oocytes and size of the largest oocyte were used as measurements of ovarian development. Due to difficulties hand feeding the larvae, no data was obtained concerning the effect of larval nutrition on ovarian development. Data from the first emergence nests of Minnesota were in conclusive. However, data from the second emergence nests of Utah, which were about three times larger than the nests from Minnesota, indicated that the position within the nest does have an effect on the total number and size of the oocytes. The Utah *Polistes* which emerged from the interior cells of the nest had more numerous oocytes than those from the exterior cells. The results indicate that there may be additional factors, such as nest size or nest age, which may affect the size and number of oocytes. Parasitized and non-parasitized *Polistes* from the same colony were examined to determine the effect of parasitism on ovarian development. Data indicated that parasitized *Polistes* have a smaller size and number of oocytes than non-parasitized *Polistes*.

INTRODUCTION

Wasps of the genus *Polistes*, commonly known as paper wasps, are eusocial insects of the family Vespidae. *Polistes* meet all three of the classic criteria for eusociality: 1) overlapping generations in which adults from two or more generations interact; 2) cooperative brood care in which adults assist in caring for the immature larvae or newly eclosed adults most of which are not their own offspring; and 3) reproductive division of labor where some of the females are reproductives who lay the eggs while other females are sterile workers which forage for pulp and food, care for the brood, and build new cells (West-Eberhard 1969).

. Typically, a single queen or foundress initiates a nest. Occasionally there may be multiple foundresses, but in these cases one of the foundresses becomes the predominant reproductive. When the queen begins constructing a nest, she first builds a pedicel which attaches the nest to a substrate, such as the eave of a building. The first cell of the nest, constructed from wood pulp, extends from the pedicel. Additional cells are added around the first cell in a circular pattern so that the first cell is in the center. As the cells are built, the queen lays an egg in each one. The eggs are attached to a cell wall next to an adjacent cell rather than on a cell wall at the periphery of the nest (West-Eberhard 1969).

Approximately two weeks later, depending on the temperature, the first egg hatches and a first instar larva emerges. In *Polistes* there are four larval instars which can be readily determined by observing the width of the larval head capsule. As the larvae develop, all of the queen's time is required for foraging for food and caring for the larvae, as a result she stops foraging for pulp, building new cells, and laying more eggs. After two to three weeks, the larvae have matured and each one spins a silk cap for its cell and pupates. As the larvae become non-feeding pupae, the queen, released from her feeding duties, resumes her previous activities of foraging for pulp, building new cells, and laying more eggs (West-Eberhard 1969).

The first adults to emerge are typically all females and function as workers. An individual worker generally forages, cares for the brood, or adds cells to the nest. The foragers tend to be specialized as either wood pulp or food foragers. They carry their loads to the nest to give to the workers who build new cells and care for the brood. While the first workers to emerge are doing the foraging, feeding, and building, the queen lays more eggs and oversees the activities on the nest (West-Eberhard 1969).

A few weeks after the first emergence of adults, the second emergence begins. The second emergence wasps include both males and females. The males do not do any foraging or caring for the brood, rather they solicit food from the foragers and wait for opportunities to mate. The newly emerged females are the reproductives which will found colonies the next spring. They do not assist in caring for the brood or foraging either. During the period of time when emergence of future reproductives is occurring, the original queen disappears. The workers are unable to feed both the new adult wasps and larvae so the colony disassembles. The newly emerged wasps often cannibalize the rest of the larvae. The reproductive females and males leave the parent colony to seek mates. The mated females accumulate fat reserves and go into diapause until the next spring when they will emerge to begin the cycle again. Workers and males die with the onset of cold weather (West-Eberhard 1969).

Important questions about species of *Polistes* revolve around the feeding and reproductive potential of the female wasps. Does food consumption affect ovarian development? Are some larvae in the nest fed more than others? If yes, which are fed more and why? Are there other factors which could cause differences in ovarian development? What effect does parasitism have on ovarian development?

According to Rossi and Hunt (1988), larval nutrition is indirectly related to ovarian development in *Polistes metricus*. An increase in the quantity and quality of food eaten by a larva will result in a higher level of non-cuticular fat, which positively correlates with ovarian development. In wasps of other genera, such as those in the Vespinae, it is believed that larval nutrition is a determinant of caste position, hence dominance (Hunt 1991). Dominance is directly related to ovarian development: the more dominant an individual *Polistes* is, the more developed are its ovaries (West-Eberhard 1969). Therefore, it would appear that larval nutrition at the very least has an indirect affect on ovarian development.

One of the key questions involving larval nutrition is, do some larvae receive more food because of their cell location in the nest? In particular, do the larvae from the interior cells of the nest receive more food than those from the exterior cells? Strassman and Orgren (1983) found no difference in the amount of food distributed among the brood members in *Polistes exclamans* in Texas. They cited several factors which support their evidence. First, they stress that there is great uniformity in size of larvae that are from the same emergence group. The larvae from the first emergence are all essentially the same size, as are those from the second emergence, even though the larvae from the first and second emergence are not the same size. If some of the larvae had been fed more, there should have been some adults within an emergence group which were larger than others. They found no evidence to support this idea. Secondly, Strassman and Orgren (1983) tried relating brood development time to position within the nest. They found no support that larvae in certain regions, specifically the central region, of the nest developed faster than others. Thus, they believe that food is evenly distributed to the larvae of the nest by the worker wasps.

However, West-Eberhard (1969) reported evidence suggesting that some larvae in *Polistes fuscatus* do receive more food than others. She observed that the female workers distributing food spend more time in areas of high larval concentration. She proposes that the centrally located larvae receive more time and food from workers caring for the brood, because the larvae are clustered together. The larvae on the periphery of the nest are not clustered together, therefore, they do not receive as much time or food. Since the centrally located larvae receive more food, their ovaries should be more developed if there is a correlation between the amount of food received and the degree of ovarian development.

In the United States *Polistes* are subject to attack by a parasitic strepsipteran, *Stylops* spp. Strepsipterans are endoparasites which attack the larvae of many species of bees and wasps without killing them (Ross 1948). The motile first instar strepsipteran larvae, known as triungulins, burrow into a host, molt, and begin development as endoparasitic larvae absorbing food from the host through diffusion across the body wall. As the parasite grows, the posterior tip of its abdomen gradually extends between the abdominal sclerites of the wasp, while the rest of the parasite body remains within the abdominal cavity of the wasp. The male strepsipteran pupates in the host and then the winged adult emerges, leaves the host, and begins searching for a female. The female pupates within the larval skin inside the host. The males mate with females while the females are still in their host. After mating, thousands of eggs develop and hatch within the female's body. Eventually the triungulins crawl through the extended abdomen of the female parasite and leave the host, usually as the wasp visits a flower. There the parasites wait until a bee or wasp visits the flower. They then attach to the wasp or bee and are carried back to the nest where they invade new larval hosts (Ross 1948). Since the strepsipterans develop within the wasp as nutritive parasites, they may affect the nutritive balance within the host (Spradbery 1973). This may be a major factor in explaining why parasitism by *Stylops* spp. may decrease the ovarian development of its *Polistes* host (Spradbery 1973).

Based on this information gained from previous studies, I predicted that *Polistes* larvae which are fed more would have better developed ovaries, *Polistes* reared from the interior cells of the nest would have more developed ovaries than those from the exterior cells, and *Polistes* infested with the strepsipteran *Stylops* spp. would have diminished ovarian development in comparison with non-parasitized *Polistes*.

METHODS

Three different groups of *Polistes* nests were collected for analysis in this project (Table 1). The first group of twenty-three nests was collected from several sites in southwestern Iowa on May 23 and 24, 1994. The majority of the nests were gathered from Waubonsie State Park; other nests were collected from Lake of Three Fires State Park and city parks in Osceola, Avoca, and Stuart, Iowa. The second group of six *Polistes* nests was collected from Greenfield, Minnesota on June 15, 1994. The third group of three nests was collected from Logan, Utah on August 11, 1994. Once the nests were located, usually under the eaves of buildings, the queen(s) was (were) netted and the nest taken down by prying the pedicel from the substrate.

A map (diagram) was drawn of each nest indicating the life cycle stage present in each of the cells. Egg and larval position within the cell were shown. Each larva was classified according to its instar: first through fourth.

In an effort to control the relative nutritional status of the developing larvae, I attempted to hand feed them. The first and second instar larvae were too small to be fed successfully, so only the third and fourth instar larvae were fed. The larvae were given a mixture of foods they would have been fed in the wild: crickets, mealworms, honey, and water (Appendix A). The ingredients were blended together and gelatin was added to improve the consistency of the mixture. The exact proportions of the ingredients in the diet varied slightly from batch to batch, but the wasps in each group were all fed from the same food batch.

The larvae from each nest were randomly separated into three feeding groups. The first group was fed twice a day. The second group was fed once a day, the third once every other day. Using a desk magnifier and lamp to aid visibility, the food was placed near the mouth of the larva with a pin. When the larvae were satiated, or stopped feeding, the excess food was carefully removed from the cell.

Each adult female which emerged from a cell in the nests of Minnesota and Utah was isolated from the nest and other adults and fed a continuous supply of honey and water for eight days, a length of time sufficient for any parasites to develop and be visible. In the event that more than one adult emerged in a day and it was not possible to determine from which cell each emerged, the adults were isolated together for the eight day period. After the eight days, the wasps were asphyxiated with ethyl acetate and preserved in Kahle's solution (Appendix A).

The wasps were dissected in Kahle's solution under a dissection scope at 25X. The number of oocytes in each ovariole was counted and the number of developed ovarioles in each ovary was determined (Figure 1). Also, the largest oocyte in each ovary was measured to the nearest 0.1 mm. Oocytes were discerned by a milky coloring and a rounded appearance within the ovariole. Special care was taken to not include nurse cells, which were significantly smaller and preceded the larger oocytes in the ovariole.

A group of adult *Polistes* spp., some of which were parasitized by the strepsipteran *Stylops* spp., were collected in Washington County, Idaho on July 14, 1994. These wasps were preserved in ethyl acetate (West-Eberhard, pers. comm.) until they were dissected. The total number of oocytes was counted and the size of the two largest oocytes was determined. The size and number of parasites associated with each wasp was also determined.

Climate data

Normal mean temperature and total precipitation data for April through August and for 1994 were obtained from the state climatologists in Des Moines, Iowa; Logan, Utah; and Boise, Idaho. Mean temperature and total precipitation data for May through June in Collegeville, Minnesota was acquired from Fr. Melchoir Freund (pers. comm.) at St. John's University and was compared to the normal temperature and precipitation data for St. Cloud, Minnesota from The Universal Almanac (1994). T-tests were used to determine whether the climate data for the summer of 1994 was significantly different from the normal.

Voucher specimens

Voucher specimens of *Polistes* spp. and the strepsipterans are in the research collection at St. John's University in Collegeville, Minnesota.

Analysis

T-tests were used to determine whether or not the mean size of the *Polistes* oocytes from the wasps reared from interior cells of the nest was significantly different from that of wasps reared from the exterior cells. Differences were considered significant when the probability of error was less than five percent ($p<0.05$). For purposes of analysis the exterior cells of the nest were defined as those in the two outer rows and all others were interior cells (Figure 2). However, in a small nest, the exterior cells were those which were not included in the centermost seven cells (Figure 3).

RESULTS

All of the hand fed larvae from both Iowa and Minnesota died within a week and a half. Death was recognized in the third and fourth instar larvae when they could not be seen eating, their mouthparts became black and hard, and their body turned yellow and shriveled. Also, the larvae did not secrete appeasement liquid when the region around their mouth was probed.

The nests collected in Minnesota contained some pupae. These pupae were allowed to emerge and were used in the study of the effect of larval position within the nest. A total of twenty-four adult females emerged and were dissected (Table 2). Nineteen of the twenty-four wasps emerged from interior cells, while five emerged from exterior cells. Wasps reared from the exterior cells of the nests had significantly larger oocytes than wasps from the interior cells ($p<0.05$; interior $\bar{x}=0.30\pm0.1$mm (S.D.), $n=19$; exterior $\bar{x}=0.38\pm0.1$mm, $n=5$). The wasps that emerged from the interior cells of the nest had fewer oocytes (interior=17.2 ± 5.5; exterior=19.2 ± 1.7), but the difference was not statistically significantly.

The female wasps that emerged from the nests collected in Utah were also used for the study of nest position effects (Table 2). The largest oocytes from wasps which emerged from interior cells were significantly larger than those of wasps from exterior cells ($p<0.05$; interior=0.63±0.25mm, n=21; exterior=0.53±0.23mm, n=13). Wasps reared from interior cells had more oocytes than wasps reared from exterior cells ($p<0.05$; interior=14.9±3.3; exterior=11.3±4.0).

The *Polistes* females collected from Idaho were used to examine the effect of parasitism on ovarian development (Table 2). Non-parasitized wasps had significantly larger oocytes than did parasitized females from the same population ($p<0.05$; non-parasitized=0.38±0.67mm, n=22; parasitized=0.14±0.10mm, n=7). The non-parasitized wasps also had a greater number of developed oocytes than did the parasitized wasps ($p<0.05$; non-parasitized=7.2±6.1; parasitized=2.0±2.3).

Climate

The normal mean temperature for April through September and for 1994 were all comparable in Iowa, Utah, and Idaho (Table 3). Minnesota, however, had a normal mean temperature ten degrees higher than the mean temperature of 1994, but this large deviation was not significantly distinguishable from long term averages. As shown in Table 3, the mean total precipitation in 1994 did not differ from Minnesota's long term average. Precipitation was lower, although not significantly so, in Iowa and Idaho; in Utah the total precipitation was significantly lower than long term averages ($p<0.05$). Iowa and Idaho had 1.42 inches and 0.33 inches less precipitation, respectively, in 1994 than normal. Utah had 1.11 inches less rainfall than normal in April through September of 1994. Since the data were collected during one field season and the results for the groups from different states were not compared against each other, the differences in the temperature and precipitation of 1994 from the normal should not matter. However, if further studies were done and comparisons were made, the temperature difference in Minnesota should be taken into account. The differences in precipitation should not be a major factor as neither wasps nor the food they consume rely directly on precipitation for their water supply. The climate data were obtained and documented so future studies may be aware of atypical climate conditions if comparisons are made.

DISCUSSION

There were several difficulties involved in hand feeding the larvae. The first difficulty was trying to obtain a good consistency in the food that was being fed to them. A standard blender was used to mix the ingredients and it left some larger chunks than was intended. In order to remedy the situation, larger amounts of each of the ingredients were added which created a better consistency.

A second problem that occurred while feeding the larvae was that when the food was presented directly to the them, it stuck to their mouthparts and appeared to "glue" them together. To prevent this from occurring, the larvae were fed indirectly by placing bits of food on the wall of the larva's cell, close enough to its head so that it could reach the food on its own. When the larva stopped eating, any remaining food was scraped from its mouth and the side of the cell and removed.

The fact that the larvae died indicates that something about the feeding process which was attempted was not acceptable. Part of the problem may have been that the food did not have a fine enough consistency. Possibly, the larvae do not have developed mouthparts which allow them to chew food that is not fine enough for their digestive tract to accept. In the wild the larvae are fed food directly from the mouth of a worker who has already chewed and softened it. In fact, according to Hunt (1984), the female *Polistes* actually ingests and digests part of the food within her midgut. Perhaps the initial digestion and the regurgitation of the food by the worker is necessary for the larvae to entirely digest its food, meaning the digestive tract is not fully developed. Further studies would have to be done to determine which of these or possibly which combination of these was responsible.

Another factor which may have affected the success of the feeding was the ability to clean off the food from around the mouth of the larva. It was difficult to determine whether or not all of the excess food had been removed. Actually, there was almost certainly at least some traces which could not be seen or removed. The larva did not appear to have the ability to remove excess food from the outside of its mouth, thus the food could have hardened and sealed the mouthparts together.

Since the hand feeding did not succeed in giving quantitative results, alternative ways to examine the relationship between nutrition and ovarian development were explored: position within the nest and parasitism.

There is still controversy about a possible relationship between a larva's position within the nest and its ovarian development. The question is whether or not some larvae are fed more than others, because if some are fed more and better quality food they have an increased reproductive potential. According to Strassman and Orgren (1983), in *Polistes exclamans* feeding is not disproportionate between larvae located in the interior or exterior cells of the nest. However, West-Eberhard (1969) reported evidence in *Polistes fuscatus* suggesting that larvae in the interior cells of the nest are clustered together and receive more food, thus they have better reproductive potential.

The first measurement of ovarian development that was used was the size of the largest oocyte. Presumably, a wasp with a large oocyte would be further along in its ovarian development than one with a smaller oocyte. Since the wasps which emerged from the interior cells of the nest are fed more and should therefore be more reproductively developed, they should have larger oocytes. As can be seen in Table 2, this relationship does not always hold. The Minnesota *Polistes* from the exterior cells of the nest had larger oocytes, while in the Utah *Polistes,* the wasps from the interior cells had significantly larger oocytes.

Before the disparity between the results can be examined, an explanation of differences between the Minnesota samples and the Utah samples is necessary. It is evident from Table 2 that the mean size of oocytes from the Utah *Polistes* is almost two times larger than the Minnesota *Polistes*. There are several factors which may be involved. The Minnesota *Polistes* were from a first emergence nest, while the Utah *Polistes* were from a second emergence nest. There are several differences between first and second emergence nests which are relevant. First of all, the queen, alone, builds the nest, forages for pulp and food, and cares for the larvae in the first emergence nest, while many workers share those responsibilities in a second emergence nest. Therefore, the second emergence larvae are able to be fed a great deal more food and more of them are able to develop at the same time. Second, the first emergence larvae are predominantly sterile female workers who do not need to have developed ovaries. The female larvae from the second emergence nests are the potential reproductive queens who need to be able to survive the winter. They are generally larger in size than first emergence females.

There could be several reasons why the results of the study of the relationship between position within the nest and ovarian development are contradictory between the *Polistes* of Minnesota and Utah (Table 2). The first explanation could be due to the age differences in the nest. As stated previously, the nests from Minnesota were first emergence nests, while the nests from Utah were second emergence nests. This means that the larvae from the Minnesota nests were fed by the queen, while the larvae from the nests of Utah were fed by the workers. It is possible that the queen feeds the larvae in a different way than the workers. This could account for the notable size differences between adults from a first versus a second emergence nest. The queen has many larvae to feed by herself, so it's possible that these larvae do not receive as much food as those fed by workers. The queen fed larvae occur earlier in the summer so there may not be as much food available or the food may not have the same nutritional quality as the food accessible later in the summer. Or, the workers may be able to expend more energy searching for food and are then able to find food of better quality. Therefore, there are many differences in larval nutrition that could be caused by being fed by either a queen or a worker.

There are additional explanations which could describe why conflicting results were obtained while trying to determine the relationship between a larva's position within the nest and the ovarian development in the adult wasp. Due to the high level of subjectivity involved in determining interior and exterior cells in the small nests of Minnesota, the results may not be accurate representations of the relationship between ovarian development and nest position. The average number of cells in the Minnesota nests was 26.3. The interior cells were defined as the centermost seven cells (Figure 3). However, when determining the centermost seven cells, the location of the pedicel was not taken into account. The pedicel and the oldest cells of the nest should theoretically be in the center of the nest. The oldest cells contain the most developed larvae and would require more attention from the queen than cells with less developed larvae. The nests are not constructed in perfect geometric circles revolving around the pedicel, rather, they seem to be misshapen depending on where the queen constructed more cells. Thus, it might be better not to classify the cells as either interior or exterior as was first done for small nests but in relation to their proximity to the pedicel of the nest.

In reviewing the nests with pedicel position in mind, all of the adults which emerged from the "exterior" cells of the nest actually came from cells close to the pedicel and should be considered interior cells. In this case, the definition of interior cells should be redefined to mean the centermost cells in closest proximity to the pedicel. Therefore the results from the Minnesota *Polistes* using the old definition of interior cells are inaccurate and do not represent the relationship between wasps emerging from interior or exterior cells. According to the new definition of interior cells, the centermost cells closest to the pedicel, no adults emerged from exterior cells. Therefore, no comparison could be made between adults emerging from interior and exterior cells using the new definition.

The Utah *Polistes* came from larger nests averaging 84.5 cells. The determination of interior and exterior cells was not as subjective as it was for the small nest because the two outside rows of the nest were considered exterior cells and the rest were interior cells (Figure 2). There were approximately equal numbers of interior and exterior cells in each of these nests. The pedicel of the nest was always attached more than two rows from the edge of the nest.

One factor which must be addressed is whether or not the larvae were in clusters. According to West-Eberhard (1969), the larvae from the interior cells of the nest receive more food because they are more clustered together than the larvae in the exterior cells. Clusters of larvae would presumably be visited more frequently by workers distributing food and would therefore receive more food. Consequently, the larvae from the interior cells, because they are clustered together, receive more food and therefore have a greater reproductive potential.

After a careful review of the nest maps of the Utah *Polistes*, it is evident that many of the larvae from the exterior cells were part of a huge cluster of larvae which all emerged within a few days of each other. In both nests the cluster encompassed almost the entire nest. The larvae on the edge of the cluster were predominantly also near the outskirts of the nest. These larvae were designated as coming from exterior cells because they were in the outer two rows of the nest. Since the majority of the larvae that were classified as being from exterior cells were also the exterior cells of the cluster, they fit two definitions of being exterior cells. The first definition of an exterior cell is a cell in the two outer rows of the nest and the second is a cell on the edge of a cluster (West-Eberhard 1969). Therefore, the *Polistes* from Utah should yield useful data for determining the relationship between nest position and ovarian development.

Polistes from Utah which emerged from the interior cells of the nest, had larger and more numerous oocytes (Table 2). The larvae from the interior cells of the nest must have received more food than those from exterior cells in order to have a greater reproductive potential as measured by oocyte size and number. Since the entire nest seemed to be a large cluster, a variation of the cluster theory of West-Eberhard seems to have been demonstrated. The larvae in the center of a group of larvae, whether it be a cluster or a nest, receive more food from workers, although the size of the cluster must be taken into consideration. The larvae are able to utilize this food to increase their reproductive potential.

My data indicate that the mean size and number of oocytes in non-parasitized *Polistes* are significantly greater than those parasitized by the strepsipteran *Stylops* spp. (Table 2). The non-parasitized wasps have three times as many developed oocytes and the oocytes were two times larger than those in parasitized wasps. Thus, parasitism inhibited the reproductive development of *Polistes*. This is most likely because parasites use many of the nutrients and calories ingested by the wasp. Consequently, the larvae do not have enough nutrients to devote to reproductive development. Therefore, parasitism by strepsipterans has a negative impact on ovarian development in *Polistes*.

CONCLUSION

It is plausible that the digestive tract of the third and fourth instar larvae is not well enough developed to properly digest food which has not been regurgitated and partially digested by an adult wasp. If this is correct, the larvae would not have been able to digest the food regardless of its consistency. Also, it would not have mattered how well the excess food was removed around the mouthparts of the larvae. However, if the larvae are capable of digesting food without the aid of an adult wasp, the hand feeding process would need to be refined. The food would have to be made with the finest consistency possible and a more precise method of food removal would need to be developed.

The correlation between a larva's position within the nest and ovarian development is not entirely clear. The first emergence *Polistes* from Minnesota are most likely not adequate representatives. The extremely small size of the nests and the subjectivity involved in determining the center cells did not accommodate a precise definition between interior and exterior cells.

The second emergence *Polistes* from Utah consisted of larger nests which are not exposed to the same subjectivity in determining the interior and exterior cells. Therefore, the results should be good representatives for determining the relationship between position within the nest and ovarian development. The results indicate that the there is a significant difference in mean oocyte size and number between *Polistes* reared from interior and exterior cells. The wasps reared from interior cells had a greater mean number and size of oocytes. As a result of evidence that feeding patterns differ in accordance with clusters of developing larvae instead of interior/exterior nest position feeding differences, the nests were viewed in terms of the presence of a cluster. It was determined that the exterior cells were also the exterior cells of the cluster.

The data indicated that the wasps which emerged from the interior cells had a greater mean size and number of developed oocytes than those wasps reared from exterior cells. Since the wasps from the interior cells were significantly more developed reproductively, they must have been fed more food. It seems logical that worker wasps would spend more time in an area with a high concentration of larvae than an area with a lower concentration. Therefore, the larvae in the interior cells of the nest, which are also the interior cells of the cluster, most likely received more food. The extra food was utilized by the developing larvae to increase their reproductive potential.

The strepsipteran parasite *Stylops* spp. had a negative effect on the reproductive potential of the infected *Polistes.* The parasites utilized a large fraction of the nutrients and calories ingested by the wasp. As a result, the wasp had less energy and nutrients to invest in ovarian development. The wasp's reproductive potential was decreased by a significant amount.

In summary, the hand feeding did not work out as expected. Further studies are needed to determine whether or not *Polistes* larvae are physically able to digest food that has not been processed by an adult wasp. Position within the nest may have an effect on the ovarian development of *Polistes*, however the effect may be manifested only in second emergence nest when the larvae are worker fed. Whether there is differential feeding in queen nests is a question for future research. Parasitism by the strepsipteran *Stylops* spp. negatively affects the ovarian development of *Polistes*.

ACKNOWLEDGMENTS

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Figure 1. A Polistes' ovary and its components.

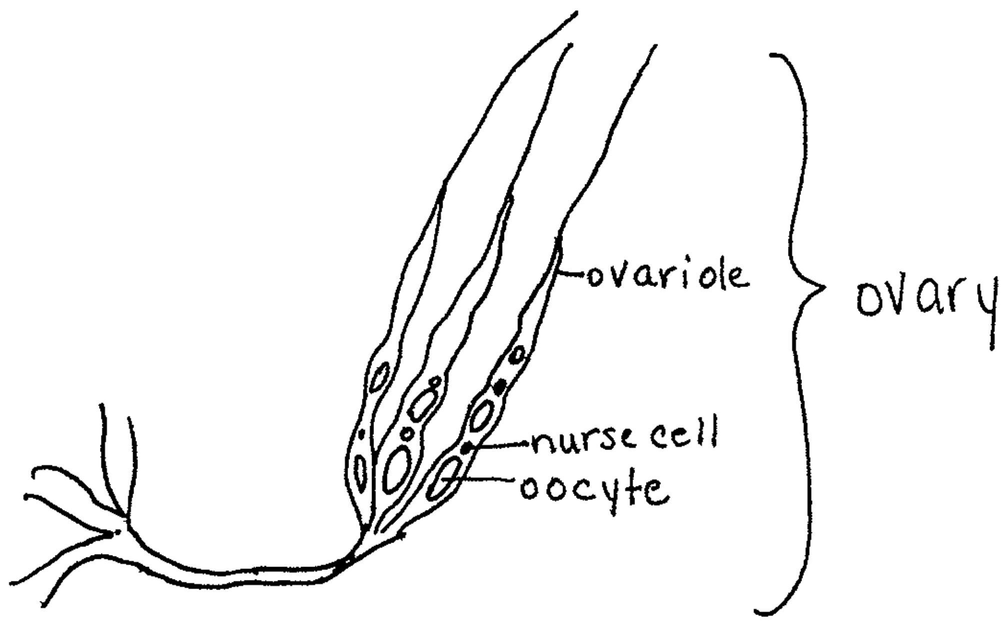

Figure 2. A large Polistes spp. nest.
Exterior cells are open.
Interior cells are darkened.

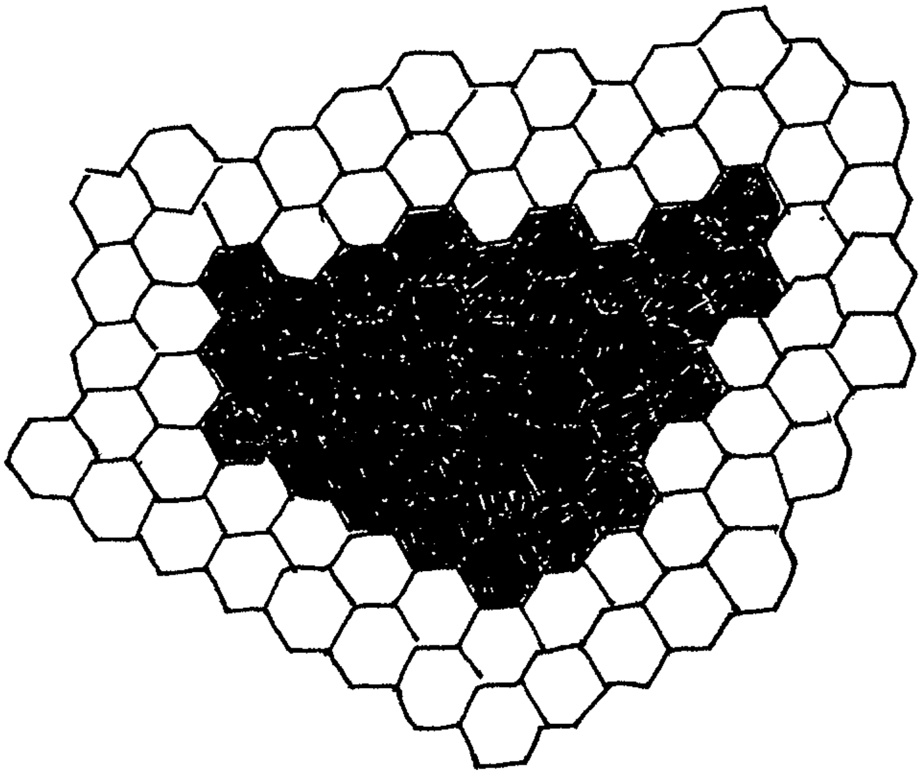

Figure 3. A small *Polistes* spp. nest.
Exterior cells are open.
Interior cells are darkened.

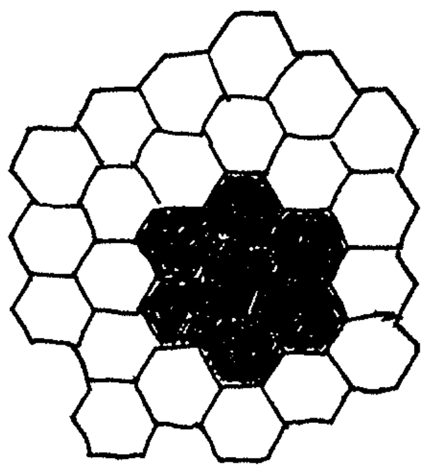

Table 1
Location of Nest Collection, Species of Polistes, and Nest Size in Number of Cells

Location	Species	Nest Size (# of Cells)
Waubonsie State Park, Iowa, Fremont County	*P. metricus*	32
	P. metricus	21
	P. metricus	37
	P. metricus	21
	P. metricus	33
	P. metricus	24
	P. metricus	19
	P. metricus	23
	P. metricus	26
	P. metricus	24
	P. metricus	20
	P. metricus	20
	P. metricus	21
	P. metricus	20
	P. fuscatus	19
Lake of Three Fires State Park, Iowa, Taylor County	*P. metricus*	14
Avoca, Iowa, Pottawattamie County	*P. fuscatus*	18
	P. fuscatus	20
Stuart, Iowa, Guthrie County	*P. fuscatus*	16
	P. fuscatus	21
Bedford, Iowa Taylor County	*P. metricus*	20
Osceola, Iowa Clarke County	*P. fuscatus*	16
Greenfield, Minnesota, Hennepin County	*P. fuscatus*	32
	P. fuscatus	31
	P. fuscatus	21
	P. fuscatus	22
	P. fuscatus	28
	P. fuscatus	24
Logan, Utah, Cache County	*P. fuscatus*	94
	P. fuscatus	75

Table 2 T-test Climate

Mean Temperature (F)	Summer 1994	p
Des Moines, IA	56.70	p>0.2
St. Cloud, MN	64.70	0.2>p>0.05
Logan. UT	61.48	p>0.2
Boise ID	70.50	p>0.2

Mean Precipitation (inches)	Summer 1994	p
Des Moines, IA	2.24	0.2>p>0.05
St. Cloud, MN	3.08	p>0.2
Logan, UT	0.23	p<0.05
Boise, ID	0.34	0.2>p>0.05

Table 3
The Mean Size and Number of Oocytes for *Polistes* from the Interior and Exterior Cells of the Nests from Minnesota and Utah.

Size of Largest Oocyte (mm)

Location	Interior	Exterior	p
Minnesota	0.30±0.1 (n=19)	0.38±0.1 (n=5)	$p<0.05$
Utah	0.63±0.3 (n=21)	0.53±0.2 (n=13)	$p<0.05$

Number of Oocytes

Location	Interior	Exterior	p
Minnesota	17.2±5.5 (n=19)	19.2±1.7 (n=5)	$0.2>p>0.05$
Utah	14.9±3.3 (n=21)	11.3±4.0 (n=13)	$p<0.05$

Table 4
The Mean Size and Number of Oocytes for the Parasitized and Non-parasitized *Polistes* from Utah

Size of Largest Oocyte (mm)

Location	Parasitized	Non-parasitized	p
Idaho	0.14±0.10 (n=7)	0.38±0.67 (n=22)	$p<0.05$

Number of Oocytes

Location	Parasitized	Non-parasitized	p
Idaho	2.0±2.3 (n=7)	7.1±6.1 (n=22)	$p<0.05$

APPENDIX A

The food mixture with the best consistency was prepared as follows:

100 mealworms, 100 crickets, and 16mL of water were mixed in a standard blender.

8mL of water, 8mL of honey were heated and 2.40g gelatin was added and dissolved.

The two mixtures were combined in a 100mL beaker and were mixed.

Kahle's solution was prepared according to Borror et al (1981).

95% ethyl alcohol...........30 cm^3

Formaldehyde................12 cm^3

Glacial acetic acid........... 4 cm^3

Water............................60 cm^3

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