

THE BIOLOGY OF THE SPIDER WASP, *PEPSIS THISBE*
(HYMENOPTERA: POMPILIDAE) FROM TRANS PECOS,
TEXAS. I. ADULT MORPHOMETRICS, LARVAL
DEVELOPMENT AND THE ONTOGENY OF LARVAL
FEEDING PATTERNS

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ABSTRACT

Aspects of the natural history and behavioral ecology of the spider wasp, *Pepsis thisbe* were studied in Trans Pecos, Texas with special emphasis on larval development and host interactions. Additional parameters studied include the physical dimensions of the egg, larval and adult size, fecundity, egg survivorship and duration of embryonic and postembryonic development as a function of temperature and relative humidity (RH), larval growth and behavior, the relationship between adult wasp and host sizes, and ontogenetic changes in larval feeding patterns. Eggs and larvae did not survive when exposed to xeric conditions (10% RH). Forty-one days were required to progress from egg to emerged adult at 30°C and 70% RH.

INTRODUCTION

The genus *Pepsis* (Hymenoptera : Pompilidae), comprising numerous species, is found in North and South America, and the West Indies, ranging from Utah (latitude 42°N) to Argentina (47°S) (Hurd, 1952). Fifteen species are found within the Nearctic region. Wasps in this genus are characterized by the following behavioral traits: 1) utilization of spiders as a larval food source with each wasp larva provided with a single paralyzed host, 2) the female wasp drags the paralyzed host backwards over the ground

Manuscript received 22 August 1994.

and places it in a nest (burrow), 3) a single egg is attached to the abdomen of the spider and, 4) the abdomen of the wasp is used to compress the loose soil in the closure of the nest entrance (Evans, 1953; Evans and Yoshimoto, 1962).

Adult male and female *Pepsis* wasps are nectivorous, and females utilize mygalomorph spiders almost exclusively as a food source for their carnivorous larvae (Hurd, 1952; Cazier and Mortenson, 1964; Punzo and Garman, 1989; Punzo, 1990, 1991). For this reason, these wasps have been frequently referred to as tarantula hawks (Passmore, 1936; Petrunkevitch, 1926, 1952; Williams, 1956). Relatively little is known concerning the comparative life histories of these spider wasps (Evans, 1953; Alcock, 1983).

This paper describes various aspects of the biology and natural history of *Pepsis thisbe* Lucas from the Big Bend Region of Trans Pecos, Texas. I report data collected from field studies and laboratory experiments conducted from 1985 to the present time. Most of the field data were collected during late spring through the summer (April–September) except for 1986 when I spent eight months in the field (May–January). Wasps and hosts were transported to the University of Tampa (UT) as described by Punzo (1990) where laboratory studies were conducted. My objectives were to determine or describe: 1) physical dimensions of the egg (length, width, and weight), 2) larval and adult size (total body length, head capsule width, and wing length), 3) survivorship and duration of embryonic and postembryonic development as a function of temperature and relative humidity (RH), 4) larval growth (weight gain) and behavior, 5) correlation between adult wasp and host sizes (weight), and 6) ontogenetic changes in larval feeding patterns.

DESCRIPTION OF THE STUDY AREA

Studies were conducted on wasps located within a 7-km radius of Study Butte (Brewster Co., Texas; 32° 24'N, 103° 12'W; elevation: 920 m), located within the northern region of the Chihuahuan Desert. A detailed description of the geology and vegetational zones of this region is given by Tinkam (1948). The study area is characterized by a mixture of sand, gravel, and adobe soils associated with a predominantly sotol-lechuguilla community. The dominant vegetation consists of sotol (*Dasyliirion leiophyllum*),

lechguilla (*Agave lechuguilla*), creosote (*Larrea divaricata*), mesa sacahuista (*Nolina erumpens*), tarbrush (*Flourensia cernua*), mesquite (*Prosopis glandulosa*), catclaw (*Acadia roemeriana*), Mexican jara (*Bacharis glutinosa*), saltbush (*Atriplex cunescens*), ocotillo (*Fouquieria splendens*), and scattered clumps of chino grass (*Bouteloua breviseta*). In this region, *Pepsis thisbe* females are host-specific on the tarantula spider, *Aphonopelma echina* Chamberlin (Orthogntha: Theraphosidae). Males and females of the host are strongly fossorial and construct or occupy burrows primarily in adobe soils. The burrows are usually located at the base of clumps of grass or mesquite.

MATERIALS AND METHODS

Adult wasps were collected with sweep nets. Eggs, larvae, and pupae of *P. thisbe* were collected from the burrows of parasitized spiders as described by Punzo and Garman (1989). Statistical methods used throughout this study follow those described by Sokal and Rohlf (1981).

A Unitron Model 110A dissecting microscope fitted with an ocular micrometer was used to measure the length and width of wasp eggs (N = 1235) as well as body length, forewing length, and head capsule width of adult males (N = 307) and females (N = 235). Forewing length was measured from the base of the wing to the outermost edge as described by Alcock (1979). Egg weight was determined using a Mettler electronic balance. All egg measurements were conducted on eggs immediately following their attachment to the host spider. A random sample of 200 gravid female wasps collected in the field was used to determine mean potential fecundity (number of eggs/female). Females were anesthetized with carbon dioxide and the ovarioles dissected in order to determine fecundity.

I also conducted a series of experiments to determine the combined effect of temperature and relative humidity (RH) on the survivorship and duration of embryonic and postembryonic development for eggs and all larval instars (L1-L5) of *P. thisbe*. The protocol for these experiments was similar to that described by Punzo and Mutchmor (1980). Eggs and larvae were exposed to both mesic (70% RH) and xeric (10% RH) conditions at test temperatures of 20 and 30°C. These values represent non-stressful as

well as stressful conditions and are within the range of values observed in the study area. Five replications of 10 eggs or larvae ($N = 50$) were exposed to each combination of temperature and RH. All experiments were conducted under constant darkness (to simulate sealed burrow conditions) in a Percival Model I-35VL Environmental Chamber (Boone, Iowa) which allowed for precise temperature, RH, and photoperiod control. Ten fertilized eggs were placed on a piece of filter paper (Whatman No. 3) lining the bottom of a glass petri dish and then placed in the environmental chamber and allowed to develop. The percent surviving and hatching into first instar larvae was recorded.

I obtained larvae from eggs deposited on host spiders during laboratory encounters between wasp and host as described by Punzo and Garman (1989) for the wasp, *P. formosa*. After hatching, individual larvae and their hosts were placed in glass finger bowls in the environmental chamber and the duration (hr) and percent survival of each larval instar was recorded. Larval instars were identified following each molt.

Additional parasitized hosts were used to obtain wasp larvae for observation of larval feeding patterns in the laboratory. After eclosion, 50 first-instar larvae were observed carefully using a hand-held magnifying glass ($5\times$) as well as a dissecting microscope. Their feeding behavior was recorded photographically with a Nikon FE2 35mm camera and a Panasonic L3 video recorder. A Lafayette Analyzer (Model 1026) was used for frame-by-frame analyses. Ontogenetic changes in feeding patterns (host tissues selectively consumed) were analyzed throughout larval development. Larvae were also weighted 24 hr (± 2 hr) prior to each molt in order to determine larval weight gain as a function of development.

These data were compared to growth rates obtained for 50 developing larvae in the field. Female wasps were observed searching for *Aphonopelma echina* burrows. Once an occupied spider burrow was located and the host parasitized, the burrow was monitored every 48 hr. The burrow entrances were opened by removing packed soil with a metal spatula and the parasitized hosts removed from the nest. The larvae were gently removed from the host with a camel hair brush and weighed on a Sartorius electronic balance operated with a 110 V portable power supply. After weighing, larvae

were returned to the same location on the host from which they were removed, and allowed to resume feeding. The hosts with attached larvae were then placed back in the burrow and the entrance closed until the next observation.

I conducted additional laboratory experiments to determine the relationship between the size of the adult wasp (total body length) and the size (weight) of the host on which the larva fed. The weight (g) of 40 hosts was measured between 3–5 hr prior to parasitization. Wasp larvae were allowed to develop on the host and pupate at 21°C and 70–75% RH. After emergence, adult wasps were anesthetized with carbon dioxide and their total body length (mm) measured. Wasps were anesthetized to prevent any movement; this resulted in reliable and accurate (standardized) length measurements.

RESULTS

Reproductive And Developmental Parameters

The mean potential fecundity was 13.4 eggs/female with a range of 9–17. Mean values for egg length (4.7 mm; \pm 0.3 S.D.), width (1.4 mm; \pm 0.2) and weight (7.3 mg; \pm 0.8) are similar to those reported for *P. marginata* from Puerto Rico (Petrunkevitch, 1952) and *P. formosa* from Arizona (Cazier and Mortenson, 1964).

The morphometric data for adult *P. thisbe* males and females are listed in Table 1. Sexual dimorphism with respect to body size is common in *Pepsis* wasps (Hurd, 1952; Evans and Yoshimoto, 1962). In *P. thisbe*, body size ranges from 18.7–24.8 mm for males, and 27.1–38.7 for females.

The eggs and larvae of *P. thisbe* are intolerant of xeric conditions (Table 2). These developmental stages exhibited 100% mortality when exposed to 10% RH regardless of ambient temperature. This is not surprising because all larval stages are characterized by a very thin and lightly chitinized integument that is not a very efficient barrier to evaporative water loss. In the field, moisture is usually not a limiting factor since RH in sealed burrows is relatively high (68–77%).

Moisture and temperature had a significant effect ($F = 19.2$; $df = 5122$; $p < 0.01$) on the duration of embryonic development (Table 2). The mean time required for fertilized eggs to complete development

Table 1. Morphological dimensions (mm) for adult *Pepsis thisbe* males and females. Values represent means \pm S.D. Values in parentheses represent the range.

Sex	N	Body length	Head capsule width	Wing length ¹
Males	307	22.3 \pm 2.1 (18.7–24.8)	3.2 \pm 0.4 (2.7–3.3)	21.9 \pm 1.6 (17.2–23.1)
Females	235	29.6 \pm 3.2 (27.1–38.7)	4.4 \pm 0.3 (3.7–4.5)	24.9 \pm 2.8 (23.2–31.7)

¹Forewing length measured from base of forewing to the outermost edge as described by Alcock (1979)

Table 2. Duration (hr) of embryonic and postembryonic development and percent survival for various life cycle stages of *Pepsis thisbe* exposed to various conditions of temperature ($^{\circ}$ C) and relative humidity (% RH). N = 50 eggs, larvae or pupae were exposed to each condition of temperature and RH.

Stage	$^{\circ}$ C/RH ¹	Mean duration ² (hr) (\pm S.D.)	Percent survival
Egg	20 $^{\circ}$ /10%	—	0
	30 $^{\circ}$ /10%	—	0
	20 $^{\circ}$ /70%	187.6 (17.2)	74
First larval instar	30 $^{\circ}$ /70%	102.4 (10.1)	68
	20 $^{\circ}$ /70%	76.4 (9.2)	72
Second larval instar	30 $^{\circ}$ /70%	50.4 (6.7)	74
	20 $^{\circ}$ /70%	88.3 (11.6)	76
Third larval instar	30 $^{\circ}$ /70%	59.7 (7.8)	70
	20 $^{\circ}$ /70%	105.6 (14.4)	72
Fourth larval instar	30 $^{\circ}$ /70%	84.3 (7.7)	66
	20 $^{\circ}$ /70%	156.2 (17.1)	68
Fifth larval instar	30 $^{\circ}$ /70%	121.4 (11.6)	74
	20 $^{\circ}$ /70%	163.2 (13.7)	76
Pupal stage	30 $^{\circ}$ /70%	135.2 (10.3)	68
	20 $^{\circ}$ /70%	504.3 (32.2)	80
	30 $^{\circ}$ /70%	432.7 (18.7)	74

¹There was 100% mortality of all life cycle stages exposed to xeric (10% RH) conditions

²ANOVA showed an overall significant effect of temperature on duration of development (F = 19.2, df = 5, 122; p < 0.01)

was 102.4 and 187.6 hr at temperatures of 20 and 30°, respectively). The amount of time required from the moment of oviposition to the formation of the cocoon by fifth instar larvae ranged from 553.4–777.3 hr (23–32 days). *Pepsis thisbe* has five larval instars in its life cycle (L1–L5). The mean duration for the pupal stage ranged from 432.7–504.3 hr.

Approximately 4–5 days after oviposition, a small area at the free end of the cream-colored egg begins to turn white. A pair of dark mandibles can be seen at this time through the thin egg shell. The shell then splits open revealing the first instar larva which is white in coloration. Its posterior end is attached to the ventral area of the host abdomen near the book lungs. The larva curves the anterior end of its body forward until the head capsule makes contact with the host and begins to feed. With the exception of changes in size, no significant morphological differences exist between larval instars 1–4 although the head capsule becomes more heavily chitinized and darker brown in coloration. At the end of L1, larvae range from 7.1–8.8 mm and weigh 310–327 mg, depending on ambient temperature. The mean weights for subsequent larval instars under both field and laboratory conditions are shown in Table 3. No significant differences in growth rates were found between laboratory and field conditions ($F = 1.56$; $p > 0.5$). Larval weight increased from 310–327 mg at the end of the L1 stage to over 1460 mg (length: 21.3–30.8 mm) just before cocoon formation (L5). Following the fourth molt, the last larval instar (L5) emerges and exhibits some obvious morphological changes. The previously pointed mandibles are thicker and possess deeper toothed ridges. The spiracles are markedly larger. It is during this stage that the host is finally killed.

Table 3. Weight gain (mg) as a function of development for various larval instars (L1–L5) of *Pepsis thisbe* (N = 50) under both laboratory and field conditions. Values represent means (\pm S.D.).

Larval Instar	Laboratory Conditions	Field Conditions
1	322.2 (24.6)	337.3 (31.2)
2	427.5 (34.3)	419.3 (19.5)
3	1208.3 (48.9)	1221.6 (38.7)
4	1385.6 (58.3)	1369.4 (70.1)
5	1489.7 (80.2)	1468.4 (69.4)

Larval Feeding Patterns And Pupation

Upon emergence, the first instar larva uses its mandibles to break through the host integument in the vicinity of the book lungs and begins to feed on cuticular lamellae and underlying connective tissues. This occupies the first 3–7 hr of feeding. The ontogenetic changes in larval feeding patterns are outlined in Table 4. It should be noted that only in the last larval instar are vital host tissues (heart and nerve) ingested.

Table 4. Ontogenetic changes in feeding patterns for larvae of *Pepsis thisbe*. Data indicate host spider tissues progressively consumed by wasp larvae as a function of time (hr) following hatching. Observations based on 50 developing larvae.

Stage ¹	Hours after hatching	Spider tissues ingested
L1	0–7	Meso- and endo-cuticular lamellae of the abdomen and associated underlying connective tissues
	7–24	Underlying cuticular longitudinal muscles of the abdomen
	24–70	Medial region of the midgut and dorsal region of the ovaries
L2	76–150	L1 moves posteriorly and begins to ingest posterior region of the gut, ovaries, and associated muscles and connective tissues
L3	160–180	Movement anteriorly to ingest anterior regions of the gut and ovaries, spinning glands, and book lungs
	190–250	Intestine, abdominal nerves, midgut diverticulum, pharynx elevator musculature
L4	270–370	Pharynx elevator and depressor musculature
	370–410	Connective tissues of the prosoma, esophagus, sucking stomach
L5	425–560	Tissues of the subesophageal and supraesophageal ganglia, and the heart

¹Larval stages 1 through 5 (L1–L5)

The larva uses the remains of the host as a substrate for cocoon formation. At the end of L5, the larva spins a very thin outer capsule which will support the finished cocoon. Silk emanates from labial silk glands. Silk strands are attached to the spider integument and then slowly worked around the body of the larva starting at its posterior end. After 28–34 hr the larva is completely concealed by a thin silk covering. At this time, the larval meconium is discharged and forms a hardened mass at the posterior end of the body. The cocoon becomes progressively thicker and darker.

Observations in the field indicate that in this study area, cocoon formation can occur from early July through September. If cocoons were formed in early summer, adults will emerge, mate, and search for hosts during the same season. If cocoon formation does not occur until late summer or early fall, wasps will overwinter in the cocoon stage.

Correlation Between Adult Wasp Size And Host Weight

There is a significant correlation between adult wasp body length and the weight of the host spider ($r = 0.924$, $p < 0.01$). This relationship is shown in Fig. 1. The regression equation is: $y = .43x - 4.705$. Data points for wasp sizes below 27 mm represent males; those above this value represent females. Wasp body size increased significantly with increasing host weight (regression: $r^2 = 0.91$, $p < 0.001$, $N = 40$).

DISCUSSION

The low fecundity that characterizes this pompilid species reflects the highly efficient hunting strategy characteristic of this genus (Punzo, 1991). The high survival rates of eggs and larvae of *P. thisbe* observed in the field and laboratory suggest that this wasp is well adapted to its environment. Once an egg is deposited on a paralyzed host and the burrow entrance sealed, mortality rates are less than 35%, ensuring a high percentage of emerging adults. Stomach content analyses of potential predators have not reported this wasp. Apparently the adult wasps have few natural predators. Twice I observed a roadrunner (*Geococcyx californianus*) attacking a wasp on the ground. The bird grasped the wasp with its beak and beat it against the substrate prior to ingestion. I have not seen one

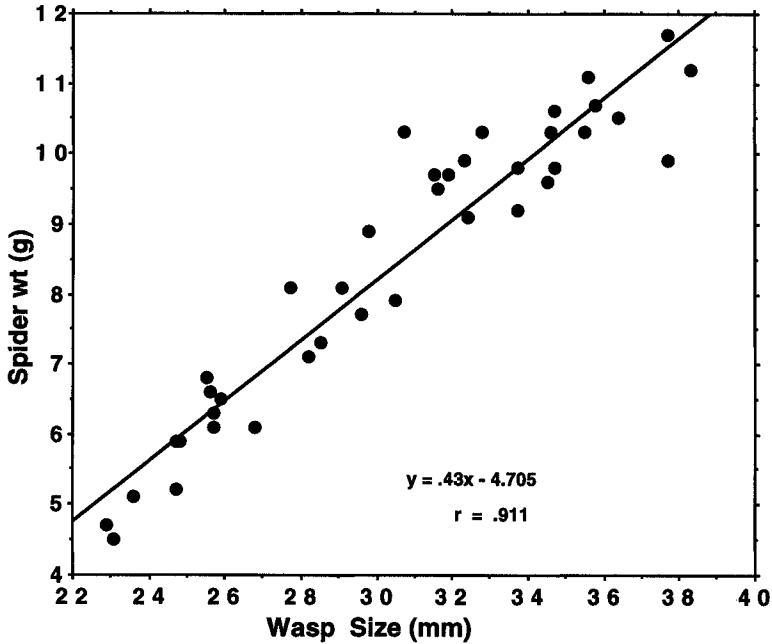


Fig. 1. Relationship between the total body length (mm) of *Pepsis thisbe* adults and the weight of the host spider, *Aphonopelma echina*. Values <27 mm represent males; >27 mm, females.

of these wasps captured in any of the spider webs frequently encountered in this area. In over 400 encounters observed between a female wasp and its tarantula host in the field, on only one occasion have I witnessed a spider successfully biting, penetrating, and killing a wasp. These wasps have heavily sclerotized bodies that appear to be relatively resistant to penetration by the (spider) fangs even though the incidence of the host actually attempting to strike at the wasp is rare (Punzo and Garman, 1989). Although male and female *Pepsis* wasps frequently engage in inter- and intra-specific territorial contests (Williams, 1956; Alcock, 1983; Field, 1992), these disputes are rarely fatal.

The results of this study have shown a strong correlation between adult wasp size and the weight of the host that was consumed. The question remains as to whether or not a larger body size confers any selective advantage to adult wasps. There was also

a wide range of adult body sizes for both sexes in this population. Why do smaller individuals persist? The males are strongly territorial and will aggressively defend perch sites on mesquite, ocotillo, and various trees by aerial combative contests with conspecific males that stray too close. Males will alight on a perch site and wait for females to fly through their territory. I have witnessed a male copulating with a female on only five occasions. Although viewed from a distance through binoculars, in each case copulation occurred when a female landed near the perch site of a male. Although there is no experimental evidence yet available for members of this genus, studies on Diptera and Lepidoptera (Shields, 1967) as well as the closely related *Hemipepsis* wasps (Alcock, 1979), suggest that larger males are more successful in gaining and holding perch sites most conducive to successful mating. Larger males tend to occupy perch sites both at higher elevations ("hill-topping," Shields, 1967) and on taller vegetation which appear to be more attractive to females. Alcock (1978) has suggested that hilltopping behavior in the pompilid *H. ustulata* evolved because it facilitates the ability of a male to locate and monopolize emerging virgin females that are characterized by unpredictable and erratic dispersal patterns. Once hilltopping behavior evolved, selection should favor females who could choose the best possible mate. In insects such as pompilid wasps, where males make no parental investment in their progeny, female mate choice may be based primarily on social dominance (Emlen and Oring, 1977; Thornhill and Alcock, 1983). Social dominance is often correlated with body size in many animal groups (Daly, 1978; Berry and Shine, 1980). Dominance status can be communicated through the competitive ability of larger males to exclude conspecifics from their territories. Perhaps males occupying higher perch sites are capable of monitoring a broader area for the presence of females.

If this holds true for *P. thisbe* males, why is there a rather wide variation in size (18.7–24.8 mm) maintained in the population? In solitary wasps, adult size is determined by the maternal parent (Evans, 1953). This study has shown that the size of a *P. thisbe* adult is determined by the size of the host that was provided for that wasp by its mother. Therefore, the seasonal frequency distribution of host size classes in a given area will determine the size variation found in adult wasps.

What about the size variation exhibited by female wasps (27.1–38.7 mm)? Once again, female size will be a function of the size distribution for available hosts in a given area. Do larger females have an advantage over smaller individuals? Perhaps larger females are capable of storing more nutrient reserves and can therefore travel over greater distances in search for hosts. In addition, there is no experimental evidence yet available to support the hypothesis that larger females might experience greater success at attacking larger spiders. It would also be interesting to determine if host selection is random or if it is directly influenced by the size of the wasp.

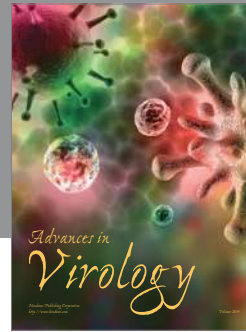
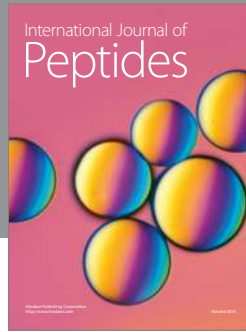
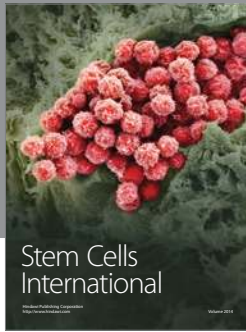
ACKNOWLEDGEMENTS

I thank James Bottrell and Thomas Punzo for assistance in the collection and monitoring of wasps and spiders in the field, and Brian Garman, Dept. of Mathematics, and Ali Jenzarli, College of Business, for consultation on statistical analyses. I also thank the University of Tampa for a Faculty Development Grant which made much of this work possible, and anonymous reviewers for comments on an earlier draft of the manuscript. Finally, I would like to thank the Dean of the College of Liberal Arts and Sciences, Terry Parssinen, for his support and encouragement of scholarly activities.

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