BIOLOGICAL STUDIES ON *GONIOZUS LEGNERI* GORDH (HYMENOPTERA: BETHYLIDAE) A PRIMARY EXTERNAL PARASITE OF THE NAVEL ORANGEWORM *AMYELOIS TRANSITELLA* AND PINK BOLLWORM *PECTINOPHORA GOSSYPIELLA* (LEPIDOPTERA: PYRALIDAE, GELECHIIDAE)

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Abstract

Goniozus legneri Gordh is a primary external parasite of Microlepidoptera larvae (Gelechiidae, Pyralidae), which was imported into California from southern Uruguay for the biological control of Navel Orangeworm (NOW), *Amyelois transitella* (Walker), a serious pest on almonds. Details of the biology of this parasite are described and compared with its performance on the Pink Bollworm (PBW), *Pectinophora gossypiella* (Saunders). Studies showed that on NOW, *G. legneri* attacked 17.23 ± 2.97 hosts to sperm depletion, attacked 6.12 ± 3.34 hosts after sperm depletion, and parasitized 23.35 ± 2.58 hosts at 25 ± 2°C, 50 ± 2% RH, LD 14:10 (n = 26). On PBW, *G. legneri* attacked 21.45 ± 3.91 hosts to sperm depletion, and 25.05 ± 3.55 during the life of the female parasite under the same environmental conditions (n = 20). Differences between means were not statistically significant.

On NOW, sting to oviposition time was 1.19 ± 0.47 days for broods producing male and female progeny (n = 437, and 1.82 ± 1.16 days for broods producing only male progeny (n = 159). The period from oviposition to eclosion was 1.25 ± 0.27 days for broods producing male and female progeny (n = 436), and 1.23 ± 0.27 days for broods producing only males (n = 155). Development time from larva to cocoon was 3.75 ± 0.35 days for broods of males and females (n = 430), and 3.60 ± 0.21 days for broods of only males (n = 155). Development time from cocoon to adult was 9.26 ± 0.53 days for broods producing male and female progeny (n = 430), and 8.63 ± 0.40 days for broods producing only male progeny (n = 155). Mean development time from egg to adult for broods of male and female parasites was 14.26 ± 0.97 days (n = 430), and 13.45 ± 0.46 days for broods composed of only males (n = 155).

On PBW, sting to oviposition time was 1.40 ± 0.59 days for broods producing only male and female progeny (n = 429), and 1.96 ± 1.07 days for broods producing only male progeny (n = 71). The period from oviposition to eclosion was 1.44 ± 0.18 days for broods producing male and female progeny (n = 428), and 1.46 ± 0.13 days for broods producing only male progeny (n = 71). Development time from larva to cocoon was 3.61 ± 0.26 days for broods producing male and female progeny (n = 428), and 3.58 ± 0.23 days for broods producing only male progeny (n = 71). Development time from cocoon to adult was 8.93 ± 0.57 days for broods producing male and female progeny (n = 428), and 8.96 ± 0.38 days for broods producing only male progeny (n = 71). Mean development time from egg to adult was 13.98 ± 0.53 days for broods producing male and female progeny (n = 427), and 14.00 ± 0.47 days for broods producing only male progeny (n = 71).

The egg and larval stages are described; they do not differ from other species of *Goniozus* which have been examined. The pattern and sequence of

pupal pigmentation is described. This character may be important in recognizing subtle morphological differences among closely related species or possibly has phylogenetic significance.

Goniozus legneri prefers to oviposit on the dorsal aspect of the host's body, followed by the lateral and ventral surfaces. On NOW, segment preference is 5 - 9 for all aspects, with a normal distribution peaking on segments 7 - 8 for all aspects. Segment and aspect preference is identical on PBW. This data was compared with data collected in a similar manner for *G. gordhi* Evans and *G. aethops* Evans.

Goniozus legneri has a precise sex ratio. The sex ratio tends to remain constant over a wide range of host weights with supplemental males produced on heavier hosts which, presumably, can sustain larger broods of parasite progeny without superparasitism.

We found that on NOW (n = 26) and PBW (n = 20) *G. legneri* has a normal distribution of eggs on the host body and that when host weight varies between 20.0 and 50.0 mg, on PBW there was a steady increase in the number of eggs laid per host with increasing host weight with a maximum of 16.0 eggs per host in the largest host weight class observed (42.5 - 45.0 mg). On NOW oviposition increased with increasing host weight to a maximum of 18.0 eggs per host in the 45.0 - 47.5 mg host weight class for female parasites provided with a 24 hour interval between ovipositions, and reached a maximum of 13.2 eggs per host in the 37.5 - 40.0 mg host weight class and then remained relatively constant (11.1 - 13.0 eggs per host) for females provided with fresh hosts immediately following oviposition. Fewer eggs laid on lighter hosts suggest that the parasite can regulate the number of eggs laid to prevent superparasitism; a relatively constant number of eggs laid at higher host weights suggests a depletion of fully developed eggs. These data were compared with other species of *Goniozus*.

Life tables were constructed for *G. legneri* on NOW and PBW, and demographic statistics were computed and compared with those generated from a life table analysis of *G. emigratus* reared on NOW. Intrinsic rates of increase (r_m) for *G. legneri* on PBW and NOW, and *G. emigratus* on NOW were 0.157, 0.162, and 0.178 females per female per day, respectively. Capacities for increase (r_c) were substantially less than corresponding r_m values: 0.0985 and 0.110 females per female per day for *G. legneri* on PBW and NOW, respectively; generation times (T_c) were 51.5 and 45.1 days, respectively; and net reproductive rates (R_0) were 160.2 and 145.1 females per female per lifetime, respectively.

Longevity studies showed that mated females deprived of hosts lived 75.0 ± 5.81 days (n = 50) at 25 ± 2°C, unmated females lived 71.0 ± 10.81 days (n = 50), and unmated males lived 61.3 ± 15.87 days (n = 30) under the same conditions. Longevity of mated female parasites on PBW was 82.35 ± 14.74 days. Regarding host survival time, one set of 10 NOW hosts was provided female *G. legneri* which stung the host and oviposited on the NOW larvae. Eggs hatched and larval development was completed. Based on haemolymph flow observed and dorsal aorta contraction, longevity of the host was 5.0 ± 0.00 days at 25 ± 2°C, 50 ± 2% RH, and LD 14:10 (n = 10). Pulse rates of parasitized NOW were compared during the morning and evening, these were not significantly different for each day of life but were significantly different on the first and last day of host life. Similar

information was collected for paralyzed, but not parasitized hosts. Paralyzed hosts lived 29.20 ± 6.49 days (n = 10) under the same environmental conditions. Data on pulse rate (morning vs afternoon, first day after sting and last day of life) is presented.

A stepwide regression procedure was used to analyze sex ratio of the first 12 broods of *G. legneri* attacking NOW (n = 6) and was performed for sex ratio (dependent variable) against six independent variables (weight of the host, age of the parasite, number of eggs deposited, days since the last sting, female adult longevity, and brood mortality). The regression was statistically significant for sex ratio and days to last sting (i.e., days since the last host was attacked) with an r^2 of 0.0811 and an F statistic of 6.18 (p = 0.0153, 70 degrees of freedom).

Similarly, a correlation analysis was conducted on 26 female *G. legneri* attacking NOW and 20 females attacking PBW. Correlation coefficients for egg, larval and pupal mortality on a given host were not statistically significant.

INTRODUCTION

This report concerns the biology of *Goniozus legneri* Gordh, a member of the Bethylidae. Bethylids presumably represent a primitive family of aculeate Hymenoptera. The family now consists of about 40 valid genera and about 2,000 nominal species. The Nearctic species have recently been revised by Evans (1978b), and he has also treated the Neotropical species (1962; 1964; 1969 a,b,c; 1970; 1973; 1978a; 1979 a,b). Substantial contributions on the Palearctic and Ethiopian faunas have been made by Móczár (1966; 1969; 1970 a,b,c; 1971; 1974; 1975; 1976 a,b; 1978; 1981) and Nagy (1966, 1967; 1968 a,b,c; 1969; 1970 a,b; 1972; 1974; 1976). A world catalog is in preparation (Gordh and Hawkins).

All bethylids are primary external parasites of Microlepidoptera and Coleoptera larvae. There are no known bethylid hyperparasites. Due to their host associations they are of potential benefit in the biological control of agricultural and stored product pests (Chatterjee 1941, Cushman and Gordh 1976, Gordh 1976, Gordh and Evans 1976, Gordh and Hartman in press, Gordh and Hawkins 1981, Kishitani 1961, Kuhne and Becker 1974, Mertens 1981, Remadevi *et al.* 1978, Venkatraman and Chacko 1961, Voukassovitch 1924, Yamada 1955).

The genus *Goniozus* is probably the most well studied genus of bethylids and displays excellent promise for biological control of Microlepidoptera. The genus is cosmopolitan in distribution and contains more than 50 nominal species. Of the species which have been studied, it appears particularly effective on Gelechiidae and Pyralidae. No species has been demonstrated to be host specific.

Goniozus legneri was imported by Dr. E. F. Legner into California from southern Uruguay for the biological control of Navel Orangeworm, *Amyelois transitella* (Walker) (hereafter designated NOW). This pyralid is the most serious orchard pest of pecans and almonds in the Central Valley of California. Initial importation was made in 1978, and releases were made in the Central Valley in 1979. The parasite was recovered in the

spring of 1980 and innoculative releases were made in 1981 and 1982. Studies by Legner (Legner *et al.* 1982 a,b) have shown that the parasite is established and that it is an important component in the natural enemy complex of NOW on almonds on study sites in the Central Valley. This paper provides laboratory-generated biological information on the parasite which supplements field-collected data by Legner, and provides new information intended to supplement existing knowledge on the genus *Goniozus*.

Voucher specimens of *G. legneri* have been deposited in the following institutions: Beneficial Insects Introduction Institute, Beltsville, MD; Biosystematics Research Institute, Agriculture Canada, Ottawa; Zoological Institute, Academy of Sciences of the U.S.S.R., Leningrad; California Academy of Science, San Francisco; All Union Plant Protection Institute, Pretoria, South Africa; Faculty of Agriculture, Ehime University, Shikoku, Japan; Department of Entomology, University of Florida, Gainesville; Department of Zoology and Entomology, Fort Collins, Colorado; University of California, Riverside, Entomology Department; Queensland Museum, Brisbane, Australia; American Museum of Natural History, New York.

MATERIALS AND METHODS

Goniozus legneri was reared in the laboratory on NOW and Pink Bollworm, *Pectinophora gossypiella* (Walker) (hereafter designated PBW). Individual parasites were placed in four-dram, plastic snap-cap vials with a few droplets of honey provided as a supplemental source of nutrition. Vials were lodged in a Percival Temperature Cabinet set at 25 ± 2°C, 50 ± 2% RH, and LD 14:10. Experience has shown that containers must have extremely tight fitting lids because the parasites are fossorial and will escape from other types of containers.

To determine parasite longevity, we performed the following experiment. Broods which developed on NOW were followed through to adult emergence and individuals placed in four-dram, snap-cap vials with a few droplets of honey provided as a supplemental source of nutrition. Two experimental groups were used, with fifty replicates per group. One group was provided with hosts (NOW and PBW, 50 replicates each) and one group was deprived of hosts. The group deprived of hosts consisted of 50 mated and 50 unmated female parasites. Additionally, we included a group of 30 unmated male *G. legneri* in the experiment. The vials were placed in a Percival Cabinet set at environmental conditions specified earlier. On all experimental studies, parasites were newly emerged and copulation had been observed.

In subsequent studies we were interested in examining several aspects of the biology of *G. legneri*. In the longevity study we learned that 50 replicates per experiment were unmanageable from the standpoint of maintaining host cultures and studying parasite biology (time required to collect data). Thus we conducted a detailed analysis of the biology of *G. legneri* using 26 females on NOW and 21 females on PBW. Initially, 30 parasites were set up on NOW, but four females were killed or escaped during host transfer. We decided to set up 21 parasites on PBW because of problems with the host culture. PBW is cannibalistic under crowded conditions and it was not always possible to maintain the culture at high density, or a

population density necessary to conduct experiments under conditions similar to those used for NOW.

Individual female parasites were isolated in numbered vials in the above mentioned manner and given one fourth instar host at a time. The hosts were weighed with a Metler analytical balance to the nearest tenth of a milligram before being offered to female parasites. The following information was tabulated for each parasite: (1) time of paralysis (day since emergence or day since last sting); (2) time interval between paralysis and oviposition; (3) number of eggs laid and the position of eggs on each body segment of the host (i.e., dorsal, lateral, ventral); (4) orientation of the paralyzed larva in the container (i.e., dorsal, lateral, ventral); and (5) extent of host feeding by the adult female parasite. In no instance was an alternate host species provided to a female parasite attacking a given host (NOW or PBW).

Parasitized hosts were isolated in 000 size gelatin capsules (Lilly Pharmaceutical Company) and the capsules were sequentially taped on 5 x 8 inch cards and placed in an environmental control cabinet under the conditions specified above. Daily observations were made of this material and progeny development time, sex ratio of progeny, and immature mortality were tabulated and computed. In turn, this information was correlated to adult parasite age and the number of previous reproductive episodes for each female of the parental generation. After each reproductive episode the adult female parasite was isolated for 24 hours (deprived of hosts, but not honey) and then given another 4th instar host. This procedure was repeated throughout the lifetime of each parasite on either host.

Following the deaths of the 26 females on NOW and the 21 females on PBW, life table statistics were calculated for *G. legneri* on each host using the computational methods of Andrewartha and Birch (1954) and Birch (1948). Age was measured in days. The counts of live 1st instar parasite larvae 24 hours after oviposition were used to estimate egg viability. The number of viable female eggs was counted (in egg clutches with no further mortality) or estimated (in clutches with larval or pupal mortality) from the number of adult female progeny in each egg clutch. Age specific fecundity (m_x) was calculated as the number of viable female eggs produced per day divided by the number of females alive on that day. Daily survivorship (1_x) for the immature stages of the parental females was estimated from that noted in their progeny. Daily survivorship (1_x) for adult females was calculated directly as the number of females surviving over the initial number of females times the estimated survivorship at adult emergence.

Hosts were cultured in the following manner. The NOW culture was about 2.5 years and came from field-collected material taken in the Central Valley. Adult moths were placed in 0.5 gallon ice cream containers fitted with wire screen lids. Filter paper was placed on the screens and the moths oviposited on the paper. Eggs were treated in 10% formalin and then rinsed in cool running water for 45 minutes. The sheets were then hung to air dry. First instar larvae were transferred with a 0000 size camel's hair brush to one ounce jelly cups filled with artificial media. The media consisted on two parts honey, two parts glycerine and one part water (total volume 250 ml). Two teaspoons of yeast and six grams of vitamins were then mixed into the solution and then poured over 1200 ml of bran. Development time of the hosts required about 28 days at 25°C.

The PBW culture was about one year old and also was from field-recovered material. Females were placed in 0.5 gallon ice cream containers fitted with wire screen lids and filter paper used as an ovipositional substrate. After egg hatch the first instar larvae were transferred to one ounce jelly cups filled with an artificial media. The media consisted of 75 gr Agar, 180 gr Casein, 50 gr salt, 180 gr sugar, 25 gr Alphacel, 8 gr MPH, 150 gr wheat germ, 115 gr vitamins, 15 ml 40% formaldehyde, 25 ml 10% KOH, and 55 ml acetic acid. The mixture was blended and boiled and put in the jelly cups and allowed to cool and solidify before the larvae were transferred. About 21 days at 25°C were necessary for pupation.

RESULTS

1. Parasite Longevity: Results of the parasite longevity experiment are indicated in Figure 1. Mated females deprived of hosts lived 75.0 ± 5.81 days; unmated females deprived of hosts lived 71.0 ± 10.81 days. The differences were statistically different at P = 0.05. We attributed this difference to unmated females wandering around the container and in general being more active. Unmated males lived 61.3 ± 15.87 days, and this was also statistically significantly different from mated and unmated females at P = 0.05.

Mated female parasites provided PBW hosts throughout their lifetime lived 95.76 ± 10.53 days. Mated female parasites provided NOW lived 97.35 ± 14.74 days. These results were not statistically significantly different, but were significantly different from the host deprived group (P = 0.01). We suspect that host feeding and/or reproductive activity may be involved in the observed differences. When daily observations were made, it appeared as if the host deprived class was visibly more active. This aspect of parasite longevity will be investigated in a subsequent study.

2. Parasite Host-attack: We found that on NOW the 26 parasites attacked 23.35 ± 2.58 hosts each, and that on PBW the 21 parasites attacked 24.76 ± 3.81 hosts each. The differences between hosts attacked were not statistically significant. Based on the sex ratio of progeny produced, we found that *G. legneri* attacked 17.23 ± 2.97 hosts until sperm depletion (i.e., on the average 17 broods produced females and that subsequent hosts produced all male broods) on NOW and on PBW the females attacked 21.38 ± 3.82 hosts until sperm depletion. The differences are not statistically different, but the slightly higher number noted for PBW was attributed to the fact that it is a slightly larger host and a few more males were produced per brood; the parental stock used in the study was generated from sib mating. That is, replicates represented all of the females mated to brothers issuing from a few clutches of eggs. From these data we noted that on NOW mean female progeny production was 149.21 ± 17.62 per parental life time while parental females attacking PBW produced 169.55 ± 28.80 female progeny. Again, we interpret the higher production of females to the fact that more males per brood were produced on PBW, hence, on PBW an individual male had more sperm available for each ejaculation. *Goniozus legneri* is arrhenotokous; unfertilized eggs produce males, fertilized eggs produce females. Thus it would appear that *G. legneri* averages at least 150 sperm on NOW and about 170 sperm on PBW. The rather high standard deviations may be attributable to variation in ejaculate size in the mating

sequence (sister number one getting more sperm than sister number six), size of the spermatheca limiting sperm accommodation, or both.

3. Host Attack and Oviposition: Immediately after adult emergence, *G. legneri* has a preovipositional period of 3.12 ± 0.67 days on NOW (n = 26), and 4.05 ± 2.16 days on PBW (n = 20). During this period the parasite is capable of stinging and paralyzing the host larva, but it is not capable of oviposition. Dissection of newly emerged female parasites shows that the ovaries are developed, but that eggs are not.

We have not determined the behavioral modalities used in host finding. Under the experimental conditions used, the parasite seemed to wander randomly in the arena until the host was located. Once detected, the parasite quickly mounted the host. The attack is rather specific. The female attaches to the host's integument with her mandibles embedded in the dorsum just posteriad of the head capsule. She then thrusts her metasoma ventrad and stings the host, presumably in the ganglion of the ventral nerve cord just posteriad of the gula. We believe the site is important because in many instances the parasite would repeatedly thrust her sting while the host larva writhed in an attempt to dislodge the parasite. In other instances one thrust was sufficient to immediately paralyze the host. In some instances total paralysis required about one minute during which the female parasite waited 3-4 cm from the host, grooming herself. We found that 90 day old, senescent parasites incapable of oviposition were capable of paralyzing their NOW hosts. Although the paralysis prevents locomotion, the paralyzed host is still capable of lateral flexion when stimulated with a probe. Physiologically, the venom is interesting because if the host was paralyzed just prior to the time of pupation, the host pupated and eggs deposited on such hosts did not develop.

We analyzed host survival based on the number of contractions per minutes of the dorsal aorta of paralyzed versus paralyzed and parasitized hosts (Fig. 2). Two groups of ten newly emerged *G. legneri* were allowed to paralyze NOW larvae and one group was allowed to parasitize their hosts. The second group was removed after host paralysis, but before oviposition. The pulse rate was counted each morning and evening for each paralyzed and paralyzed and parasitized host. There was no significant difference between morning and evening counts, but within the paralyzed and parasitized group there was a linear decline in pulse rate over five days, with all hosts "dead" (no haemolymph flow) on the sixth day. The variance in haemolymph flow among hosts in this group was nearly constant (i.e., not significantly different among individuals).

Hosts which were paralyzed and not parasitized lived 28.30 ± 6.65 days, based on contraction of the dorsal aorta. After an initial decline and upshift of heart beat rate, pulse rate remained relatively constant between the 10th and 30th days. The variance was rather constant until the 24th day, after which it became somewhat erratic. The temperature was constant (25°C) throughout the experiment, so the increase in variance was attributed to a smaller sample size and varying degrees of moribundity within the sample population.

Oviposition requires two to four hours. The period from sting to oviposition requires 1.19 ± 0.47 days for females producing male and female

progeny, and 1.82 ± 1.16 days for females producing only male progeny on NOW (n = 437, 159, respectively). On PBW, sting to oviposition was 1.40 ± 0.59 days for females producing male and female progeny, and 1.96 ± 1.07 days for females producing only male progeny (n = 429, 71, respectively). The differences between hosts were not statistically significant, but females producing only male progeny were old (ca. 50-60 days) and had depleted their sperm supply. Presumably their senescent condition was responsible for the longer sting-to-oviposition period. Summary data on oviposition to eclosion, larval development to cocoon formation, cocoon to adult emergence (pupation), and oviposition to adult emergence is provided for parasites attacking NOW and PBW (Table 1).

Occasionally, a female may leave a host for a few minutes or become quiescent, but she returns to the host or becomes ovipositionally active until the appropriate number of eggs have been deposited on the host (see below). Once the full complement of eggs has been deposited, the female leaves the host and wanders around the arena. If an ovipositing female is confronted with a pencil or probe, she will act aggressively toward it by spreading her mandibles and attempting to bite or sting the object. Similar behavior has been observed in females near paralyzed and arasitized hosts.

Eggs may be deposited one hour after paralysis of the host or the parasite may wait up to five days. The period from oviposition to eclosion was 1.25 ± 0.27 days for broods producing male and female progeny on NOW (n = 436) and 1.23 ± 0.27 days for broods producing only male progeny (n = 155). Parasite eggs on PBW required 1.44 ± 0.18 days to develop for broods producing male and female progeny (n = 428), and 1.46 ± 0.13 days for broods producing only males (n = 71). We are unable to explain the slightly longer period of the egg stage on PBW. In all instances observations were made in the morning and evening.

During the period of oviposition the host remains alive and haemolymph flows metasynchronously in the dorsal aorta. Females will host feed before oviposition and frequently necrotic areas on the host's integument appear at the site of feeding. Males have not been observed to host feed.

The larval to cocoon interval was slightly shorter for all male broods, for broods on NOW (3.75 ± 0.35 (n = 430) versus 3.60 ± 0.21 (n = 155) and PBW (3.61 ± 0.26 [n = 428] versus 3.58 ± 0.23 [n = 71]), but the differences were not statistically significant. Males are invariably smaller than females and emerge before sibling sisters. It seems that larval stage is responsible for this difference between sexes, although it is not statistically significant. Males emerge less than 12 hours before females of the same brood, but the data was collected twice daily. This could have a confounding effect on the statistics presented in Table 2, as more frequent observations might have produced a statistically significant results.

The larval head of *G. legneri* does not project through the hosts's integument but rather only the mandibles are embedded in the cuticle. As with the egg, removing the parasite larva from the host results in its death. During the first two days of larval development the parasites consume about 50% of the internal contents of the host. Development time for the larval stage for mixed and male only broods on both hosts at 25°C and 50% RH are given above and in Table 1. The larvae eventually consume the contents of

the host's body and all that remains is a shriveled cuticle and the head capsule. We believe that haemolymph flow is essential to parasite development because in several instances when the adult female parasite killed the host (determined by lack of contraction of the dorsal aorta) and oviposited upon it, the eggs would hatch but invariably the larvae died.

After completing feeding, the larvae detach from the host but remain *in situ* and begin to spin a cocoon. The spinning larva differs from the feeding larva in that the integument is no longer transparent and urate cells aggregate near the integument and form white spherules.

The cocoon of *G. legneri* is loosely woven, white, 5 mm long and 1.5 mm in diameter. Its construction requires 14 - 16 hours at 25°C. After completion of the cocoon a dark orange fluid is secreted from the anus. The amount of time between the onset of spinning and voiding the fluid is about 30 hours. The fluid hardens in several minutes, depending on ambient temperature and relative humidity. Stimulation, such as probing or squeezing with a pair of forceps causes the hindgut to be voided. In all instances, however, the hindgut is voided in less than five seconds.

The pupal period, defined as the termination of cocoon formation to adult emergence, is 9.26 ± 0.53 days on NOW (n = 430) at 25°C and 50% RH, for female and male broods, and 8.63 ± 0.40 days for broods producing only male progeny (n = 155). On PBW pupal development requires 8.93 ± 0.57 days for broods producing males and females (n = 428), and 8.96 ± 0.38 days for broods composed exclusively of males (n = 71). The differences between PBW and NOW were different, but not statistically significant. However, the difference between the means for mixed and all male broods on NOW is highly significant ($p < 0.001$). This was to be expected because males are protandrous and emerge before their sibling sisters. Mixed broods would be expected to have a longer mean development time. There was no significant difference in the period of pupation when progeny from a young parasite was compared to the progeny of an old parasite on either host. In fact, we found no statistically significant correlation between age of the parental female and progeny development.

The newly formed pupa is entirely white with translucent appendages. Pigmentation occurs in a definite, predictable pattern (Fig. 3). Initially the eyes become pink. As they darken the dorsum of the propodeum and scutellum also darken. Ventrad, the middle and hind coxae darken and the medial portion of the sternum becomes dusky. Later the darkening of these areas becomes more pronounced and the posterior portions of metasomal sterna I-III, and the ventral aspect of the head becomes dusky. Darkening of the above mentioned regions proceeds and spreads such that within 96 hours the entire body assumes adult coloration.

Total development time from egg to adult was 14.26 ± 0.97 days on NOW at 25°C and 50% RH for broods producing males and females (n = 430). Development time under the same conditions for broods producing only males was 13.45 ± 0.46 days (n = 155). The difference is highly significant ($p < 0.001$) and due to the combined effect of shorter larval and pupal periods for all male broods. Development time for broods producing males and females on PBW was 13.98 ± 0.53 days (n = 427), and 14.00 ± 0.47 days for broods producing only males (n = 71). The differences between

development times for equivalent broods on NOW versus PBW are highly significant ($p < 0.001$) but opposite in sign and are attributable to the larval and pupal development periods. We have no explanation for the high variance in development time (oviposition to adult) for mixed broods developing on NOW.

4. Courtship, Copulation, and Sex Ratio: Males of *G. legneri* are protandrous and emerge 10-12 hours before their sibling sisters. After emergence, a male remains at the site of pupation and chews a hole in the female's cocoon. No particular site is preferred for the hole and the male may chew into the anterior or posterior end of the female's cocoon. Once inside the cocoon, the male orients toward the female head-to-head and dorsum-to-venter, with the male assuming the superior position. The female will deflect her metasoma in an upward position and the male will extend his metasoma to the ventral surface of the female's metasoma. Little overt courtship behavior exists in this species and copulation requires 3-15 minutes. The seemingly wide variation in copulation time is probably due to female receptivity, male sperm depletion (ejaculate size), or both. After inseminating the female, the male leaves the cocoon and chews a hole in another female's cocoon and the procedure is repeated. In the meantime, the inseminated female leaves her cocoon and grooms her body. Copulation also occurs between males and newly emerged, uninseminated females.

Inseminated females repel subsequent copulatory attempts by males. If a male succeeds in mounting an unreceptive female, she runs rapidly around the container. If this behavior does not repel the male, she uses her hind legs in an attempt to dislodge the male. Frequently, females will turn in an attempt to bite the male.

In one experiment, cocoons of both sexes were isolated and placed individually in 000 gelatin capsules. After ten days individual virgin males and females were placed together in four-dram vials. Observing ten such couples revealed that not all females were readily receptive to courtship and copulatory attempts of virgin males. Receptive females remained quiescent with their antennae vibrating. Insemination in these episodes lasted three to five minutes.

Goniozus legneri has a precise sex ratio and regulates the number of male eggs based on the size of its host. The overall sex ratio for 26 female parasites throughout their lifetime on NOW (including clutches which produced only males) was 1.23:1.00 in favor of females (n = 6,761 eggs). However, when only the first twelve broods are considered, i.e., ignoring all-male broods produced by females which have depleted their sperm supply, the sex ratio shifts to 4.15:1.00 in favor of females.

In order to analyze the effects of various factors on sex ratio a stepwise regression procedure was performed on the data for the first 12 broods of *G. legneri* on NOW (n = 6). Sex ratio (as number of females over the total brood, arcsin transformation) was treated as the dependent variable against six independent variables: host weight, age of the parasite, number of eggs in the brood, days since the last sting, female adult longevity, and brood mortality. The regression was statistically significant for sex ratio and days since last sting with an r^2 of 0.081 and an F statistic of 6.18

($p = 0.0153$, 70 degrees of freedom). That is, the proportion of females in a brood tends to increase as the number of days since the last oviposition increases. A longer period between oviposition may provide for increased sperm availability during the next reproductive episode.

Table 2 represents a joint frequency distribution for the first 12 broods of 191 clutches of eggs of *G. legneri* laid on NOW for which there was no immature mortality. From the data presented it is obvious that the number of males produced is strongly correlated with brood size. Small broods have only one male; intermediate sized broods have two males while large broods produce three males. It seems apparent that supplemental males are produced for intermediate and large broods to insure adequate sperm to inseminate all females of the brood. We have observed numerous inseminative episodes in multiple male broods and have not witnessed combat among males for uninseminated females in a brood.

5. Egg Production and Host Size: Studies with other species of *Goniozus* suggest that the number of eggs per clutch is strongly correlated with host size. In order to evaluate the relationship between host size and clutch size we used the data from the detailed tests of 26 *G. legneri* females on NOW and 20 *G. legneri* females on PBW (the 21st female on *G. legneri* was originally set up as an alternate in case of parasite mortality. Thus, the data from this female was not included in some analyses. It was in no way atypical). These parasites were provided with weighed hosts following a 24 hour isolation interval after each oviposition, as described above. Hosts were chosen at random from host cultures. In addition, concurrently with the 26 females on NOW described above, 6 females were set up on NOW under identical conditions with the exception that these 6 females were given fresh hosts immediately after oviposition was noted (i.e., no 24 hour isolation interval). Due to logistical reasons, the NOW and PBW tests could not be run concurrently. However, the replicates were exposed to identical conditions in all tests.

The weight of hosts was broken down into 2.5 mg increments and the total number of parasite eggs, the mean number of eggs per host (clutch), and the number of such clutches observed was tabulated for each host weight class for each of the 3 tests. The data are presented in Table 3.

The distribution of host weights for NOW and PBW is apparently normal, as one would expect, with the largest number of hosts in the ranges 22.5 to 35.0 mg for PBW and 25.0 to 40.0 mg for NOW. The absolute number of eggs in each weight class follows these distributions. However, the mean number of eggs per host shows an increase with increasing host weight for PBW and for NOW with and without a 24 hour isolation interval. The trend is monotonic with one exception on PBW, and on this host the number of eggs per host reaches a maximum in the largest weight class provided. It is unknown, of course, if clutch size on PBW would increase if larger PBW larvae were available. On NOW, however, the data for clutch size suggest a plateau in the weight classes of 45.0 to over 50.0 mg and 42.5 and 50.0 mg for parasites with and without the 24 hour isolation interval, respectively. This suggests that parasites presented with large hosts under these conditions may be utilizing the maximum number of ovarian eggs suitable for oviposition. Clutch size is somewhat smaller on NOW in the largest weight classes for parasites which were not given 24 hour isolation intervals between

hosts. This would be expected if egg utilization is at a maximum with large hosts, as less time would be available for egg maturation between reproductive episodes.

6. Egg Production and Position: In addition to analyzing egg production and host size, we examined the position of eggs with regard to segment number and aspect (dorsal, lateral, ventral) of the host's body. Data presented in Table 4 were collected from the detailed tests on NOW (n = 26) and PBW (n = 20) (both with 24 hour isolation interval) described above. Data collected from NOW and PBW were maintained as distinct. From Table 4 it is evident that there is a strong preference for the dorsal aspect of the host's body, followed by a moderate preference for the lateral aspect of the host's body, while the ventral aspect of the host's body is strongly rejected. The trend was consistent for PBW and NOW. *Goniozus legneri* prefers to oviposit on segment 5 - 9 when attacking NOW and segments 4 - 9 when attacking PBW. Both trends were seen on the dorsal and lateral aspects of the host's body for NOW and PBW. It was also noted for the ventral surface of segments 5 - 9 on NOW and 5 - 8 on PBW.

This data was compared to similar data collected on two related species, *G. gordhi* Evans (attacking *Deoclona yuccasella* Busck) (Gelichiidae) and *G. aethops* Evans (attacking PBW). Interestingly, *G. gordhi* prefers to oviposit on the dorsal aspect of segments 6 - 9, has a moderate preference to the lateral aspect of segments 6 - 9, and is reluctant to oviposit on the venter. This data is consistent with the findings for *G. legneri*, but is in sharp contrast with the findings for *G. aethops* , which demonstrates a strong preference for the lateral aspect of segments 5 - 9, but strongly rejects the dorsal and ventral aspects of the host's body.

7. Immature Mortality: Mortality of larvae and pupae were compared for the 26 females attacking NOW and the 20 females attacking PBW (Table 5). Mean egg production (at 25 ± 2°C, 50% RH, LD 14:10) per female per lifetime was 288.00 ± 33.91 on NOW, and 294.75 ± 47.74 on PBW. These results were not significantly different. These females produced 272.08 ± 32.09 larvae on NOW and 284.50 ± 46.24 larvae on PBW (not significantly different). Thus egg-larval mortality was 15.54 ± 6.21 individuals on NOW, and 10.70 ± 3.74 individuals on PBW. Pupal mortality was 6.20 ± 3.80 individuals on NOW and 8.70 ± 11.25 individuals on PBW.

8. Life Tables: Life tables were constructed for 25 female *G. legneri* on NOW (one female was lost during the experiment) and the 21 female *G. legneri* on PBW. These parasites were provided with 24 hour isolation intervals between ovipositions and hosts were chosen at random from host cultures. Age (x) was counted in days; survivorship (l_x) and age-specific fecundity (m_x) values were calculated by the methods described above.

The life table incorporating age (x), survivorship (l_x) and fecundity (m_x) values for *G. legneri* on NOW is presented as Table 6. Only the values through the age of last female egg production (x = 105 days) are shown. Table 7 is a life table for *G. legneri* on PBW and is presented in a similar manner (age of last female egg production is x = 119 days).

From the life tables, demographic statistics were estimated using the methods discussed in Birch (1948). Net reproductive rates (R_0) were calculated by the formula:

$$R_0 = \Sigma l_x m_x. \quad (1)$$

Generation times (T_c) were calculated using the formula for cohort generation time:

$$T_c = \Sigma\ x l_x m_x / R_0 \quad (2)$$

Two population growth rate parameters were calculated. Capacities for increase (r_c) were derived using:

$$r_c = \ln R_0 / T_c \quad (3)$$

Intrinsic rates of increase (r_m) were estimated by iterative solutions of the equation:

$$1 = \sum_{x=1}^{\infty} l_x m_x e^{-r_m x} \quad (4)$$

By this method, successive values of r_m are tried until the desired degree of accuracy is achieved. The capacity for increase (r_c) is often used as an approximation of the intrinsic rate of increase (r_m), but is often discussed by Laughlin (1965), May (1976), and others, both statistics have relevance to discussions of population growth phenomena. The capacity for increase (r_c) can be thought of as the growth rate of populations with non-overlapping generations, or as the actual growth rate of a population founded by a single cohort of females until a stable age distribution is obtained (i.e., for the first several generations). Once a stable age distribution is obtained, a population grows at the intrinsic rate of increase (r_m) in an unlimited environment. The capacity for increase (r_c) is typically less than r_m and Laughlin (1965) states that the difference is usually small (5% or less) while May (1976) provides a formula to estimate the relative error in estimating the relative error in estimating r_m by r_c.

The demographic statistics we calculated for *G. legneri* are presented in Table 8. Net reproductive rates (R_0) for this parasite on PBW and NOW are 160.2 and 145.1 females per female per lifetime, respectively. Values for generation time (T_c) and capacity for increase (r_c) were 51.5 days and 0.0985 females per female per day on PBW and 45.1 days and 0.110 females per female per day on NOW. The intrinsic rates of increase (r_m) were 0.157 females per female per day on PBW and 0.162 females per female per day on NOW. On both hosts, the differences between r_m and r_c were substantial: r_m exceeded r_c by 37.3% on PBW and by 32.1% on NOW. The differences are due to the large R_0 values and, possibly, to large variances in the $l_x m_x$ distributions (see May [1976] for a discussion of this problem).

We wished to compare the demographic statistics for *G. legneri* with those produced for *G. emigratus* on NOW by Gordh and Hawkins (1981). However, the value given for r_m in that paper was calculated using formula (3) and is therefore better referred to as r_c. We have included this statistic (as r_c) and those for net reproductive rate (R_0) and cohort generation time (T_c) in Table 8. In order to compare intrinsic rates of increase between the 2 species of *Goniozus*, we have used the life table data presented in Gordh and Hawkins (1981) to calculate r_m for *G. legneri* using equation (4). This is also included in Table 8. A similar trend for the "approximation" statistic (r_c) versus the "accurate" statistic (r_m) was noted for *G. emigratus* on NOW: r_m was 0.178 and exceeded r_c (0.131) by 26.4%. These empirical results indicate that the choice of one method or another to estimate population growth rates is not necessarily trivial as substantially different results may be obtained. The differences between r_m and r_c values for these *Goniozus* spp. are only slightly greater than the differences predicted by applying May's (1976) formula to our life table data.

The life table for *G. emigratus* on NOW (Gordh and Hawkins 1981) was obtained using an experimental protocol virtually identical to that used for *G. legneri* as described above. We note one difference: *G. emigratus* females were maintained at 26.7 ± 1°C and *G. legneri* was maintained at 25. ± 2°C on both hosts in our experiments. Nevertheless, values for demographic statistics computed by equivalent methods should be directly comparable between the two species reared on NOW, and between hosts for *G. legneri*. The value for r_m for *G. emigratus* on NOW is substantially greater than that obtained for *G. legneri* on the same host, 0.178 versus 0.162 females per female per day, respectively, even though the net reproductive rate for *G. emigratus* on NOW (R_0 = 128.0 females per female per lifetime) is substantially less than that for *G. legneri* on NOW (R_0 = 145.1 females per female per lifetime). This effect is due to the shorter generation time for *G. emigratus* on NOW (T = 27.3 days) versus *legneri* on NOW (T = 30.7 days), and may be due, in part, to the temperature difference noted above. Similarly, *G. legneri* has a slightly higher r_m on NOW than on PBW (0.162 and 0.157 females per female per day, respectively) despite the lower R_0 obtained for this parasite on NOW (145.1 females per female per lifetime versus R_0 = 160.2 females per female per lifetime on PBW). Again, the slightly higher r_m on NOW is due to the shorter generation time for *G. legneri* on this host: 30.7 days versus 32.4 days on PBW.

The net reproductive rates (R_0) for *G. legneri* on PBW and NOW obtained by analyses of life tables were very close to the mean number of female progeny on PBW and NOW (169.55 ± 28.80 and 149.21 ± 17.62 females per female per lifetime, respectively) obtained by direct averaging of the data. One possible reason for the greater total production of female progeny by *G. legneri* on PBW is discussed above under 2. Parasite Host-Attack. That is, the greater number of males in the original broods of *G. legneri* on PBW resulted in more sperm per female per insemination.

The difference cannot be due to host size (larger hosts supporting larger broods with more females) as PBW hosts tended to be smaller than NOW hosts in these experiments (see Table 3). The shorter generation time (T) for *G. legneri* on NOW is difficult to account for, but it may be related to host size or host quality.

DISCUSSION

In recent years there has been considerable interest in the study of bethylid biology and the potential of bethylids in biological control of various agricultural and urban pests. Much of this work has been reviewed elsewhere and need not be repeated here (see Gordh 1976, Gordh and Evans 1976, Gordh and Hawkins 1981, and papers cited therein).

Studies have shown that several species are of value to biological control, and *G. legneri* seems to be another useful species in attacking Microlepidoptera. The fossorial habits of bethylids, their longevity, and high reproductive potential would be desirable attributes for biological control agents attacking Lepidoptera and Coleoptera larvae, especially in concealed situations. Although not host specific, they do demonstrate strong preference at the family or superfamily level.

Although considered among the most primitive of aculeate Hymenoptera, bethylids display a highly complex biology. Within the genus *Goniozus*, several species are known to regulate the number of eggs deposited based on an estimate of host size. The modalities responsible for this phenomenon are not known, but they are currently under investigation. Regulation of sex ratio based on egg clutch size is also apparently widespread in *Goniozus*, and will perhaps be found in other bethylids as well. Further research on other bethylids will prove exceptionally rewarding in understanding the evolution of the aculeate Hymenoptera.

The morphology of the immature stages of *G. legneri* do not differ from other species of *Goniozus* (cf. *G. columbianus*, *G. japonicus*, *G. emigratus*, *G. gordhi*, *G. aethops*, *G. claripennis* Foerster, *G. nigrifemur* [Ashmead]). There are some indications that the manner in which pupal pigmentation is formed differs among species, and may be of some taxonomic value (Gordh 1976, Gordh and Evans 1976). Unfortunately this aspect of immature development has not been critically examined for most species.

The longevity of *G. legneri* is substantially longer than many other species of *Goniozus* which have been studied. For instance, Gordh and Evans (1976) found that *G. aethops* lived 13.35 ± 8.48 days, Gordh and Hawkins (1981) found that *G. emigratus* lived 52.60 ± 7.30 days when provided hosts and 37.10 ± 12.40 days when deprived of hosts, and Gordh (1976) found that *G. gordhi* females lived 62.43 ± 8.48 days when provided hosts. Thus it appears that there is considerable variability in the longevity of *Goniozus* species.

There is similarly some variability in the number, size and position of eggs of *Goniozus*. Gordh (1976) reported that *G. gordhi* deposited 153.78 ± 48.59 eggs during the course of a female's lifetime, Gordh and Evans (1976)

reported that *G. gordhi* deposited 153.78 ± 48.59 eggs during the course of a female's lifetime, Gordh and Evans (1976) reported that *G. aethops* deposited 16.23 ± 8.18 eggs during the course of its lifetime, and Gordh and Hawkins (1981) found that *G. emigratus* deposited 232.9 ± 91.5 eggs per lifetime under conditions similar to those provided *G. legneri*.

Goniozus legneri has a strong ovipositional preference for the dorsal aspect of the host's body. This site preference is also seen in *G. gordhi* (Gordh 1976), *G. cellularis* (Say) (Gordh and Evans 1976), *G. nigrifemur* (Gordh, unpubl.), and *G. emigratus* (Gordh and Hawkins 1981). Other species (*G. aethops*, Gordh and Evans 1976, *G. nephantidis*, Antony and Kurian 1960) prefer the lateral aspect of the host's body while Cherian and Israel (1942) indicated that *G. indicus* prefers the ventral aspect of the host's body as an ovipositional site.

The size and shape of *Goniozus* eggs can vary also. Most species have the typical sausage-shaped (hymenopteriform) eggs which are deposited longitudinally along the host's body, but some species have "football" shaped eggs which are deposited intersegmentally within the integumental folds (*G. aethops*, Gordh and Evans, 1976). The thickness of the chorion also appears to be related to the position of the egg and the extent of paralysis. Permanently paralyzed hosts with eggs deposited on segments have relatively thin chorions; eggs which are deposited on hosts which recover from paralysis and resume activity tend to have football shaped eggs which have thick chorions and are deposited intersegmentally.

In all species of *Goniozus* studied, there appears to be a normal distribution of eggs over the integument of the host. That is, all species prefer to oviposit on the middle segments of the host's body, irrespective of the aspects which it prefers (i.e., dorsal, lateral, ventral) and progressively fewer eggs are deposited on segments toward the head or anus. The purpose for this behavior is not clear. Hosts paralyzed permanently can exhibit some lateral movement. Considering the thin chorion of most eggs, and the possibility of dislodgement, and subsequent mortality, then it is unlikely that the middle segments of the body would be a suitable ovipositional site because in lateral flexure, these segments are exposed to the most deformation. Alternatively, it appears that maximum haemolymph flow is the most important consideration in survival of the parasite. At least, hosts which have been killed by the female parasite and oviposited upon yield no parasite progeny. Given the shape of the host larva, it seems probable that maximum haemolymph flow (volumetrically) is located along the middle segments of the host's body. Thus we infer that the reason the middle segments are preferred is due to haemolymph flow.

Courtship in *G. legneri* is not different from that noted for *G. gordhi*, *G. aethops*, *G. emigratus*, *G. nephantidis*, *G. montanus*, or *G. claripennis*. Indeed, in all species of *Goniozus* and related genera courtship is overtly simple. In all species of *Goniozus* it appears that the male chews into the female's cocoon. Thus sib mating in broods producing males and females appears to be the rule.

The host attack by *G. legneri* does not differ from other species of the genus. Invariably the female stings her host in the ventral nerve cord near the head. The only noted exception to this site specificity is a report

by Bridwell (1919) in which he remarked that in *G. emigratus* the parasite stung its host in three places - the head region, the middle of the body, and near the anus. In a subsequent study (Gordh and Hawkins 1981) this behavior was not observed in *G. emigratus*. We suspect that Bridwell's comments were based on a very limited number of observations, and that in fact what he noted was a female parasite initially mounting the host at the posterior end of its body and that in the ensuing struggle, the parasite shifted to the head. This sort of behavior has been observed in *G. emigratus*, *G. aethops*, *G. legneri*, and *G. gordhi*.

There does appear to be some variability in the effect of venom in *Goniozus*. In most species the paralysis is permanent, but in *G. japonicus* (Iwata 1961, Kishitani 1961), *G. rugosus* (Samad 1973), and *G. claripennis* (Voukassovitch 1924), the host regains the ability to walk after the parasite has oviposited. Although the reports on regaining locomotion are not clear on this point, it is suspected that any species of *Goniozus* which temporarily paralyzes its host probably has small eggs with thick chorions, and deposits its eggs in the intersegmental folds of the host's integument. Otherwise, high egg mortality could be suspected.

A post-adult emergence period during which the parasite is incapable of oviposition seems common in *Goniozus*, but its duration is highly variable. Gerling (1979) found that *Goniozus* sp. had a preovipositional period of up to nine days, and Iwata (1961) found that *G. japonicus* has a preovipositional period of about seven days. Most other species of *Goniozus* which have been studied have a preovipositional period of 3 - 5 days.

Demographic statistics such as we have calculated for *G. legneri* may eventually prove to be useful to biological control workers in evaluating the potential of natural enemies or in analyzing performance in particular habitats. Certainly, many other attributes of natural enemies are responsible for success or failure in a given program. These statistics do provide a good measure of reproductive potential in the laboratory. The choice of which population growth statistic to use is best determined by the context of particular comparisons. For example, r may be close to the actual growth rate of a population of natural enemies soon after a release has been made. If hosts are abundant and competition effects negligible, the growth rate may increase for several generations and approach r_m, if a stable age distribution of parasites is obtained. The r_m values which we have calculated for *G. legneri* on PBW and NOW (0.157 and 0.162) and for *G. emigratus* on NOW (0.178) are rather high, even for insects (see Connell and Scheiring (1982) for a recent tabulation of r_m values for various insects). This indicates that these species of *Goniozus* are capable of rapid increases in population size under favorable conditions.

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Table 1. Mean and standard deviation for sting to oviposition, egg deposition to eclosion, larval stage duration, pupal stage duration, and egg to adult duration for broods producing only males and broods producing males and females on NOW and PBW.

Interval	Host PBW	NOW
Sting - Oviposition		
♂♀	1.40 ± 0.59 (n = 429)	1.19 ± 0.47 (n = 437)
♂♂	1.96 ± 1.07 (n = 71)	1.82 ± 1.16 (n = 159)
Oviposition - Eclosion		
♂♀	1.44 ± 0.18 (n = 428)	1.25 ± 0.27 (n = 436)
♂♂	1.46 ± 0.13 (n = 71)	1.23 ± 0.27 (n = 155)
Larva - Cocoon		
♂♀	3.61 ± 0.26 (n = 428)	3.75 ± 0.35 (n = 430)
♂♂	3.58 ± 0.23 (n = 71)	3.60 ± 0.21 (n = 155)
Cocoon - Adult		
♂♀	8.93 ± 0.57 (n = 428)	9.26 ± 0.53 (n = 430)
♂♂	8.96 ± 0.38 (n = 71)	8.63 ± 0.40 (n = 155)
Egg - Adult		
♂♀	13.98 ± 0.53 (n = 427)	14.26 ± 0.97 (n = 430)
♂♂	14.00 ± 0.47 (n = 71)	13.45 ± 0.46 (n = 155)

Table 2. Summary (joint frequency distribution) of data for complete broods for first 12 broods for each female parasite. (Female parasites began exhausting sperm supply on 13th brood.)

	NUMBER OF MALES					
Brood size	0	1	2	3	4	Total
5		3				3
6		4				4
7		8				8
8		10	2			12
9		5	8			13
10			21	1		22
11			29	3		32
12			33	8		41
13			15	14		29
14			6	9		15
15				9		9
16				2		2
17						0
18						0
19						0
20					1	1
Total	0	30	114	46	1	191

Table 3. Total egg production and mean number of eggs per host on NOW and PBW as a function of host weight, with and without 24 hour interval between hosts. For each mean, n = number of hosts observed.

	Host								
	PBW (n = 20♀) (24 hour interval)			NOW (n = 26♀) (24 hour interval)			NOW (n = 6♀) (no interval)		
Host weight (mg)	Total eggs	Eggs per host	n	Total eggs	Eggs per host	n	Total eggs	Eggs per host	n
Under 20	45	7.5	6	0	--		0	--	--
20.0-22.5	204	9.3	22	67	8.4	8	0	--	--
22.5-25.0	405	10.7	38	150	9.4	16	20	10.0	2
25.0-27.5	1029	12.0	86	499	11.1	45	109	9.1	12
27.5-30.0	1224	11.3	108	952	11.8	81	236	11.2	21
30.0-32.5	1563	11.8	132	1294	11.9	109	397	12.0	33
32.5-35.0	733	13.0	56	1319	12.2	108	229	11.4	20
35.0-37.5	89	12.7	7	1156	12.7	91	248	12.4	20
37.5-40.0	157	14.3	11	832	13.9	60	251	13.2	19
40.0-42.5	106	15.1	7	419	15.0	28	111	11.1	10
42.5-45.0	48	16.0	3	277	13.8	20	78	13.0	6
45.0-47.5	0	--	--	225	18.8	12	25	12.5	2
47.5-50.0	0	--	--	0	--		26	13.0	3
Over 50	0	--	--	82	16.2	5	0	--	--

Table 4. Cumulative number of eggs produced per segment and egg position by G. legneri attacking NOW (n = 26 female parasites) and PBW (n = 20 female parasites). Data compared with similar data collected for G. gordhi Evans, G. aethops Evans.

	Segment of host's body										
Aspect	1	2	3	4	5	6	7	8	9	10	11
					G. LEGNERI (NOW)						
Dorsal	0	5	8	58	258	962	1454	1456	699	118	0
Lateral	0	0	3	10	85	431	751	649	292	40	0
Ventral	0	0	1	0	13	38	72	54	15	0	0
					G. LEGNERI (PBW)						
Dorsal	1	14	67	323	678	1021	1067	924	426	76	2
Lateral	1	1	11	57	144	278	312	245	117	25	2
Ventral	0	2	8	8	27	35	25	17	5	2	1
					G. GORDHI (Deoclona yuccasella Busck)						
Dorsal	0	0	5	12	56	120	193	202	153	3	0
Lateral	0	0	3	9	21	39	67	42	32	14	5
Ventral	0	0	1	2	5	4	3	6	3	2	0
					G. AETHOPS (PBW)						
Dorsal	0	0	0	2	2	3	6	8	4	0	0
Lateral	0	4	6	26	71	72	111	118	81	22	1
Ventral	0	0	0	2	1	0	5	0	0	0	0

Table 5. Immature mortality of G. legneri on PBW and NOW. Each figure represents the total lifetime production of one female parasite. Figures in parenthesis refer to mortality in that stage.

NOW			PBW		
Eggs	Larvae	Adults	Eggs	Larvae	Adults
329	301 (28)	293 (8)	227	222 (5)	281 (4)
207	197 (10)	191 (6)	319	308 (11)	290 (18)
358	337 (21)	335 (2)	334	323 (11)	318 (5)
326	308 (18)	298 (10)	326	319 (7)	272 (47)
317	285 (22)	283 (2)	225	219 (6)	210 (9)
338	331 (17)	311 (10)	187	178 (9)	175 (3)
295	284 (11)	282 (2)	332	321 (11)	319 (2)
287	272 (15)	272 (0)	270	261 (9)	254 (7)
274	255 (19)	246 (9)	341	328 (13)	324 (4)
317	307 (10)	304 (3)	344	332 (12)	324 (8)
318	302 (16)	298 (4)	284	271 (13)	268 (3)
253	234 (19)	230 (4)	267	250 (17)	249 (1)
293	271 (22)	260 (11)	342	325 (17)	317 (8)
263	251 (12)	243 (8)	368	359 (9)	356 (3)
278	271 (7)	263 (8)	304	286 (18)	282 (4)
288	270 (18)	264 (6)	254	245 (9)	215 (30)
273	265 (8)	256 (9)	300	286 (14)	276 (10)
263	253 (10)	251 (2)	329	322 (7)	319 (3)
315	301 (14)	297 (4)	274	265 (9)	263 (2)
267	257 (10)	248 (9)	268	261 (7)	258 (3)
267	263 (4)	260 (3)			
269	250 (19)	244 (6)	294.75	284.50	275.45
299	281 (18)	280 (1)	±47.74	±46.24	±46.85
226	205 (21)	195 (10)			
280	272 (8)	256 (16)			
288	261 (27)	259 (2)			
288.00	272.08	266.12			
±33.91	±32.09	±32.86			

Table 6. Life table for G. legneri on NOW. Developmental stage, age (x) in days, survivorship (l_x), and age-specific fecundity (m_x), n = 25 ♀.

Developmental Stage	Age x	Survivorship l_x	Fecundity m_x
eggs	0	1.000	0
1st instar larvae	1	.945	0
larvae to adult emergence	2 - 13	.924	0
mating and isolation period	14 - 15	.924	0
hosts available	16	.924	0
	17	.924	0
	18	.924	1.200
	19	.924	6.620
	20	.924	.480
	21	.924	0
	22	.924	9.480
	23	.924	0
	24	.924	4.760
	25	.924	3.600
	26	.924	.760
	27	.924	4.400
	28	.924	3.560
	29	.924	2.840
	30	.924	0
	31	.924	5.600
	32	.924	2.640
	33	.924	.600

Table 6 (continued).

Age x	Survivorship l_x	Fecundity m_x	Age x	Survivorship l_x	Fecundity m_x
34	.924	7.720	58	.924	.960
35	.924	.440	59	.924	4.080
36	.924	.640	60	.924	2.880
37	.924	2.800	61	.924	1.360
38	.924	4.760	62	.924	2.760
39	.924	1.000	63	.924	2.840
40	.924	2.680	64	.924	1.680
41	.924	4.760	65	.924	1.360
42	.924	2.080	66	.924	1.640
43	.924	2.000	67	.924	3.000
44	.924	4.160	68	.924	1.320
45	.924	2.520	69	.924	1.720
46	.924	3.400	70	.924	1.880
47	.924	2.520	71	.924	1.400
48	.924	3.720	72	.924	1.640
49	.924	2.760	73	.924	1.520
50	.924	1.160	74	.924	.840
51	.924	3.240	75	.924	.840
52	.924	3.520	76	.924	.960
53	.924	3.640	77	.924	1.160
54	.924	1.280	78	.924	.080
55	.924	2.080	79	.924	.480
56	.924	5.960	80	.924	.880
57	.924	1.800	81	.924	.760

Table 6 (continued).

Age x	Survivorship l_x	Fecundity m_x	Age x	Survivorship l_x	Fecundity m_x
82	.924	.240	104	.813	0
83	.924	.040	105	.813	.046
84	.924	.240	106	.813	0
85	.924	.720			
86	.924	.160			
87	.924	.040			
88	.924	0			
89	.924	.080			
90	.924	.160			
91	.924	0			
92	.924	.040			
93	.924	0			
94	.924	.040			
95	.924	.080			
96	.924	0			
97	.887	.042			
98	.887	0			
99	.887	0			
100	.887	0			
101	.887	0			
102	.887	0			
103	.887	0			

Table 7. Life table for G. legneri on NOW. Developmental stage, age (x) in days, survivorship (l_x), and age-specific fecundity (m_x), n = 21 ♀.

Developmental Stage	Age x	Survivorship l_x	Fecundity m_x
eggs	0	1.0000	0
1st instar larvae	1	.9637	0
larvae to adult emergence	2 - 13	.9345	0
mating and isolation period	14 - 15	.9345	0
hosts available	16	.9345	0
	17	.9345	0
	18	.9345	2.143
	19	.9345	5.238
	20	.9345	.333
	21	.9345	2.095
	22	.9345	3.560
	23	.9345	2.047
	24	.9345	1.905
	25	.9345	3.471
	26	.9345	1.286
	27	.9345	1.952
	28	.9345	3.905
	29	.9345	2.762
	30	.9345	2.286
	31	.9345	2.762
	32	.9345	2.143
	33	.9345	2.492

Table 7 (continued).

Age x	Survivorship l_x	Fecundity m_x	Age x	Survivorship l_x	Fecundity m_x
34	.9345	2.762	58	.9345	2.143
35	.9345	2.714	59	.9345	1.286
36	.9345	2.571	60	.9345	5.238
37	.9345	3.762	61	.9345	2.333
38	.9345	1.190	62	.9345	1.810
39	.9345	3.524	63	.9345	1.381
40	.9345	2.762	64	.9345	4.095
41	.9345	.714	65	.9345	2.905
42	.9345	3.619	66	.9345	1.429
43	.9345	3.476	67	.9345	1.476
44	.9345	.476	68	.9345	2.857
45	.9345	4.048	69	.9345	2.905
46	.9345	4.095	70	.9345	.810
47	.9345	1.429	71	.9345	1.524
48	.9345	2.333	72	.9345	2.714
49	.9345	4.571	73	.9345	2.571
50	.9345	1.714	74	.8900	.700
51	.9345	2.143	75	.8900	1.450
52	.9345	3.286	76	.8900	2.500
53	.9345	2.714	77	.8900	1.400
54	.9345	.952	78	.8900	.850
55	.9345	3.667	79	.8900	3.100
56	.9345	3.524	80	.8900	1.150
57	.9345	2.381	81	.8900	1.500

Table 7 (continued).

Age x	Survivorship l_x	Fecundity m_x	Age x	Survivorship l_x	Fecundity m_x
82	.8900	.700	105	.6230	0
83	.8900	2.350	106	.5340	.083
84	.8455	1.368	107	.5340	0
85	.8455	.947	108	.5340	.333
86	.8455	1.263	109	.5340	.250
87	.8455	.579	110	.5340	0
88	.8455	.684	111	.4450	.100
89	.8455	1.632	112	.4450	0
90	.8455	.368	113	.4450	.700
91	.8455	.158	114	.4450	0
92	.8455	.947	115	.4450	0
93	.8010	.444	116	.4450	0
94	.7565	.176	117	.4005	.222
95	.7565	.706	118	.3115	0
96	.7565	.529	119	.3115	.286
97	.7565	.059	120	.2670	0
98	.7565	.824			
99	.7120	1.000			
100	.6675	.533			
101	.6675	0			
102	.6675	.467			
103	.6230	1.500			
104	.6230	.214			

Table 8. Demographic statistics for G. legneri on PBW (n = 21), G. legneri on NOW (n = 25), and G. emigratus on NOW. Statistics for G. emigratus taken from (*) or calculated from (**) Gordh and Hawkins (1981).

Statistic	G. legneri PBW	G. legneri NOW	G. emigratus NOW
1. R_0	160.2	145.1	128.0*
2. T_c	51.5	45.1	37.1*
3. r_c	.0985	.110	.131*
4. r_m	.157	.162	.178**

1. Net Reproductive Rate, females per females per lifetime, $R_0 = \Sigma l_x m_x$
2. Cohort Generation Time, in days, $T_c = \Sigma\ x l_x m_x / R_0$
3. Capacity for Increase, females per female per day, $r_c = \ln R_0 / T_c$
4. Intrinsic Rate of Increase, females per female per day, $r_m = \sum_{x=1}^{\infty} l_x m_x e^{-rx}$

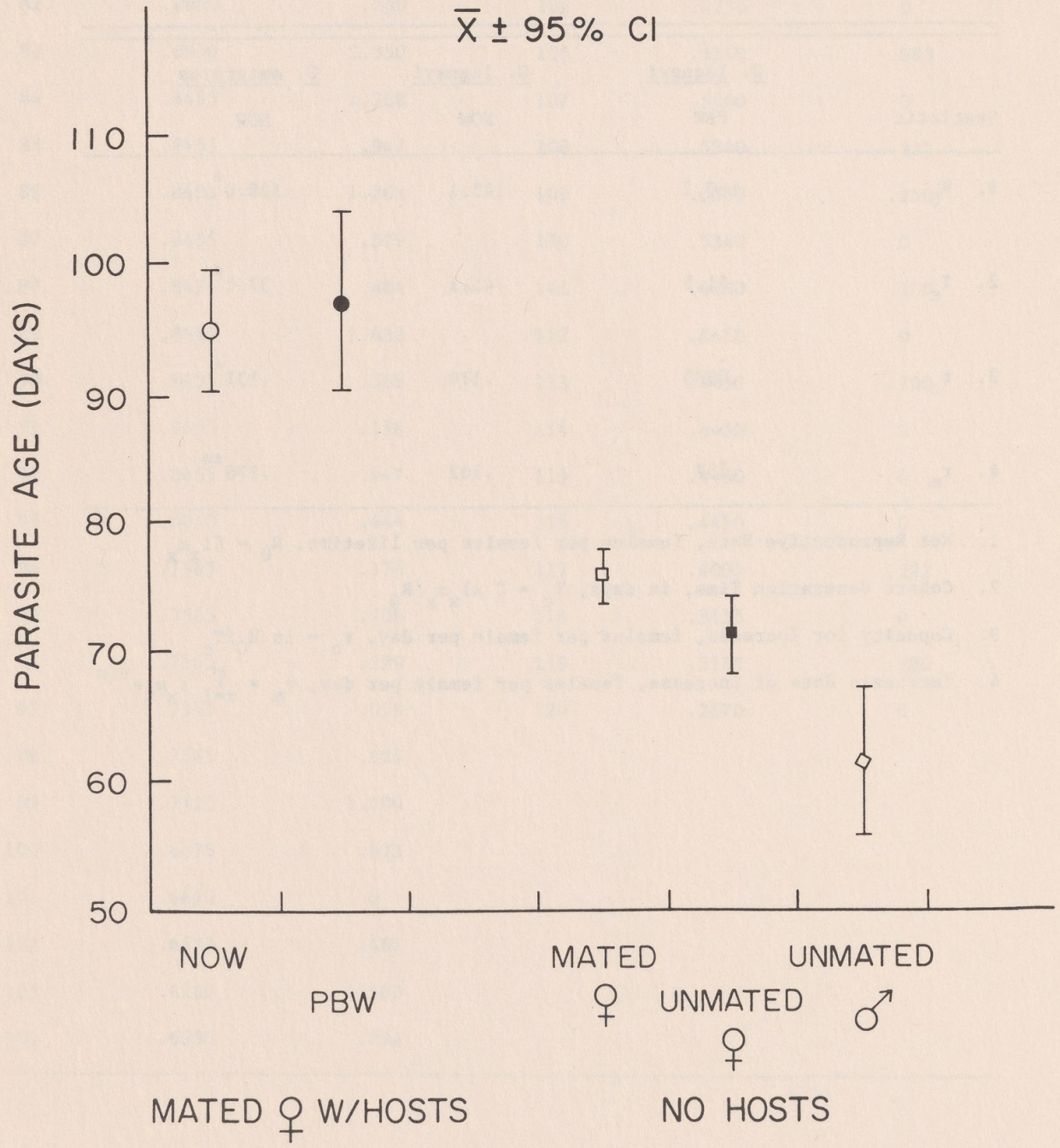

Fig. 1. Mean and variance of longivity of **G. legneri** comparing mated parasites provided hosts (NOW, PBW) (n = 50 each), and mated and unmated females deprived of hosts (n = 50each), and unmated males (n = 30).

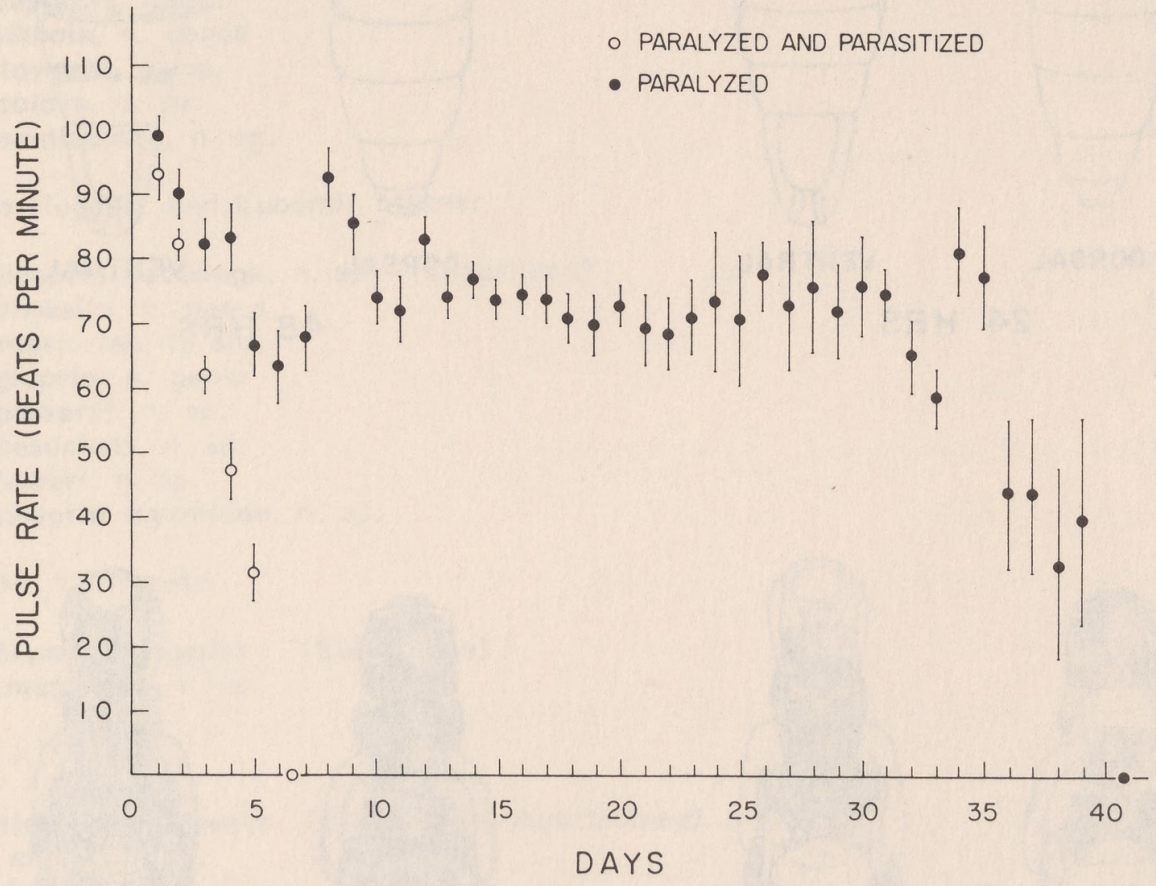

Fig. 2. Mean and variance of pulse rate of NOW which were paralyzed (dots) and which were paralyzed and parasitized (circles) by **G. legneri** during their lifetime (n = 10 for each sample).

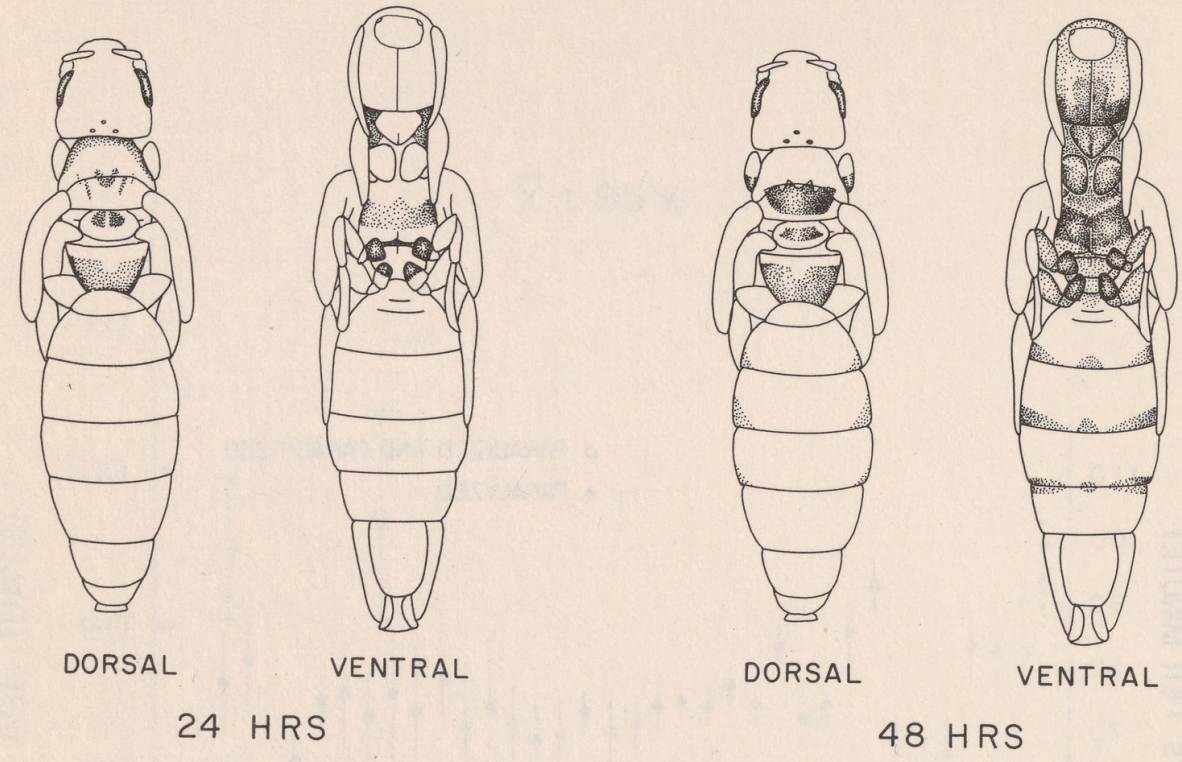

Fig. 3. Dorsal and ventral aspects of 24, 48, 72, and 96 hour old pupae of **G. legneri**, illustrating the sequence of pupal pigmentation.