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Influences of Host Density, Temperature, and Parasite Age on the Reproductive Potential of *Bathyplectes Curculionis* (Hymenoptera: Ichneumonidae), an Endoparasite of the Alfalfa Weevil (Coleoptera: Curculionidae)

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INFLUENCES OF HOST DENSITY, TEMPERATURE, AND PARASITE AGE ON THE REPRODUCTIVE POTENTIAL OF *BATHYPLECTES CURCULIONIS* (HYMENOPTERA: ICHNEUMONIDAE), AN ENDOPARASITE OF THE ALFALFA WEEVIL (COLEOPTERA: CURCULIONIDAE)

Robert J. Barney¹, Daniel P. Bartell², and W. G. Ruesink¹

ABSTRACT

Alfalfa weevil larvae were exposed to *Bathyplectes curculionis* (Thomson) to determine the effect of host density, temperature, and parasite age on the reproductive potential of *curculionis*. Percent parasitism was found to be inversely proportional to host density and most of the parasites distributed their eggs randomly regardless of host density. The number of eggs deposited was largely independent of temperature. Peak egg laying was reached in three days from which point the parasite's capabilities diminished with increasing age. The longevity of ovipositing females was shorter than females that were not exposed to larvae.

Many species of parasitic Hymenoptera have been imported and released in the U.S. and Canada to help regulate populations of the alfalfa weevil, *Hypera postica* (Gyllenhal). One of the most important and successful species to be introduced is *Bathyplectes curculionis* (Thomson), an endoparasite of alfalfa weevil larvae. Through initial releases in 1911 (Chamberlin, 1924), subsequent releases, and natural dispersal, *curculionis* is now established throughout the range of its host (Brunson and Coles, 1968).

Dynamic models of the alfalfa weevil's life system are being developed for use in pest management programs. Since *curculionis* is such an important natural enemy, it is essential that these models include its effect on the weevil. Among the more important processes in the parasitism submodel are: 1) egg production and deposition by the parasite, and 2) distribution of those eggs among available hosts. Writing equations to describe these processes is relatively simple once the biological relations are described quantitatively.

Although there is an abundance of literature pertaining to *curculionis*, only a few researchers have dealt with quantitative aspects of the host/parasite interactions, or with the effect of these interactions on the population dynamics of the alfalfa weevil (van den Bosch, 1964; Armbrust et al., 1970; Duodu and Davis, 1974). This investigation was designed to determine the effect of host density, temperature, and parasite age on the reproductive potential of *curculionis*.

MATERIALS AND METHODS

Alfalfa weevil larvae were field-collected in the spring and reared in the laboratory on fresh-cut alfalfa. Adult alfalfa weevils and cocoons of *curculionis* that developed from these larvae were retrieved to establish laboratory cultures.

Adult alfalfa weevils were fed and then stored at 7°C during summer and early fall diapause. Upon removal from storage in January, the adult weevils were placed in 1-gallon plastic containers supplied with bouquets of alfalfa which provided food and oviposition sites for the adults. Cultures were maintained in a TWINcubator® (Scientific Systems Corp.) at 20°C with a 9-hour photophase alternated with a 15-hour scotophase.

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Alfalfa weevil eggs were removed from the bouquets and incubated on moistened filter paper in 10 × 2.5 cm Pyrex[®] petri dishes. The eggs hatched in 10±1 days at 20°C with relative humidity near saturation in the petri dishes. Newly emerged larvae (less than 24 hours old) were placed on the terminal tips of alfalfa bouquets using a moistened camel hair brush. The alfalfa bouquets were held in Mallinckrodt[®] plastic funnels (10 cm dia.) suspended in Ball[®] jars and covered with Saran Wrap[®] as described by Bartell (1973). The rearing units were held in TWINcubators programmed for a 9-hour photophase alternated with a 15-hour scotophase. RH fluctuated between 40% and 60% in the incubators, but was near saturation in the rearing units.

Cocoons containing *curculionis* larvae were stored at 7°C and when needed were transferred to a chamber at 20°C to induce emergence. Adult parasites emerged from these cocoons in 12±2 days and were held in Erlenmeyer flasks sealed with cotton plugs. The plugs were moistened with 2% sucrose solution to provide food for the parasites. Flasks were held under a 9-hour photophase at 25°C, alternated with a 15-hour scotophase at 7°C.

A pair (1 male-1 female) of *curculionis* adults was removed from a holding flask and isolated in each rearing unit with potential host larvae. After 24 hours the parasites were removed, and the alfalfa weevil larvae were dissected. By removing the larval head capsule and teasing the internal structures, the parasite eggs were liberated from the host's haemocoel. The white parasite eggs were easily located against the black background of the microscope stage. The number and condition of all eggs found were recorded for each alfalfa weevil larva.

The effect of host density, temperature, and parasite age on the reproductive potential of *curculionis* was determined by evaluating the following variables: 1) percent parasitism, 2) percent superparasitism, 3) eggs laid/female, and 4) eggs laid/larva parasitized.

The influence of host density was examined by isolating newly emerged larvae at densities of 5, 10, 20, 30, 50 or 100 per treatment. The weevil larvae were then allowed six to eight days to mature to late second or early third instars before exposing them to parasites. Five replications per host density were made using three-day old parasites, and a 20°C constant temperature was maintained during the 24-hour exposure period.

The effect of temperature was examined by isolating 50 newly emerged larvae at 10, 15, 20, 25 or 30°C for the 24-hour exposure period. Again the weevil larvae were allowed to mature for six to eight days before introducing the three-day old parasites, and five replications were made per treatment.

The influence of parasite age was examined by providing a newly emerged female with a new cohort of host larvae each day until the parasite died. In this study, each cohort started with 30 newly emerged larvae; they were then held six to eight days before introducing the parasites. Rearing units were held at a constant 20°C and contained a food supply and male parasites at all times. This study was replicated 10 times.

Two regression equations were calculated to evaluate the effect of host density on each of the four factors measured: a simple linear regression on host density and a regression on the log of host density. The effects of temperature and parasite age were evaluated using simple linear regression and a 2nd order polynomial. In each case we present only the equation which better fits the data.

RESULTS AND DISCUSSION

Host Density

Reproductive potential of parasitic Hymenoptera is affected by many factors, one of these being the availability of hosts to attack. Our results show that for *curculionis* nearly 100% of the host larvae were parasitized at the lowest densities, whereas at the higher densities tested, about 50% were parasitized (Fig. 1). This observation agrees with the generally accepted concept of low parasitism rates at high host populations and higher rates when host densities are lower. At the population level and under field conditions Clancy (1969) and Davis (1974) have observed an identical relationship between host density and percent parasitism.

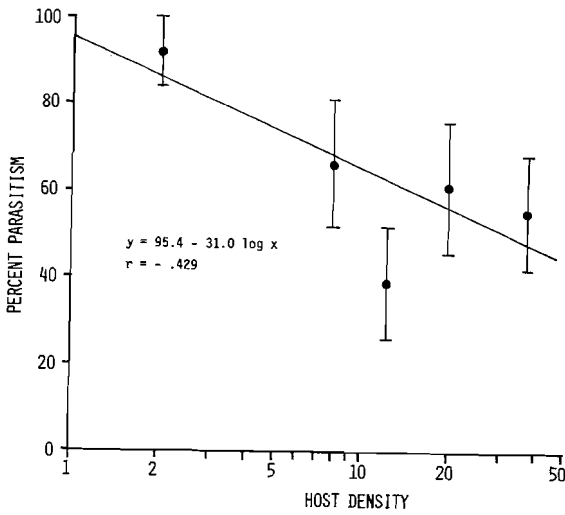


Fig. 1. Host density influence on percent parasitism by *B. curculionis* (points represent mean \pm one standard error for experiments with similar host densities).

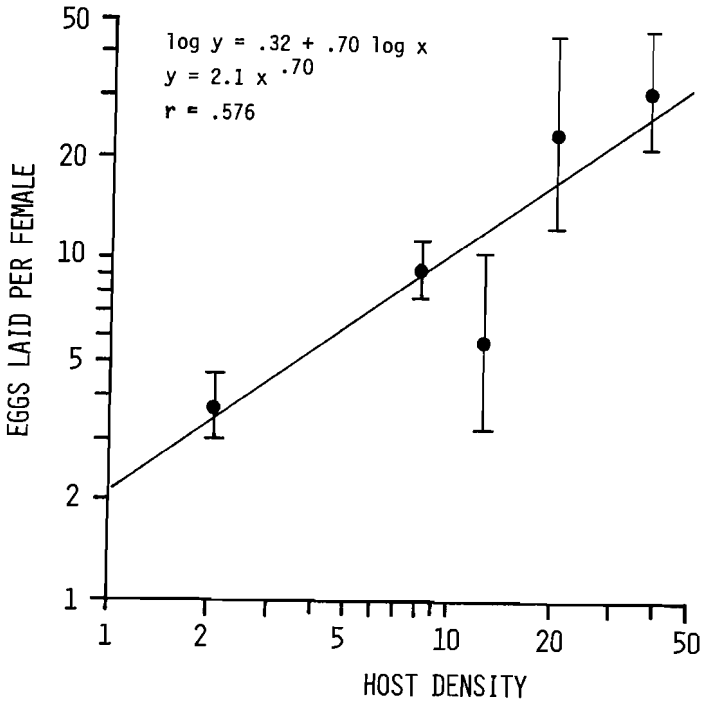


Fig. 2. Egg deposition by *B. curculionis* as a function of host density (points represent mean \pm one standard error for experiments with similar host densities).

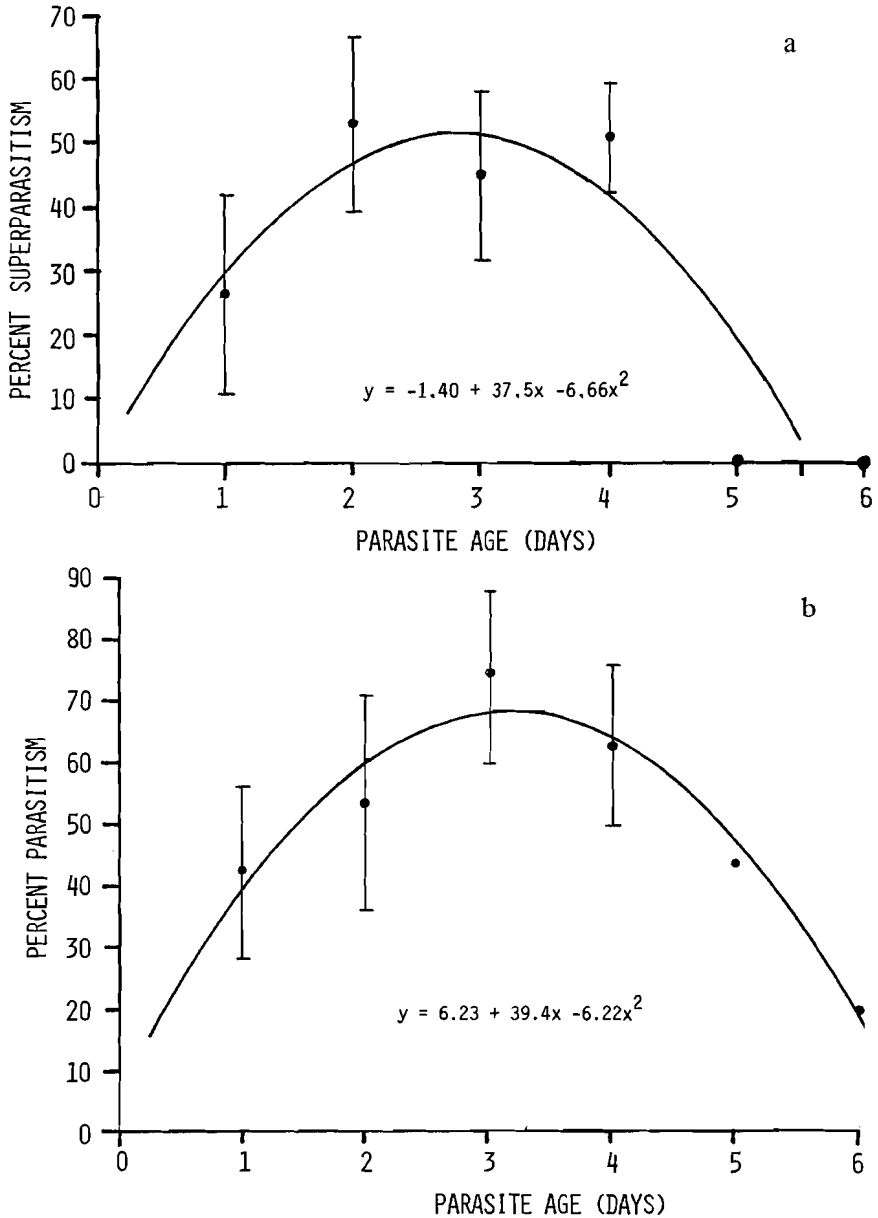
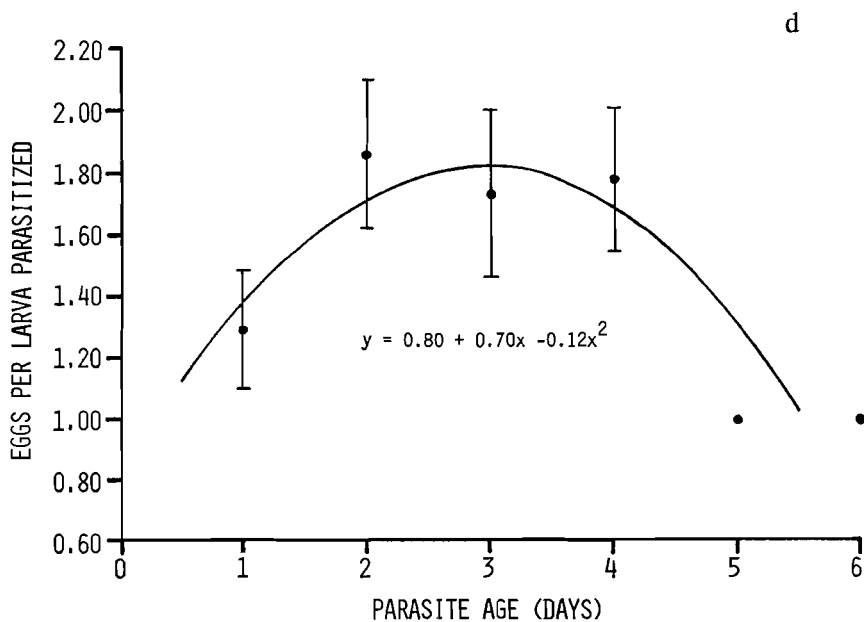
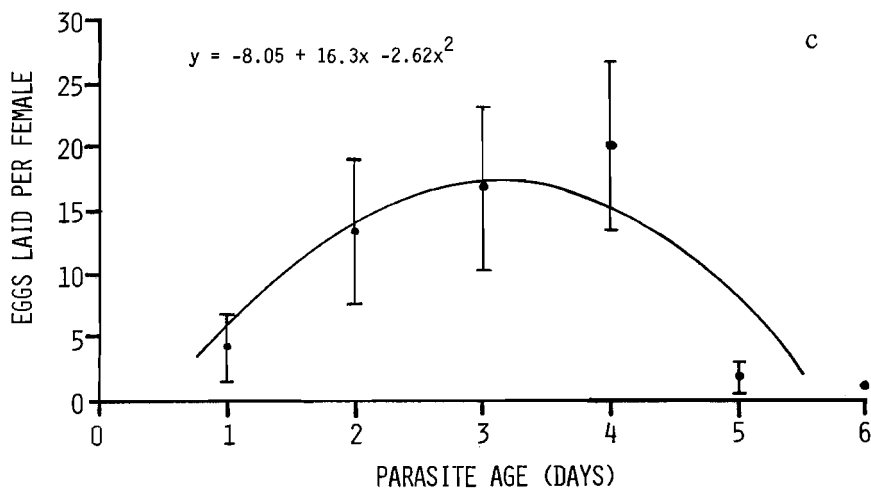


Fig. 3. Influence of parasite age on a) percent parasitism, b) percent superparasitism, c) eggs laid/female, and d) eggs/larva parasitized ($\bar{x} \pm SE$) showing peak oviposition at age three days.



Host availability also effects the number of eggs laid per female parasite. Population theory predicts an increase as host availability increases eventually approaching an upper limit corresponding to the potential of the parasite species. Our observations are summarized in Figure 2. Over the range of densities tested, there was a significant increase in the number of eggs laid per female, with little or no evidence that a maximum had been reached. Our experimental arena did not allow us to test host densities exceeding 50 per female parasite; thus we cannot say that the highest number of eggs per female found (98) is the maximum level. Dowell³ has dissected female *curculionis* and found that the number of available mature eggs seldom exceeds 140; thus we expect the eggs laid per female in 24 hours should not greatly exceed this number. Certainly the number of eggs laid cannot continue to increase as host availability climbs into the hundreds. At very high host densities the number of eggs laid per female must approach a limit, and therefore the straight lines shown in Figures 1 and 2 cannot be extrapolated to higher densities. Both lines must curve, with percent parasitism asymptotically approaching zero and eggs per female approaching the upper limit for the species.

Under our laboratory conditions, *curculionis* did not discriminate between previously parasitized hosts and unparasitized ones. Utilizing the equation given by Salt (1932) for calculating the expected random distribution of eggs among available hosts, we found that most female *curculionis* parasites distribute their eggs randomly. Those few parasites which departed from the random pattern tended to superparasitize their hosts rather than discriminate between parasitized and non-parasitized larvae. This observation does not agree with the conclusion by Hamlin et al. (1949) that this parasite can partially discriminate. Apparently that conclusion was based on counts of parasite eggs and larvae in field collected hosts. Since parasite larvae are known to eliminate supernumeries, Hamlin's technique would produce a biased count of singly parasitized hosts. This bias can only be avoided by excluding from the analysis those hosts containing parasite larvae. The situation is further complicated by the fact that in field populations not all hosts have been exposed to parasites for the same length of time. For example, a newly emerged first instar larva probably will not be parasitized even if the parasitism rate is high. An accurate interpretation of parasitism data gathered from field populations is probably impossible without models for the dynamics of both parasite and host populations.

The average number of eggs found in each parasitized larva was 2.32 and did not vary with host density. This supports Flanders' (1942) statement that for most parasitic Hymenoptera the number of eggs laid in each individual host is fairly constant and largely independent of host density.

The mortality of alfalfa weevil larvae in our rearing units increased significantly as host densities increased. This mortality was probably caused by exceeding the carrying capacity of the rearing units rather than from parasite ovipositional activity, as there was no significant difference in mortality between the controls and the units containing parasites. Duodu and Davis (1974) found that host mortality due to stings by *curculionis* is observable by the second day following parasitization, but we did not detect this phenomenon in our experiments, probably because our observations did not extend beyond 24 hours after parasitization.

Temperature

We found no statistically significant relationship between temperature and any of the biological responses we studied. A curvilinear relationship between temperature and egg deposition was expected, such as the one found by Force and Messenger (1964) for *Praon exsoletum* Nees (as *P. palitans* Muesebeck), a parasite of the spotted alfalfa aphid, *Therioaphis maculata* (Buckton), but no significant correlation was detected.

We conclude that for *curculionis* any temperature from 10° to 30°C is adequate for searching out hosts and ovipositing in them. We expect that temperatures below 10° would

³R. Dowell. 1975. Personal communication. Ohio State University.

reduce the searching and oviposition rates, but we do not have data to show this. We also expect that oogenesis and egg maturation with *curculionis* are significantly affected by temperature, but evaluating this hypothesis would require a quite different experimental design with adult parasites being held at the experimental temperatures from the time they are formed within the cocoon until host larvae are offered.

Parasite Age

We found the relationships of parasite age vs. percent parasitism, percent superparasitism, eggs laid/female, and eggs/larva parasitized to be very similar (Figs. 3a, b, c, and d). The peak egg laying rate was reached by the third day from which point it declined with increasing age. The average percent parasitism at age three days was $74.5 \pm 14.7\%$ ($\bar{x} \pm SE$).

Subba Rao et al. (1967) reported *curculionis* females parasitizing hosts within 48 hours of emergence. In our experiments we observed oviposition during the first 24 hours after emergence. *B. curculionis* probably can parasitize host larvae immediately upon emergence from the cocoon, but a day or two must pass before they reach their maximum egg laying potential. This is consistent with the report by Puttler and Coles (1962), in which they state that *Bathyplectes* (as *Biolysia*) *tristis* Gavenhorst, a parasite of the clover leaf weevil, *Hypera punctata* (Fabricius), emerges containing fully mature eggs in the oviducts and is capable of ovipositing almost immediately after emergence.

The average age at death of the adult female parasites exposed to larvae in our experiments was 4.8 ± 1.2 days ($\bar{x} \pm SD$), and for those not exposed to hosts it was 8.4 ± 3.8 days. The parasites not exposed to larvae were held under a fluctuating temperature regime. We do not know whether the action of searching for, handling, and stinging larvae shortened the life of the *curculionis* females, or whether there was an effect of constant versus fluctuating temperatures.

Subba Rao et al. (1967) estimated the longevity of adult *curculionis* as two to seven days, which compares well with our data. However, Richardson (1972) considered three to four weeks as the average longevity for *Bathyplectes* species. Supplemental feeding has been found to increase the life span and fecundity of some parasites (Leius, 1961a; 1961b; 1963), and although this may be an important factor in determining the longevity of *curculionis* females, it was not responsible for the short life span in our study. Our parasites were supplied with food as described earlier; still none approached three to four weeks of age.

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