

PREDATOR-PREY RELATIONSHIP OF GEOCORIS PUNCTIPES (SAY)
AND HELIOTHIS VIRESCENS (F.)

by

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ABSTRACT

Predator-prey relationships between Geocoris punctipes (Say) and Heliothis virescens (F.) were studied in the laboratory. G. punctipes nymphs were caged individually with H. virescens eggs or larvae. The primary objective of the study was to determine which stages of H. virescens were acceptable as prey for each nymphal instar of G. punctipes and how this predation affected the developmental rate and per cent survival of the predator's five instars.

In the feeding tests, first-instar G. punctipes nymphs were discovered to be almost exclusively egg predators. The last four G. punctipes instars fed on both eggs and small larvae. All predator stages attained a rate of survival of over 96% when they fed on eggs. When feeding on first-instar larvae, the rate of survival had a range of 5.6-69.0% for all G. punctipes instars.

Some major trends in the predation data were observed to be related to the developmental levels of the predator and the prey. When the developmental level of the prey increased, the per cent survival, the feeding rate and the developmental rate of the predator decreased. With an increase in the developmental level of the predator,

corresponding increases in per cent survival and feeding rates were observed.

INTRODUCTION

Members of the genus Geocoris have been reported as abundant insect predators in many cotton-growing areas of the United States. Geocoris punctipes (Say) is the most common species found in southern Arizona (Wene et al. 1965).

These predators are known to feed on several of the common arthropod pests of cotton. Their apparent effectiveness as natural control agents has been frequently reported in the results of large-scale field tests. Bell and Whitcomb (1964) studied the predation of Heliothis spp. eggs in Arkansas cotton fields. They determined that insect predators such as G. punctipes, that had piercing mouthparts, destroyed more eggs than did those predators with chewing mouthparts. In Arizona Heliothis virescens (F.) and H. zea (Boddie) are common insect pests of cotton. Past efforts to quantify the capabilities of G. punctipes to prey on these two pest species have been limited.

With the increasing concern over the environmental effects of heavy pesticide use, a greater need has developed for research into the practical applications of biological control. To intelligently implement biological control in a pest management system, a quantitative understanding of the existing predator-prey relationships is a basic prerequisite.

This study is concerned with the ability of G. punctipes nymphs to successfully feed on H. virescens eggs and larvae. The primary objectives proposed for this research were to determine (1) which stages of H. virescens were acceptable as prey to each nymphal instar of G. punctipes, (2) what number of individuals from each prey stage was consumed by each instar of G. punctipes nymphs, and (3) how did predation on the various prey stages affect the developmental rates of G. punctipes nymphs.

LITERATURE REVIEW

Geocoris spp.

Description

Most of the Lygaeidae are phytophagous insects. Sweet (1960) described seed feeding as the generalized and characteristic feeding habit of the Lygaeids. He also observed that Geocorinae was the only subfamily within this group known to be predaceous. Wene et al. (1965) stated that Geocoris punctipes (Say) was the most common Geocoris species found in Arizona. G. pallens Stal, G. atricolor Montandon and G. carinatus McAtee are also present. G. punctipes can generally be differentiated from these by its slightly larger size and its lighter color. The important distinguishing characteristics of G. punctipes were described by Torre-Bueno (1946). A fine longitudinal sulcus extends from the sulcus of the tylus onto the vertex. The head is smooth, polished and not granulose.

Geographical and Seasonal Distribution

Slater (1964) stated that within the United States G. punctipes has been recorded in Alabama, Arizona, Arkansas, California, Colorado, District of Columbia, Florida, Georgia, Hawaii, Illinois, Indiana, Louisiana, Maryland, Michigan,

Mississippi, Missouri, New Jersey, New Mexico, North Carolina, Oklahoma, South Carolina, Texas, and Virginia. The distribution of this species also includes the Bahama Islands, Colombia, Guatemala, the Johnson Islands, Mexico, and Panama.

In Arizona, several crops and weeds have been recorded as reservoirs for Geocoris spp. populations. Fye (1973) observed seasonal population levels of several Hemipteran predators (Geocoris, Nabis, Orius, Sinea, and Zelus) in Arizona's Avra Valley. He found large numbers of these predators on London Rocket (Sisymbrium irio L.) in January and February and on globemallow (Sphaeralcea spp.), wheat, barley and alfalfa in the spring months. Cotton, alfalfa and grain sorghum held large populations of these predators during the summer. Whitcomb and Bell (1964) observed that in Arkansas G. punctipes overwintered in alfalfa, winter grains and various dry grasses.

Wene and Sheets (1962) reported that in central Arizona cotton fields Geocoris spp. populations reached their highest peak in June. These population levels dropped drastically in July and continued to decrease during August. Fye (1971) also observed these population trends in Arizona. He noted that the sharp decline of the Geocoris spp. and other predator populations in mid-July immediately followed insecticide applications for control of the pink bollworm, Pectinophora gossypiella (Saunders). In the Coachella

Valley of California, Staten (1970) determined that G. punctipes was capable of maintaining relatively high populations in cotton until mid-October. This occurred in fields where insecticide use was either non-existent or limited to one application.

Importance of Geocoris spp. as a Predator

Bell and Whitcomb (1964) studied the predation of bollworm, Heliothis zea (Boddie), eggs in Arkansas cotton fields. They observed that insects with piercing mouthparts destroyed more eggs than did those with chewing mouthparts. G. punctipes and Orius insidiosus (Say) were the two predators with piercing mouthparts which predominated.

Field cage studies of Geocoris spp. have shown it to be an effective predator against both eggs and larvae of Heliothis spp. on cotton. Following the introduction of fresh tobacco budworm, H. virescens (F.), adults into field cages, Lingren, Ridgway, and Jones (1968) introduced G. punctipes adults at a rate equal to 252,000/acre. H. virescens eggs in predator-free cages reached a peak rate of 260,000/acre in 6 days following adult release. The larval counts reached 47,840/acre in 8 days. When compared to these check cages, G. punctipes reduced the egg populations about 51% by the 8th day. The larval populations were reduced 67% by the 13th day.

Predation of pink bollworm eggs by G. punctipes was investigated by Orphanides, Gonzalez, and Bartlett (1971). Small cards with attached pink bollworm eggs were placed within the bracts of bolls and squares on individually caged cotton plants. Five G. punctipes adults were maintained on each plant for 48 hours. In two series of tests G. punctipes reduced the number of eggs by 42.0% and 49.5%, respectively. It was also noted that G. punctipes adults had been observed to reach and destroy pink bollworm eggs which had been naturally oviposited beneath the calyx of the boll. In tests where freshly hatched first-instar pink bollworm larvae were confined in vials, G. punctipes was also observed to feed upon these larvae.

Clancy and Pierce (1966) reported that G. punctipes easily preyed upon early instars of Lygus spp. nymphs. G. punctipes also destroyed Lygus spp. eggs that had been oviposited in green beans. These were destroyed at a rate of 1.5-4.2 eggs per predator per day.

In addition to those prey species noted above, G. punctipes has been reported as a predator of the following arthropods: spider mites (McGregor and McDonough 1917, Reynolds and Swift 1951); larvae and pupae of the banded-wing whitefly, Trialeurodes abutilonea (Haldeman) (Dysart 1966); spotted alfalfa aphid, Therioaphis maculata (Buckton) (Nielson and Henderson 1959); adults and eggs of the beet leafhopper, Circulifer tenellus (Baker) (York 1944); flea

beetles, Epitrix parvula Fab. (Chamberlin and Tenhet 1923); and eggs of the tobacco hornworm, Manduca sexta (Johannson) (Gilmore 1936).

In a few cases Geocoris spp. have been reported as predators of other beneficial insects. Geocoris sp. predation was suspected by van den Bosch, Reynolds, and Dietrick (1956) as the cause of a decline in Orius sp. populations in cotton. Whitcomb and Bell (1964) stated that G. punctipes and G. uliginosus (Say) will attack O. insidiosus (Say) and O. tristicolor (White), although plant bugs are preferred, when they are in abundance. G. pallens was discovered to be predaceous upon two species of beneficial weevils (Microleptinus spp.), which were introduced to California to control the puncture vine, Tribulus terrestris L. (Goeden and Ricker 1967).

Staten (1970) established the role of G. punctipes as a pathogen vector. He determined that nymphs of this species were capable of transmitting the nuclear polyhedrosis virus of the cabbage looper, Trichoplusia ni (Hubner). The virus was transmitted to the T. ni larvae during non-fatal feeding attempts by the vector G. punctipes.

Geocoris spp. Feeding Habits

The apparent feeding upon plant tissue by Geocoris spp. was first clearly demonstrated by King and Cook (1932). They reported that such feeding on cotton plants yielded

"positive internal reactions" but "no external swelling or damage." York (1944) observed that feeding on both animal matter and plants or other water source was necessary for the survival of Geocoris spp. The longevity of Geocoris spp. held on sugar beet leaves was not greater than those supplied with water-soaked wicks alone. Therefore, it was also assumed that plant juices were taken for their moisture content only, and not for any nutritional value. Ridgway and Jones (1968) reported very similar results when they tested G. pallens on cotton plants. Using radio-labeled cotton terminals, they also discovered that the plant-feeding habits were not greatly affected by the introduction of prey material (Heliothis spp. eggs) to the plants.

Sweet (1960) and Stoner (1970) demonstrated that Geocoris spp. feeding on seeds only, such as sunflower seeds, had a much increased longevity when compared to those which fed only on leaves (York 1944, Ridgway and Jones 1968). Tamaki and Weeks (1972) observed G. pallens and G. bullatus (Say) feeding upon pea aphids, Acyrtosiphon pisum (Harris), with green plants provided as a moisture source. When sunflower seeds were added to the diet, it was noted that there was a shorter developmental time, higher egg production and a greater per cent survival. Stoner (1970) suggested that feeding on seeds might actually be for food rather than for moisture content. He also determined that although a diet including both prey and plant material appeared necessary

for complete development and adult fertility, G. punctipes nymphs can develop to some extent on plant foods only. In the event prey was in short supply, this ability to maintain itself temporarily on plant foods might allow G. punctipes to survive until prey was available again.

In contrast to the conclusions by York (1944) and Stoner (1970), Dunbar and Bacon (1972a) reared G. punctipes on animal food only. With a diet of only potato tuber moth, Phthorimaea operculella (Zeller), eggs, 57.4% of the nymphs survived to the adult stage. More than half of the resulting female adults produced viable eggs. It was noted that increased egg production and egg viability resulted when plant food (green beans) was added to this diet.

Ridgway et al. (1967) observed that Geocoris, Nabis and Orius were particularly affected by systemic insecticides. It was implied that the plant feeding habits of these Hemipteran predators were possibly the main mechanisms through which contact with these insecticides occurred. An inverse relationship between the predator and prey populations was apparent after the applications of systemic insecticides. Heliothis spp. infestation and damage levels increased as the populations of systemic-susceptible predators decreased.

Several studies have implied that the behavioral activity of potential prey affects its suitability as a food source for Geocoris spp. When Geocoris spp. feeding on

live beet leafhopper adults were also supplied with various dead insects, there was very little effect upon the rate at which living leafhoppers were consumed (York 1944). It was assumed then, that the predators preferred living prey. In tests with the pink bollworm, Orphanides et al. (1971) stated that G. punctipes and O. tristicolor preyed upon first-instar larvae in preference to the stationary egg stage. These preferences though, could be related to factors other than prey activity.

Butler (1967) observed that when G. punctipes adults were fed various instars of Lygus spp. nymphs; fewer of these were fed upon when older nymphs were provided. He determined that the larger nymphs were more difficult to subdue, therefore they were less frequently killed.

The most convincing evidence of suitability based on prey activity was reported by Dunbar and Bacon (1972a). They reared G. punctipes nymphs on eight different diets. A predator growth rate index based upon maturation time and adult weight was calculated for each of the eight diets. The four diets producing highest growth rates were those composed of insect eggs or dead larvae. Prey that were active or had defense behavior apparently were less suitable as food sources.

Consumption rate data for individual Geocoris sp., when fed Heliothis spp. eggs, were first obtained by Butler (1966a). He tested the first four nymphal instars and the

adults of G. punctipes for daily consumption rates of Heliothis spp. eggs. For the four instars the mean daily egg consumption per predator averaged 3.0, 2.7, 2.9, and 7.5, respectively. The adults were observed to consume an average of 36.2 eggs per predator per day.

Lingren et al. (1968) tested G. punctipes individual consumption on H. virescens and H. zea eggs and first-instar larvae. In small containers an average of 9.3 eggs/day were consumed by G. punctipes adult males, and 26.7 eggs/day were consumed by adult females. Consumption of first-instar larvae averaged 26.5 larvae/day for the males and 31.9 larvae/day for the females. In studies on cotton terminals, combinations of 20 Heliothis spp. eggs or larvae and 4 G. punctipes adults were placed on each terminal. On the terminals with eggs, 1.9 eggs were consumed per predator per day during the first two days. This resulted in a 78% total reduction of eggs. Larval predation was measured at 1.4 larvae consumed per predator per day for a 94% total reduction of larvae during the two-day period. In a four-day test period there was 98% reduction of eggs and 94% reduction of larvae.

Geocoris spp. Life History

The first complete study of the life history of G. punctipes was reported by Champlain and Sholdt (1967a). These Geocoris were reared at 25.5°C, about 50% RH and with

a 14 hr-light photoperiod. The predators fed upon killed larvae of the beet armyworm, Spodoptera exigua (Hübner), and green beans.

Duration of the egg incubation period averaged 9.9 days. About 25% mortality was recorded for this stage. Duration of the five nymphal instars in the females averaged 8.2, 5.2, 4.1, 4.1, and 6.1 days, respectively. The males averaged 7.6, 4.8, 4.1, 4.0, and 6.3 days, respectively. The total nymphal period was 27.7 days for the females and 26.8 days for the males. Mean adult longevity was measured at 67.7 days for the females and 41.5 days for the males. The preoviposition period averaged 5.2 days, and the mean egg-laying period was 30.8 days. Oviposition was measured at an average of 177.7 total eggs laid per female.

Dunbar (1972) observed G. punctipes mating behavior at 30°C, 60% RH and with 14 hr of light per day. He determined that the adult premating period was 2-5 days in females and 3-5 days in males. The preoviposition period had a duration of 3.6 days for mated females and 4.0 days for nonmated females. The period of oviposition averaged 62.1 days in mated females and resulted in an average of 496.5 total eggs laid per female.

Three major studies have dealt with the relationship of temperature to G. punctipes. Butler (1966b) reared G. punctipes on killed larvae of the beet armyworm, S. exigua, at 3 different temperature regimes and 15 hours of light

per day. Mean duration of the egg stage ranged from 5.8 days at 30°C to 17.9 days at 20°C. Mean duration of the nymphal stage was 21.3 days at 30°C and 54.2 days at 20°C.

Champlain and Sholdt (1967b) conducted tests under conditions similar to those of Butler, except that they employed a much broader range of temperatures. They determined that 10°C was below the developmental threshold for G. punctipes eggs, and only minimal developmental success occurred at 15°C. No successful hatching was observed at the high temperature of 40°C. The mean egg incubation time ranged from 5.0 days at 35°C to 16.0 days at 20°C. Successful nymphal development was recorded at temperatures from 20°C to 35°C with limited success at 40°C. Mean nymphal durations ranged from 17.8 days at 35°C to 53.9 days at 20°C.

Dunbar and Bacon (1972b) provided G. punctipes with potato tuber moth larvae and green beans at 14 hours of light per day. Their results agree with the developmental pattern observed by Champlain and Sholdt (1967b), except that they found no egg or nymphal development at the high temperature of 37.8°C. Observations of the effects on reproduction indicated that fecundity and fertility varied in direct relation to temperature. Fecundity ranged from 75.4 total eggs laid per female at 23.9°C to 200.8 total eggs laid per female at 32.3°C. Fertility evidenced a range of 19.9% hatched eggs at 23.9°C to 53.8% hatched eggs at 32.2°C.

Enemies of Geocoris spp.

Whitcomb and Bell (1964) reported that nymphal G. punctipes and G. uliginosus are preyed upon by all species of Nabis. Nymphal assassin bugs were observed to occasionally prey upon adult Geocoris spp. Champlain and Sholdt (1967b) observed that large nymphs of Lygus hesperus Knight can act as predators upon smaller nymphs of G. punctipes.

Several species of Geocoris have been observed to be parasitized by a Tachinid, Hyalomya aldrichii Townsend. Dunbar (1971) found 0.1% parasitization of Geocoris spp. females sampled in the San Joaquin and Sacramento Valleys of California. Clancy and Pierce (1966) reported 11.0% parasitization of Geocoris spp. adults in California's Coachella Valley.

Parasitization of Geocoris spp. eggs by a Scelionid, Telenomus sp., was reported by McGregor and McDonough (1917) and van den Bosch and Hagen (1966). Clancy and Pierce (1966) observed that Telenomus sp. near opacus (Howard) parasitized Geocoris spp. eggs collected from alfalfa in Yuma, Arizona and southern California. The percentage of parasitization ranged from 27 to 68%.

Heliothis spp.

Importance of Heliothis spp.

Two principal pests of cotton in the southwestern United States are the tobacco budworm, Heliothis virescens (F.), and the cotton bollworm, Heliothis zea (Boddie). Neunzig (1969) noted that these two species are found throughout most of the Western Hemisphere. He characterized H. virescens as a major pest of tobacco and cotton. Although he observed H. zea on 16 cultivated hosts in North Carolina, Neunzig reported that corn and cotton were the two primary hosts of this species. The presence of H. zea on such crops as alfalfa, soybeans, sorghum, okra, tomatoes and tobacco was termed as sporadic. Graham and Robertson (1970) reported that in Texas occasionally H. virescens was also found on okra, tomatoes and alfalfa, and H. zea was observed on lettuce.

Both species of Heliothis are known to have several wild hosts. Graham and Robertson (1970) found a few H. zea on burclover, Medicago hispida Baertn., and sunflower, Helianthus annuus L., in the spring. They observed both Heliothis species on a wild tobacco, Nicotiana repanda Willd., in the spring and on a passionflower vine, Passiflora foetida L., in the fall. Pigweed, Amaranthus spp., is known to be a wild host of H. zea in Arizona in the fall (Fye 1973). Snow and Brazzel (1965) in Mississippi found eleven

wild host species of H. virescens. They stated, that wild hosts were probably more vital to the biology of H. virescens than to that of H. zea.

Seasonal abundance of Heliothis spp. in cotton has been studied by Henry and Adkisson (1965) in Texas and by Snow (1964) in Georgia. They observed that H. virescens was the prominent species of Heliothis during June. By early- and mid-July H. zea was beginning to predominate, and it continued to increase throughout the season. The increase of the H. zea population within the cotton was credited to an immigration of this species from some of its alternate hosts, such as corn. In contrast, Cole, Adkisson, and Fye (1973) found no H. virescens in cotton until early July, although H. zea had been present since early June. The H. virescens population then rose to 50% of the total Heliothis population by the second week in August and up to 85% of the total by the second week in October.

Heliothis spp. Life History

Fye and McAda (1972) studied the life history of H. virescens in the laboratory. Larvae were reared on an artificial diet. A series of these insects was maintained at four different 24-hr temperature programs. These programs provided daily mean temperatures of 20, 25, 30, and 33°C, respectively. At the mean temperature of 25°C the durations of the five larval instars for the males were

3.5, 2.0, 2.0, 2.5, and 7.5 days, respectively. The five instars of females averaged 3.4, 2.0, 2.0, 2.5, and 7.2 days, respectively. Occasionally a few individuals required a sixth larval instar to complete development. Duration of the male pupae averaged 16.2 days, and that of the female averaged 14.8 days. The total larval-pupal periods averaged 33.9 days for the males and 32.2 days for the females. Adult total longevity was 19.6 days for the males and 20.7 days for the female. The minimum preoviposition period was 2 days, and by the fifth day of the adult stage most females had oviposited. Longer oviposition periods were prevalent in the cooler temperature regimes. The hotter temperatures reduced the fecundity. Fecundity for the four temperature programs ranged from a mean of 495 eggs per female at 33°C to 1626 eggs per female at 20°C. In the programmed 25°C regime, fecundity averaged a total of 963 eggs per female. Duration of the egg stage, based upon a constant temperature of 25°C, was approximately 3.1 days.

Neunzig (1969) studied the life history of H. virescens on tobacco in North Carolina. He determined that during mid-summer a minimum developmental time of 17-18 days for the larval period and 15-16 days for the prepupal and pupal period was required. During the earlier months of May and June the larval period was increased by 3-4 days, and the prepupal and pupal period averaged about 17 days. The developmental time required during August and September

was extended considerably beyond that of even the early season individuals. Both H. virescens and H. zea were observed to have a total of four generations per year on all hosts combined. In Mississippi, Snow and Brazzel (1965) reported five generations per year for H. virescens. Wene et al. (1965) indicated that H. zea passed through 6-8 generations per year in Arizona.

Enemies of Heliothis spp.

Lingren et al. (1968) listed several major insect predators of Heliothis spp. eggs and small larvae. These included Chrysopa, Nabis, Geocoris, Orius, Collops, Zelus, Hippodamia and Scymnus. Whitcomb and Bell (1964) listed about 600 species of predaceous arthropods associated with cotton. In addition to those named above, they listed many species of spiders, ants, mites, several beetles and a few Dipterans and Orthopterans as predators of Heliothis spp. All stages of Heliothis spp. were observed to be attacked by at least a few of these predators.

Parasites of Heliothis spp. have been observed by Lewis and Brazzel (1968). Two Braconids were the predominant species in Mississippi. Microplitis croceipes (Cresson) parasitized both Heliothis species, and Cardiochiles nigriceps Viereck was a successful parasite of H. virescens only. One other Braconid and a few species of Ichneumonidae and Tachinidae were also identified as

Heliothis spp. parasites. Six families of egg and larval parasites of H. zea in California were listed by van den Bosch and Hagen (1966).

METHODS AND MATERIALS

Source of Insects

Sweep-net collections for Geocoris spp. adults were made in alfalfa fields near Tucson, Arizona in August, 1972 and June, 1973. The preliminary determination of species in the field was based upon the generally lighter color and larger size of G. punctipes in relation to the other Geocoris species present. Subsequently a more precise identification was obtained in the laboratory using the characteristics described by Torre-Bueno (1946). The primary distinguishing feature of G. punctipes is a dorsal longitudinal sulcus extending posteriorly from the most anterior portion of the head onto the vertex.

A stock culture of H. virescens was developed from eggs and larvae collected from cotton near La Palma, Arizona during July and August of 1972 and 1973. Field-collected Heliothis spp. were reared individually, and the resulting adults were differentiated by the characteristic striped pattern and green color of the wings of H. virescens.

Rearing of Geocoris punctipes

Rearing cabinets used for the G. punctipes stock culture consisted of converted refrigerators. The culture

was maintained at $26.1 \pm 2.3^{\circ}\text{C}$ (mean \pm standard deviation) and $46 \pm 14\%$ RH. Fluorescent lights were used to provide 15 hr light/day.

The G. punctipes adults were caged in transparent plastic storage boxes (34.6 x 27.0 x 8.7 cm). Five 1.6 cm diam holes were bored into each of the two longest sides of each box. Trays to hold food and oviposition substrate were positioned in each of these holes. The trays were constructed from 7 cm sections of rigid plastic tubing (1.4 cm diam) which had been cut in half longitudinally. Each concave half was attached at one end to a cork stopper, and the opposite end was inserted through the cage wall to form an interiorly projecting tray.

Five trays in each adult cage were used to hold the food for the predators. This consisted of fifth-instar H. virescens larvae that had been killed by placing them in hot tap water (about 60°C) for 15-20 seconds. One or two larvae were placed in each tray. Fresh larvae were provided every two days.

Distilled water served as the moisture source for the predators. A reservoir was constructed from a glass vial, stoppered with a cotton dental wick, and mounted in an inverted position in the roof of the adult cage.

The five remaining trays in each cage were filled with loosely packed cotton lint as oviposition sites. Preliminary investigations showed agreement with the

findings of Champlain and Sholdt (1966), which described cotton lint as a readily acceptable oviposition substrate for G. punctipes females. The cotton was replaced at 3-day intervals, and the egg-laden cotton from each cage was placed in a 9.0 cm plastic petri dish.

The G. punctipes eggs hatched after a total incubation period of 7-8 days. Freshly-hatched nymphs were aspirated daily from the petri dishes and deposited in 1/2-pint mason jars. Generally, only those nymphs hatching within one 24-hr period were placed in each jar. The mouth of the jar was covered by a 7.0 cm diam piece of filter paper, which was held in place by the lid ring. Nymphs also received killed late-instar H. virescens larvae as food. The moisture source in each of the nymph jars was supplied by a cotton dental wick positioned at the bottom of the jar. The wick was soaked daily with distilled water. A folded piece of 9.0 cm diam filter paper was also placed in each jar to increase the surface area upon which the nymphs moved, and to provide a site upon which exuviae were shed during the molting process. After an average of about 21 days in the nymphal stages, the final molt to the adult stage occurred. The new adults were then removed from the jars with an aspirator and introduced into an adult cage.

When large numbers of a particular nymphal instar were needed for testing purposes, the nymphs in the stock culture were lightly dusted with Day-Glo® fluorescent

powder. Using different colors of powder provided an efficient method of differentiating between the various instars, and also determining those individuals which had recently molted. After molting, a nymph was either introduced into a test situation, or was dusted with a new color and placed in a rearing jar for the next nymphal stage.

Although no adverse effects were apparent with light applications of this dust, it was used only intermittently when large numbers of certain instars were to be removed from the stock culture. No dusting was used in any of the actual test situations.

No plant material was ever supplied to G. punctipes in stock culture or in feeding tests. The distilled water available in the cotton wicks was the only moisture source provided. The colony was maintained on killed larvae and free water for more than two years with no apparent decline in the vitality of the culture.

Rearing of Heliothis virescens

The larval stages of the H. virescens stock culture were maintained in a walk-in style, temperature-controlled chamber at $27.4 \pm 0.5^{\circ}\text{C}$ and $64 \pm 13\%$ RH. A 15-hr photoperiod was provided by fluorescent lights. All other stages of the H. virescens culture were held in the open laboratory, which maintained temperatures between 22 and 27°C .

The basic rearing procedures used for H. virescens were adapted from those described by Patana (1969). Adults were caged in one-gallon, wide-mouth glass jars. Two strips of paper towelling extending down the inside walls of the jar and a circular piece of towelling covering the mouth of the jar served as oviposition sites. An inverted glass vial protruding through the top sheet of towelling was utilized as a dispenser for a 5% sugar solution fed to the moths.

At two- or three-day intervals the sections of towelling containing eggs were removed from the jars. Eggs were surface sterilized by washing them in a 0.3% solution of sodium hypochlorite, rinsing in 10% sodium thiosulfate and rinsing finally in distilled water (Ignoffo 1963). Washed egg sheets were allowed to air dry, and then placed in clean one-gallon glass jars until hatching.

Freshly-hatched first-instar larvae were removed daily from the egg sheet jars. Camel's hair brushes were used to transfer them to the larval rearing cups. These one-ounce plastic cups were half filled with an artificial lima bean diet (Patana 1969). The cups were closed with cardboard tab lids. Several larvae were introduced into each cup initially. During the third-instar stage the larvae were separated into individual cups. After pupation the pupae were removed from their cells within the diet and placed in one-gallon jars to await adult emergence.

Feeding and Development Tests

The primary objective of this study was to determine which stages of H. virescens could be fed upon and destroyed by G. punctipes, and how this feeding affected the developmental rate and per cent survival of the predator. The basic procedure involved feeding several H. virescens of one stage to individual G. punctipes first-instar nymphs. These nymphs were maintained on this prey until they developed to the adult stage or until their death prior to that time. Feeding and developmental data were recorded for all five instars of these nymphs. After successful completion of this portion of the tests, the next larger stage of H. virescens was fed to a new group of first-instar G. punctipes. These nymphal predators were allowed to feed on this prey and develop to the adult stage if possible.

In feeding tests on H. virescens eggs, a very high percentage of the predators survived through all five developmental stages. However, when first-instar G. punctipes were fed H. virescens first-instar larvae, none of the predators survived beyond the second instar. The testing procedure was then modified for all tests in which larvae were the prey. After the testing of first-instar G. punctipes, second-instar nymphs were taken fresh from the stock culture and tested on the same H. virescens larval stage. These nymphs were also allowed to develop to the oldest stage possible. This procedure was repeated for

third-, fourth- and fifth-instar G. punctipes. Feeding tests with second- and third-instar H. virescens as prey continued this schedule of introducing individuals of all five instars of G. punctipes to a test and monitoring them through the remainder of their nymphal life.

All tests were maintained in a temperature-controlled cabinet at $26.1 \pm 1.4^{\circ}\text{C}$ and $52 \pm 11\%$ RH. Fluorescent lights provided 15 hours of light/day.

Cages used in the tests consisted of the upper halves of 10 cm diam glass petri dishes, which were inverted, and the opening on each dish was covered with a transparent plastic lid. The lid, the type found on 1 lb. coffee cans, provided a tight seal with the lip of the glass dish. For ventilation an 8 mm diam hole was bored into each lid and covered with fine mesh nylon organdy.

In the egg predation tests, a first-instar G. punctipes, less than six hours old, was placed into each cage. A cotton dental wick, soaked daily with distilled water, served as the moisture source. Based on data from preliminary tests, each nymph was supplied daily with unwashed H. virescens eggs in excess of the number on which it would feed within a 24-hr period. Egg oviposition sheets from the H. virescens stock culture were removed daily for the purposes of this test. The one-day old eggs on these sheets were first examined under a stereomicroscope to discover any obvious damage that had resulted from handling

or from cannibalism by stray H. virescens first-instar larvae in the adult jars. Sections of the egg sheets, each containing the G. punctipes nymph's daily supply of apparently healthy eggs, were then cut out from the sheets and placed into each individual test cage. No previously damaged eggs were allowed to remain on these test sheets. The number of eggs/day supplied to each nymph is presented in Table 1.

Table 1. Number of each Heliothis virescens stage presented daily to each Geocoris punctipes nymph in all predator-prey combinations.

<u>Geocoris</u> <u>instars</u>	<u>Heliothis</u> stages			
	Eggs	1st instar	2nd instar	3rd instar
1st	20	6	4	3
2nd	20	6	4	3
3rd	30	8	4	3
4th	30	12	4	3
5th	40	16	4	3

At 24-hr intervals the egg sheets were replaced in each cage. The eggs were then examined under a stereomicroscope for visible damage. Initially an attempt was made to classify damage into the categories of partially

collapsed eggs, completely collapsed eggs and undamaged eggs. To determine the accuracy of this evaluation, eggs from these three groups were randomly selected and were cut out individually from the egg sheets. Each egg was held in a 5 cm diam plastic petri dish until the per cent hatch could be determined.

In the tests of predation on larvae the cages were the same as those used in the previous tests. To reduce the amount of larval cannibalism present, H. virescens lima bean diet was added to the cage. Approximately a 10 mm layer of the hot diet was poured into the dish and allowed to cool and solidify before use in the test. About a fourth of the diet was cut out and removed from one side of the dish to provide a place for the water-soaked cotton wick.

All G. punctipes used in these tests were introduced into individual cages within six hours following the previous molt. During the test no dusting with fluorescent powder was used. Determining nymphal molts was based entirely upon the presence of the exuviae.

Each nymph was given a daily supply of H. virescens larvae in excess of its feeding capacity. The number of larvae placed in each predator cage daily is presented in Table 1. Each cage was checked at approximately 24-hr intervals. The difference between the original number of larvae in the cage and the number of live larvae remaining after 24 hours was recorded as the number killed by the

G. punctipes nymph. All live larvae and larval corpses were removed daily, and a new supply of larvae was introduced. This helped to maintain a constant number of prey of a uniform age group.

Young first-instar H. virescens larvae taken directly from the egg hatching jar and placed in the test were found to have a higher rate of cannibalism than those which had been allowed to feed on the stock culture diet for at least one day. Therefore, in tests in which first-instar larvae were the prey, only 1-2 day old individuals were used.

To determine the prevailing levels of natural mortality of the H. virescens larvae, identical test cages were set up without the presence of any G. punctipes nymphs. For each combination of larval instar and number of larvae per cage used in the feeding tests, 20 "Geocoris-free" cages were tested. Each cage was tested for five days, and the larvae were replaced daily as in the feeding tests.

Because of the plant feeding habits of Geocoris spp., it was desirable to know if the presence of the H. virescens lima bean diet in these tests was providing any significant nutritional benefit to the nymphs. Starvation tests on all G. punctipes nymphal instars were designed to measure the longevity of the predators when fed lima bean diet and water or water alone. Individual nymphs were caged in one-ounce transparent plastic cups with cardboard tab lids. Each cup contained a cotton dental wick, which was soaked daily with

distilled water. Half the cups were also about 1/4-filled with lima bean diet. Daily checks of the cups were made to determine the occurrence of mortality and possible molting.

Data Analysis

The mean (\bar{x}) and the standard error ($s_{\bar{x}}$) of the mean were calculated for developmental rates, feeding rates and natural prey mortality. Determining the presence of significant differences between means was accomplished through the use of t tests and Student-Newman-Keuls' multiple range test. Significance was evaluated at the 0.05 level throughout all analyses. Statistical calculations were performed according to the procedures as described by Steel and Torrie (1960).

Feeding and developmental rate data for each G. punctipes instar was based on all individuals successfully completing that instar. Successful completion was defined as development through an instar concluding with a complete molt into the subsequent stage.

Nymphs that died with the first 24-hr period after introduction into a predation test were not included in the analyses of mortality and survival rate. Death during this time was attributed to injury resulting from handling. Dunbar and Bacon (1972a) followed this procedure. They stated that death of G. punctipes during this period would not be caused by absence of the nutritive value of food,

because they found that nymphs could survive for about one day without any animal or plant food.

In analyzing the developmental rate and feeding data for tests on the predation of larvae, it was realized that the level of complexity of the data was possibly greater than merely a single set of values for each predator instar. It was considered a possibility that those G. punctipes nymphs which survived on a certain larval prey until reaching the adult stage might have significantly different values from those nymphs that may have completed a given instar but subsequently died before completing nymphal development (e.g., a fourth-instar nymph may have survived successfully to the adult stage, while another fourth-instar, feeding on the same prey, may have completed the fourth-instar but died during the fifth-instar). This aspect was tested in all applicable cases where sample size was sufficient. No significant difference was ever found between the two groups at the 0.05 level (Student-Newman-Keuls' test). Therefore, no segregation of these groups of data was included in the final analysis.

It was also initially theorized that those nymphs initiated into the test at a later instar might have values significantly different from those of nymphs initiated into the test in an earlier instar (e.g., when examining the data for all fifth-instar feeding on a certain prey, those nymphs which were initiated into the test as fifth-instars might

have values significantly different from those of the nymphs initiated into the test as third instars). In only one combination of predator and prey stages was a significant difference found at the 0.05 level (Student-Newman-Keuls' test).

Significantly different values between males and females were discovered in only two predator-prey combinations. Analysis of such significantly different components within a single G. punctipes instar are detailed where appropriate in the results of this report.

RESULTS AND DISCUSSION

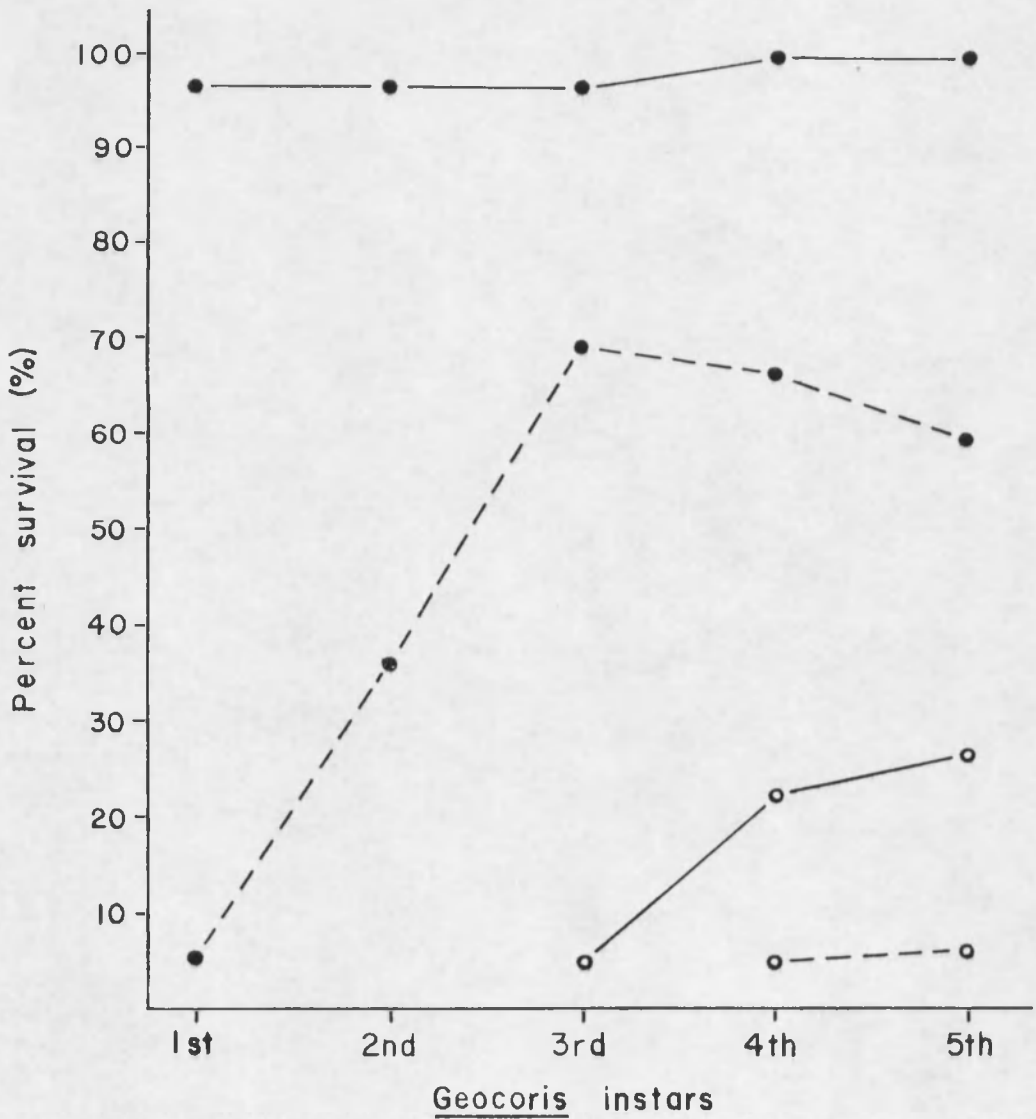
Rate of Survival

Table 2 details the per cent of G. punctipes nymphs completing each instar for all predator-prey combinations tested. It is evident, that for each G. punctipes instar, the per cent survival decreased as the developmental level of the prey increased. In contrast, the per cent survival increased as the predator's developmental level increased. Fourth- and fifth-instar G. punctipes generally had the highest survival records on all four prey stages tested. Predator-prey combinations resulting in no G. punctipes nymph completing the instar were those in which the greatest disparity in size favoring the prey existed. First- and second-instar nymphs were not able to complete their respective instars when second- or third-instar H. virescens larvae were provided as food.

The distinctly different rates of survival derived from feeding on the various prey stages is demonstrated in Figure 1. This graph is similarly based upon the per cent of G. punctipes successfully completing each particular instar. Figure 2 presents the per cent survival based upon the number of individuals in each instar which subsequently completed development to the adult stage. With the second type of analysis there is a much greater separation of

Table 2. Per cent survival of each Geocoris punctipes instar when feeding on the various stages of Heliothis virescens.

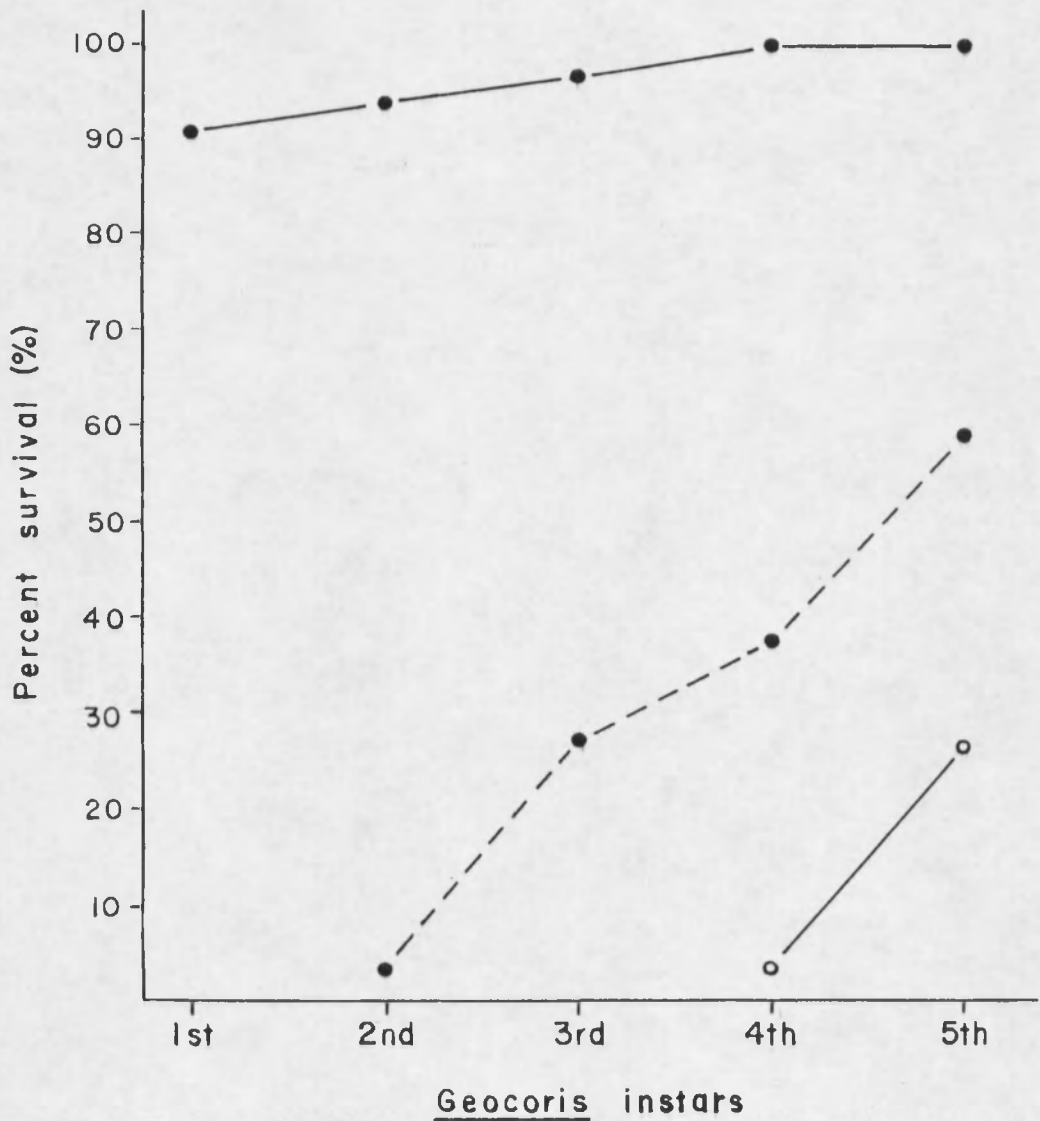
<u>Geocoris</u> instars	<u>Heliothis</u> stages	No. <u>Geocoris</u>	No. completing each instar	Per cent survival
1st	eggs	34	33	97.1
2nd		33	32	97.0
3rd		32	31	96.9
4th		31	31	100.0
5th		31	31	100.0
1st	1st instar	18	1	5.6
2nd		33	12	36.4
3rd		58	40	69.0
4th		72	48	66.7
5th		88	52	59.1
1st	2nd instar	10	0	0.0
2nd		10	0	0.0
3rd		20	1	5.0
4th		31	7	22.6
5th		37	10	27.0
1st	3rd instar	10	0	0.0
2nd		10	0	0.0
3rd		10	0	0.0
4th		20	1	5.0
5th		31	2	6.5



Heliothis stages:

- | | | | |
|---------|------------|---------|------------|
| ●—● | egg | ○—○ | 2nd instar |
| ●- - -● | 1st instar | ○- - -○ | 3rd instar |

Figure 1. Mean per cent survival through each instar of *Geocoris punctipes* when feeding on various stages of *Heliothis virescens*.



Heliothis stages :

● ——— ● egg ○ ——— ○ 2nd instar
 ● - - - ● 1st instar

Figure 2. Mean per cent survival to the adult stage by each instar of Geocoris punctipes when feeding on various stages of Heliothis virescens.

survival success between feeding on H. virescens eggs and feeding on H. virescens larvae. While feeding on eggs, the per cent survival to adult was relatively the same as the survival rates recorded for completing each instar. When feeding on larvae, the G. punctipes nymphs' per cent survival to adult was considerably less than the survival through individual instars.

In addition to the data presented in Figure 2, two fifth-instar nymphs feeding on third-instar larvae completed development to the adult stage. No individuals from earlier G. punctipes instars were capable of surviving to the adult stage, while feeding on H. virescens third-instar larvae.

In preliminary testing, one female G. punctipes fifth-instar feeding on H. virescens fourth-instar larvae survived and subsequently molted into the adult stage. This was the only successful feeding observed on H. virescens fourth-instars. Because of these observations and the low survival rate previously determined for feeding on the smaller third-instars, it is assumed that successful predation of H. virescens fourth instars by G. punctipes nymphs occurs only rarely.

During predation tests in which H. virescens larvae were the intended prey, the larvae were occasionally observed feeding on the G. punctipes nymphs. No larval attack on G. punctipes was observed, therefore it is not

known if the larvae actually killed the nymphs. It is possible that the larvae fed on the corpses of G. punctipes after they had died from other causes. However, because of the cannibalism observed among H. virescens larvae, the possibility of such aggression against G. punctipes can not be eliminated.

Evidence of feeding on the G. punctipes nymphs by H. virescens larvae was present only in the tests with second- and third-instar larvae. Such feeding by these two larval stages was found in a range of 10-47% of all G. punctipes fatalities.

The effect of predator and prey size differences should be considered as a possible cause of the above results. The differing levels of activity of the prey are also possibly related causes. G. punctipes predation on eggs, which are a stationary, non-defensive form of prey, resulted in a very high predator survival rate. This rate dropped drastically when G. punctipes was provided only the active defensive larvae as prey. As the developmental level of the larvae increased, the G. punctipes rate of survival decreased, and the level of prey feeding on G. punctipes nymphs increased.

With the existence of these broadly ranging survival rates, analyses of the feeding and developmental rates of the G. punctipes nymphs were limited to those predator-prey combinations in which a sufficient sample size was

available. Such combinations were defined as those with ten or more test individuals completing their respective instars.

Predator Feeding

Initially, H. virescens eggs which had been subjected to G. punctipes feeding tests were categorized as either partially collapsed, completely collapsed or undamaged eggs. Tests were set up to determine the accuracy of this damage evaluation method. No significant difference was found at the 0.05 level (t test) between the per cent hatch of the partially collapsed eggs (n = 240) and the per cent hatch of the completely collapsed eggs (n = 250). Therefore, all egg consumption data are based on the total number of damaged eggs. The mean per cent hatch for all eggs which were visually determined to be damaged (n = 490) was found to be 3.1%. Eggs described as undamaged showed a mean per cent hatch of 94.8%.

The levels of natural mortality of H. virescens larvae are reported in Table 3. These data are based upon observations from the Geocoris-free cages. A large portion of this natural mortality appeared to be the result of larval cannibalism. In analyzing the feeding data of G. punctipes no attempt has been made to correct for this natural prey mortality. G. punctipes nymphs were often observed feeding on larval remains which had obviously been killed by H.

Table 3. Natural mortality of Heliothis virescens larvae.

<u>Heliothis</u> instars	Larval density (No./cage/day)	Mean daily mortality per cage
1st	6	0.4 ± 0.13 ^a
	8	0.5 ± 0.11
	12	1.3 ± 0.26
	16	1.2 ± 0.19
2nd	4	0.7 ± 0.08
3rd	3	0.2 ± 0.05

^aMean ± standard error of the mean.

virescens cannibalism. Because these predators are very easily reared in laboratory cultures with killed larvae as a food source, it is logical to assume that they can act as scavengers in this situation. This is especially probable if the only live prey available are those with strong defensive behavior. If a G. punctipes nymph can partially satiate its desire to feed by scavenging on cannibalized larvae, then the amount of predation on live prey will probably be affected. Therefore, to correct for natural prey mortality would considerably minimize estimates of G. punctipes feeding capabilities.

The amount that G. punctipes fed upon each prey individual varied slightly. Usually the prey body was greatly shrunken and most of the body fluids had been drained from it during the G. punctipes feeding. Occasionally the nymphs fatally injured the prey, but did not completely suck all fluids from the egg or larva. The term, "number of prey consumed," which is used in the following analysis of the feeding data, refers to all prey fed upon and killed by G. punctipes, although in some cases the actual physical consumption of the prey was not complete.

Table 4 presents the average number of H. virescens individuals consumed per G. punctipes nymph per day. The daily rate of prey consumed increased steadily with the successive instars of the predator. This trend was evident for feeding on both eggs and larvae and is clearly illustrated in Figure 3. As the size and developmental level of the prey increased, the number consumed by the predator decreased. In the fifth-instar of G. punctipes, comparison of feeding on larval forms is possible. The number of third-instar H. virescens consumed was significantly less (at the 0.05 level, t test) than the number of second-instars consumed.

The average number of H. virescens consumed by each G. punctipes nymph during each instar is reported in Table 5. The general trends seen in the daily consumption data are manifested also in these data for the total

Table 4. Average number of Heliothis virescens individuals consumed per predator per day for the various instars of Geocoris punctipes.

<u>Geocoris</u> <u>instars</u>	<u>Heliothis</u> stages		
	Eggs	1st instar	2nd instar
1st	2.5 ± 0.15 ^a	--	--
2nd	3.7 ± 0.28	0.8 ± 0.15	--
3rd	6.4 ± 0.40	1.4 ± 0.09	--
4th	10.0 ± 0.46	3.2 ± 0.14	--
5th	11.6 ± 0.41	5.6 ± 0.21	1.8 ± 0.18

^aMean ± standard error of the mean.

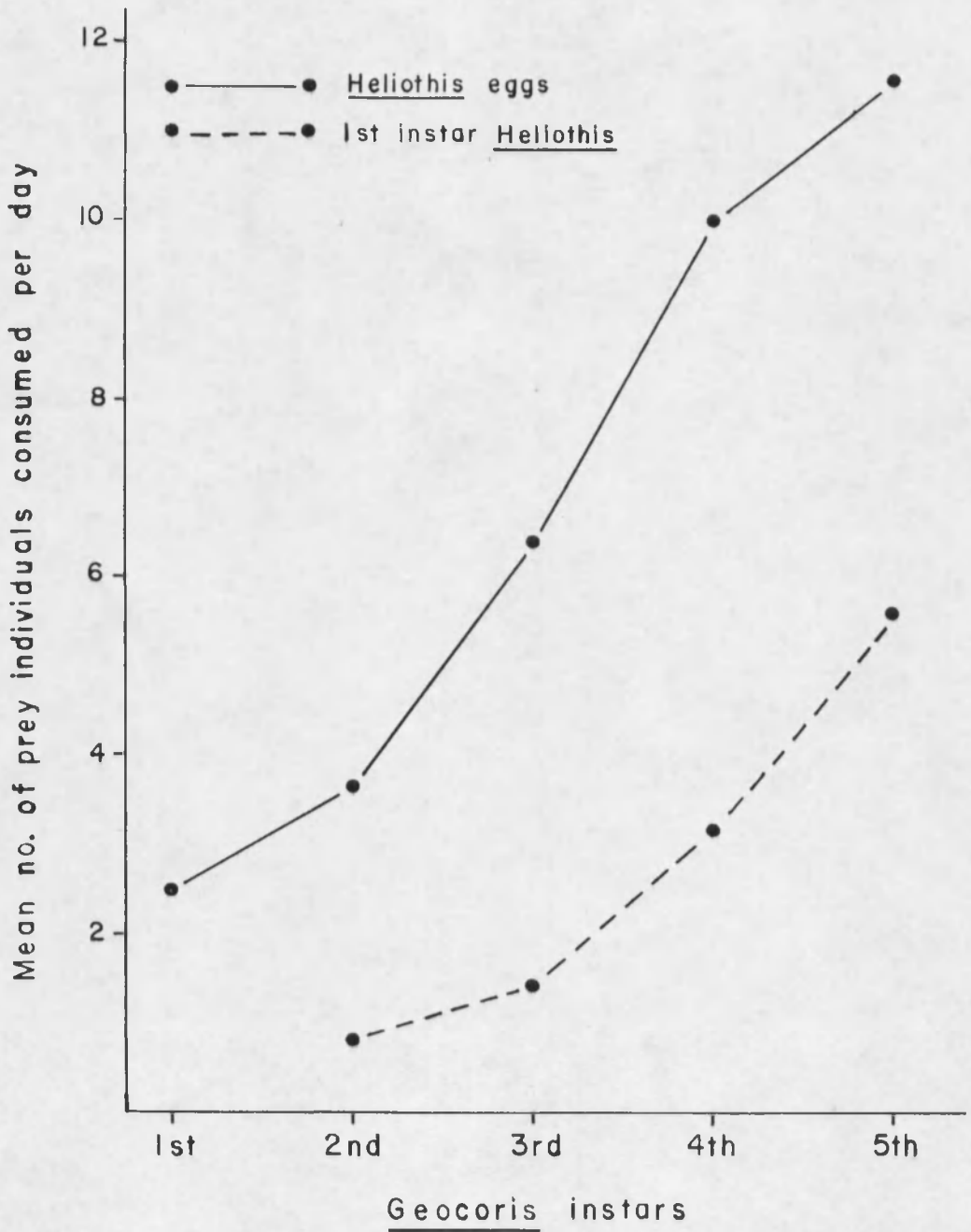


Figure 3. Average daily consumption of Heliothis virescens eggs and larvae by Geocoris punctipes nymphs.

Table 5. Average number of Heliothis virescens individuals consumed per predator during each instar of Geocoris punctipes.

<u>Geocoris</u> instars	<u>Heliothis</u> stages		
	Eggs	1st instar	2nd instar
1st	11.6 \pm 0.82 ^a	--	--
2nd	12.8 \pm 1.03	5.5 \pm 0.98	--
3rd	23.1 \pm 1.68	8.0 \pm 0.54	--
4th	38.8 \pm 2.29	19.2 \pm 0.87	--
5th	64.4 \pm 2.03	43.8 \pm 1.69	14.3 \pm 1.35

^aMean \pm standard error of the mean.

nymphal instar periods. A rapid increase in consumption of prey was again evident with each increase in the developmental level of G. punctipes. In egg predation by the last four instars of G. punctipes, the rate of feeding increased by a factor of about two-thirds with each successive instar. Feeding on H. virescens first-instar larvae was more than doubled by each successive step through the third-, fourth- and fifth-instars of G. punctipes. These increasing feeding rates of each nymphal instar are depicted in Figure 4.

Total consumption of each H. virescens stage during G. punctipes nymphal development is summarized in Figure 5. Considering only the number of prey consumed, the most effective predation by G. punctipes occurred on H. virescens eggs. All five nymphal instars were capable of feeding on the eggs. The mean number of eggs consumed during G. punctipes development extended to 150.7 eggs. With only the last four G. punctipes instars feeding on first-instar H. virescens larvae, a mean total of 76.5 of this prey stage was consumed.

The presence of the lima bean diet in test cages containing H. virescens larvae, appeared to have no effect on the longevity of G. punctipes nymphs. The starvation tests conducted on individual nymphs determined the longevity of G. punctipes nymphs that were given lima bean diet and water and the longevity of those that were given only water. No significant difference at the 0.05 level

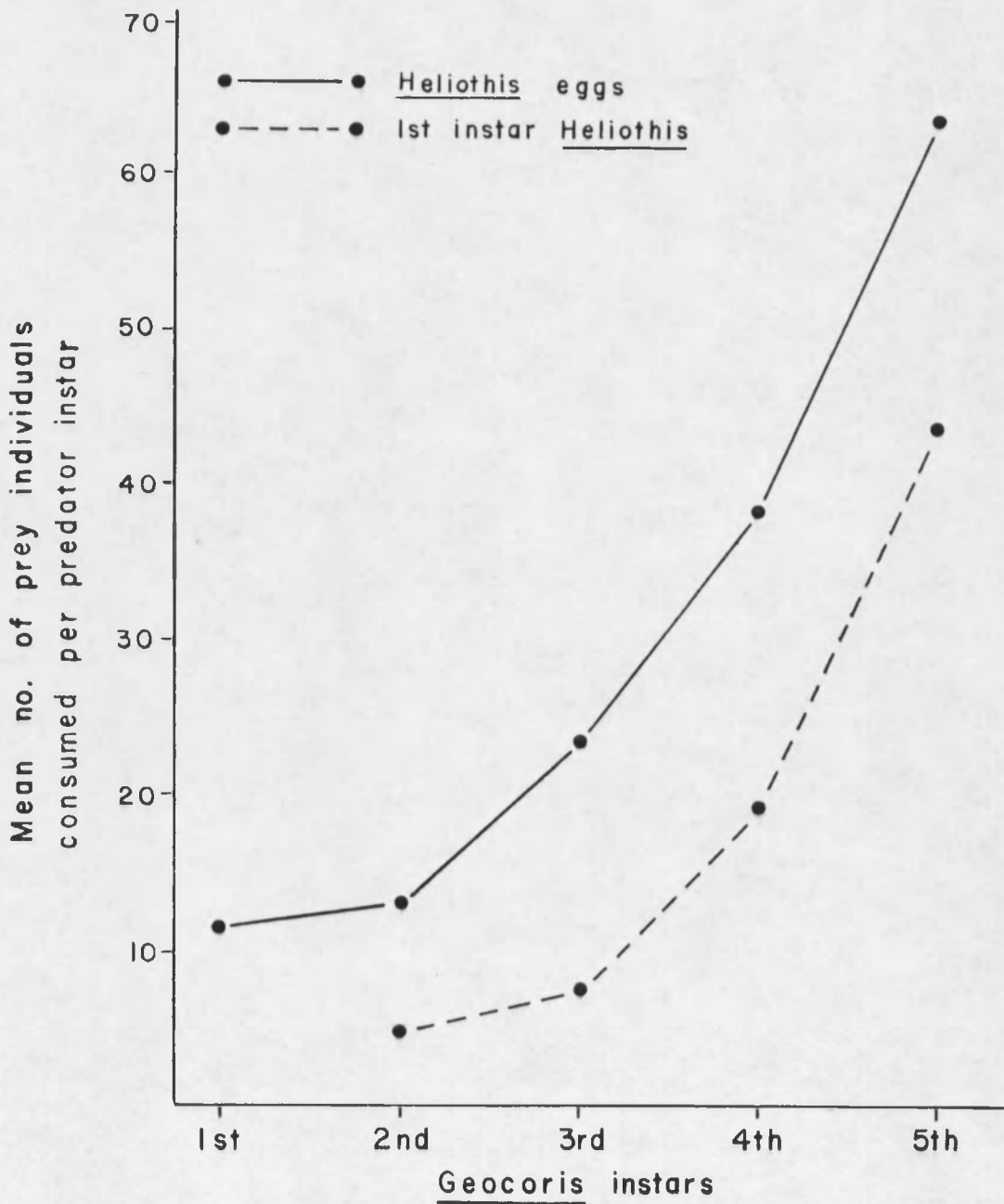


Figure 4. Average total consumption of Heliiothis virescens eggs and larvae during each instar of Geocoris punctipes.

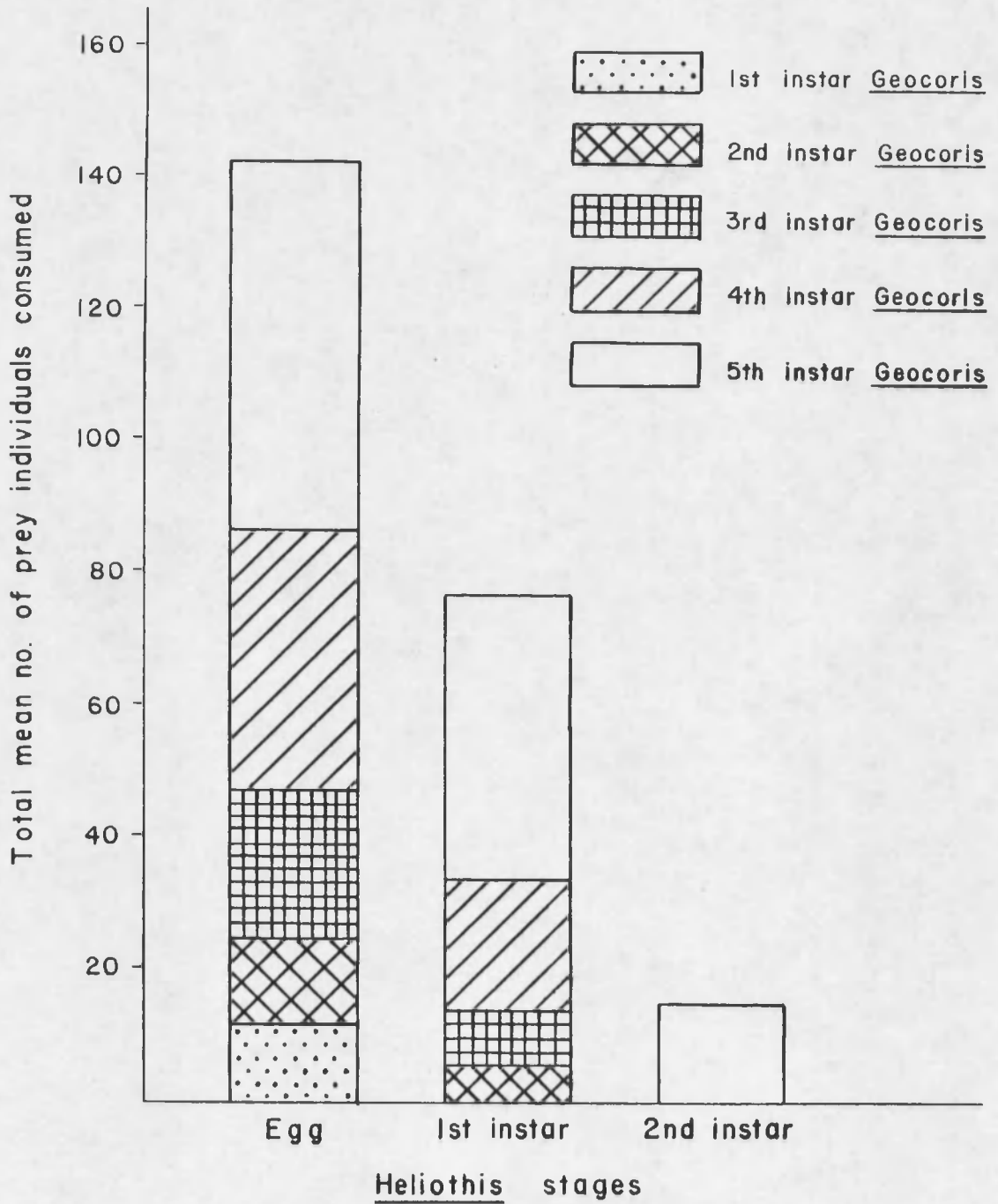


Figure 5. Total number of Heliothis virescens eggs and larvae consumed during the nymphal development of Geocoris punctipes.

(t test) was evident between the two groups. Therefore, it is reasonable to assume that no significant amount of nutritional benefit was received by those G. punctipes which had access to the lima bean diet.

Rate of Development

The mean duration of time required to complete each G. punctipes instar is recorded in Table 6. Those nymphs feeding on H. virescens eggs exhibited instar periods significantly shorter (at the 0.05 level, t test), than those of the nymphs feeding on H. virescens larvae. This was true for each individual instar of G. punctipes. For fifth-instar G. punctipes no significant difference in instar lengths (at the 0.05 level) was determined for those feeding on first-instar larvae and those feeding on second-instar larvae.

The slower rate of development for the feeding on larvae can be clearly demonstrated by the total length of time required for nymphal development. Although only the last four instars of G. punctipes were successful in feeding on first-instar larvae, their total developmental time was greater than that of all five instars which fed on eggs. The nymphs feeding on eggs completed five instars in a total mean of 21.2 days. The nymphs feeding on first-instar larvae completed the last four nymphal instars in a total mean of 26.6 days.

Table 6. Average number of days required by Geocoris punctipes nymphs to complete each instar when feeding on various stages of Heliothis virescens.

<u>Geocoris</u> instars	<u>Heliothis</u> stages		
	Eggs	1st instar	2nd instar
1st	4.7 ± 0.13 ^a	--	--
2nd	3.5 ± 0.13	6.6 ± 0.31	--
3rd	3.6 ± 0.13	6.0 ± 0.19	--
4th	3.8 ± 0.10	6.1 ± 0.12	--
5th	5.6 ± 0.09	7.9 ± 0.10	8.2 ± 0.49

^aMean ± standard error of the mean.

Summary of Predation by Individual Instars

First-instar G. punctipes

Results of the feeding tests involving G. punctipes first-instar nymphs are summarized in Table 7. Although over 97% of these nymphs completed the instar on a diet of eggs, only one from a sample size of 18 (5.6%) completed the instar when feeding on first-instar larvae. None were observed to survive when feeding on larger H. virescens. These data appear to indicate that in relation to the H. virescens prey, first-instar nymphs of G. punctipes act almost exclusively as egg predators.

Table 7. Summary of predation by first-instar Geocoris punctipes on the various stages of Heliothis virescens.

	<u>Heliothis</u> stages			
	Eggs	1st instar	2nd instar	3rd instar
Number of predators in each test	34	18	10	10
Number completing the instar	33	1	0	0
Per cent survival	97.1	5.6	0.0	0.0
Mean number of prey consumed per day	2.5	--	--	--
Mean number of prey consumed during the entire instar	11.6	--	--	--
Mean instar length (days)	4.7	--	--	--

Second- and Third-instar
G. punctipes

Tables 8 and 9 summarize the results of the feeding tests for G. punctipes second- and third-instar nymphs, respectively. Effective feeding by these nymphs was limited to the eggs and first-instar larvae of H. virescens. A value for the mean daily natural mortality of H. virescens larvae has been included in the summaries of the feeding tests. As was discussed above, G. punctipes consumption

Table 8. Summary of predation by second-instar Geocoris punctipes on the various stages of Heliothis virescens.

	<u>Heliothis</u> stages			
	Eggs	1st instar	2nd instar	3rd instar
Number of predators in each test	33	33	10	10
Number completing the instar	32	12	0	0
Per cent survival	97.0	36.4	0.0	0.0
Mean number of prey consumed per day	3.7	0.8	--	--
Mean daily natural mortality of prey larvae	--	0.4	--	--
Mean number of prey consumed during the entire instar	12.8	5.5	--	--
Mean instar length (days)	3.5	6.6	--	--

Table 9. Summary of predation by third-instar Geocoris punctipes on the various stages of Heliothis virescens.

	<u>Heliothis</u> stages			
	Eggs	1st instar	2nd instar	3rd instar
Number of predators in each test	32	58	20	10
Number completing the instar	31	40	1	0
Per cent survival	96.9	69.0	5.0	0.0
Mean number of prey consumed per day	6.4	1.4	--	--
Mean daily natural mortality of prey larvae	--	0.5	--	--
Mean number of prey consumed during the entire instar	23.1	8.0	--	--
Mean instar length (days)	3.6	6.0	--	--

rates have not been corrected for natural prey mortality, because G. punctipes have been observed acting as scavengers of prey killed by cannibalism.

Fourth-instar G. punctipes

The results from the G. punctipes fourth-instar feeding tests are presented in Table 10. No mortality was recorded, when this instar fed on eggs. When feeding on larvae, fourth-instar nymphs were observed to survive at varying degrees on all three prey instars tested. However, low survival rates when feeding on second- and third-instar larvae did not result in adequate sample sizes for analysis of consumption rates and instar duration.

Results from the starvation tests of individual G. punctipes nymphs indicated that a few fourth-instars were capable of molting without feeding in that instar. Two out of the total of 100 fourth-instar nymphs in the starvation tests successfully molted to the fifth-instar without any access to prey individuals. Such molting without prior feeding was not observed in any other nymphal instar.

Statistical tests were conducted on all pertinent predator-prey feeding combinations to determine if significantly different groups of G. punctipes existed within any one test combination. Such significantly different components were found only within the fourth- and fifth-instars of G. punctipes.

Table 10. Summary of predation by fourth-instar Geocoris punctipes on the various stages of Heliothis virescens.

	<u>Heliothis</u> stages			
	Eggs	1st instar	2nd instar	3rd instar
Number of predators in each test	31	72	31	20
Number completing the instar 3	31	48	7	1
Per cent survival	100.0	66.7	22.6	5.0
Mean number of prey consumed per day	10.0	3.2	--	--
Mean daily natural mortality of prey larvae	--	1.3	--	--
Mean number of prey consumed during the entire instar	38.8	19.2	--	--
Mean instar length (days)	3.8	6.1	--	--

The males and females within the fourth-instar displayed significantly different values (at the 0.05 level, Student-Newman-Keuls' test) for the mean rates of consumption. The data, which are detailed in Table 11, indicate that the females had the higher rates. No significant difference was discovered for instar durations.

Table 11. Relationship between males and females of fourth-instar Geocoris punctipes feeding on Heliothis virescens eggs.^a

	Males (n=14)	Females (n=17)
Mean number of prey consumed per day	8.7 ± 0.59 a	11.1 ± 0.58 b
Mean number of prey consumed during the entire instar	33.1 ± 2.92 a	43.5 ± 3.03 b
Mean instar length (days)	3.8 ± 0.15 a	3.9 ± 0.10 a

^aMeans in the same row followed by the same letter are not significantly different at the 0.05 level (Student-Newman-Keuls' test).

Fifth-instar G. punctipes

The results of the G. punctipes fifth-instar feeding tests are summarized in Table 12. Analyses of feeding data and instar duration are complete for those tests in which eggs and first- and second-instar larvae were the prey. Only 6.5% of the fifth-instar nymphs survived when feeding on third-instar larvae. As was also noted with the fourth-instar G. punctipes, fifth-instars feeding on eggs had a 100% rate of survival.

Two factors within the fifth-instar feeding tests resulted in values with significant differences. These are the sex and the prior feeding histories of the nymphs. Table 13 illustrates the differences between male and female

Table 12. Summary of predation by fifth-instar Geocoris punctipes on the various stages of Heliothis virescens.

	<u>Heliothis</u> stages			
	Eggs	1st instar	2nd instar	3rd instar
Number of predators in each test	31	88	37	31
Number completing the instar	31	52	10	2
Per cent survival	100.0	59.1	27.0	6.5
Mean number of prey consumed per day	11.6	5.6	1.8	--
Mean daily natural mortality of prey larvae	--	1.2	0.7	--
Mean number of prey consumed during the entire instar	64.4	43.8	14.3	--
Mean instar length (days)	5.6	7.9	8.2	--

Table 13. Relationship between males and females of fifth-instar Geocoris punctipes feeding on Heliothis virescens eggs.

	Males (n=14)	Females (n=17)
Mean number of prey consumed per day	10.0 ± 0.45 a	12.9 ± 0.46 b
Mean number of prey consumed during the entire instar	58.1 ± 2.94 a	69.5 ± 2.16 b
Mean instar length (days)	5.8 ± 0.11 a	5.4 ± 0.12 b

^aMeans in the same row followed by the same letter are not significantly different at the 0.05 level (Student-Newman-Keuls' test).

fifth-instars feeding on eggs. The males showed mean consumption rates significantly lower (at the 0.05 level, Student-Newman-Keuls' test) than those of the females. The mean instar duration was also significantly greater for the males.

The reasons for these differences between males and females feeding on eggs are not clear. No such differences were exhibited when larvae were the prey, or when G. punctipes nymphs other than fourth- or fifth-instars were the predators. It is possible that these later nymphal instars approached their maximum consumption capabilities for each sex by feeding on what might be termed a highly desirable form of prey. The eggs were non-defensive, immobile prey which were available in sufficient quantities. Feeding on eggs by these nymphs resulted in 100% predator survival and shorter instar duration than when larvae were the prey. Therefore, it is reasonable to assume that G. punctipes nymphs experienced the least difficulty when attempting feeding in these two predator-prey combinations. In the absence of significant behavioral restrictions on predation, the biological and size differences between the older male and female nymphs might be the primary factors affecting variations in the rates of feeding and development.

Fifth-instar G. punctipes nymphs feeding on first-instar larvae demonstrated significant differences based

on the prior feeding histories of the nymphs. The first group under this category is composed of those nymphs which had prior feeding under test conditions. They were introduced into the tests as second-, third- or fourth-instar nymphs and subsequently survived through the fifth-instar. The second group of nymphs had no prior feeding under test conditions and were introduced into the test as fifth-instars. The data for these two groups are presented in Table 14. The group with prior test feeding had significantly higher consumption rates (at the 0.05 level, Student-Newman-Keuls' test) than those of the nymphs which had been introduced into the test as fifth-instars. The instar durations of the two groups were not significantly different.

Such differences based on prior feeding histories were not observed in any other predator-prey combination. The cause of the differences in this situation may also be related to the desirability of the prey. A first-instar larva is a form of prey capable of locomotion and defensive behavior. Table 2 demonstrates that G. punctipes nymphs which fed on first-instar larvae had a much lower rate of survival than those which fed on eggs. When G. punctipes fed only on the first-instar larvae, the younger nymphs had much lower survival rates than did the older nymphs. It may be assumed that the earlier G. punctipes nymphs experienced the greatest difficulty in overcoming the active prey. It is also reasonable to assume, that as the predator

Table 14. Relationship of the prior feeding history of fifth-instar Geocoris punctipes to the predation of Heliothis virescens first-instar larvae.

	Prior feeding history ^a	
	Predation tests (n=27)	Stock culture (n=25)
Mean number of prey consumed per day	6.0 ± 0.28 a	5.1 ± 0.28 b
Mean number of prey consumed during the entire instar	47.8 ± 2.27 a	39.4 ± 2.26 b
Mean instar length (days)	8.0 ± 0.16 a	7.8 ± 0.11 a

^aMeans in the same row followed by the same letter are not significantly different at the 0.05 level (Student-Newman-Keuls' test).

grew in size through the successive instars, its ability to overpower and feed on the prey also increased. This assumption appears to be corroborated by the steadily increasing rate of survival for the successive instars of G. punctipes.

The G. punctipes fifth-instars, with no prior feeding under test conditions, had previously been feeding on an inactive prey source. In the stock culture, these nymphs fed on killed larvae, which represented an immobile form of prey with no defensive behavior. In contrast, the fifth-instars with prior feeding under test conditions were

preying upon the active, defensive first-instar larvae. Therefore, based on the above data from Table 2, it is probable that those fifth-instars with prior test feeding on active prey experienced greater difficulty in obtaining an adequate amount of food, than did the fifth-instars which were taken fresh from the stock culture. Dunbar and Bacon (1972a) developed similar conclusions, when they tested G. punctipes nymphs on eight different diets. The four diets producing the highest growth rates were those composed of insect eggs or dead larvae. Prey that were active or had defensive behavior were considered to be less suitable as food sources.

By the time G. punctipes nymphs have reached the fifth-instar, their increased size has resulted in a greater ability to overcome the active larvae. However, if the nymphs with prior test feeding have a greater nutritional deficit, than do the nymphs which were introduced as fifth-instars, this might account for greater consumption rates by the former (Table 14).

SUMMARY

Nymphs of Geocoris punctipes were studied in laboratory feeding tests to determine their capabilities for predation of Heliothis virescens. The results of this predation were correlated with the developmental success of the G. punctipes nymphs.

All five nymphal instars of G. punctipes were observed to have very high rates of survival when feeding on H. virescens eggs. G. punctipes first-instar nymphs were determined to be almost exclusively egg predators of H. virescens. All of the last four G. punctipes instars were capable of feeding on H. virescens first-instar larvae. During the last half of nymphal development, G. punctipes nymphs also fed on second-instar larvae with limited success. G. punctipes fifth-instars were observed to rarely maintain successful feeding on the larger third- and fourth-instar larvae.

The results of the feeding tests showed several major trends related to the developmental ages of the predator and of the prey. As the developmental level of the prey increased, the per cent survival of the predator decreased. A decrease in predator feeding rates and a decrease in predator developmental rates were also observed to be concurrent with an increase in the developmental level

of the prey. With the larger prey larvae which were tested (second- and third-instar H. virescens), these intended prey were frequently observed to be feeding on the corpses of the G. punctipes predators.

Major trends were also observed as the developmental level of the predator increased. The per cent survival and the feeding rates of the predator increased directly as the predator developed.

Several related factors were proposed as the causes of the trends in predator success. Disparity in size appeared to have a direct effect on feeding success by the predator. The poorest overall predation success was exhibited by the first- and second-instar G. punctipes nymphs, when they were fed second- and third-instar H. virescens larvae. Conversely, the highest level of success was attained by the fourth- and fifth-instar G. punctipes, when they fed on H. virescens eggs.

Activity of the prey was an important causative factor in the variation of predator success. H. virescens eggs represented a stationary form of prey with no defensive behavior. H. virescens first-instar larvae were prey which possessed both the capability for locomotion and for defensive behavior. G. punctipes nymphs feeding on eggs exhibited survival rates for the individual instars which ranged from 96.9 to 100.0%. G. punctipes which fed on first-instar larvae displayed survival rates with a range

of 5.6-69.0%. The total mean developmental time for all five G. punctipes instars feeding on eggs was 21.2 days. Only the last four G. punctipes instars successfully fed on first-instar larvae. The total mean developmental time for those four instars was 26.6 days.

Based on the results of all tests, G. punctipes were most effective as egg predators of H. virescens. Egg predation resulted in the highest per cent survival and the shortest developmental time. Considering only the number of prey consumed during the predator's nymphal development, G. punctipes feeding on eggs were capable of consuming a much greater number than when they fed on the larval stages.

Significantly different groups were found within each of three predator-prey combinations. Male and female fourth-instar G. punctipes showed different consumption rates when they fed on H. virescens eggs. In the fifth-instar males and females which fed on eggs, there were different consumption rates and different instar durations. Fifth-instar G. punctipes which fed on first-instar H. virescens larvae, showed significant differences based on the prior feeding histories of the nymphs. Those nymphs which had prior feeding under test conditions, displayed significantly higher consumption rates than did those nymphs which were introduced into the tests as fifth-instars.

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