AN ABSTRACT OF THE THESIS OF

<u>Diane Lyn Belnavis</u> for the degree of <u>Master of Science</u> in <u>Entomology</u> presented on <u>December 16, 1988</u>. Title: <u>HOST EXPLOITATION BY DINOCAMPUS COCCINELLAE</u> (SCHRANK) [HYMENOPTERA: BRACONIDAE].

Abstract approved by:_____

Ecological relationships between <u>D. coccinellae</u> and its coccinellid hosts were examined in the Willamette Valley, Oregon, in 1982. The distribution and relative abundance of seven species of coccinellids from eight collecting sites were monitored to determine percent parasitism by <u>D. coccinellae</u> on a spatial and temporal basis. Host size and host suitability were addressed in the laboratory.

Overall, <u>D. coccinellae</u> parasitized approximately 27% of the 2272 beetles collected from April through August. The number of beetles collected and the number parasitized were highest in July and August. Levels of parasitism significantly differed according to host species, host habitats and month collected. Coccinellids collected on peppermint and clover showed significantly higher levels of parasitism than the other six sites. A significantly higher degree of parasitism was seen in the coccinellids <u>Hippodamia convergens</u> Guerin-Meneville and <u>Hippodamia</u> <u>sinuata</u> Mulsant. <u>Coccinella californica</u> Mann was parasitized significantly less than the other coccinellid species in this study. One common species of predaceous coccinellid, <u>Adalia bipunctata</u> (L.) was never found parasitized. Host density did not affect parasitism.

Size did not appear to be a factor in the selection of hosts at the species level of selection. Two of the three most heavily parasitized coccinellid species were the smallest species in this study, the other was the second largest species. The largest species, <u>C. californica</u>, showed a low level of parasitism (4%). Within species, there appeared to be a size effect in the smaller hosts. Individuals of suitable host species below a volume of 10mm³ were never found parasitized by <u>D. coccinellae</u>.

The non-suitability of <u>Adalia bipunctata</u> as a host for <u>D. coccinellae</u> was examined in the laboratory. Parasitoids always selected other hosts if given a choice in laboratory experiments. Ovipositor probing by <u>D.</u> <u>coccinellae</u> into <u>A. bipunctata</u> could be provoked by isolating female parasitoids without hosts for three days and then exposing them to <u>A. bipunctata</u> with no other host species present. Females appeared to oviposit but no evidence of parasitism was detected in dissections of the hosts.

HOST EXPLOITATION BY <u>DINOCAMPUS COCCINELLAE</u> (SCHRANK) [HYMENOPTERA: BRACONIDAE]

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HOST EXPLOITATION BY <u>DINOCAMPUS COCCINELLAE</u> (SCHRANK) [HYMENOPTERA: BRACONIDAE]

INTRODUCTION

The parasitoid <u>Dinocampus coccinellae</u> (Schrank) [Hymenoptera: Braconidae: Euphorinae] is known most commonly in the literature as <u>Perilitus coccinellae</u> (Schrank). The original description was given by Schrank in 1803 under the name <u>Ichneumon</u> (Muesbeck and Walkley, 1951). The taxonomy of this species was recently revised by Shaw (1985), though there has been much confusion concerning the classification of the Euphorinae (Matthews, 1974; Smith, 1953).

Cosmopolitan in distribution, <u>D. coccinellae</u> has been recorded as a parasitoid of 18 genera and 42 species of predaceous Coccinellidae (Richerson, 1970). Females primarily exploit hosts in the tribe Coccinellini in the sub-family Coccinellinae (Belicek, 1976), ladybird beetles which feed primarily on aphids. It is not known if <u>D.</u> <u>coccinellae</u> was introduced into the United States from Europe or if it is a native species.

A solitary endoparasitoid, <u>D. coccinellae</u> has been generally regarded as a parasitoid of adult coccinellids (Semyanov, 1981; Hodek, 1973; Richerson and DeLoach, 1972; Tobias, 1965; Balduf, 1926). However, laboratory studies have shown that immature stages will be accepted and the parasitoid will then emerge from the adult beetle (Obrycki et.al., 1985; Semyanov, 1979; David and Wilde, 1973; Smith, 1960). Field collections of larvae and pupae have shown low levels of parasitism (Semyanov, 1979; Smith, 1960). David and Wilde (1973) noted no difference in preference when larvae and adults of Hippodamia convergens (Guerin-Meneville) were exposed to D. coccinellae. Obrycki et.al. (1985) found that later instars were preferred over early instars and that the percent of successful parasitism was higher in later developmental stages of the host <u>Coleomegilla maculata</u> (DeGeer). It is likely that some parasitization of immatures occurs in the field. Other euphorine species are reported to attack the adult, pupa, and larva of their beetle hosts, all of which often occur in the same habitat (Loan, 1963; Clausen, 1940).

LIFE CYCLE AND SEASONAL OCCURRENCE

In temperate areas coccinellids are parasitized in autumn before they migrate to their overwintering sites. Parasitoids overwinter as first instars in the abdomen of adult coccinellids (Balduf, 1926). Several authors have studied thermal requirements and development of the overwintering parasitoid and its host (Obrycki and Tauber, 1979 and 1978; Wright and Laing, 1978; Hodek et.al., 1977). Obrycki and Tauber (1979) studied the seasonal interactions of this parasitoid and the coccinellid, <u>C.</u> <u>maculata</u>, in upstate New York. Both the host and the parasitoid are in diapause from autumn to the winter solstice. Diapause is maintained by short daylengths. The photoperiodic maintenance of diapause ends for most individuals of <u>D. coccinellae</u> by the end of January. Postdiapause development in the parasitoid does not begin until early April when temperatures increase. Diapause is maintained until May in the host. It is believed that <u>D.</u> <u>cocccinellae</u> emerges after the beetles disperse from their overwintering sites in the spring (Obrycki and Tauber, 1979).

Balduf (1926) summarizes the life cycle of <u>D</u>. <u>coccinellae</u>. The adult parasitoid will pursue a moving beetle with the ovipositor bent forward between its front legs. Eggs are deposited in the abdomen of the host through the soft membranes between the abdominal plates. Usually only one egg is laid, though superparasitism occurs in a small percentage of beetles. In these cases, only one parasitoid will survive to the adult stage. It is believed that the mandibulate first instar will destroy other parasitoids in the same host (Harvey and Partridge, 1987; Vinson and Iwantsch, 1980; Salt, 1961).

The egg stage lasts from 6 to 9 days (Balduf, 1926). During this time the egg increases in size 1000 times. The first instar possesses a sclerotized head capsule with

long piercing mandibles, supposedly used in defense against other larval parasitoids. The head capsule is lost in subsequent instars. There appear to be three larval instars with a total duration of 15 days. The primary resource of the larva is derived from the fat body of the beetle and the internal organs remain intact (Sluss, 1968). The mature larva emerges from the host through the posterior of the abdomen and spins a cocoon beneath the host. At this point the host is alive. Timberlake (1916) reported that hosts can recover from the effects of parasitism and that twice he succeeded in rearing a second generation of <u>D. coccinellae</u> from a In field situations the host's legs are beetle host. entangled in the cocoon and therefore immobilized; the beetle dies of starvation within a few days. The pupal stage lasts for seven days. Reproduction is parthenogenetic and thelytokous: only females are produced. Males are rare, only five have been recorded (Wright, 1978; Hudon, 1959). The adult parasitoid can oviposit within minutes of emergence.

Under field conditions the total developmental time from egg to adult is approximately one month. Four to five generations may occur from early spring to September, depending on summer temperatures and food availability for the beetle (Cartwright et.al., 1982; Obrycki and Tauber, 1979).

BIOLOGY OF THE COCCINELLID HOSTS

General biology and life history of the predaceous Coccinellidae are reviewed in several publications (Hodek, 1973; Hodek, 1967; Hodek, 1965; Hagen, 1962). Coccinellids oviposit when they arrive at feeding sites in the spring. Eggs are laid in the vicinity of prey. Both larvae and adults feed primarily on aphids. Most species of aphids are acceptable though some are preferred over others (Hodek, 1973). Olszak (1986) found that the fecundity and longevity of Propylea quatuordecimpunctata (L.), an aphidophagous coccinellid, was significantly affected by different aphid species. During periods of low prey density, many species of coccinellids feed on pollen (Hemptinne and Desprets, 1986; Putman, 1964; Hagen, 1962; Smith, 1961). Most coccinellid species have 1 to 2 generations per year.

Ladybird beetles are known to occur in many terrestrial habitats including field crops, orchards, forested areas and roadside vegetation (Hodek, 1973; Rockwood, 1952). Within habitats, coccinellids are often distributed according to food preference, humidity, geotactic and phototactic preferences (Coderre and Tourneur, 1986; Kokubu and Duelli, 1986; Honek, 1982; Smith, 1971; Ewert and Chiang, 1966).

Rockwood (1952) and Ewing (1913) describe the

distribution and seasonal abundance of coccinellid species in the Pacific Northwest. In the Willamette Valley, Oregon, beetles are active from mid-April through September, depending on food availability and species. Several species common in 1913 and 1952 are no longer common in the Willamette Valley, the area in which both of these studies were concentrated. Several species not mentioned by these authors are now present.

In the Willamette Valley, <u>Adalia bipunctata</u> (L.) is the first coccinellid species active as adults in the spring. By June, most others are present. The most common species are Coccinella trifasciata L., <u>Cycloneda</u> <u>polita</u> Casey, <u>Hippodamia sinuata</u> Mulsant, <u>H. convergens</u>, and two species not collected by Rockwood or Ewing, <u>Coccinella undecimpunctata</u> L. and <u>Coccinella californica</u> Mann. All of these show some affinity for certain types of habitat. <u>A. bipunctata</u> and <u>C. polita</u> are mainly arboreal; the others are generally found in field crops (peppermint, alfalfa), weeds, and herbaceous plants such as vetch (Rockwood, 1952; Ewing, 1913).

Historically, coccinellids have been known to migrate from feeding sites in midsummer when aphid populations decrease (Hagen, 1962). Before the modification of plant communities by the introduction of irrigated crops and exotic aphids, summer vegetation could not support large populations of aphids. Many species aggregated in large

numbers in mountain canyons or on prominent dry hillsides, depending on the species (Harper and Lilly, 1982; Rockwood, 1952). It has been suggested that aggregating behavior serves to bring the sexes together for mating (Hagen, 1962).

In the Willamette Valley, populations of coccinellids in agricultural areas decrease in July only slightly and subsequently increase in August. It is possible that the continued supply of aphids in agricultural crops throughout the summer has altered the migrating behavior of coccinellids so that they are better synchronized with prey populations. By mid-September, most species of coccinellids have migrated to overwintering sites and entered reproductive diapause (Obrycki and Tauber, 1981,1979).

INTERACTIONS OF D. COCCINELLAE WITH ITS COCCINELLID HOSTS

There are several steps necessary for successful parasitism in insects: host habitat location, host location, host acceptance, host suitability, and host regulation. This process has been reviewed in several publications (van Alphen and Vet, 1986; Vinson, 1984, 1981; Vinson and Iwantsch, 1980; Vinson, 1975, 1976; Matthews, 1974; Doutt, 1959; Laing, 1937; Salt, 1935). A hierarchy of physical and chemical cues serve to lead the female parasitoid to its potential host. Upon encounter, another set of cues is used to determine the suitability of that host. A breakdown in the stimuli from one step to the next may result in parasitism failure.

HOST/HABITAT LOCATION. The cues involved in location may differ with the habitat type and host and food specificity of either the parasitoid or its host. Several combinations are possible: host-specific parasitoid of a habitat-specific host (parasitoid must also be habitatspecific); host-specific parasitoid of a habitat generalist host; host-generalist parasitoid of a habitat specific host; and a host-generalist parasitoid of a habitat generalist host. In the last three cases the parasitoid may show different levels of habitat

The steps in host location have been examined in detail in parasitoids that are specific on hosts that are restricted to a particular habitat (Vinson, 1976; Read, et al. 1970). The parasitoid has coevolved with its host and is able to locate it through physical and chemical cues from the host's environment and the host itself.

Varying cues may be used by a specific parasitoid of a host that is not restricted in its choice of habitat. Weseloh (1972) found that gypsy moths in clear cuts were parasitized less than those in forested areas. Arthur (1962) reported that pine shoot moth pupae were parasitized more readily on certain species of pines.

Caging experiments with <u>Trichogramma pretiosum</u> Riley on two different crops showed significantly different levels of parasitism (Orphanides and Gonzalvez, 1970).

Generalist parasitoids may depend on less specific methods of host location. Townes (1960) cites several examples of generalist ichneumonid parasitoids that select hosts on the basis of the species that occur in the parasite's preferred habitat. Unrelated hosts are often attacked by the same parasitoid species. Read et al. (1970) found that aphids on sugar beets were parasitized more readily by <u>Diaeretiella rapae</u> (M'Intosh), a generalist aphid parasitoid, when the beets were interspersed with collard plants. The collards attracted the parasitoid initially and the sugar beets would also be searched.

Host location strategies by a polyphagous parasitoid (ie. <u>D. coccinellae</u>) on hosts with unrestricted habitat requirements (ie. ladybird beetles) are not well understood. Habitat preference may be a major factor that determines the type of habitat searched and the hosts which are selected. Cross and Chestnut (1971) found that there was less tendency to select phylogenetically related hosts than unrelated hosts on the same plant.

Most habitat/host location studies have recorded empirical observations rather than addressed the mechanisms involved. However, some mechanistic data do

General habitat preferences of parasitoids have exist. been shown to be influenced by temperature, humidity, light intensity and wind (Vinson, 1975); movement habits of the parasitoid (Weseloh, 1972); and sources of food for the adult (Simmons et al. 1975). There is considerable evidence that parasitoids can be conditioned to certain hosts and habitats (van Alphen and Vet, 1986). Vet (1983) found that Leptopilina clavipes (Hartig) could be conditioned to search for its Drosophila spp. hosts using yeast odors (a potential microhabitat: fermenting fruits) over decaying fungi once the adult parasitoid was given oviposition experience with hosts feeding on yeast. The ability to learn cues in host searching, as opposed to genetically fixed searching behavior, may be more adaptive in polyphagous parasitoids that are exposed to different host species occupying several habitats (van Alphen and Vet, 1986).

The family Coccinellidae contains species which exhibit a wide range of habitat preferences from stenotopic to eurytopic (Hodek, 1973), though there is evidence that the eurytopic species prefer certain habitat types (Hodek, 1965, Hagen, 1962). Many coccinellids show specific microhabitat affinities (Coderre and Tourneur, 1986; Kokubu and Duelli, 1986; Honek, 1982; Radwan and Lovei, 1982; Smith, 1971; Ewert and Chiang, 1966). Records of <u>D. coccinellae</u> parasitism show varying degrees within both species and habitat types (Cartwright et al., 1982; Semyanov, 1981; Richerson and DeLoach, 1973, 1972; Walker, 1961; Smith, 1960; Hudon, 1959; Smith, 1953; Bryden and Bishop, 1945; Liu, 1944; Balduf, 1926). In Illinois, parasitism of <u>C. maculata</u> (reported as <u>C.</u> <u>fuscilabris</u>) varied from 36% in roadside vegetation to 12% in a woods margin to 5% in corn, while parasitism among species varied from an average of 11% for C. maculata to 23% for <u>Coccinella sanguinea</u> (L.) (Balduf, 1926). Parasitism varied from 2% to 27% among beetle species in Missouri (Richerson and DeLoach, 1973), and from 17% (<u>Coccinella septempunctata</u>) to 48% (<u>Coccinella</u> <u>undecimpunctata</u>) in Scotch Pine in New Jersey (Cartwright et al. 1982). The mechanisms involved in host location have not been addressed in <u>D. coccinellae</u>.

Seasonal synchrony of <u>D. coccinellae</u> and its host<u>C.</u> <u>maculata</u> has been observed in several studies (Obrycki and Tauber, 1979; Wright and Laing, 1978; Parker et al. 1977). No other host species of <u>D. coccinellae</u> have been examined for temporal synchrony.

HOST ACCEPTANCE. Studies on host acceptance by <u>D.</u> <u>coccinellae</u> are limited to the laboratory (Semyanov, 1981; Richerson and DeLoach, 1972; Walker, 1961). These investigations have shown that olfaction plays a major role in host recognition. The response of <u>D. coccinellae</u> increased when coxal secretion of <u>H. convergens</u> (a preferred host) was applied to non-host beetles (Richerson and DeLoach, 1972). Semyanov (1981) found that the parasitoid could locate a suitable host with only one antenna and blackened eyes, but lost the ability to find hosts when both antennae were amputated. Many studies have shown the importance of chemical cues at this step of host selection in insect parasitoids. This subject has been reviewed by Vinson (1984, 1976, 1975).

Possible reasons for the differences in preference among host species in field situations are discussed in Balduf (1926). These include: synchrony of life cycles; habitat and microhabitat preferences; host density; host behavior; and size of host. Several of these have been addressed in laboratory studies (Obrycki et al. 1985; Obrycki and Tauber, 1979, 1978; Wright and Laing, 1978; Hodek et al. 1977; Parker et al. 1977; David and Wilde, 1973; Richerson and DeLoach, 1972; Sluss, 1968). Sluss (1968) found that active H. convergens attracted a parasitoid up to four inches away but a motionless pupa was recognized only when the parasitoid was within 3/4 of an inch. It is believed that D. coccinellae can only parasitize a moving beetle, exposure of the soft tissue between the abdominal plates is necessary for oviposition (Balduf, 1926). Host species reacted differently to parasitoid attack in the study by Richerson and DeLoach (1973). Cycloneda munda Say, A. bipunctata, and

<u>Coccinella novemnotata</u> Herbst became immobile when attacked, and <u>C. maculata</u> was extremely active and often escaped.

Size was implicated as a factor in host species preference by Richerson and DeLoach (1972). Preference appeared to diminish with the size of the host. Survival of the immature stages of the parasitoid was higher in the larger hosts. Obrycki et al. (1985) found that <u>D.</u> <u>coccinellae</u> preferred later instars of larval <u>C. maculata</u> over earlier ones and that survival was higher in these larger individuals. Preferences for a certain size of immature hosts in other species of insect parasitoids has been reported (Vinson, 1976).

The adaptive significance of preference for particular host species by generalist parasitoids has been addressed in the review by van Alphen and Vet (1986). Their theories suggest that a parasitoid will select a host based on fitness gain or relative abundance of host species.

Within a habitat, <u>D. coccinellae</u> often encounters more than one suitable host species. Several of the common species of coccinellids in the Willamette Valley occur together in field crops and orchards. However, field and laboratory studies have not addressed the role of fitness or relative abundance of host species in host selection.

HOST SUITABILITY. Once a host is discovered, the successful development of a parasitoid to the adult stage depends on several factors: evasion of or defense against host defenses; competition with other parasitoids; and nutritional suitability (Vinson and Iwantsch, 1980; Salt, 1938). Several studies on host species preference in D. coccinellae have reported greater parasitism when hosts were dissected than by rearing the parasitoid to the pupal stage (Cartwright, et al., 1982; Richerson and DeLoach, 1972; Bryden and Bishop, 1945; Balduf, 1926). This discrepancy is an indication of larval mortality of the parasitoid. The difference between the data derived from dissection and rearing techniques varied among host species in the study by Cartwright et al. (1982). The highest survival for larval <u>D. coccinellae</u> was in <u>C.</u> <u>maculata</u>. The greatest mortality occurred in <u>C.</u> undecimpunctata, the species with the highest % parasitism by dissection. Parasitism decreased from 48% by dissection to 20% by rearing for this species. No parasitoids emerged from <u>A. bipunctata</u>, though 12% (n=100) were found parasitized when dissected. These results were similar to those in other studies on A. bipunctata (Hodek, 1973; Richerson and DeLoach, 1972; Bryden and Bishop, 1945). Larval mortality may be an indication of differential host suitability among host species.

The objectives of this study were: 1. To examine how the spatial and temporal distribution and relative abundance of host species relate to parasitism by <u>D.</u> <u>coccinellae</u> in the Willamette Valley; 2. To determine the effect of host size on parasitism by <u>D. coccinellae</u>; 3. To determine the suitability of <u>A. bipunctata</u> as a host for <u>D. coccinellae</u>.

MATERIALS AND METHODS

DISTRIBUTION AND RELATIVE ABUNDANCE OF HOST SPECIES

In 1982, coccinellids were collected weekly from 8 sites near Corvallis, Benton County, Oregon. A diversity of habitat types previously recorded as suitable for coccinellids were sampled. Beetles were obtained from 3 alfalfa fields, 1 peppermint field, 1 clover field, 1 filbert orchard, 1 forested site and 1 riparian area. Α total of 9 other habitats were sampled on a limited basis depending on availability of beetles: 2 peppermint fields, 3 filbert orchards, 2 forested sites, 1 roadside vegetation area and an urban site within city limits. In January, 1983, beetles were collected from an overwintering aggregation in McDonald Forest. These sites were not included when seasonal patterns were examined because of harvest, spray schedules and/or unexplained absence of coccinellids for extended periods.

Entomology alfalfa: a 2-acre field of first-year alfalfa at the Entomology Farm adjacent to the OSU campus. Bordered by weedy vegetation, a road, and on 2 sides by filbert orchards. This site was used concurrently in another research project and was not sprayed. Harvested in early August.

Peoria alfalfa: a 10-acre field of second-year alfalfa 3 miles southeast of Corvallis on Peoria Road. Bordered by the Willamette River, Peoria Road, houses and weedy

vegetation. Spray schedule is unknown but traditional management practices were used. Harvested early August.

Horticulture alfalfa: a 2-acre alfalfa field at the Horticulture Farm 1 mile east of Corvallis on Hwy. 34. Bordered by mixed crops which varied somewhat over the season and included corn, cabbage and other cole crops, bush beans, filberts and peaches. Spray schedule is unknown but a variety of experimental management practices were used at the farm. Harvested mid-July.

Peppermint: A 10-acre field of second-year peppermint 2 miles northeast of Corvallis on Hwy. 20. Bordered by weedy vegetation, another peppermint field, houses and a road with moderate to heavy traffic. Traditional management practices were used, sprayed in mid-July, harvested in mid-August and burned.

Clover: A 7-acre crimson clover field 10 miles north of Corvallis on Hwy. 99. Bordered by winter wheat and a road with moderate traffic. Chemical pesticides had not been used for several years. Harvested in late August.

Entomology filbert: A 2-acre orchard of over 20-year old filbert trees at the Entomology Farm adjacent to the OSU campus. Bordered by weedy vegetation, mixed orchards: apple, cherry, pear and plum, and the alfalfa field mentioned previously. A variety of management practices were used at the farm.

McDonald Forest: A mixed oak (<u>Quercus garryana</u> Dougl.), Douglas fir (<u>Pseudotsuga menziesii</u> (Mirbel)Franco) forest adjacent to meadow and riparian area along Oak Creek 5 miles northwest of Corvallis. This area was also an overwintering site for aggregating <u>H.</u> <u>convergens</u>.

Kiger riparian: A disturbed area along the banks of the Willamette River on Kiger Island 5 miles south of Corvallis. Vegetation was mainly blackberry (<u>Rubus</u> <u>ursinus</u> Cham. & Schlecht) and garden tansy (<u>Tanacetum</u> <u>vulgare</u> L.) with an adjacent field of sweet corn along the entire length.

Three different collecting methods were used depending on the type of plant at each site. A standard 38 cm diameter sweep net was used in field crops (peppermint, clover and alfalfa) and at the McDonald Forest meadow. In filbert orchards and at the McDonald Forest site a 36cm x 36cm beating sheet was used to catch beetles knocked from tree foliage. At the overwintering aggregation site and at the Kiger site an aspirator was used to individually collect beetles. In an effort to standardize these collecting methods, 30 minutes of collecting time was allotted at each site. Sampling was conducted from late April through August.

All field-collected beetles were kept in 50x30x45cm sleeve cages at 22°C for 1 week. Beetles were fed green peach aphids (<u>Myzus persicae</u> [Sulzer]) which had been reared on chinese cabbage (<u>Brassica campestris</u> L.) at the OSU greenhouses. The 1 week period allowed parasitoid eggs (if present) to hatch into first instars, a stage easier to detect during dissection. All parasitoids that pupated during that week were reared to the adult stage to maintain a laboratory culture of <u>D. coccinellae</u>.

After 1 week, all surviving beetles were preserved in a KASA solution for 24 hours and then permanently preserved in 75% ETOH. These beetles were dissected to determine if they had been parasitized by <u>D. coccinellae</u>.

Species and sex of the coccinellids, parasitoid instar, habitat and date collected were recorded for each beetle. Beetles were identified using the key to the Coccinellidae of Western Canada and Alaska (Belicek, 1976). Chi-square tests were done to determine significance of the effects of host species, habitat and sex of host on <u>D. coccinellae</u> parasitism. Expected values were computed by multiplying total number by expected proportion in the sample.

EFFECT OF HOST SIZE ON PARASITISM

All field-collected coccinellids were measured previous to dissection. The maximum length, width and

height of the elytra were measured to compute relative volume ($1 \times w \times h = v$). This measurement was used to estimate the potential resource available to a parasitoid since the larva is confined to the abdomen and mesa and metathorax of the host. One-way Analysis of Variance (ANOVA) using Least Significant Difference (LSD) range tests were conducted to evaluate the effect of host size on parasitism. Data were examined over all coccinellids combined, among host species, within species, and between sexes of hosts. Regression analyis determined the relationship of parasitism to average species size.

A total of 84 adult <u>D. coccinellae</u> which had emerged from beetles under laboratory conditions were used to determine the effect of host size on the size of the parasitoid. Adult parasitoids were dried for 24 hours in an oven (40°C) and weighed on a Cahn electronic analytical balance. Host beetles were measured as described above. A One-Way ANOVA using an LSD range test was used to determine the effect of host species size on weight of parasitoid. A regression analysis determined the overall relationship (all host species combined) of host volume to parasitoid weight.

EFFECT OF FAT BODY WEIGHT ON PARASITISM

Since the actual resource of the larval parasitoid is the fat body of the host, a separate group of field collected coccinellids were used to determine the relationship between weight of fat body and dry weight of the beetle. Individuals of 5 species were used: <u>C.</u> <u>undecimpunctata</u>, <u>C. trifasciata</u>, <u>C. californica</u>, <u>H.</u> <u>convergens</u>, and <u>A. bipunctata</u>. To control for seasonal differences in fat content, beetles were all collected during the first week of August, 1984.

Lipids were extracted with ether using a Soxhlet apparatus (Fig.1). Beetles were dried for 24 hours in a 40^oC oven and then weighed on a Cahn electronic analytical balance. Each beetle was placed in a 10mm cotton Whatman extraction thimble and the thimble was placed in the extractor. The flask was 3/4 filled with petroleum ether and cold water was passed through the condenser jacket. The flask was heated, solvent vapors ascended through the side arm, condensed and dripped onto the thimble. The solvent, now containing soluble lipids from the beetle, siphoned over into the flask. The extraction was run for 8 hours and the apparatus was then cooled for 10 minutes. Beetles were dried in a 40^oC oven for 24 hours to remove the ether and then reweighed. Weight of fat body was determined from the difference in beetle dry weight before and after extraction. This extraction method was a modification of the procedure used for mosquitoes at the Department of Entomology, Oregon State University.

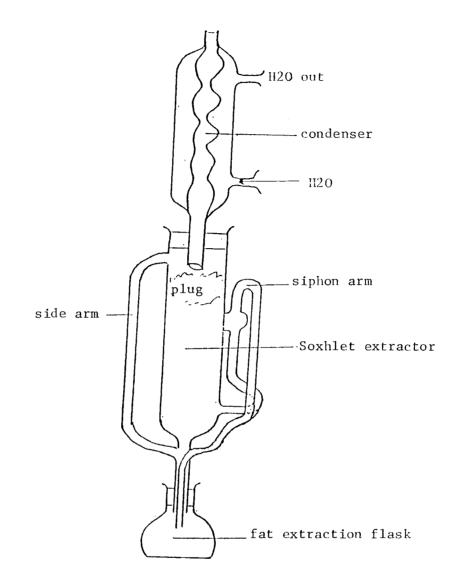


Figure 1. Diagram of Soxhlet apparatus used in lipid extraction of coccinellid hosts of <u>D. coccinellae</u>.

A regression analysis demonstrated the relationship between fat body weight and dry weight of the beetle in order to determine if beetle size was an accurate estimation of actual resource for the parasitoid.

HOST SUITABILITY OF ADALIA BIPUNCTATA

The interaction between <u>D. coccinellae</u> adults and <u>A.</u> <u>bipunctata</u>, a species of aphidophagous coccinellid rarely found parasitized, was observed in the laboratory. A culture of parasitoids was maintained in the laboratory at 22° C in a 50x40x35cm sleeve cage. Parasitoids were given a honey-water solution and field-collected coccinellids several times weekly. Several acceptable host species were introduced to serve both as an ovipositional resource for newly emerged parasitoids and a reservoir for fieldcollected parasitoid larvae. The beetles were maintained on green peach aphids (<u>M. persicae</u>) raised on chinese cabbage.

One adult parasitoid was placed in a Petri dish containing 6 active adult coccinellids. These included 2 <u>A. bipunctata</u>, 2 <u>H. convergens</u> and 2 <u>C. trifasciata</u>. They were observed for 15 minutes. Antennal tapping, pursuit, ovipositional stance (abdomen folded under thorax so that tip extends beyond head), oviposition attempts and beetle behavior were recorded. This procedure was repeated 5 times using 5 different parasitoids and 30 different beetles. All beetles were maintained at 22°C for one week and then dissected.

One adult <u>D. coccinellae</u> was then presented with 5 adult <u>A. bipunctata</u> in a Petri dish. Procedures, observations, and replications were the same as for the previous experiment. A total of 5 parasitoids and 25 <u>A.</u> <u>bipunctata</u> were used. The time allotment was 30 minutes in order to increase the probability of parasitoid oviposition. All beetles were maintained at 22° C for 1 week and then dissected.

At this point it was observed that <u>D. coccinellae</u> did not attempt oviposition in <u>A. bipunctata</u>. In order to stimulate <u>D. coccinellae</u> to use <u>A. bipunctata</u> as a host, parasitoids were isolated without hosts for 3 days after emergence. The above procedure was then repeated using these host-starved individuals. Parasitoids remained with the beetles until oviposition was observed. A total of 50 <u>A. bipunctata</u> were exposed to 10 parasitoids and subsequently dissected to determine the outcome of the oviposition attempts. To follow development of <u>D.</u> <u>coccinellae</u>, 2 beetles were dissected every half-hour for 8 hours immediately following exposure to the parasitoid and then 3 beetles were dissected daily for 2 weeks.

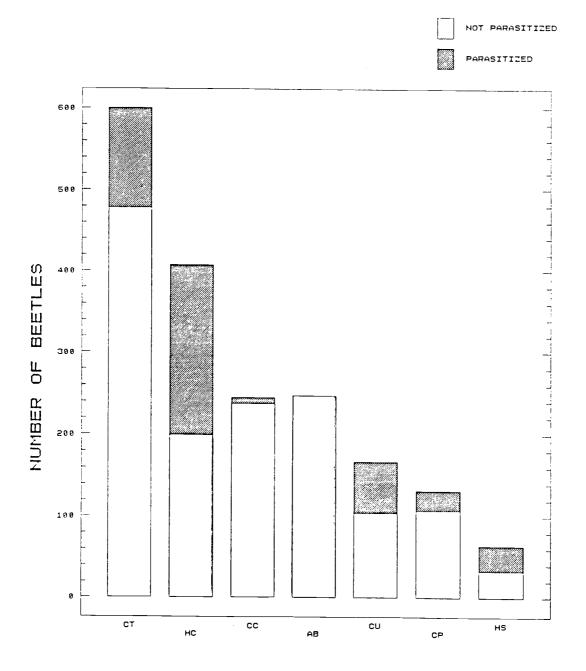
RESULTS AND DISCUSSION

A total of 2272 coccinellid adults consisting of 11 species were collected from 19 sites in 1982-1983 (Table 1). Of these, 27% were found to be parasitized by <u>D</u>. <u>coccinellae</u>. Four species found parasitized were previously unrecorded as hosts: <u>Calvia</u> <u>quatuordecimguttatta</u> (L.) (9%, n=22); <u>Coccinella</u> <u>california Mann (4%, n=265); Cycloneda polita</u> Casey (23%, n=157); and <u>Mulsantina picta</u> (Randall). Three species were never found parasitized: <u>A. bipunctata, Adalia</u> <u>frigida</u> Mulsant and <u>Chilocorus</u> sp.

Degree of parasitism varied among the 8 remaining species and ranged from 4% for <u>C. californica</u> (n=265) to 56% for <u>H. sinuata</u> (n=70). <u>H. convergens</u>, <u>H. sinuata</u> and <u>C. undecimpunctata</u> were parasitized at significantly higher levels, and <u>C. californica</u> significantly lower levels than expected (X^2 , p<0.005). Figure 2 shows the total number collected and the number parasitized for each species. It is obvious that some coccinellids were much more common than others, and that host species were parasitized non-randomly by <u>D. coccinellae</u>. There does not appear to be a relationship between number collected and degree of parasitism; the effect of relative abundance on parasitism will be addressed more completely in a later section. These differences suggest that <u>D. coccinellae</u> Table 1. Number collected and % parasitized by D.coccinellae of coccinellids from seven habitats in theWillamette Valley, Oregon, 1982.

SPECIES	No. Collected	<u>Parasi</u> No.	<u>tized</u> %
<u>Adalia bipunctata</u>	295	0	0
<u>Adalia frigida</u>	31	0	0
<u>Calvia quatuordecim-</u> guttatta*	22	2	9
<u>Chilocorus</u> sp.	1	0	0
<u>Coccinella californica</u> *	265	11	4
<u>Coccinella_trifasciata</u>	757	189	25
<u>Coccinella undecimpunctata</u>	202	. 85	42
<u>Cycloneda polita</u> *	157	36	23
<u>Hippodamia convergens</u>	492	256	52
<u>Hippodamia sinuata</u>	70	39	56
<u>Mulsantina picta</u> *	2	1	50

* New host record for **D. coccinellae**



SPECIES

Figure 2. Number of parasitized and non-parasitized beetles of seven coccinellid species collected in the Willamette Valley, Oregon, 1982: <u>H. convergens</u> (HC); <u>C. trifasciata</u> (CT); <u>C. californica</u> (CC); <u>C. undecimpunctata</u> (CU); <u>C.</u> <u>polita</u> (CP); <u>H. sinuata</u> (HS); <u>A. bipunctata</u> (AB).

parasitizes coccinellids based on species or some aspect of the beetle's biology (ie. habitat, phenology, size). In this study, the 7 most common species of coccinellids were used to examine patterns of parasitism in 8 different habitats over the 5 month period (Table A1). These species will be discussed separately in order of increasing parasitism. Aspects of temporal and habitat distribution and abundance will then be considered.

The use of percent parasitism (number yielding parasitoids by dissection divided by total beetles collected) is sufficient only for broad comparisons in this study. van Driesche (1983) discussed the biases associated with this method of analysis for parasitism impact. Stamp (1981) and Smith Trail (1980) found that parasitism changed the behavior of hosts. Parasitized caterpillars occurred higher and more exposed on vegetation. Sampling by sweep net (a method which selects for more exposed insects) as opposed to hand-picking insects in soybeans resulted in significantly higher parasitism. Sampling methods and analysis by percent parasitism may have biased results in this study.

ADALIA BIPUNCTATA. PARASITISM 0% (N=295). The first coccinellid present at collecting sites in the spring was <u>A. bipunctata</u>. Obrycki and Tauber (1981) found that the threshold temperature for post-diapause reproductive

development in <u>A. bipunctata</u> was lower than that for other aphid predators. Consequently, <u>A. bipunctata</u> was active when populations of filbert aphid (<u>Myzocallis coryli</u> Goetze) began to increase in April.

In May, the number of <u>A. bipunctata</u> collected decreased. This coincided with an increase in coccinellid species richness (5 species) in the Entomology filbert orchard, the only habitat where <u>A. bipunctata</u> was found in May (Fig. 3). Total number of coccinellids collected in filbert remained the same from April to May. In June the population of <u>A. bipunctata</u> increased in filbert, again the only habitat where <u>A. bipunctata</u> was encountered during that month (Fig. 4).

Numbers of <u>A. bipunctata</u> peaked at 142 in July and individuals were collected in 5 habitats: filbert, mint, Kiger, Entomology alfalfa and Peoria alfalfa (Fig. 5). More than half of the <u>A. bipunctata</u> collected in July were from filbert. Mint and filbert contained <u>A. bipunctata</u> in August but numbers of individuals decreased in both from July (Fig. 6). Total number collected in August was the same as for June (Fig. 7).

Adalia bipunctata is considered more arboreal in habit than are most other coccinellid species (Messing, 1982), and was collected in filbert 75% of the time (Fig. 8). <u>A. bipunctata</u> was never found parasitized (Fig. 9), though other coccinellid species which co-occurred with \underline{A} . <u>bipunctata</u> were parasitized by <u>D. coccinellae</u>.

COCCINELLA CALIFORNICA. PARASITISM 4% (N=265). New host record for <u>D. coccinellae</u>. Only 11 individuals of <u>C.</u> <u>californica</u> were collected from April through June. The first parasitized individuals were found at the Entomology alfalfa site in June, when 3 of 8 <u>C. californica</u> were parasitized by <u>D. coccinellae</u> (Fig. 4). Two individuals were found at the horticulture alfalfa site in June but were not parasitized.

The number of <u>C. californica</u> increased steadily through July and August (Fig. 7). A total of 110 individuals were collected over 5 habitats in July: Entomology alfalfa, Peoria alfalfa, clover, mint, and Kiger (Fig. 5). Parasitized <u>C. californica</u> were found on clover, mint and at the Kiger site on garden tansy (<u>T.</u> <u>Vulgare</u>); the highest level of parasitism was 15% (n=20) in mint. Overall % parasitism in July was 6% (Fig. 9), a decrease most probably caused by the increase in number collected.

Parasitism of <u>C. californica</u> decreased in August (Fig. 9) and the number collected increased to 141 (Fig. 7). Individuals of <u>C. californica</u> were found in 6 of the 8 habitats in August (Fig. 6) though Peoria alfalfa produced

over 50% n=78). None was collected at entomology alfalfa or McDonald Forest.

CYCLONEDA POLITA. PARASITISM 23% (N=157). New host record for <u>D. coccinellae</u>. The first individuals of <u>C.</u> <u>polita</u> were collected in McDonald Forest and filbert in May, 5 of the 7 collected were parasitized (Fig. 3). In June, numbers collected increased (n=24) and parasitism decreased from 71% in May to 22% (Fig. 9). The majority were found in filbert (n=20); 4 of these were parasitized (Fig. 4). Messing (1982) reported that <u>C. polita</u> was the second most common coccinellid found in filbert orchards in western Oregon.

In July, 67 of the 76 <u>C. polita</u> collected were found in filbert. Parasitism for the month was 19%, slightly lower than for June (Fig. 9). A decrease in populations of <u>C. polita</u> in August (n=27) did not affect parasitism (22%), (Fig. 9). Although 7 individuals were found in other habitats (clover, mint, McDonald Forest and Horticulture alfalfa), most <u>C. polita</u> were collected on filbert.

Parasitism of <u>C. polita</u> remained fairly constant from June through August (Fig. 9). This species was fairly habitat specific throughout the season (Fig. 8). **<u>COCCINELLA TRIFASCIATA</u>** L. PARASITISM 25% (N=757). By far the most abundant aphidophagous coccinellid in the Willamette Valley, <u>C. trifasciata</u> was present in all 8 habitats (Fig. 8). Numbers collected increased steadily from April through August (Fig. 7).

Parasitized individuals were first found in May, at all 3 sites that produced <u>C. trifasciata</u>: McDonald Forest, Entomology alfalfa and filbert (Fig. 3). Parasitism peaked at 39% in June (n=115) and was distributed over 3 habitats (Fig. 4). The highest parasitism for the month was in Entomology alfalfa (48%), the habitat that produced the most number of <u>C. trifasciata</u> (n=62). At the Entomology farm, it appeared that <u>C. trifasciata</u> moved from the filbert orchard in May to the adjacent alfalfa field in June.

In July numbers of <u>C. trifasciata</u> increased (n=239) (Fig. 7) and parasitism decreased (Fig. 9). It is possible that <u>D. coccinellae</u> cannot respond proportionally to the increase in host density. <u>Coccinella trifasciata</u> were found parasitized in 6 of the 7 habitats in July (Fig. 5). Five individuals were collected at the Kiger site but none were parasitized.

In August the numbers of <u>C. trifasciata</u> were concentrated in clover and Peoria alfalfa although a few individuals were encountered at all other sites (Fig. 6).

Total number collected continued to increase as parasitism decreased. (Figs. 7,9).

<u>C. trifasciata</u> was common throughout the season in field crops, orchards and in McDonald Forest in both arboreal and meadow habitats (Fig. 8).

COCCINELLA UNDECIMPUNCTATA L. PARASITISM 42% (N=202). From April to June, only 11 individuals were collected. In May, parasitism was 100% (n=9), and distributed over 2 habitats, Entomology alfalfa and filbert (Fig. 3); these 2 habitats were adjacent to each other. No <u>C.</u> <u>undecimpunctata</u> were collected the entire month of June. It is possible that the 100% parasitism observed in May was an accurate indication of the effect of <u>D. coccinellae</u> on <u>C. undecimpunctata</u>.

In July <u>C. undecimpunctata</u> occurred in 5 habitats and parasitism ranged from 16% (Kiger, n=32) to 59% (mint, n=32). One individual was found in Entomology and 1 in Peoria alfalfa; both were parasitized.

Number of <u>C. undecimpunctata</u> increased in August (n=118) and parasitism decreased (36%) (Figs. 7,9). Parasitized individuals were collected from 5 of the 6 habitats where <u>C. undecimpunctata</u> were found. A total of 99 of the 118 <u>C. undecimpunctata</u> collected in August were from Peoria and clover (Fig. 6). **HIPPODAMIA CONVERGENS**. PARASITISM 52% (N=492). A total of 139 <u>H. convergens</u> were collected from overwintering aggregations in addition to the 492 considered in seasonal comparisons with other species from April through August. Parasitism in aggregations was 60%, which was significantly higher than that in the summer.

From April through June, only 25 individuals were collected (Fig. 5). Of these 25 individuals, 9 were parasitized and were distributed over the 3 habitats where <u>H. convergens</u> was collected: filbert, Entomology alfalfa and mint (Figs. 3,4).

Parasitism remained fairly constant from May through July (Fig. 9) though numbers and distribution varied greatly. In July, <u>H. convergens</u> occurred in 6 habitats (all but Entomology alfalfa) but most were collected in Peoria, clover, mint and Kiger. Parasitism varied from 33% (n=70) at Kiger to 53% (n=30) in mint (Fig. 5). The higher numbers of <u>H. convergens</u> collected at Kiger (70 compared to an average of 30 for the other 3 sites) may be an indication of midsummer aggregating behavior. Historically, <u>H. convergens</u> will leave feeding sites in midsummer when prey populations crash and migrate to outlying areas where they will enter diapause or feed on alternate food sources (ie. pollen) (Hodek, 1973). Most coccinellids at Kiger in July appeared to be feeding on pollen of the garden tansy plants (<u>T. vulgare</u>). It is

probable that midsummer aggregating behavior has been modified due to the introduction of irrigated crops and exotic aphids.

It appeared that <u>H. convergens</u> returned to agricultural areas in August and were collected mainly in Peoria alfalfa and clover. However, parasitized individuals were found at all sites except filbert (Fig. 6). Overall parasitism for the month was 57% (n=141) (Fig. 9). Parasitism and number collected were highest in clover, 72% (n=60) but parasitism of <u>H. convergens</u> increased at all sites (Fig. 6).

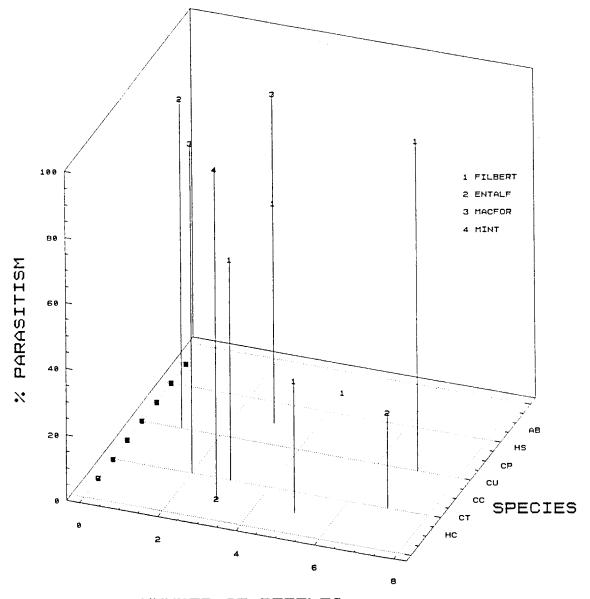
The increase in parasitism late in the season coincided with 60% parasitism at the aggregation sites, the highest of the year for <u>H. convergens</u>. The lower level of parasitism in the spring and early summer may be a result of high winter mortality in parasitized individuals.

HIPPODAMIA SINUATA Mulsant. PARASITISM 56% (N=70). Although <u>H. sinuata</u> was a relatively uncommon species throughout the collecting season, degree of parasitism was high (Fig. 9). Individuals of <u>H. sinuata</u> were not encountered until July, and only 34 and 33 individuals were collected in July and August respectively (Fig. 7).

With the exception of 3 individuals collected at Peoria in August, all <u>H. sinuata</u> were found at the clover site. The high levels of parasitism of all coccinellids in this habitat (39%, n=390) may be related to the presence of <u>H. sinuata</u> (a preferred species) in clover, if <u>D. coccinellae</u> searched for this particular species of host. More probably the fact that this site was not sprayed resulted in higher numbers of parasitoids.

SEASONAL RESULTS

Figure 10 shows the weekly number of beetles collected as it compared to parasitism from late April (week 1) through August. Figure 11 pools the weekly data by months. The first parasitized beetle was found during the last week of April in a small field of peppermint at the OSU Entomology Farm in Corvallis. Only 25 coccinellids were collected in April. A. bipunctata was present in filbert at this time, probably because of the lower temperature threshold required for reproductive development as mentioned earlier and because of the early population of filbert aphids at this site. In May, parasitism was 30%, the highest of the entire season. D. coccinellae may have arrived at collecting sites before the populations of coccinellids increased. Of the 90 beetles collected in May, 27 were parasitized. In the Willamette Valley, coccinellids do not migrate in great numbers to agricultural areas until July. It is possible that early concentrations of a few suitable host species



NUMBER OF BEETLES

Figure 3. Number collected and percent parasitized by <u>D.</u> <u>coccinellae</u> of seven coccinellid species in four habitats (filbert, entomology alfalfa, McDonald Forest, peppermint) in May; Willamette Valley, Oregon, 1982: <u>H. convergens</u> (HC); <u>C. trifasciata</u> (CT); <u>C. californica</u> (CC); <u>C. undecimpunctata</u> (CU); <u>C. polita</u> (CP); <u>H. sinuata</u> (HS); <u>A. bipunctata</u> (AB).

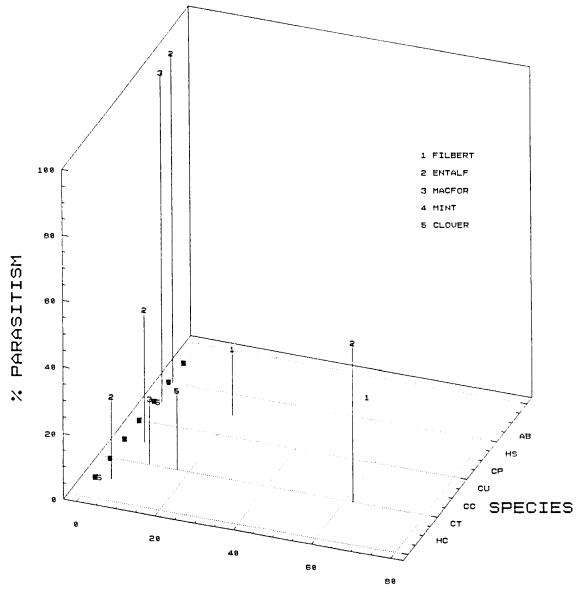




Figure 4. Number collected and percent parasitized by <u>D</u>. <u>coccinellae</u> of seven coccinellid species in five habitats (filbert, entomology alfalfa, McDonald Forest, peppermint, clover) in June; Willamette Valley, Oregon, 1982: <u>H</u>. <u>convergens</u> (HC); <u>C. trifasciata</u> (CT); <u>C. californica</u> (CC); <u>C. undecimpunctata</u> (CU); <u>C. polita</u> (CP); <u>H. sinuata</u> (HS); <u>A.</u> <u>bipunctata</u> (AB).

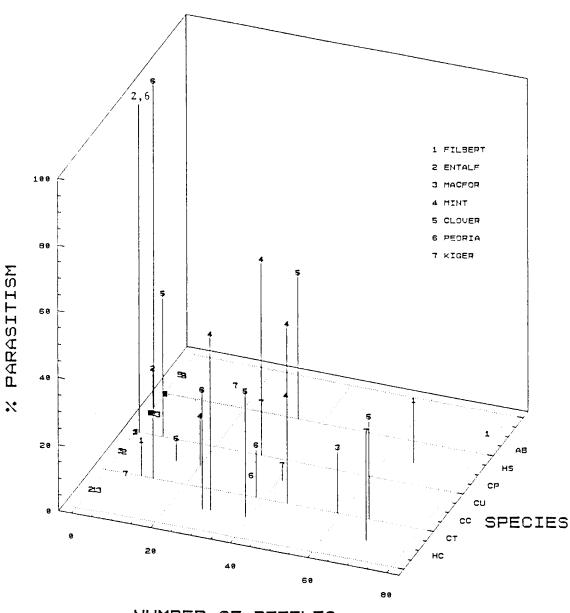
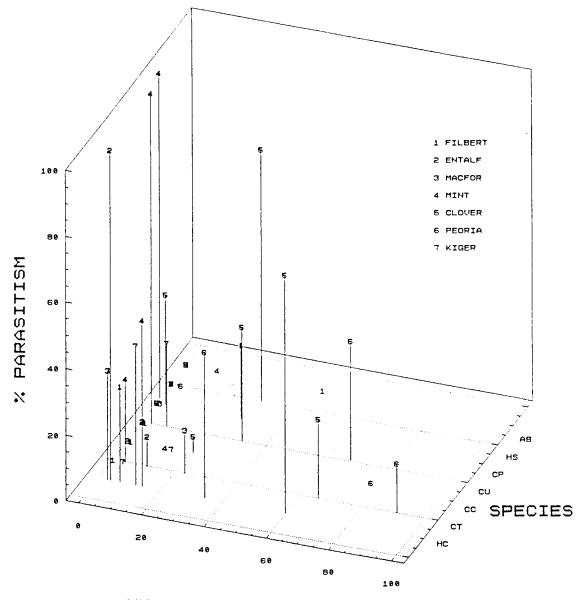




Figure 5. Number collected and percent parasitized by <u>D.</u> <u>coccinellae</u> of seven coccinellid species in seven habitats (filbert, entomology alfalfa, McDonald Forest, peppermint, clover, Peoria alfalfa, Kiger) in July; Willamette Valley, Oregon, 1982: <u>H. convergens</u> (HC); <u>C. trifasciata</u> (CT); <u>C.</u> <u>californica</u> (CC); <u>C. undecimpunctata</u> (CU); <u>C. polita</u> (CP); <u>H. sinuata</u> (HS); <u>A. bipunctata</u> (AB).



NUMBER OF BEETLES

Figure 6. Number collected and percent parasitized by <u>D.</u> <u>coccinellae</u> of seven coccinellid species in seven habitats (filbert, entomology alfalfa, McDonald Forest, peppermint, clover, Peoria alfalfa, Kiger) in August; Willamette Valley, Oregon, 1982: <u>H. convergens</u> (HC); <u>C. trifasciata</u> (CT); <u>C.</u> <u>californica</u> (CC); <u>C. undecimpunctata</u> (CU); <u>C. polita</u> (CP); H. sinuata (HS); <u>A. bipunctata</u> (AB).

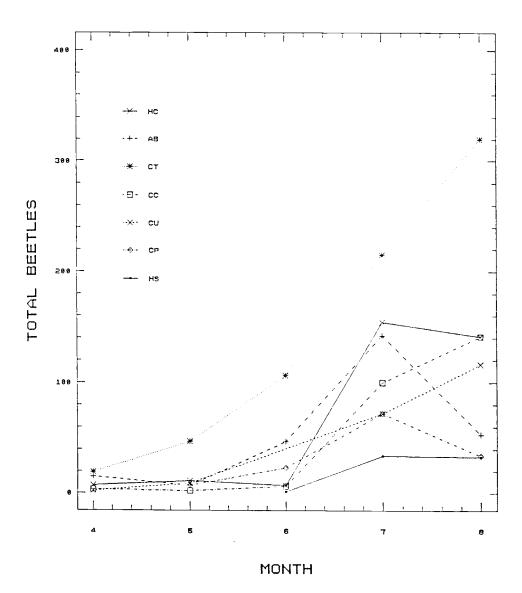


Figure 7. Number of beetles collected monthly April through August in the Willamette Valley, Oregon, 1982: <u>H. convergens</u> (HC); <u>C. trifasciata</u> (CT); <u>C. californica</u> (CC); <u>C.</u> <u>undecimpunctata</u> (CU); <u>C. polita</u> (CP); <u>H. sinuata</u> (HS); <u>A.</u> <u>bipunctata</u> (AB).

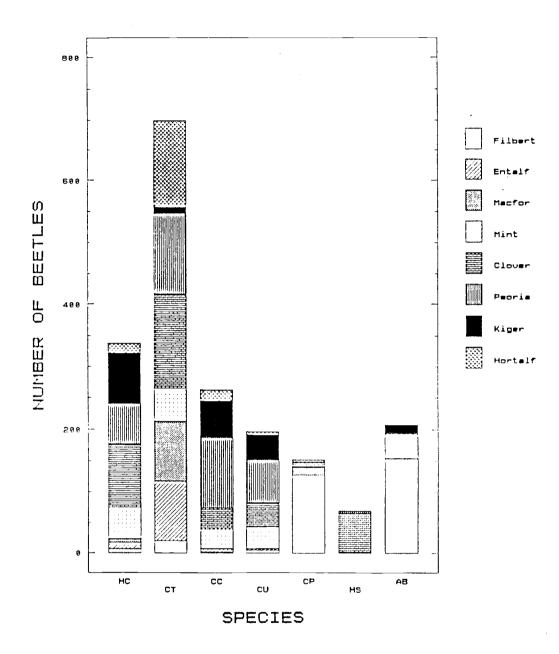
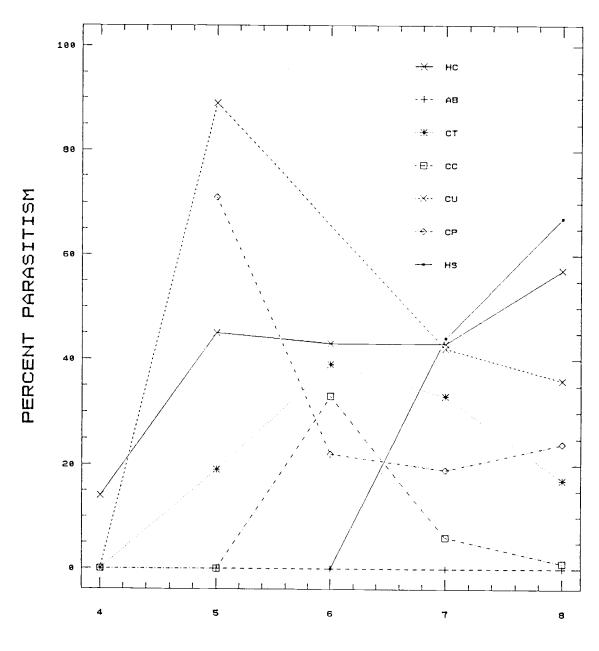
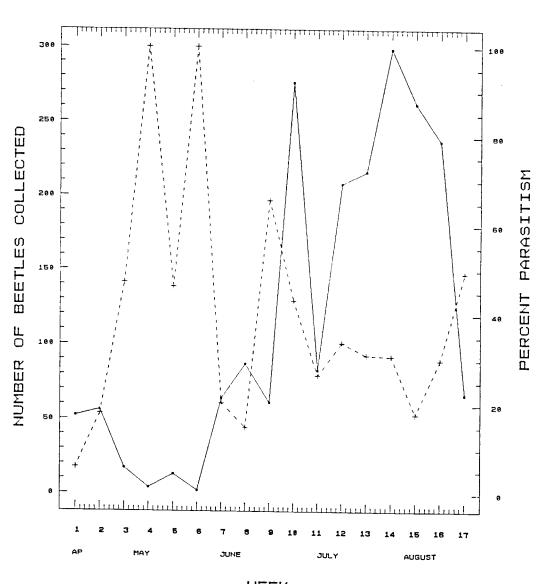


Figure 8. Distribution of seven coccinellid species over eight habitats (filbert, entomology alfalfa, McDonald Forest, peppermint, clover, Peoria alfalfa, Kiger, horticulture alfalfa) in the Willamette Valley, Oregon, 1982: <u>H. convergens</u> (HC); <u>C. trifasciata</u> (CT); <u>C.</u> <u>californica</u> (CC); <u>C. undecimpunctata</u> (CU); <u>C. polita</u> (CP); <u>H. sinuata</u> (HS); <u>A. bipunctata</u> (AB).



MONTH

Figure 9. Parasitism by <u>D. coccinellae</u> of seven species of coccinellids April through August in the Willamette Valley, Oregon, 1982: <u>H. convergens</u> (HC); <u>C. trifasciata</u> (CT); <u>C. californica</u> (CC); <u>C. undecimpunctata</u> (CU); <u>C. polita</u> (CP); <u>H. sinuata</u> (HS); <u>A. bipunctata</u> (AB).



WEEK

Figure 10. Parasitism by <u>D. coccinellae</u> and number of coccinellids collected weekly April through August in the Willamette Valley, Oregon, 1982.

NUMBER

PERCENT

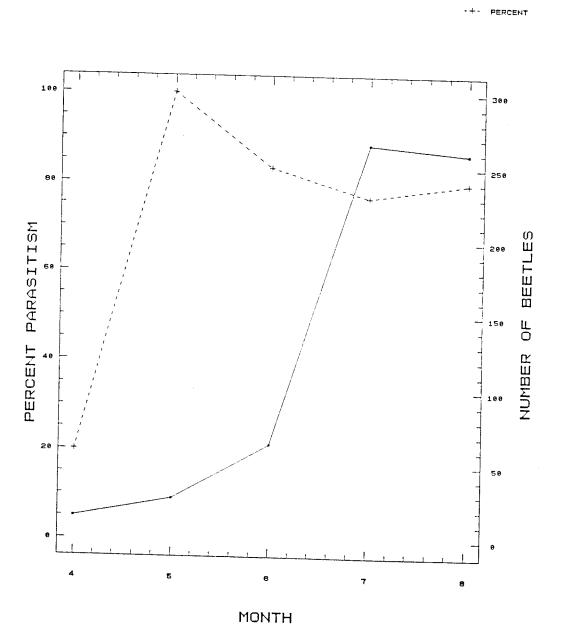


Figure 11. Parasitism by <u>D. coccinellae</u> and number of coccinellids collected monthly April through August in the Willamette Valley, Oregon, 1982.

NUMBER

resulted in intense parasitization by just a few <u>D.</u> <u>coccinellae</u> individuals.

In June, total number of beetles collected increased to 213 and parasitism dropped to 25% (Fig. 10). However, parasitism peaked in the fourth week of the month (week 9) at 66% (n=61). Parasitism decreased to 23% of the 886 coccinellids collected in July (Fig. 11). It is possible that <u>D._coccinellae</u> cannot respond proportionally to this host increase. However, a total of 276 coccinellids were collected in the first week of July, and parasitism was 43%. The high level of parasitism for 2 consecutive weeks (week 9,10) may be an indication of the emergence of the second generation of adult parasitoids. Parasitism remained fairly stable for the next 4 weeks and varied from 27% to 34%. This coincided with a continuous increase in the number of beetles collected. The peak occurred the first week of August at 299 beetles. Parasitism decreased to 18% the next week (week 15), the lowest since mid-June, and then increased to 49% in the last week of August. Number of coccinellids sharply decreased in one week from 237 to 33 collected the final week.

There is no indication of a third generation of <u>D</u>. <u>coccinellae</u> at the end of July, the approximate week that emergence should have occurred if the peak at the end of June was the beginning of a second generation. However,

the increase to almost 50% at the end of August suggests that another generation may have emerged. Populations of adult <u>D. coccinellae</u> peaked at 54 parasitoids collected/hr per site in late August in the study by Richerson and DeLoach in 1972. It is believed that <u>D. coccinellae</u> may have 4 to 5 generations a year (Obrycki and Tauber, 1979; Richerson and DeLoach, 1972). Agricultural sites were less stable towards the end of August and into September because of harvest, spray schedules and field burnings. Seasonal data on parasitism and host density were not used past August because of these events.

It is necessary to consider both species and habitat in an examination of seasonal trends in this parasitoid. There is evidence that <u>D. coccinellae</u> may select hosts based on coccinellid species. Preference for particular habitats is common in hymenopteran parasitoids (van Alphen and Vet, 1986). Since 7 species of beetles and 8 habitats were combined in Figs. 10 and 11, species and habitat patterns are unknown.

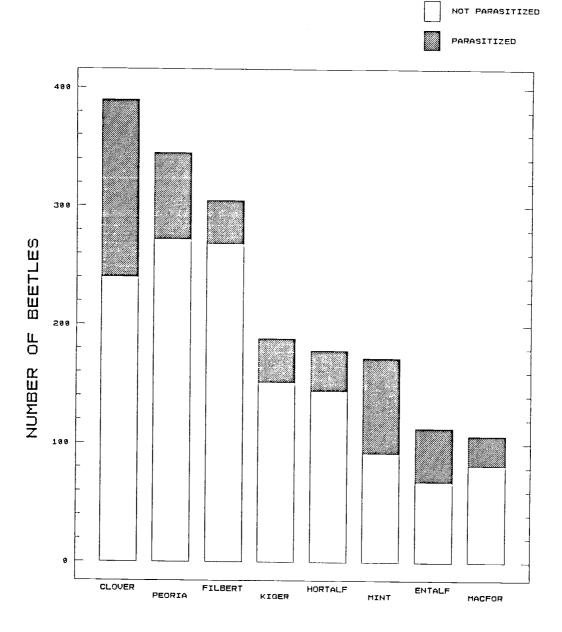
The seasonal pattern of parasitism shown in Fig. 10 indicates that adult <u>D. coccinellae</u> were present from late April to September. Percent parasitism was never below 15% for any week. Although numbers of available hosts fluctuated from April through August, there was a general increase in number collected of all species in July which remained fairly stable through August (Fig. 7). It is

probable that adult <u>D. coccinellae</u> were temporally synchronized with the 7 coccinellid species used in this study.

HABITAT EFFECTS

Of the 17 total habitats that produced coccinellids, 7 were considered when seasonal and species patterns of parasitism were examined. Sites were selected based on the number of beetles collected and the consistency in numbers over the season. In August, 145 beetles were collected from the alfalfa site at the Horticulture farm in Corvallis but none during the 5 previous weeks. Therefore this site was not included when seasonal trends were examined. Relative abundance of coccinellids and degree of parasitism over habitats were used only for broad comparisons because sampling efforts could not be strictly standardized.

Overall parasitism and number of beetles collected in each habitat is shown in Fig. 12. Parasitism differed significantly for the 7 sites discussed and the McDonald aggregation site ($X^2=192$, p<.001). This chi-square goodness of fit test indicates that parasitism was significantly higher in clover, mint and the aggregation, and lower in filbert. It is possible that <u>D. coccinellae</u> searched for hosts by selecting particular habitats.



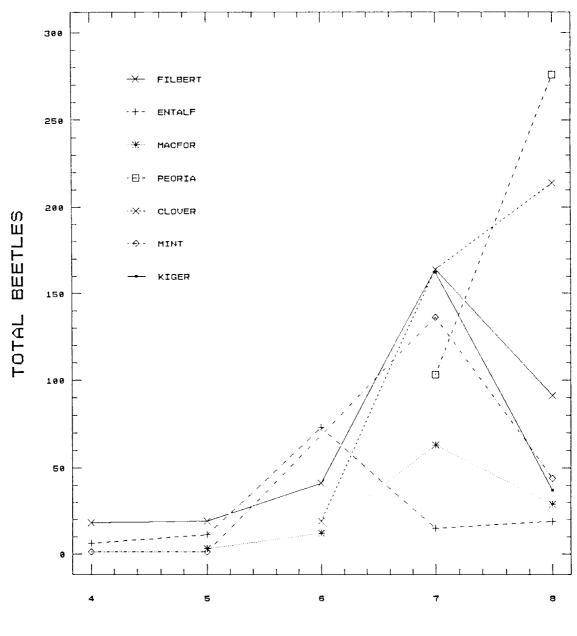
COLLECTING SITE

Figure 12. Number of parasitized and non-parasitized coccinellids collected from eight habitats (clover, Peoria alfalfa, filbert, Kiger riparian, horticulture alfalfa, peppermint, entomology alfalfa, McDonald Forest) in the Willamette Valley, Oregon, 1982.

Figure 13 shows the number collected in each habitat by month. Coccinellids were found in the filbert orchard at the OSU Entomology Farm earlier in the spring than other habitats, probably due to the presence of filbert aphid at that time. In May, parasitism peaked for the season at 53% (n=22) (Fig. 14). This was probably due to the species present rather than an affinity for filbert by <u>D. coccinellae</u>. By June, parasitism had decreased to 12% and remained fairly stable for the remainder of the season in spite of the fluctuation in beetle numbers. Number collected peaked in July at 164 beetles.

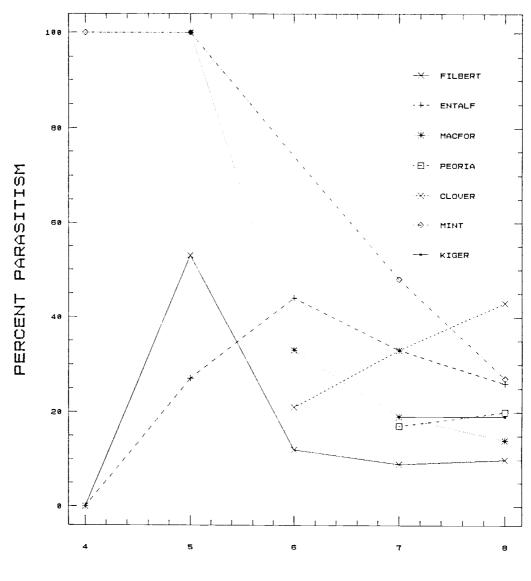
The alfalfa field adjacent to the filberts at the Entomology Farm was the only other habitat where more than 5 beetles were collected in April or May (Fig. 13). Parasitism peaked in June at 44% (n=73) and then decreased through July and August (Fig. 14). The decrease may have been the result of a build-up of host populations at other sites. Only 34 beetles were collected in this habitat after June.

Beetle density at McDonald Forest was moderate compared to other sites. Parasitism was below 20% in July and August. Number of beetles collected peaked in July at 63, possibly due to the habit of coccinellids to migrate to outlying areas when prey populations crash. A subsequent decrease in host numbers in August suggests that beetles may have returned to feeding sites. There



MONTH

Figure 13. Number of coccinellids collected monthly April through August from seven habitats in the Willamette Valley, Oregon, 1982: filbert, entomology alfalfa, McDonald Forest, Peoria alfalfa, clover, peppermint, Kiger.



MONTH

Figure 14. Parasitism by <u>D. coccinellae</u> of coccinellids collected from seven habitats (filbert, entomology alfalfa, McDonald Forest, Peoria alfalfa, clover, peppermint, Kiger) April through August in the Willamette Valley, Oregon, 1982. have been several accounts in the literature of similar occurrences (Hodek, 1973; Hagen, 1962).

McDonald Forest was the site of overwintering aggregations of <u>H. convergens</u> from October to March and parasitism was 60% (n=139) although <u>H. convergens</u> were rare during the collecting season.

Overall beetle density was relatively high at the alfalfa field on Peoria Road northeast of Corvallis (n=378). This site was the main source of coccinellids in August (Fig. 13). A total of 273 individuals were collected in that month. However, parasitism was relatively low in July and August (17% and 20% respectively) (Fig. 14).

Parasitism and number of coccinellids collected increased steadily from June through August at the clover field north of Corvallis (Figs. 13,14). Overall, the highest number of beetles (n=388) were found at this site and August parasitism reached 43% (n=214). The high number of beetles and parasitoids at this site may be due to the use of organic methods of pest control from 1980 through the collecting season of this study.

Due to spray schedules and harvest, the peppermint field on Hwy. 99 was an inconsistent source of beetles. A total of 136 were collected in July, but high numbers of beetles per collecting effort suggest that the potential number of hosts was much higher at this site. Only 44

beetles were collected in August (Fig. 13). Parasitism was relatively high at this site; in July and August it was 48% and 27% respectively (Fig. 14).

At the Kiger site along the Willamette River south of Corvallis, coccinellids were not encountered until mid-July. It is possible that the midsummer influx of beetles was a result of the coccinellid migration away from feeding sites that was mentioned earlier in this discussion. Hodek (1973) reports that coccinellids will change their diet to pollen in midsummer when prev populations crash. It appeared that the beetles at the Kiger site were feeding on pollen from the garden tansy plants (T. vulgare). Parasitism was consistently low at 19% for both July (n=162) and August (n=37). It is possible that D. coccinellae did not enter the Kiger site as adults to search for hosts since the populations of coccinellids were very temporary. Collection of adult D. coccinellae was not attempted. Coccinellids may have flown into this site already parasitized.

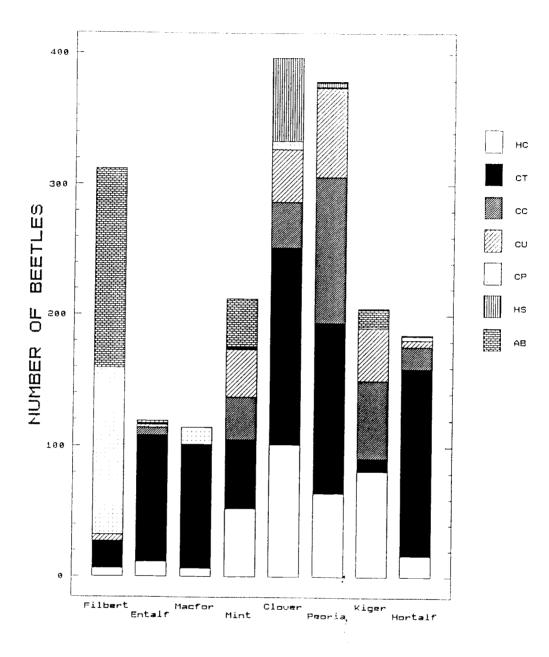
The monthly parasitism for each habitat is shown in Fig. 14. Until June, fluctuations were mainly a function of the low numbers of host species in addition to a possible species and habitat preference by <u>D. coccinellae</u>. Overall parasitism of these 7 habitats varied from a low of 12% in Entomology filbert to 47% in mint (Fig. 12). In

all months except April parasitism was 12% or more in habitats producing beetles (Fig. 14). Although this study did not take into account the fact that beetles could have flown into the site already parasitized, it is probable that adult <u>D. coccinellae</u> were present at all of these sites from June through August if coccinellids are present. This implies that spatial synchrony at the habitat level was not a factor that affected parasitism among host species. Microhabitat preference and behavior of coccinellid species could have affected number of encounters with the parasitoid. The searching behavior of the parasitoid may have differed among habitats due to the architecture of the plants (trees vs. herbs). The interaction of host species, host habitat and time of year as it relates to <u>D. coccinellae</u> parasitism needs to be examined for an overall perspective.

EFFECT OF HOST SPECIES, HOST HABITAT AND TIME OF YEAR

Parasitism has been determined to be significantly different among species and among habitats. If <u>D.</u> <u>coccinellae</u> preferred certain host species, this preference may have affected habitat parasitism. If an affinity for types of habitats existed, degree of species parasitism may have been affected.

Fig. 15 shows the host species distribution in habitats for the collecting season. Most sites were



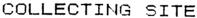


Figure 15. Relative abundance of seven species of coccinellids in eight habitats (filbert, entomology alfalfa, McDonald Forest, Peoria alfalfa, clover, peppermint, Kiger, horticulture alfalfa) in the Willamette Valley, Oregon, 1982: <u>H. convergens</u> (HC); <u>C. trifasciata</u> (CT); <u>C.</u> <u>californica</u> (CC); <u>C. undecimpunctata</u> (CU); <u>C. polita</u> (CP); <u>H. sinuata</u> (HS); <u>A. bipunctata</u> (AB). dominated by a few species. <u>A. bipunctata</u> and <u>C. polita</u> dominated the filbert site. <u>C. trifasciata</u>, though common in most habitats, was the most significant species in Entomology alfalfa, McDonald Forest and Horticulture alfalfa.

Some species were less restricted in their habitat than others. C. trifasciata was the most eurytopic and was at least as common as any other species at all sites except Kiger and filbert. Numbers of H. convergens, C. californica and C. undecimpunctata were also distributed over several sites. <u>C. polita</u> and <u>A. bipunctata were</u> fairly restricted to filbert. Since filbert was dominated by these two species it is probable that any preference by the parasitoid for either the habitat or the host species would have directly affected the parasitism of the other. H. sinuata was found almost exclusively in clover though all other species were also found at this site. If D. coccinellae preferred clover over other habitats, then parasitism in <u>H. sinuata</u> may have been high for this reason.

The monthly distribution of beetle species in habitats is shown in Fig. 16. The coccinellid guild for each habitat appears to change monthly. At the Kiger site, 6 species were present in July and <u>H. convergens</u>, <u>C.</u> <u>californica</u>, <u>C. undecimpunctata</u> and <u>A. bipunctata</u> were common. In August at Kiger, a few individuals of 4

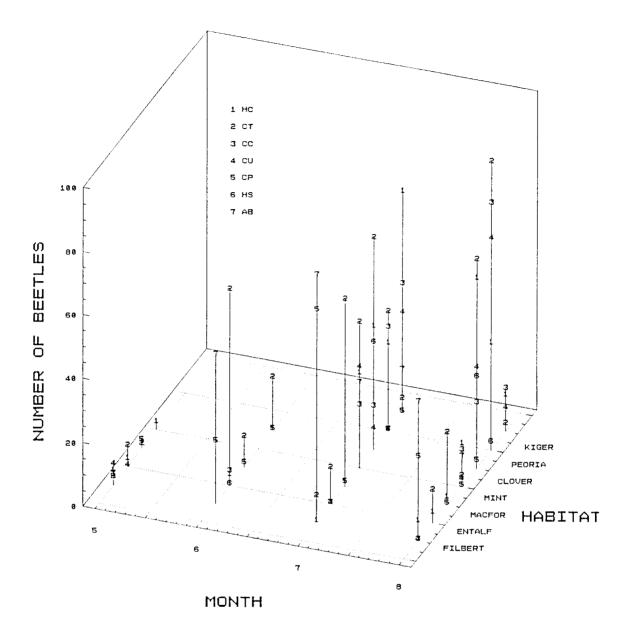


Figure 16. Distribution of seven species of coccinellids over seven habitats (filbert, entomology alfalfa, McDonald Forest, Peoria alfalfa, clover, peppermint, Kiger) collected May through August in the Willamette Valley, Oregon, 1982: <u>H. convergens</u> (HC); <u>C. trifasciata</u> (CT); <u>C. californica</u> (CC); <u>C. undecimpunctata</u> (CU); <u>C. polita</u> (CP); <u>H. sinuata</u> (HS); <u>A. bipunctata</u> (AB).

species were collected. At Peoria alfalfa, <u>C.</u> <u>undecimpunctata</u> was absent in July and over 80 individuals were collected in August. The seasonal fluctuations of parasitism in habitats has been discussed. Monthly fluctuations in parasitism may be a result of coccinellid guild variation.

The monthly parasitism for each species is shown by habitat in Fig. 17. Parasitism for most species varied by month and by habitat. In order to determine if <u>D</u>. <u>coccinellae</u> cued in on particular habitats, the difference in species parasitism was examined over different habitats. For <u>H. convergens</u>, parasitism was almost equal for July in clover, Peoria alfalfa and Kiger. It was slightly higher in mint. The difference among habitats was not significant ($X^2=3.3$, p<.1). In August, parasitism for this species was the same in mint, Peoria alfalfa and Kiger, slightly lower in McDonald Forest and filbert, and higher in clover (p<.002). Parasitism then increased to 60% at the overwintering sites. The difference between winter and total summer sites for this species is significant (p<.05).

The degree of parasitism for <u>C. trifasciata</u> was significantly different among habitats in July (p<.05). In mint, 25 of 46 individuals were parasitized (54%) as opposed to 31 % in clover and 16% at Peoria. In August, there was no difference among habitats ($X^2=3.3$). A

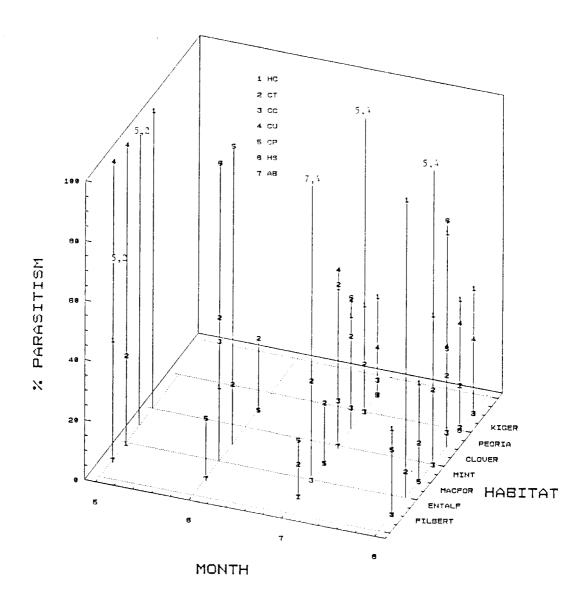


Figure 17. Parasitism by <u>D. coccinellae</u> of seven species of coccinellids collected from seven habitats (filbert, entomology alfalfa, McDonald Forest, Peoria alfalfa, clover, peppermint, Kiger) May through August in the Willamette Valley, Oregon, 1982: <u>H. convergens</u> (HC); <u>C. trifasciata</u> (CT); <u>C. californica</u> (CC); <u>C. undecimpunctata</u> (CU); <u>C. polita</u> (CP); <u>H. sinuata</u> (HS); <u>A. bipunctata</u> (AB).

similar trend was seen in <u>C. undecimpunctata</u>. This is the opposite of what occurred in <u>H. convergens</u>, whose parasitism increased in certain habitats in August.

It is difficult to interpret these results as a habitat effect in <u>D. coccinellae</u>, since they were not consistent over species. It does appear that there was some preference for mint in July, since parasitism for most species was somewhat higher if not significant. A follow-up in August was not possible because of a pesticide application followed two weeks later by harvest; only 44 coccinellids were collected the entire month. At the clover site in August, parasitism was higher only in the <u>Hippodamia</u> species. At this site it is most probable that the grower's organic practices was the reason for the high numbers of beetles and parasitoids. Parasitism was significantly lower in filbert overall. This is probably due to the abundance of A. bipunctata (parasitism=0%) at this site.

In August, it appears that <u>D. coccinellae</u> switched host preference. At all sites, parasitism of <u>H.</u> <u>convergens</u> increased. The species had the highest percent parasitism in 5 of the 7 habitats and was second highest in the remaining 2. At the same time, numbers of <u>H.</u> <u>convergens</u> did not fluctuate greatly from July to August. A similar trend was seen in the study by Richerson and DeLoach (1973). They found that parasitism increased to

nearly 100% before <u>H. convergens</u> left for aggregation sites in September.

Total parasitism of <u>H. sinuata</u> also increased in August, from 44% in July to 67%. Parasitism of C. trifasciata decreased in all habitats in August. Since the life cycle of D. coccinellae is approximately 1 month it is possible that there was 1 more generation of adults in September before diapause began in host and parasitoid. If <u>H. convergens</u> migrated to overwintering sites before the pupation of this last generation, <u>D. coccinellae</u> would have had the opportunity to infect aggregated populations of hosts. In October, 1984, a pupal cocoon from D. coccinellae was found attached to a <u>H. convergens</u> at the aggregation site in McDonald Forest. Lee (1980) often found pupal cocoons with H. convergens in winter aggregations on the shores of lakes in the Midwest. Askew and Shaw (1979, 1978) found that in temperate climates there is often an overall greater level of parasitism in late summer generations of hosts. The increased parasitism in August would then be one explanation for the high overwintering parasitism in <u>H. convergens</u>.

It is possible that <u>D. coccinellae</u> used cues from the host species' habitat for location. However, both parasitoid and hosts are polyphagous. Most examples of the use of habitat cues for location in insect parasitoids involve more habitat specific species (van Alphen and Vet,

1986). It seems unlikely that this parasitoid would have evolved the ability to locate hosts using these diverse habitat cues.

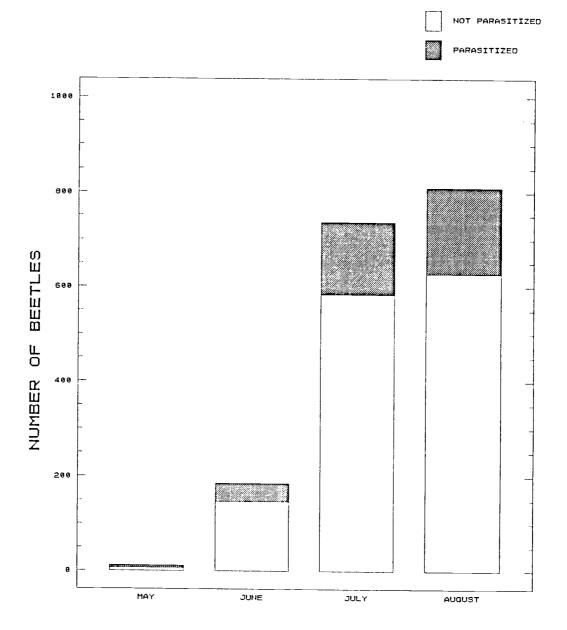
Individuals may be more specific than the species as a whole. This may be true for both parasitoid and coccinellid. In this case the host or parasitoid may prefer certain habitats because of past experience or success, or a genetic line may have evolved the ability to discriminate among particular habitats.

EFFECT OF RELATIVE ABUNDANCE OF HOST SPECIES

A comparison of parasitism and total beetles collected by species (Fig. 2), habitat (Fig. 12) and month (Fig. 18) showed no relationship between relative abundance of hosts and level of parasitism. The highest species parasitism was in <u>H. sinuata</u>, the least common. Two species, <u>C.</u> <u>californica</u> and <u>A. bipunctata</u>, were fairly common and were not preferred hosts.

The highest monthly percent parasitism was in May, when the fewest beetles were collected (Fig. 18). The lowest habitat parasitism level was in filbert, which produced the third highest number of beetles (Fig. 12).

The number of hosts available in a habitat at a given time needs to be examined since the relative abundance of beetles in each habitat fluctuates monthly. Figure 19 shows the monthly habitat trends. In May, numbers were



MONTH

Figure 18. Number of parasitized and non-parasitized coccinellids collected monthly from May through August in the Willamette Valley, Oregon, 1982.

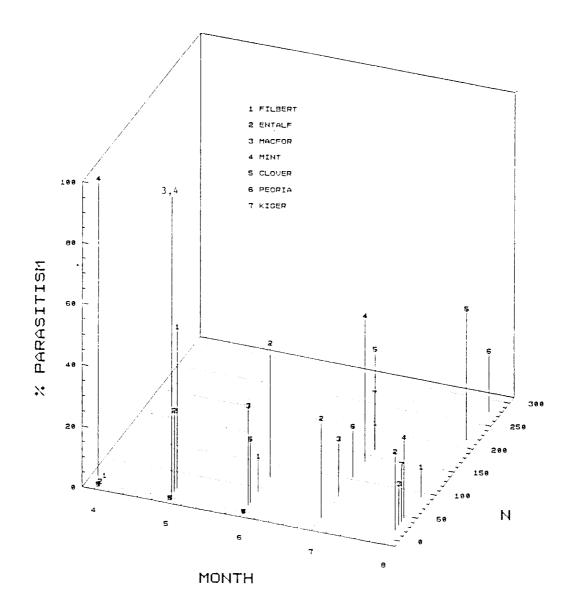


Figure 19. Parasitism by <u>D. coccinellae</u> and number of coccinellids collected from seven habitats (filbert, entomology alfalfa, McDonald Forest, Peoria alfalfa, clover, peppermint, Kiger) April through August in the Willamette Valley, Oregon, 1982.

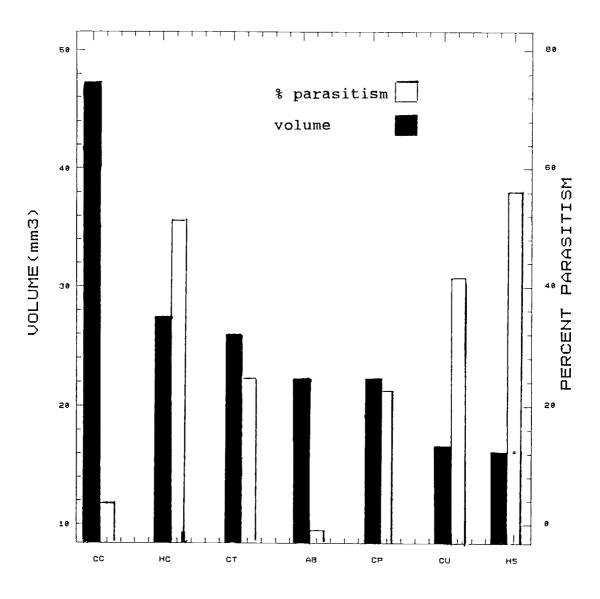
low and parasitism was high in the 4 habitats. In June, numbers increased slightly and parasitism was moderate. The highest parasitism in July was in mint, the habitat with the median number of beetles. The 3 sites which produced the most beetles had low, medium and high parasitism. Less than 50 beetles were collected from most sites in August. Most coccinellids were at the Peoria alfalfa and clover habitats. Although clover had the highest parasitism for the month (43%) and produced over 200 beetles, almost 300 beetles were collected from Peoria and the percent parasitism (20%) was the same as those sites with a minimum number of coccinellids.

At a species level, relative abundance of hosts in a habitat at a given time does not appear to affect parasitism. Figs. 3, 4, 5, and 6 portray the interaction of all 5 factors (species, habitat, month, parasitism and abundance) simultaneously. This estimates the actual number of hosts available to an individual <u>D. coccinellae</u> during a search in a given month, the assumption being that numbers of hosts remained fairly constant over that time period. No patterns are obvious; low, moderate and high degrees of parasitism existed at all levels of abundance.

EFFECT OF HOST SIZE

The 7 beetle species used in this project were in 5 different size classes according to a multiple range test of One-Way ANOVA Least Significant Difference results. Fig. 20 gives the level of parasitism and mean volume for each species. The smallest group included <u>H. sinuata</u> (16.19mm³) and <u>C.undecimpunctata</u> (16.57mm³). <u>A.</u> <u>bipunctata</u> (22.23mm³) and <u>C. polita</u> (22.23mm³) were in the next largest size class. The remaining 3 species were in size classes by themselves: <u>C. trifasciata</u> (25.88mm³), <u>H.</u> <u>convergens</u> (27.34mm³) and <u>C. californica</u> with an average volume of 47.32mm³, 40% larger than the next largest species.

The 2 smallest species, <u>H. sinuata</u> and <u>C.</u> <u>undecimpunctata</u>, showed high levels of parasitism while the largest species, <u>C. californica</u>, was parasitized 4%. The second largest species, <u>H. convergens</u>, was over 50% parasitized. A one-way ANOVA on all species combined, done to determine if there was an overall size difference between parasitized and non-parasitized individuals, resulted in 2 distinct size classes. Fig. 21 shows the 95% LSD intervals for the 2 classes. The non-parasitized group had the largest average volume, 27.99mm³. This is perhaps due to the low level of parasitism in <u>C.</u> <u>californica</u>, 4%, and its extreme size difference from the



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Figure 20. Parasitism by <u>D. coccinellae</u> and mean volume (mm³) of seven species of coccinellids collected in the Willamette Valley, Oregon, 1982: <u>H. convergens</u> (HC); <u>C. trifasciata</u> (CT); <u>C. californica</u> (CC); <u>C. undecimpunctata</u> (CU); <u>C. polita</u> (CP); <u>H. sinuata</u> (HS); <u>A. bipunctata</u> (AB).

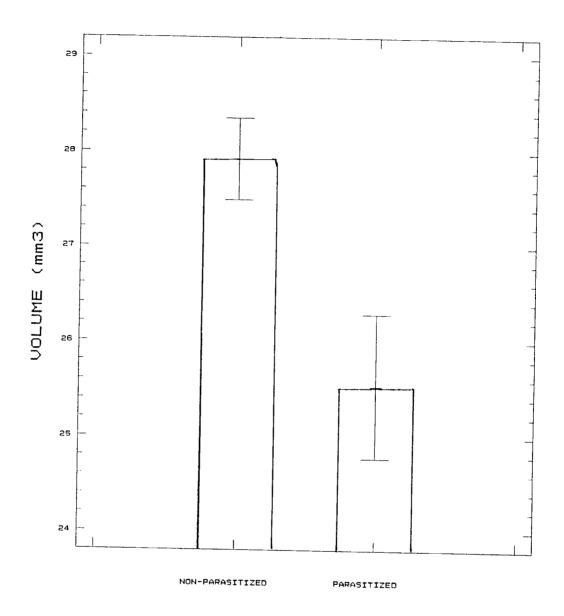


Figure 21. Comparison of mean volume (mm^3) of coccinellids non-parasitized (n=1415) and parasitized (n=465) by <u>D.</u> coccinellae. other species, 47.32 mm^3 . The next largest species, <u>H.</u> <u>convergens</u>, had an average volume of 27.34 mm^3 , 40% smaller than <u>C. californica</u>.

The parasitized group had an average volume of 25.66mm³. This smaller size was probably influenced by the low average volume of 2 of the 3 most heavily parasitized species. <u>C. undecimpunctata</u> had an average volume of 16.57mm³ and was parasitized 42%; <u>H. sinuata</u> was parasitized 56% of the time and had an average volume of 16.19mm³. The second highest parasitized species, <u>H. convergens</u> (52%), was also the second largest with an average volume of 27.34 mm³. However, individual size was highly variable in this species and ranged from 10.2mm³ to 68.15mm³. Many small individuals were found parasitized.

The average size of hosts from which adult parasitoids emerged was 21.14mm³. This value is lower than the average size of all host species except for the 2 smallest, <u>C. undecimpunctata</u> and <u>H. sinuata</u>. However, the small sample size (33) resulted in 95% LSD intervals of 18.33 to 23.96. The predominance of <u>C. undecimpunctata</u> in this group may be a result of a shorter generation time or a higher success rate for the parasitoid in this species. This would increase the probability that a parasitoid would have completed development in the first week after field collection. Walker (1961), Balduf (1926) and Belnavis (personal observation) found a generation time of 3 weeks in this host, a week shorter than the average generation time for <u>D. coccinellae</u>. Tests are needed to determine generation times and emergence success in different host species.

It is apparent that <u>D. coccinellae</u> does not select a host on the basis of size at the species level of selection. However, if host species preference is determined by other factors (fat body amount or suitability, host defenses, behavior), it is possible that selection within the species is affected by size. A One-Way ANOVA was done for 2 host species, <u>H. convergens</u> and <u>C. undecimpunctata</u>, to determine if there was a size difference between parasitized and non-parasitized individuals. The average size of parasitized (25.56mm³) and non-parasitized (25.39mm³) <u>H. convergens</u> were not significantly different. The parasitized (16.92mm³) and non-parasitized (15.59mm³) individuals of <u>C.</u> <u>undecimpunctata</u> were in 2 distinct size classes. In this species the parasitized individuals were significantly greater in size. The smallest parasitized individual in this species was 10.04mm³, non-parasitized was 7.66mm³. Small individuals of C. undecimpunctata may fall below the lower size limits for hosts in this parasitoid. It appears that <u>D. coccinellae</u> discriminated against hosts below a certain size during host selection. The larger average volume of <u>H. convergens</u> may have been the reason

that size was not a factor in host selection within this species.

EFFECT OF HOST SEX RATIO.

The sex ratio of the coccinellids collected was 3:2 (females to males). Since the size of females was significantly larger than males (p<0.05), they were compared as 2 different groups to determine if one was preferred by <u>D. coccinellae</u>. The observed values were within 3 of the expected values. This gave a p value of greater than 99%. It appears that D. coccinellae did not select hosts on the basis of sex. Cartwright, et al. (1982) found that parasitism was higher in female hosts of D. coccinellae. Sex ratio of males to females was the same in his study. Parker et al. (1977) and Hodek (1973) also found that parasitism was higher in female beetles. Wright and Laing (1982) showed no difference in levels of parasitism between male and female hosts of D. coccinellae. All of these studies were strictly observational, definitive experiments are necessary to resolve conflicting results.

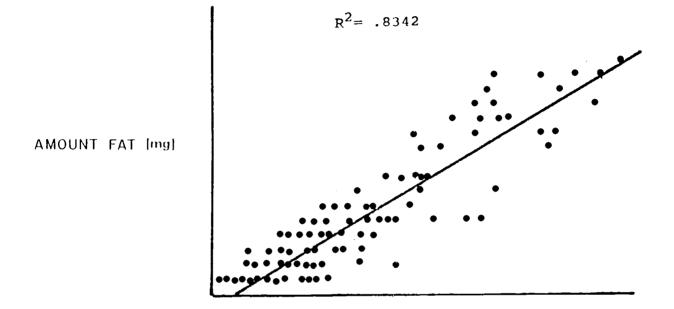
EFFECT OF FAT BODY SIZE.

Since the fat body of the host is the primary resource for this parasitoid, it was necessary to examine the relationship between host volume and fat body weight. It

is possible that different species could have different proportions of fat body to their body weight. The actual weight of the fat body was determined in 5 of the 7 hosts used in this study. The results of a regression of fat body weight to dry weight of beetle showed a positive correlation (R-squared=.8342) (Fig. 22). This test followed the assumption that larger beetles possess more fat body than smaller ones, and consequently a greater resource for the parasitoid. Figure 23 compares the degree of parasitism to the weight of the fat body for the 5 species used in this test. Size of beetle species and hence amount of available resource did not appear to have an effect on host preference. Resource nutritional suitability rather than resource (fat body) amount, may be an important factor that differed among host species. Nutritional suitability of the fat body has not been compared in these coccinellid species.

EFFECT OF HOST SIZE ON SIZE OF PARASITOID.

The ultimate test of the importance of host size is the determination of the fitness of the F1 generation of parasitoids. A larger parasitoid is presumably more fit than a smaller one. Larger individuals of a species may live longer, may be more fecund, and produce healthier offspring than do smaller ones. The volume of 84 coccinellids consisting of 5 host species was compared to



DRY WEIGHT (mg) BEFORE EXTRACTION

Figure 22. Regression of fat body weight (mg) on dry weight (mg) of coccinellids collected August, 1982 in the Willamette Valley, Oregon..

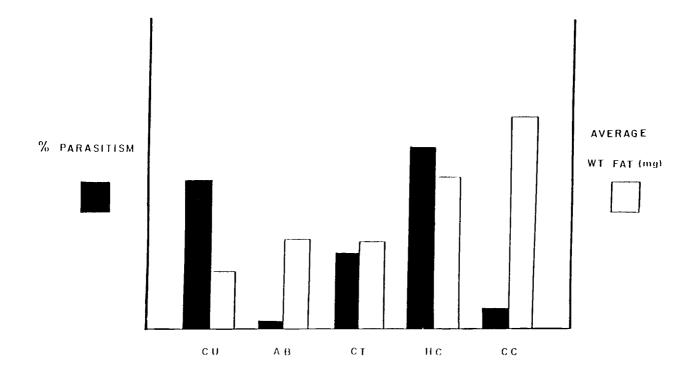
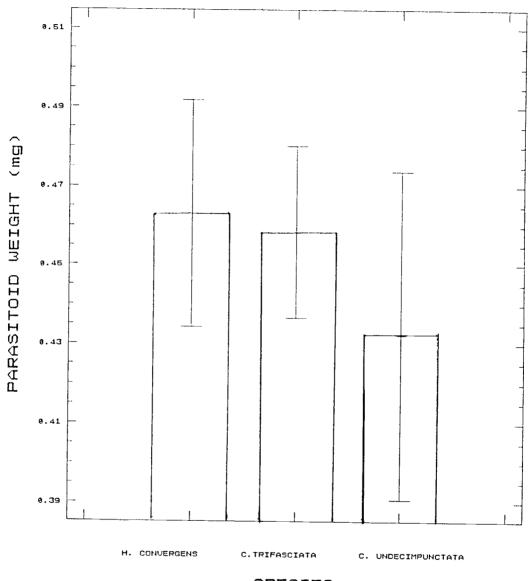


Figure 23. Comparison of parasitism by <u>D. coccinellae</u> and fat body weight (mg) of five species of coccinellids (<u>C.</u> <u>undecimpunctata</u> (CU); <u>A. bipunctata</u> (AB); <u>C. trifasciata</u> (CT); <u>H. convergens</u> (HC); <u>C. californica</u> (CC).

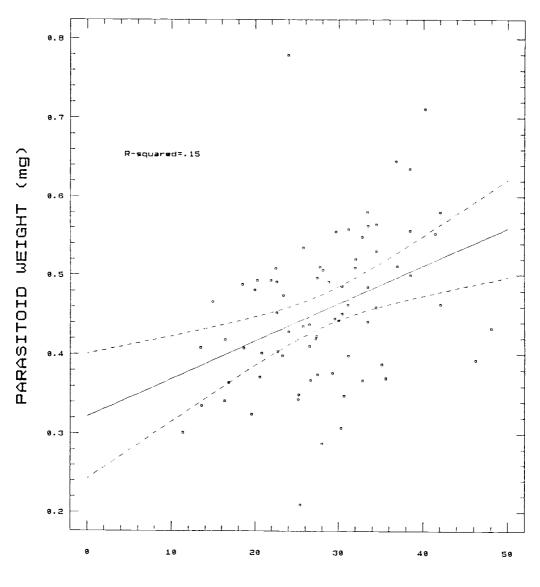
the dry weight of the emerged adult parasitoid of the individual. The differences among mean weight of parasitoids from <u>H. convergens</u>, <u>C. trifasciata</u> and <u>C.</u> undecimpunctata were not significant (Fig. 24). The regression of host volume to parasitoid weight of all species combined is shown in Fig. 25. The R-squared value of 0.15 indicates that a strong correlation did not exist. However, within species comparisons yielded different results. The R-squared values for <u>C. trifasciata</u>, H. convergens, and C. undecimpunctata were 0.05, 0.30 and 0.54 respectively. The strongest correlation of host to parasitoid weight was with the smallest species. This is consistent with the previous observation, that parasitized individuals were on the average larger than nonparasitized in this species. It appears that in hosts with a volume below a certain point, the small size of the host limited the maximum size a parasitoid would attain. Table 2 shows the mean volume of the three coccinellids and the mean dry weight of their emerged parasitoids. The largest parasitoid produced from the <u>C. undecimpunctata</u> hosts in this test was 0.53mg. This is smaller than the largest for <u>H. convergens</u> (0.71mg) and <u>C. trifasciata</u> (0.78mg).

Although smaller hosts appeared to yield smaller parasitoids, larger hosts did not necessarily produce larger parasitoids. Beetles ranged in size from 9.83mm³



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Figure 24. Mean dry weight (mg) of <u>D. coccinellae</u> adults which emerged from three species of coccinellid hosts: <u>H. convergens</u> (HC); <u>C. trifasciata</u> (CT); <u>C. undecimpunctata</u> (CU).



HOST VOLUME (mm3)

Figure 25. Regression of dry weight (mg) of adult \underline{D} . <u>coccinellae</u> on volume (mm³) of coccinellid host.

Table 2. Comparison of mean volume (mm³) of three species of coccinellid hosts and the mean dry weight (mg) of their emerged <u>D. coccinellae</u> adult parasitoids.

			PARASITOID	WEIGHT (MG)	
SPECIES	N	VOLUME (MM ³)	MEAN	RANGE	
<u>Hippodamia</u> <u>convergens</u>	23	31.32	0.463	0.21-0.71	
<u>Coccinella</u> <u>trifasciata</u>	40	29.33	0.458	0.29-0.78	
<u>Coccinella</u> <u>undecimpunctata</u>	11	18.34	0.432	0.30-0.53	

to 48.05mm^3 . Parasitoids ranged in size from 0.209mg to 0.779mg. The smallest parasitoid (0.21mg) originated from a <u>H.convergens</u> individual with a volume of 25.38mm^3 . A <u>C.</u> <u>undecimpunctata</u> with a volume of 11.31mm^3 produced the smallest <u>D. coccinellae</u> (0.30mg) for this host species. There was little correlation (R-squared=0.05) between host size and parasitoid size for <u>H. convergens</u>. The largest individual of this species had a volume of 46.20mm^3 and produced a 0.392 mg parasitoid, while the smallest <u>H.</u> <u>convergens</u> (18.65mm^3) yielded a parasitoid of 0.407 mg. These results suggest that above a certain host volume there are other factors (ie. host suitability, genetics) that govern parasitoid size.

The results of this study suggest that above a certain host volume (approximately 10mm³), host size was not a factor in the determination of the size of the resulting parasitoid. Individuals below this minimum volume were not acceptable hosts for <u>D. coccinellae</u>.

SUITABILITY OF ADALIA BIPUNCTATA

When confronted with a choice of species, <u>D.</u> <u>coccinellae</u> did not pursue individuals of <u>A. bipunctata</u> when suitable hosts were available. In all 5 trials using 3 coccinellid species, <u>D. coccinellae</u> began to pursue hosts immediately upon being placed in the Petri dish. Behavior of the parasitoid was as described by Balduf

(1926). When a host was within 2 cm, females would wave their antennae and fold their abdomen under the thorax so that the tip extended beyond the head. Antennal palpating and probing with the ovipositor would follow. Actual deposition of the egg was made by a forward thrust of the ovipositor and a subsequent backing up of the parasitoid followed by an unfolding of the abdomen (Sluss, 1968). Active beetles were pursued more readily than inactive beetles. Mobile hosts may be preferred because the exposed softer tissue between the abdominal segments and at the posterior tip of the abdomen (elevated during locomotion) facilitates oviposition (Tobias, 1965; Bryden and Bishop, 1945; Balduf, 1926). The structure of the ovipositor and the small size of the egg characteristic of the Euphorinae are probably associated with this mode of oviposition (Tobias, 1965). Parasitization of a mobile host requires speed and accuracy. The petiolate abdomen and long straight ovipositor allow accurate insertion because both the host and the end of the ovipositor is in view. The small egg size facilitates rapid oviposition.

No obvious differences in mobility among the three beetle species were observed. <u>A. bipunctata</u> did not react to the parasitoid when it approached. Individuals of both <u>H. convergens</u> and <u>C. trifasciata</u> occasionally displayed aggressive behavior towards the parasitoid.

When exposed to only <u>A. bipunctata</u> adults, <u>D.</u> <u>coccinellae</u> pursued and antennated the beetles and occasionally took the ovipositional stance and appeared to oviposit. The parasitoid spent much of the time searching for suitable hosts in the Petri dish. The movement of an <u>A. bipunctata</u> would initially stimulate <u>D. coccinellae</u> into pursuit and the ovipositional stance, but once the beetle was examined, the parasitoid returned to searching. After 20 minutes of searching, the females appeared to oviposit in several individuals. These beetles were dissected 1 week later. All contained a dark globular mass that could have indicated encapsulation of the parasitoid egg or larva. No other evidence of parasitization was found.

To explore these results in further detail, the previous procedure with <u>A. bipunctata</u> was repeated with host-starved <u>D. coccinellae</u> that had been isolated for three days after emergence. The parasitoids in all 5 trials immediately began to pursue and appeared to oviposit in the beetles. After the initial attempt, several minutes would pass before the parasitoid would pursue the coccinellids. This process was repeated several times during the hour of observation for each of the trials. Parasitoids appeared to oviposit in all beetles within that time period. No globular masses and

no evidence of parasitization was found in any of the dissected beetles.

In several studies, <u>A. bipunctata</u> has been described as a suitable host for <u>D. coccinellae</u> (Cartwright, et al. 1982; Richerson and DeLoach, 1973, 1972; Bryden and Bishop, 1945; Balduf, 1926). However, successful parasitism never exceeded 5%. Most studies that found parasitism by dissection had no successful emergence of the parasitoid from this species.

The results of this study suggest that D. coccinellae does not accept A. bipunctata when other host species are present. A. bipunctata was temporally and spatially synchronized with this parasitoid in field situations. Data suggest that both the beetle and parasitoid were present from April through August in the same macrohabitats. Parasitized individuals of other host species were found in filbert throughout the season. When parasitism was compared over habitats for C. polita, a common coccinellid in filbert, no habitat effect was observed. Adults of <u>C. polita</u> were parasitized to approximately the same degree in all habitats. This suggests that the probability of the presence of the adults parasitoids may be the same for filbert as for other sites.

It is possible that the microhabitat preferences of the beetle and parasitoid differ. Behavior of A.

bipunctata in filbert was not examined. However, observations in the lab indicate that this species is generally rejected by <u>D. coccinellae</u> at the host acceptance step in host selection. Given a choice, the parasitoid always selected another host species.

Results of this study have shown that size was not important in the selection of host species in <u>D</u>. <u>coccinellae</u>. Therefore, the relatively small size of <u>A</u>. <u>bipunctata</u> was probably not a factor in the rejection of this species. It is unlikely that shape or color of this beetle affected preference, since there is a great overlap in both of these in the aphidophagous Coccinellidae. <u>D</u>. <u>coccinellae</u> will parasitize beetles of various colors including the brown <u>M. picta</u>, the pink and black <u>C</u>. <u>quattuorodecimguttata</u>, and larvae and pupae of the Coccinellidae (Obrycki et al., 1985).

The effect of chemicals in host acceptance needs to be examined. The hemolymph of <u>Galleria mellonella</u> was found to contain compounds that induced oviposition on <u>Itoplectis conquistor</u> (Arthur et al., 1969; Hegdekar and Arthur, 1973). <u>D. coccinellae</u> will probe <u>A. bipunctata</u> and then reject the beetle. The chemical cue for oviposition may be absent in <u>A. bipunctata</u>. Richerson and DeLoach (1972) found that olfactory chemicals were important in host selection in <u>D. coccinellae</u>. <u>A.</u> <u>bipunctata</u> may lack these olfactory cues. It is still unknown if <u>A. bipunctata</u> is physiologically suitable for <u>D. coccinellae</u>. The amount of fat body in this species is sufficient, however the suitability of the fat body has not been measured. There was some evidence of encapsulation but tests were not conclusive. It is believed that a calyx virus exists in the ovipositor of many braconid parasitoids that functions to suppress the immune response of the hosts. It is possible that the calyx virus is present in <u>D. coccinellae</u> but does not function to suppress the immune response in <u>A. bipunctata</u> (Stolz and Vinson, 1979).

Fat body nutritional suitability, encapsulation of the parasitoid egg, and the function of the calyx virus, in addition to microhabitat and behavior studies in the field, are necessary to understand the interaction of <u>D</u>. <u>coccinellae</u> and <u>A. bipunctata</u>.

CONCLUSION

The braconid <u>D. coccinellae</u> parasitizes several species of coccinellids in the Willamette Valley, Oregon. Parasitism varied significantly with host species, host habitat and time of year. The species of the host was most probably the determining factor in host selection of <u>D. coccinellae</u> in field situations. Seasonal effects and variation in parasitism over habitats appeared to be related to host species present.

Size of the host beetle at the species level did not appear to be a factor in host selection. Smaller species in general were preferred by the parasitoid. Within host species, size was not important until a minimum size was encountered (approximately 10 mm³). Individuals below this size were not accepted by <u>D. coccinellae</u>. Host size was not a determining factor in the size of the adult parasitoid except in maximum physical limitations of the host.

The coccinellid <u>A. bipunctata</u> did not appear to be an acceptable host species for <u>D. coccinellae</u>. Rejection of this species by the parasitoid is probably at the host acceptance step in host selection. Physiological studies of <u>A. bipunctata</u> which examine fat body nutritional suitability, immune response to the parasitoid, and olfactory ovipositional stimuli, in addition to field

studies of behavior and microhabitat affinities, are necessary to understand the relationship of <u>A. bipunctata</u> to <u>D. coccinellae</u>.

REFERENCES CITED

- van Alphen, J.J.M. and L.E.M. Vet. 1986. An evolutionary approach to host finding and selection. pp. 23-61. In Insect Parasitoids, Waage, G. and D. Greathead [eds]. Academic Press, Inc. London. 389pp.
- Arthur, A.P. 1962. Influence of host tree on abundance of <u>Itoplectis conquisitor</u> (Say), a polyphagous parasite of the European shoot moth, <u>Rhyacionia buoliana</u> (Schiff). Can. Ent. 94: 337-47.
- Arthur, A.P., B.M. Hegdekar and C. Rollins. 1969. Component of the host hemolymph that induces oviposition in a parasitic insect. Nature 223: 966-67.
- Askew, R.R. and M.R. Shaw. 1978. Account of Chalcidoidea parasitizing leaf-mining insects of deciduous trees in Britain. Biological J. Linnean Soc. 6: 289-335.
- Askew, R.R. and M.R. Shaw. 1979. Mortality factors affecting the leaf-mining stages of <u>Phyllonorycter</u> [Lepidoptera: Gracillariidae] on oak and birch. 1. Analysis of the mortality factors. Zoological J. Of the Linnean Soc. 67: 31-49.
- Balduf, W. V. 1926. The bionomics of <u>Dinocampus</u> <u>coccinellae</u> (Schrank) [Hymenoptera: Braconidae]. Ann. Entomol. Soc. Am. 19:465-498.
- Belicek, J. 1976. Coccinellidae of western Canada and Alaska with analyses of the transmontane zoogeographic relationships between the fauna of British Columbia and Alberta [Insecta: Coleoptera: Coccinellidae]. Quaestiones Entomologicae 12: 283-409.
- Bryden, J.W. and Bishop, M.W.H. 1945. <u>Perilitus</u> <u>coccinellae</u> (Schrank) [Hymenoptera: Braconidae] in Cambridgeshire. Entomol. Mon. Mag. 81:51-52.
- Cartwright, B., R.D. Eikenbary and G.W. Angalet. 1982. Parasitism by Perilitus coccinellae (Hym.: Braconidae) of indigenous coccinellid hosts and the introduced <u>Coccinella Septempunctata</u> (Col.:Coccinellidae), with notes on winter mortality. Entomophaga 27(3):237-244.
- Clausen, C.P. 1940. Entomophagous Insects. New York: McGraw-Hill. 688pp.

- Coderre, D. and J.C. Tourneur. 1986. Vertical distribution of aphids and aphidophagous insects on maize. pp. 291-296. In: Ecology of Aphidophaga. Hodek, I. (ed). Academia, Prague. 563pp.
- Cross, W.W. and T.L. Chestnut. 1971. Arthropod parasites of the boll weevil, Anthonomus grandis: 1. An annotated list. Annu. Entomol. Soc. Am. 64: 516-27.
- David, M. H. and G. Wilde. 1973. Susceptibility of the convergent lady beetle to parasitism by <u>Perilitus</u> <u>coccinellae</u> (Schrank) [Hymenoptera: Braconidae]. J. Kansas Entomol. Soc. 46: 359-362.
- Doutt, R.L. 1959. The biology of the parasitic Hymenoptera. Ann. Rev. Entomol. 4: 161-182.
- van Driesche, R.G. 1983. Meaning of "percent parasitism"
 in studies of insect parasitism. Env. Entomol. 12:
 1611-1622.
- Ewert, M.A. and H.C. Chiang. 1966. Effects of some environmental factors on the distribution of three species of Coccinellidae in their microhabitat. pp. 195-219. In: Ecology of Aphidophagous Insects. Hodek, I. (ed), Academia, Prague.
- Ewing, H.E. 1913. Notes on Oregon Coccinellidae. J. Econ. Entomol. 6(5): 404-407.
- Hagen, K. S. 1962. Biology and ecology of predaceous Coccinellidae. Ann. Rev. Entomol. 7: 289-326.
- Harper, A.M. and C.E. Lilly. 1982. Aggregations and winter survival in southern Alberta of <u>Hippodamia</u> <u>quinquesignata</u> (Coleoptera: Coccinellidae), a predator of the pea aphid (Homoptera: Aphidiidae). Can. Entomol. 114: 303-309.
- Harvey, P.H. and L. Partridge. 1987. Murderous mandibles and black holes in hymenopteran wasps. Nature 326: 128-29.
- Hegdekar, B.M. and A.P. Arthur. 1973. Host hemolymph chemicals that induce oviposition in the parasite <u>Itoplectis conquistor</u>. Can. Entomol. 105: 787-93.
- Hemptinne, J.L. and A. Desprets. 1986. Pollen as a spring food for <u>Adalia bipunctata</u>. pp. 29-36. In: Ecology of Aphidophaga. I. Hodek, ed. Academia, Prague.

- Hodek, I. 1965. Ecology of aphidophagous insects. Academia, Prague.
- Hodek, I. 1967. Bionomics and ecology of predaceous coccinellidae. Ann. Rev. Entomol. 12: 79-104.
- Hodek, I. 1973. Biology of Coccinellidae. Dr. W. Junk, The Hague, 260pp.
- Hodek, I., G. Iperti and F. Rolley. 1977. Activation of hibernating <u>Coccinella septempunctata</u> [Coleoptera] and <u>Perilitus coccinellae</u> [Hymenoptera] and the photoperiodic response after diapause. Entomol. Exp. Appl. 21: 275-86.
- Honek, A. 1982. Factors which determine the composition of field communities of adult aphidophagous Coccinellidae (Coleoptera, Coccinellidae). Z. Ang. Entomol. 94: 157-168.
- Hudon, M. 1959. First record of <u>Perilitus coccinellae</u> Schrank [Hym: Braconidae] as a parasite of <u>Coccinella</u> <u>novemnotata</u> Hbst. and <u>Coleomegilla maculata lengi</u> Timb. [Col: Coccinellidae] in Canada. Can. Entomol. 91(1):62-63.
- Kokubu, H. and P. Duelli. 1986. Aerial population movement and vertical distribution of aphidophagous insects in cornfields (Chrysopidae, Coccinellidae and Syrphidae). pp. 279-284. In: Ecology of Aphidophaga. I. Hodek (ed). Academia, Prague. 562pp.
- Laing, J. 1937. Host-finding by insect parasites. I. Observation on the finding of hosts by <u>Alysia</u> <u>manducator</u>, <u>Mormoniella vitripennis</u>, and <u>Trichogramma</u> <u>evanescens</u>. J. Anim. Ecol. 6: 298-317.
- Lee, R.E. Jr. 1980. Aggregation of lady beetles on the shores of lakes (Coleoptera: Coccinellidae). Am. Mid. Nat. 104: 295-304.
- Liu, C.L. 1944. Contributions to the knowledge of Chinese Coccinellidae. VI. Occurrence of <u>Perilitus</u> <u>coccinellae</u> (Schrank), a parasite of adult Coccinellidae in Yunnan [Hym: Braconidae]. Entomol. News 55: 235-237.
- Loan, C.C. 1963. Parasitism of the dogwood flea beetle, <u>Altica corni</u>, in Ontario. J. Econ. Entomol. 56: 537-38.

- Matthews, R. W. 1974. Biology of Braconidae. Annu. Rev. Entomol. 19: 15-32.
- Messing, R.H. 1982. The biology of the predator complex of the filbert aphid, <u>Myzocallis coryli</u> Goetze, in Western Oregon. M.S. Thesis, Oregon St. Univ. 115pp.
- Obrycki, J.J. and M. J. Tauber. 1978. Thermal requirements for the development of <u>Coleomegilla</u> <u>maculata</u> [Col:Coccinellidae] and its parasite <u>Perilitus coccinellae</u> [Hym: Braconidae]. Can. Entomol. 110: 407-412.
- Obrycki, J.J. and M.J. Tauber. 1979. Seasonal synchrony of the parasite <u>Perilitus coccinellae</u> and its host <u>Coleomegilla maculata</u>. Environ. Entomol. 8:400-405.
- Obrycki, J.J. and M.J. Tauber. 1981. Phenology of three coccinellid species: thermal requirements for development. Annu. Entomol. Soc. Am. 74: 31-36.
- Obrycki, J.J., M.J. Tauber and C.A. Tauber. 1985. <u>Perilitus coccinellae</u> [Hymenoptera: Braconidae]: Parasitization and development in relation to host stage attacked. Annu. Entomol. Soc. Am. 78: 852-854.
- Olszak, R. W. 1986. Suitability of three aphid species as prey for <u>Propylea quatuordecimpunctata</u>. pp. 51-56. In Ecology of Aphidophaga. I. Hodek (ed.) Academia: Prague. 562pp.
- Orphanides, G. M. and D. Gonzalez. 1970. Effects of adhesive materials and host location on parasitization by uniparental race of <u>Trichogramma</u> <u>pretiosum</u>. J. Econ. Entomol. 63: 1891-98.
- Parker, B.L., M.E. Whalon and M. Warshaw. 1977. Respiration and parasitism in <u>Coleomegilla maculata</u> <u>lengi</u> [Coleoptera: Coccinellidae]. Annu. Entomol. Soc. Am. 70: 984-987.
- Putman, W.L. 1964. Occurrence and food of some coccinellids in Ontario peach orchards. Can. Entomol. 96: 1149-1155.
- Radwan, Z. and G.L. Lovei. 1982. Distribution and bionomics of ladybird beetles [Col. Coccinellidae] living in an apple orchard near Budapest, Hungary. Zeitschrift fur angewandte Entomologie 2: 169-175.
- Read, D.P., P.P. Feeney and R.B. Root. 1970. Habitat selection by the aphid parasite <u>Diaeretiella rapae</u>

and hyperparasite <u>Charips brassicae</u>. Can. Entomol. 102: 1567-78.

- Richerson, J.V. 1970. A world list of parasites of Coccinellidae. J. Entomol. Soc. Brit. Col. 67: 33-48.
- Richerson, J.V. and C.J. DeLoach. 1973. Seasonal abundance of <u>Perilitus coccinellae</u> and its coccinellid hosts and degree of parasitism in central Missouri. Environ. Entomol. 2: 138-141.20%
- Richerson, J.V. and C.J. DeLoach. 1972. Some aspects of host selection by <u>Perilitus coccinellae</u>. Ann. Entomol. Soc. Am. 65: 834-839.3
- Rockwood, L.P. 1952. Notes on coccinellids in the Pacific Northwest. Pan-Pacific Entomol. 28(3): 139-147.
- Salt, G. 1935. Experimental studies in insect parasitism. III. Host selection. Proc. Royal Entomol. Soc. London. Ser. B, Biol. Sci. 114: 413-435.
- Salt, G. 1938. Experimental studies in insect parasitism. VI. Host suitability. Bull. Entomol. Res. 29: 223-46.
- Salt, G. 1961. Competition among insect parasitoids. Symp. Soc. Exp. Biol. 15: 96-119.
- Semyanov, V.P. 1979. An unusual instance of parasitism in <u>Dinocampus coccinellae</u> [Hym: Braconidae]. Entomol. Rev. 57: 351-352.
- Semyanov, V.P. 1981. Behavior of <u>Dinocampus</u> (=Perilitus) <u>coccinellae</u> Schrank [Hym: Braconidae] during search for and infection of hosts. pp. 159-163. In V.P. Pristavko [ed], Insect behavior as a basis for developing control measures against pests of field crops and forests (published in 1975, translated from Russian in 1981). Amerind, New Delhi.
- Shaw, S.R. 1985. A phylogenetic study of the subfamilies Meteorinae and Euphorinae (Hymenoptera: Braconidae). Entomography 3: 277-370.
- Simmons, G.A., D.E. Leonard and C.W. Chen. 1975. Influence of tree species density and composition on parasitism of the spruce budworm, <u>Choristoneura</u> <u>fumiferana</u> (Clem.). Env. Entomol. 4: 832-6.

- Sluss, R. 1968. Behavioral and anatomical responses of the convergent lady beetle to parasitism by <u>Perilitus</u> <u>coccinellae</u> (schrank) [Hym: Braconidae]. J. Inv. Path. 10: 9-27.
- Smith, B.C. 1960. Note on parasitism of two coccinellids, <u>Coccinella trifasciata perplexa</u> Muls. and <u>Coleomegilla maculata lengi</u> Timb. [Col: Coccinellidae] in Ontario. Can. Entomol. 92: 652.
- Smith, B.C. 1961. Results of rearing some coccinellid
 [Col: Coccinellidae] larvae on various pollens.
 Proc. Entomol. Soc. Ontario. 91: 270-271.
- Smith, B.C. 1971. Effects of various factors on the local distribution and density of coccinellid adults on corn (Coleoptera: Coccinellidae). Can. Entomol. 103: 1115-1120.
- Smith, O.J. 1953. Species, distribution and host records
 of the braconid genera, <u>Microtonus</u> and <u>Perilitus</u>
 [Hym: Braconidae]. Ohio J. Science 53: 173-178.
- Smith Trail, D. R. 1980. Behavioral interactions between parasites and hosts: host suicide and the evolution of complex life cycles. Am. Nat. 116(1): 77-91.
- Stamp, N. E. 1981. Behavior of parasitized aposematic caterpillars: advantageous to the parasitoid or the host? Am. Nat. 118(5): 715-725.
- Stolz, D.B. and S.B. Vinson. 1979. Viruses and parasitism in insects. pp125-171. In Advances in Virus Research. Vol. 24. M.A. Lauffer; F.B. Bang; K. Maramorosch; and K.M. Smith. eds. Dalhousie U., Canada.
- Timberlake, P.H. 1916. Note on an interesting case of two generations of a parasite reared from the same individual host. Can. Entomol. 48: 89-91.
- Tobias, V.I. 1965. Generic grouping and evolution of the subfamily Euphorinae. Part 1. Entomol Rev. 41: 494-507.
- Townes, H.K. 1960. Host selection patterns in some nearctic Ichneumonids. Proc. 2nd Int. Congress Entomol. 2: 738-744.
- Vet, L.E.M. 1983. Host habitat location through olfactory cues by <u>Leptopilina clavipes</u> (Hartig) (Hym. Eucoilidae), a parasitoid of fungivorous <u>Drosophila:</u>

the influence of conditioning. Neth. J. Zool. 33: 225-248.

- Vinson, S.B. 1975. Biochemical coevolution between parasitoids and their hosts. pp. 14-48. In: Evolutionary Strategies of Parasitic Insects and Mites. P.W. Price (ed). Plenum Press, New York. 224pp.
- Vinson, S.B. 1976. Host selection by insect parasitoids. A. Rev. Entomol. 21: 109-33.
- Vinson, S. B. 1981. Habitat location. pp. 51-77. In: Semiochemicals: Their Role in Pest Control. Nordlund, D. A., R.L. Jones and W. J. Lewis (eds.). John Wiley, New York.
- Vinson, S.B. 1984. Parasitoid-host relationship, pp. 205-233. In W.J. Bell and R.T. Carde [eds.], Chemical Ecology of Insects. Chapman and Hall, London.
- Vinson, S.B. and G.F. Iwantsch. 1980. Host suitability for insect parasitoids. Annu. Rev. Entomol. 25: 397-419.
- Walker, M.F. 1961. Some observations on the biology of the ladybird parasite <u>Perilitus coccinellae</u> (Schrank) [Hym: Braconidae] with special reference to host selection and recognition. Entomol. Mon. Mag. 97: 240-244.
- Weseloh, R. M. 1972. Spatial distribution of the gypsy moth and some of its parasitoids within a forest environment. Entomophaga 17: 339-51.
- Wright, E.J. 1978. Observations on the copulatory behavior of <u>Perilitus coccinellae</u> [Hym: Braconidae]. Proc. Entomol. Soc. Ontario 109: 22.
- Wright, E.J. and J.E. Laing. 1978. The effects of temperature on development, adult longevity and fecundity of <u>Coleomegilla maculata lengi</u> and its parasite <u>Perilitus coccinellae</u>. Proc. Entomol. Soc. Ont. 109: 33-47.
- Wright, E.J. and J.E. Laing. 1982. Stage-specific mortality of <u>Coleomegilla maculata lengi</u> Timberlake on corn in southern Ontario. Env. Entomol. 11(1): 32-37.

APPENDIX

	HABITAT**												
SPECIES*	монтн	ĒĀ	PA	НА	PM	CL	ĒĒ	NF	KR	TOLV			
λΒ Apr Hay June July Aug	Apr	1(0)	0(0)	0(0)	0(0)	0(0)	14(0)	0(0)	0(0)	15			
	Hay	0(0)	0(0)	0(0)	0(0)	0(0)	4(0)	0(0)	0(0)	4			
		12(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	12			
		1 (0)	1(0)	0(0)	27(0)	0(0)	78(0)	0(0)	14(0)	121			
	0(0)	0(0)	0(0)	10(0)	ο(υ)	44(0)	0(0)	0(0)	54				
	Apr	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0			
	Hay	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0			
	June	5(40)	0(0)	2(0)	0(0)	0(0)	0(0)	0(0)	0(0)	7			
July Aug	July		33(0)	0(0)	20(15)	14(7)	0(0)	0(0)	41(5)	109			
	Aug	0(0)	78 (1)	15(0)	12(0)	21(5)	1(0)	0(0)	15(0)	142			
CP Apr Hay June July Aug		0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0			
		0(0)	0(0)	0(0)	0(0)	0(0)	3(67)	3 (100)		6			
		0(0)	0(0)	1(0)	0(0)	1(0)	20(20)	2 (100)		24			
		0 (0)	1(100)		0(0)	0(0)	67(19)	2(0)	1(0)	71			
	0(0)	0(0)	2(0)	1(100)	3(33)	27(22)	1(0)	0(0)	34				
CT A	Apr	5(0)		0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	5			
	Nay	7(29)		0(0)	0(0)	0(0)		2(100)		12			
Jul	June	62(48)		24 (29)		17(24)		10(20)	0(0)	113			
	July	12(33)				67(31)		59(20)		236			
	Aug	11(9)	91(15)1	18(14)	4(25)	66(24)	7(29)	23(13)	3(0)	323			
CU	Apr	0(0)		0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0			
	Hay	1(100)		0(0)	0(0)	0(0)	7 (100)		0(0)	8			
July	June	0(0)	0(0)	0(0)	0(0)		0(0)	0(0)	0(0)	0			
	July		1(100)		32(59)		0(0)	0(0)	32(16)				
	Λug	1(0)	67 (36)	5(40)	3(100)	32(34)	1(0)	0(0)	8(25)	117			
11 3 1 3 1	Apr	0(0)	0(0)	0(0)	1(100)		0(0)	0(0)	0(0)	1			
	Hay	3(0)	0(0)	0(0)	3(100)		5(40)	0(0)	0(0)	11			
	June	4(25)		2(100)		1(0)	0(0)	0(0)	0(0)	7			
	July		28(36)		30(53)		1(0)		70(33)				
	Aug	4 (100)	34 (44)	4(50)	14(50)	60(72)	0(0)	3(33)	12(42)	131			
Ha Ju Ju	Apr	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0			
	Нау	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0			
	June	1(100)		0(0)		0(0)	0(0)	0(0)	0(0)	1			
	July	0(0)	0(0)	0(0)		34 (44)	0(0)	0(0)	0(0)	34			
	λug	0(0)	3(0)	1(0)	0(0)	29(76)	0(0)	0(0)	0(0)	33			
OTAL		132	375	174	203	391	291	107	201	1874			

Table A). Number and **t** parasitism by \underline{p}_{\perp} coccinellae of seven species of coccinellids collected from eight habitats April through August in the Willamette Valley, Oregon, 1982.

* <u>A. bipunctata</u> (AB); <u>C. californica</u> (CC); <u>C. polita</u> (CP); <u>C. trifasciata</u> (CT) <u>C. undecimpunctata</u> (CU); <u>H. convergens</u> (HC); <u>H. sinuata</u> (HS).

**entomology alfalfa (EA); Peoria alfalfa (PA); horticulture alfalfa (HA); peppermint (PM); clover (CL); entomology filbert (EF); McDonald Forest (MF); Kiger riparian (KR).

()=percent parasitism
