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AN INVESTIGATION INTO THE FEEDING HABITS, POPULATION
DENSITY, DISPERSION, AND DISPERSAL OF SEVERAL SPECIES OF
CARABIDS FOUND IN IOWA CORNFIELDS

Iowa State University

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An investigation into the feeding habits, population density,
dispersion, and dispersal of several species of carabids
found in Iowa cornfields

by

Richard L. Best

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1979

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GENERAL INTRODUCTION

Several authors have discussed the potential usefulness of carabid beetles in biologically controlling insect pests (e.g. Wishart et al. 1956, Scherney 1960, Rivard 1964, 1966, Frank 1971, Kirk 1971, 1973, and Thiele 1977). In some cases the impact of carabids on a pest population has been sizeable. Scherney, 1960, as cited in Thiele (1977) reported that in some instances two species of carabids reduced insect damage to potatoes by at least 50%. Wishart et al. (1956) reported 70% destruction of Hylemya brassicae (Bouché) eggs and Frank (1967) reported 40% destruction of healthy Operophtera brumata (L.) pupae by predatory beetles including carabids.

Three of the species, Pterostichus chalcites Say, Harpalus pensylvanicus DeGeer and Scarites substriatus Haldeman, trapped by Esau and Peters (1975) in Iowa cornfields, are large enough and numerous enough to warrant their investigation as potential biological control agents against such pests as black cutworm, armyworm, and corn rootworm. Kirk (1973) estimated populations of H. pensylvanicus to be 18-32/m² in some cornfields. He further reported that although this species is opportunistic in its feeding habits (consuming both plant and animal material) it was observed to have fed on live insects in the field. Pterostichus chalcites is one of the most abundant species of carabids found in corn (Esau and Peters 1975) and it, too, is reported to feed on other insects (Kirk 1973, Lund and Turpin 1977b). Very little is known about the biology and habits of S. substriatus other than it is

one of the largest carabids encountered in cornfields and that it is also presumed to be predaceous.

It was the intention of this study to explore the impact of these three carabid species as natural control agents, or at least to assess their role in an integrated pest-management program for corn. Questions concerning their feeding preferences, quantity of prey consumed, population density, dispersion and dispersal were addressed in this study. In addition to studying these three species intensively, several other carabid species (Evarthrus alternans Casey, Pterostichus lucublandus Say, Bembidion quadrimaculatum L., and B. rapidum LeConte) were investigated in regards to their feeding habits. Population density, dispersion and dispersal were not determined for these species. In the case of E. alternans and P. lucublandus, population levels were too low to warrant a more detailed study. In the case of B. quadrimaculatum and B. rapidum, the adults were too small to mark individually.

PART I. FOOD PREFERENCES OF FIVE SPECIES OF CARABIDS
COMMONLY FOUND IN IOWA CORNFIELDS

INTRODUCTION

Carabids in general are regarded as both predaceous and beneficial (Borror and DeLong 1971, Comstock 1950). The literature includes many references to carabids as valuable natural control agents, attacking various insect pests (Burgess and Collins 1911, Coaker and Williams 1963, Dempster 1967, Frank 1971). The literature also includes, however, many references to the phytophagous habits of many carabids (Johnson and Cameron 1969).

The food preferences of five species of carabids (Scarites substriatus Haldeman, Evarthrus alternans Casey, Pterostichus chalcites Say, Pterostichus lucublandus Say, and Harpalus pensylvanicus DeGeer) were tested in the laboratory.

The value of carabids as predators of various insect pests has been much debated. Basic to this debate is whether the large carabids commonly found in Iowa cornfields prefer feeding on plant material, live animal material or dead animal material. By offering each species a selection of foods at one point in time under controlled laboratory conditions, it was hoped that insight into the food preferences of the five carabid species chosen for this study could be gained.

MATERIALS AND METHODS

Each food preference trial consisted of 20 replications. One 38-liter aquarium was used for each replication. Food objects were randomly placed on a piece of moistened white blotter paper covering the aquarium bottom. In each aquarium, one adult beetle was confined for 24 h, at the end of which time the aquariums were examined, and the amount of each host eaten was recorded. The beetles used in the experiment were field-collected as adults and brought to the laboratory and held until needed. They were supplied with water and fed Top Choice® dog food. Before a beetle was used in an experiment, it was starved for two days.

The experiment consisted of three parts. In the first part, beetles were tested to determine whether they preferred vegetable, detritus, or animal matter. The food choices were: seeds of prairie peppergrass, Lepidium densiflorum Schrader; sweet clover, Melilotus alba Desrousseaux; giant ragweed, Ambrosia trifida L.; velvet leaf, Abutilon theophrasti Medicus; wild parsnip, Pastinaca sativa (L.); yellow foxtail, Chaetochloa glauca (L.) Schribner; smooth dock, Rumex altissimus Wood; smartweed, Polygonum persicaria L.; Japanese brome grass, Bromus japonicus L. barnyard grass, Echinochloa crus-galli (L.) Beauvois; alfalfa, Medicago sativa L.; corn, Zea mays L.; soybean, Glycine max (L.) Merrill; and oat, Avena sativa L.; leaves of corn, soybean and alfalfa; dead larvae of black cutworm, Agrotis ipsilon (Hüfnagel); leaf detritus and male corn flowers. All seeds were soaked for 12 h before use so that

they would be in a state similar to that of seeds that had lain on moistened ground.

To compare the amount of different-sized comestibles eaten, a visual rating system based on volume was used. One unit of volume equaled the size of one peppercress seed, the smallest seed used in this experiment, and will hereafter be referred to as one unit. It was necessary to compare equal volumes of comestibles with one another. Because 20 peppercress seeds were used in a replication, an attempt was made to keep other comestible volumes close to 20 units. Some food items, such as soybean seeds and black cutworm larvae, had volumes greater than 20 units. When comparing these larger food items with 20-unit comestibles, a maximum consumption of 20 units was recorded even if more was eaten. This was done rather than cutting a food such as a black cutworm larva into a smaller unit because cutting a larva would cause body fluids to leak out and alter its natural appearance.

In the second part, beetles were tested to determine what animal hosts they preferred to feed on and whether they preferred those hosts alive or dead. Live hosts were allowed to roam about while dead hosts were randomly placed in each 38-liter aquarium. One live and one dead of each of the following species were used: green cloverworm larvae, Plathypena scabra (F.); field crickets, Gryllus sp.; angieworms, Lumbricidae; virgo tiger moth larvae, Callarethia virgo (L.); southern corn rootworm adults, Diabrotica undecimpunctata howardi Barber; black cutworm larvae, Agrotis ipsilon; terrestrial isopods, Porcellio sp.; slugs, Limacidae and phalangids, Phalangida. A different rating system

was used for the second part of the experiment. In this instance, hosts were more nearly equal in size, so comparisons were based on the fractional part of the host eaten. The ratings were: 0 = not fed on, 1 = chewed on, 2 = 1/8 eaten, 3 = 1/4 eaten, 4 = 1/2 eaten, 5 = 3/4 eaten, and 6 = completely consumed.

The data for each carabid species were analyzed separately by analysis of variance and Duncan's multiple range test.

In the third part, two of the most common and potentially more predaceous beetles, P. chalcites and S. substriatus were tested to determine whether they preferred live or dead black cutworm larvae when only this host was randomly placed in each 38-liter aquarium. Sixth-instar cutworms were used for S. substriatus, and fourth-instar larvae used for P. chalcites because of the difference in predator size. The rating system was the same as was used in the second part of the experiment.

RESULTS

Compared to various plant materials, black cutworm larvae were the most preferred food choice by all species. The following materials were totally rejected as food by all five species of carabids tested: corn flowers, wild parsnip seeds, alfalfa leaves, corn leaves, and detritus. Two of the species, P. chalcites and S. substriatus, did not feed on any vegetable material, while H. pensylvanicus and E. alternans fed upon a number of seeds.

All seeds and leaves fed upon were grouped together under the general category of vegetable material. This was done to eliminate the preponderance of 0 values. A "T"-test was then used to test whether black cutworm larvae were significantly favored over vegetable material in general. For all carabid species except H. pensylvanicus, black cutworm larvae still were favored significantly over vegetable material ($P = 0.001$).

There was no significant difference in preference between vegetable material and dead black cutworm larvae by H. pensylvanicus, so it was decided to compare those vegetable materials with means greater than one unit to one another and to black cutworm larvae. The treatments consisted of seeds of yellow foxtail, smooth dock, barnyard grass, and black cutworm larvae. The F-test was significant ($P = 0.01$), so a Duncan's test at the 0.05 level was performed on the treatment means. The results are listed in Table 1.

H. pensylvanicus did not show a significant preference for black cutworm larvae over smooth dock. There also were no significant

Table 1. Comparison of mean volumes of food greater than 1.0 eaten in 24 h by H. pensylvanicus.

Food Item	Mean ¹ volume ² consumed
Black cutworm larvae	6.00 a ³
Smooth dock seeds	3.78 ab
Barnyard grass seeds	1.75 b
Yellow foxtail seeds	1.25 b

¹ Based on 20 replications.

² Consumed volume is expressed in peppergrass units. One peppergrass unit equals the volume of one peppergrass seed.

³ Numbers not followed by the same letter are significantly different at the 5% level using Duncan's multiple range test.

differences in preferences between the seeds tested. H. pensylvanicus did, however, prefer black cutworm larvae to barnyard grass and yellow foxtail. Because all other vegetable materials had means below 1.25 units, black cutworm larvae were preferred over the other vegetable materials tested.

In the second part of the experiment, data on carabid feeding preferences between various live and dead animals were analyzed using four separate analyses of variance.

E. alternans, P. lucublandus, and H. pensylvanicus significantly preferred dead invertebrates as a group over live or dead hosts at the 0.05 level. All carabid species preferred certain host species to others ($P = 0.0001$). There was significant interaction in all instances. That is, some dead hosts were preferred over live ones, while some live hosts were preferred over dead ones, depending on the host species. The interaction was most pronounced for S. substriatus ($P = 0.0001$) and H. pensylvanicus ($P = 0.0001$).

Because there were significant treatment differences at the 0.05 level, a Duncan's multiple range test was performed on the means. Each species is listed separately (Tables 2, 3, 4, and 5).

Smooth-skinned lepidopterous larvae (both live and dead green cloverworm and dead black cutworm larvae) were significantly the most favored food of P. lucublandus. Dead crickets were significantly the most preferred food of S. substriatus, E. alternans, and H. pensylvanicus although live or dead smooth-skinned lepidopterous larvae (green cloverworm and black cutworm larvae) were also readily fed upon.

Table 2. Mean consumption of various live and dead animal hosts by P. lucublandus.

Host	Mean amount consumed ^{1,2}
Dead green cloverworm larva	3.55a ³
Dead black cutworm larva	3.25a
Live green cloverworm larva	3.20a
Dead cricket	1.80b
Live black cutworm larva	0.90bc
Live angleworm	0.55c
Dead corn rootworm adult	0.50c
Dead slug	0.50c
Dead phalangid	0.30c
Live slug	0.30c
Dead tiger moth larva	0.30c
Live isopod	0.20c
Dead angleworm	0.20c
Dead isopod	0.00c
Live phalangid	0.00c
Live cricket	0.00c
Live corn rootworm adult	0.00c
Live tiger moth larva	0.00c

¹ Means based on 20 replications. Standard error of a mean = 0.127.

² Based on a rating system where 0 = not fed upon, 1 = chewed on, 2 = 1/8 eaten, 3 = 1/4 eaten, 4 = 1/2 eaten, 5 = 3/4 eaten, 6 = completely consumed.

³ Numbers not followed by the same letter are significantly different at the 5% level using Duncan's multiple range test.

Table 3. Mean consumption of various live and dead animal hosts by E. alternans.

Host	Mean amount consumed ^{1,2}
Dead cricket	3.45a ³
Dead green cloverworm larva	3.00a
Live black cutworm larva	2.95a
Dead black cutworm larva	2.95a
Live green cloverworm larva	2.55a
Live angleworm	1.15b
Dead tiger moth larva	0.80b
Dead phalangid	0.60b
Live slug	0.60b
Dead isopod	0.35b
Live corn rootworm adult	0.30b
Live cricket	0.30b
Dead slug	0.30b
Dead angleworm	0.20b
Dead corn rootworm adult	0.20b
Live isopod	0.00b
Live tiger moth larva	0.00b
Live phalangid	0.00b

¹ Means based on 20 replications. Standard error of a mean = 0.174.

² Based on a rating system where 0 = not fed upon, 1 = chewed on, 2 = 1/8 eaten, 3 = 1/4 eaten, 4 = 1/2 eaten, 5 = 3/4 eaten, 6 = completely consumed.

³ Numbers not followed by the same letter are significantly different at the 5% level using Duncan's multiple range test.

Table 4. Mean consumption of various live and dead animal hosts by S. substriatus.

Host	Mean amount consumed ^{1,2}
Dead cricket	4.35a ³
Live green cloverworm larva	2.80b
Dead corn rootworm adult	2.35b
Live black cutworm larva	2.25bc
Dead green cloverworm larva	1.45bcd
Live isopod	0.90cd
Dead black cutworm larva	0.85cd
Live angleworm	0.70d
Dead tiger moth larva	0.55d
Dead phalangid	0.45d
Dead angleworm	0.35d
Live cricket	0.30d
Dead isopod	0.30d
Live corn rootworm adult	0.20d
Live tiger moth larva	0.00d
Live phalangid	0.00d
Live slug	0.00d
Dead slug	0.00d

¹Means based on 20 replications. Standard error of a mean = 0.217.

²Based on a rating system where 0 = not fed upon, 1 = chewed on, 2 = 1/8 eaten, 3 = 1/4 eaten, 4 = 1/2 eaten, 5 = 3/4 eaten, 6 = completely consumed.

³Numbers not followed by the same letter are significantly different at the 5% level using Duncan's multiple range test.

Table 5. Mean consumption of various live and dead animal hosts by H. pensylvanicus.

Host	Mean amount consumed ^{1,2}
Dead cricket	2.85a ³
Dead green cloverworm larva	2.70ab
Live green cloverworm larva	1.70bc
Dead black cutworm larva	1.50cd
Dead phalangid	1.25cde
Dead corn rootworm adult	0.95cde
Live isopod	0.85cde
Live corn rootworm adult	0.80cde
Live angleworm	0.50de
Live black cutworm larva	0.30e
Dead tiger moth larva	0.25e
Dead angleworm	0.20e
Live tiger moth larva	0.00e
Dead isopod	0.00e
Live phalangid	0.00e
Live cricket	0.00e
Live slug	0.00e
Dead slug	0.00e

¹ Means based on 20 replications. Standard error of a mean = 0.137.

² Based on a rating system where 0 = not fed upon, 1 = chewed on, 2 = 1/8 eaten, 3 = 1/4 eaten, 4 = 1/2 eaten, 5 = 3/4 eaten, 6 = completely consumed.

³ Numbers not followed by the same letter are significantly different at the 5% level using Duncan's multiple range test.

In the third part of the experiment, S. substriatus and P. chalcites were tested to determine whether either species preferred dead over live black cutworm larvae and whether there were species differences. Consumption of sixth-instar larvae by S. substriatus was significantly greater than consumption of fourth-instar larvae by P. chalcites ($P = 0.0001$). This can be explained by the fact that S. substriatus is a much larger beetle, and no special significance is attached to this statistic. What is significant is that dead black cutworm larvae were preferred over live ones ($P = 0.0417$) and that this preference was not significantly different between these species as indicated by the lack of interaction ($P = 0.92$).

DISCUSSION

A laboratory study such as this admittedly has limitations. Beetles will respond somewhat differently under the artificial conditions imposed by the experiment. An additional problem is that not all foods normally fed upon in the field were presented to the beetle, and many items not normally fed upon were overly abundant.

The purpose of this study was to determine whether several carabid beetles, commonly found in Iowa cornfields, were mainly carnivorous, herbivorous, or necrophagous, and whether certain food items were either highly favored or rejected. The method employed in this study was used because of the relatively large amount of information that could be gained about the feeding habits of these beetles. Such information is needed before a detailed study into their value as natural control agents is initiated.

On the basis of feeding preferences, H. pensylvanicus was shown to have relatively little potential as a natural control agent, while other species, such as S. substriatus, may be valuable predators of certain lepidopterous pests.

All carabids studied seem to be opportunistic feeders, and many items were fed on. H. pensylvanicus and E. alternans seem to have the least selectivity, feeding on both plant and animal material when given a choice. Detritus was not fed upon by any species, and certain animals also were not attractive as food sources. Specifically, isopods, slugs, phalangids, and angleworms were not preferred food items.

Isopods were not often consumed, presumably because of their protective armor. Isopods fed upon had been attacked from the ventral, and not the protected dorsal, side. Protective armament is perhaps the explanation for arctiid larvae being rejected in many cases. Cook (1936) also observed, using Calosoma inquisitor L., that hairy Lepidoptera were less favored as prey than smooth-skinned Lepidoptera. Carabids may avoid feedings on slugs and angleworms because of the protective layer of slime which these animals secrete.

In many instances, certain animals were not utilized as food because of the inability of the carabid to capture them. This may explain the fact that dead hosts, in general, were preferred over live ones. Many live hosts were able to avoid the beetles. This is most likely the case with crickets. Although dead crickets were a preferred food item, live crickets were rarely eaten. That dead insects were readily eaten has special significance. The application of insecticides that kill large numbers of insects may be indirectly poisoning potential predators because of the carabid's willingness to feed on dead or dying insects.

PART II. CONSUMPTION OF AGROTIS IPSILON
BY SEVERAL SPECIES OF CARABIDS FOUND IN IOWA

INTRODUCTION

Wishart et al. (1956) stated that, although most biological control successes utilizing predators have involved predators with specific feeding habits, predators with nonspecific feeding habits may be an important factor in reducing large populations of prey.

Carabids are generally regarded as nonspecific in their feeding habits, but several authors have mentioned that carabids are capable of consuming large amounts of prey. Burgess and Collins (1917) stated that an individual of Calosoma inquisitor L. could consume 103 large larvae of Malacosoma americana (Fabr.) or Porthetria dispar L. during its entire adult life. Cook (1936) observed that each pair of C. inquisitor ate an average of 120 caterpillars of all kinds from May 10-June 20. Rivard (1964) concluded that carabids were presumably capable of consuming large numbers of prey but that more observations were needed on their feeding habits before evaluating them as biological control agents.

Blackman (1968) stated that, if an attacker is observed under laboratory conditions to consume part or all of a victim and repeats this behavior as often as new victims are supplied, then this behavior is good evidence that the attacker is predaceous on the victim under natural conditions, provided that the two normally come into physical contact with one another in the field.

The purpose of this study was to determine the maximum consumption of various immature stages of the black cutworm, Agrotis ipsilon

(Hufnagel), by seven species of carabids: Scarites substriatus Haldeman, Evarthrus alternans Casey, Pterostichus chalcites Say, P. lucublandus Say, Bembidion quadrimaculatum L., B. rapidum LeConte, and Harpalus pensylvanicus DeGeer. All these species are commonly found in Iowa cornfields in association with black cutworm larvae and were suspected of being predaceous.

MATERIALS AND METHODS

Adult carabid beetles, captured in pitfall traps and brought back to the laboratory, were kept in 38-liter aquariums until needed. They were fed Top Choice® dog food and supplied with water. Beetles were starved for two days before their use in a feeding trial.

The experiment to determine the general level of food consumption by adult beetles was divided into two parts. In the first part of the experiment, several species of carabids were tested to determine their total consumption, during 24 h, of various stages of the black cutworm. In most instances, the stage used depended upon the size of the beetle and the likelihood that the stage would be encountered and fed upon in the field.

Beetles to be tested in the first part were placed, one per box, in plastic sandwich boxes. Moistened filter paper served as a water source. The boxes were maintained at 26.7°C, 50-80% RH, and under a 12-h photoperiod during the experiment. There were 20 replications of each feeding trial.

The mean number of black cutworm eggs consumed by adult B. rapidum, B. quadrimaculatum, and P. chalcites was recorded. Adult B. rapidum were also tested to determine the number of first-instar larvae they could consume (10 larvae/container were available to them). Scarites substriatus adults were tested to determine the number of black cutworm pupae that they could consume. Scarites substriatus, P. chalcites, P. lucublandus, and H. pensylvanicus adults were tested to determine the total consumption of fourth-instar cutworm larvae.

In the second part of the experiment, beetles were fed dead black cutworms over a four-day period to determine whether the high level of food consumption observed in the one-day feeding trials would be continued over more extended periods. Beetles to be tested were placed, one per aquarium, in 38-liter aquariums. Four dead black cutworm larvae were randomly placed on moistened filter paper lining the bottom of each aquarium. Dead larvae were used rather than live ones to eliminate problems of escape or cannibalism by the larvae. Best and Beegle (1977) have shown that dead black cutworm larvae are at least as attractive as live larvae as a food source for adults of the carabid species tested in this study. Temperature, humidity, and photoperiod for this part of the experiment were the same as for the first part.

Each beetle was allowed to feed on cutworm larvae for a 24-h period before the amount of each larva consumed was recorded and new larvae were placed in the aquarium. This was repeated so that each beetle had four freshly-killed larvae each day on which to feed over a four-day period. There were 20 replications of this feeding trial.

Consumption of an individual larva was estimated to within 1/8 of the total larval volume. Because of differences in beetle sizes, different-sized black cutworm larvae were used for the different species. Sixth-instar larvae were used for S. substriatus and E. alternans, while fourth-instar larvae were used for P. chalcites and H. pensylvanicus.

RESULTS

The mean number of black cutworm eggs consumed by P. chalcites in a 24-h period was 13.5, with a SD of 7.27 and a range of 5-23 eggs. B. quadrimaculatum consumed a mean of 10.8 eggs in 24 h, with a SD of 6.79 and a range of 0-19. Bembidion rapidum consumed a mean of 5.8 eggs, with a SD of 4.20 and a range of 0-17. None of the carabids consumed all 25 eggs offered to them, so these figures probably represent the number of eggs that these beetles could consume where a minimum amount of searching was required.

Bembidion rapidum consumed a mean of 8.25 first-instar larvae, with a SD of 2.45 and a range of 0-10. These figures would probably be higher if more larvae had been provided, as in many cases all the larvae (10) in a container were consumed. It is not known why there was a higher consumption of black cutworm larvae than eggs by this beetle. Whether an actual preference for larvae over eggs of the black cutworm was shown by B. rapidum or whether more feeding occurred because of more encounters between predator and prey remains to be explored.

Scarites substriatus, a large predatory carabid, was tested to determine its ability to consume black cutworm pupae. The adult beetle consumed a mean of 1.2 pupae in 24 h, with a SD of 0.89 and a range of 0-3. That a beetle ca. 2.5-cm long can consume three black cutworm pupae attests to the voracity of these beetles.

Scarites substriatus, P. chalcites, P. lucublandus, and H. pensylvanicus were all tested to determine the number of fourth-instar

black cutworm larvae that could be consumed in 24 h. The mean consumptions, standard deviations, and ranges are listed in Table 6.

To test whether carabids could consume a large amount of prey over more extended periods of time, we allowed S. substriatus, E. alternans, H. pensylvanicus, and P. chalcites to consume all the black cutworm larvae they could over a four-day period. Because of different seasonal activity periods of these beetles, feeding trials for each species were run at different times during the summer. For this reason, each species is discussed separately.

Scarites substriatus consumed a mean of 0.30, 0.31, 0.16, and 0.22 sixth-instar black cutworm larvae per day during the first through fourth day of the experiment, respectively. An analysis of variance showed no significant difference in consumption between days for this species.

Evarthrus alternans consumed a mean of 0.28, 0.13, 0.12, and 0.17 sixth-instar black cutworm larvae during the first through fourth day of the experiment, respectively. An analysis of variance showed a significant difference ($P = 0.01$) between days, and a Duncan's multiple range test calculated at the 0.05 level showed a significant difference in the amount of black cutworm larvae fed upon on day one compared with days two to four.

Pterostichus chalcites consumed a mean of 0.39, 0.39, 0.26, and 0.24 fourth-instar black cutworm larvae per day during the first through fourth day of the experiment, respectively. An analysis of variance showed no significant difference in consumption of black cutworms per day for this species.

Table 6. Mean consumption, SD, and range of 4th-stage black cutworm larvae consumed by 4 species of carabids in 24 h.

Species	Mean ^a	SD	Range
<u>S. substriatus</u>	5.2	1.9	1.5-8.0
<u>P. chalcites</u>	3.1	1.6	0.5-6.0
<u>P. lucublandus</u>	2.2	0.8	1.0-3.6
<u>H. pensylvanicus</u>	2.1	1.2	1.0-4.5

^aBased on 20 replications.

Harpalus pensylvanicus consumed a mean of 0.34, 0.27, 0.33, and 0.35 fourth-instar cutworm larvae per day during the first through fourth day of the experiment, respectively, and an analysis of variance showed no significant difference in consumption between days.

DISCUSSION

Because each species tested over the four-day feeding period was tested at a different time during the summer, it is questionable whether detailed comparisons between species can be made. Certain generalizations, however, can be made about the feeding behavior of these beetles.

Evarthrus alternans consumed significantly more cutworms on day one than on the remaining days. It seems that this species gorged itself on day one and thus ate less on the following days. The remaining species, however, did not show this trend. They consumed essentially the same amount of prey every day. One important point is that this relatively constant consumption was a population characteristic. That is, as a group, there was no significant difference in the amount consumed over the four-day feeding trial. The population did not gorge itself one day and then not feed the next. Some individuals, however, did display this behavior. It was not uncommon for beetles to consume a large amount of prey one day and then consume less the next.

There are obvious limitations in equating laboratory behavior to a field situation. Blackman (1968) discussed some of these limitations in reference to determining the relative predatory behavior of an insect by using laboratory observations of prey consumption. The amount of prey consumed by carabids in this study is meant to be used only as a rough measure of predation by these beetles. Such may be useful in determining the relative amount of prey that can be consumed under ideal field conditions. Results of this study would indicate that, ignoring

the problem of prey finding, a population of carabids is capable of consuming a fairly high and constant number of prey on a more or less daily basis.

PART III. POPULATION DENSITY, DISPERSION, AND DISPERSAL OF
THREE SPECIES OF PREDACEOUS CARABIDS FOUND IN IOWA CORNFIELDS

INTRODUCTION

During the summer of 1975, population parameters for three species of beetles, Pterostichus chalcites (Say), Harpalus pensylvanicus DeGeer, and Scarites substriatus (Haldeman), thought to be predaceous on cornfield insects, were investigated. Basic to the problem of assessing their importance as natural control agents was the accurate determination of population density, dispersion, and dispersal. Predator population density directly influences the numbers of host pests which can be found and consumed over time. Southwood (1978) states that the importance of obtaining absolute population estimates in the study of insect populations cannot be overemphasized. Dispersion or the description of insect distribution is of considerable ecological significance (Southwood 1978). Knowledge of dispersion is necessary for the development of a proper sampling program and affects the method of data analysis (Southwood 1978, Pieters and Sterling 1973). An understanding of dispersion is also critical to analysis of predator-prey relationships (Murdie and Hassell 1973, Hassell and May 1974). Information on dispersal rate can indicate whether predators are capable of dispersing into new areas either in response to increasing pest populations or to repopulate a field which has been treated with insecticides.

Unfortunately, it has been difficult to estimate population parameters for active epigeic invertebrates such as carabids (Ericson 1977). Pitfall traps have been the favorite method for sampling Coleoptera and

have been used to study seasonal abundance of adults, spatial patterns of distribution, relative numbers in different vegetation types and daily activity rhythms (Greenslade 1964a). Kirk (1971) stated that pitfall traps are well-suited for trapping carabids. Other methods such as direct quadrat counts, in addition to being much more labor intensive, are usually not used because population densities may be too low (Greenslade 1964a, Thiele 1977) and because direct quadrat counts involves site destruction (Greenslade 1964a). Pitfall traps, however, have serious drawbacks which have been noted by several authors. The main disadvantage in their use is that both population density and activity influence the size of the catch (Greenslade 1964a, Thiele 1977). Briggs (1961) further states that the number of carabids trapped is related more to activity than absolute population density. Factors which in turn have been reported to affect activity include vegetation (Greenslade 1964a, Rivard 1966, Thiele 1977), weather (Mitchell 1963), relative humidity (Kirk 1971), microclimate (Thiele 1977), substrate (Wishart et al. 1956), beetle behavior (Greenslade 1964a, Thomas and Sleeper 1977), and construction of the trap (Luff 1975). In spite of these problems, Greenslade (1964a) concluded that pitfall traps are often the only method available for studying carabid populations.

While simple pitfall trapping is not adequate for estimating population density, several authors (Greenslade 1964a, Nelson 1970, Gist and Crossley 1973, Thiele 1977) have stated that pitfall trapping in conjunction with a mark and recapture technique can give a valid den-

sity estimate.

Southwood (1978) gives an excellent review of various marking techniques and capture-recapture methods of estimating population parameters. Ettershank and Ettershank (1973) and Southwood (1978) discuss underlying assumptions of capture-recapture methods and their validity.

Since Lincoln's (1930) study much has been done toward the development of a capture-recapture method which could be used with a population not closed to immigration and emigration. The methods developed can either be categorized as deterministic or stochastic. Deterministic models include those of Jackson (1948), Fisher and Ford (1947) and Bailey (1951, 1952). Stochastic models, which Southwood (1978) states are more realistic in nature, include those developed by Seber (1965), Jolly (1965) and Manly and Parr (1968).

The methods developed independently by Jolly (1965) and Seber (1965) are nearly identical with the exception that Jolly's makes allowance for any individuals killed after capture and so not released (Jolly 1965, Southwood 1978). As stated earlier, both methods, in addition to being stochastic, allow for loss (death and emigration) and dilution (births and immigration), thus avoiding the difficulty of having to work with a closed population.

Since its development the Jolly-Seber method has been used widely to study insect populations (e.g. Parr 1965, Sheppard et al. 1969, Manga 1972, Fletcher 1973, Ito et al. 1974, Ericson 1977, Thomas and Sleeper 1977), and according to Southwood (1978) remains the most useful method.

Ettershank and Ettershank (1973) working with a computer-simulated

population examined 4 different methods of capture-recapture analysis- Bailey's Triple Catch (Bailey 1951, 1952), Lincoln Index (Lincoln 1930), Jolly's (1965), and Schnabel (Ricker 1958) - and concluded that Jolly's method and the Lincoln Index most accurately described changes in population density. Jolly's, however, did better than the Lincoln when birth and death rates were higher and gave estimates for those rates which the Lincoln Index did not.

Several authors discuss the problems and biases encountered when the underlying assumptions of Jolly's (1965) method are violated. It has been noted that the standard errors obtained may not be very accurate because they are correlated to the estimate of sample size, the result being that small estimates appear more accurate than large estimates (Manga 1972; Ettershank and Ettershank 1973; Ericson 1977). Jolly's method may tend toward overestimation when recapture rate is low (Carothers 1973, Ericson 1977). Cormack (1972) and Carothers (1973) discuss the problems and biases which result from violating the assumption of equal catchability. Cormack (1972) discusses problems which arise if individuals have different probabilities of survival.

As Thiele (1977) points out, an important but often neglected question determining abundance values is whether carabids are distributed randomly or are aggregated. Both situations have been recorded in the literature (Thiele 1977, Reise and Weidemann 1975). Aggregation may be due to either environmental attraction or inter-individual attraction (true aggregation) (Southwood 1978). Aggregation in response to the favorableness or unfavorableness of the environment has been reported by

several authors (Rivard 1964, Greenslade 1964a, Briggs 1965, Baker and Dunning 1975). True aggregation has been less commonly noted (Greenslade 1963, Wautier 1971, as cited in Thiele 1977); and, in fact, Thiele (1977), states that on the whole few carabid species show true aggregation.

Mathematical distributions are often used in entomological research to describe insect dispersion quantitatively. Positive binomial, Poisson, negative binomial, and logarithmic with zeros are among the most commonly used distributions to fit discrete data.

Positive binomial is an appropriate model for underdispersion, regular, or uniform distribution (Cassie 1962; Pieters and Sterling 1973). Poisson best describes a random distribution with the following assumptions: all organisms have an equal probability of capture, all traps have an equal probability of capturing an organism, and the presence of an individual in a trap does not affect the chance of capturing another individual (Pieters and Sterling 1973, Southwood 1978). Negative binomial and logarithmic with zeros represent contagious or aggregated populations. Negative binomial is widely used to describe biological populations and is one of the more flexible overdispersion models (McGuire et al. 1957, Cassie 1962). Negative binomial has two parameters: the mean and a dispersion parameter K which is usually about 2. If K is greater than 2 then the distribution approaches Poisson; whereas if K is less than 1, then it approaches the logarithmic series (Southwood 1978).

The question of dispersal rate is closely tied to distribution. Thiele (1977) states that unequal powers of dispersal can account for

differences in distribution. Several authors have attempted to measure dispersal by measuring the distance traveled over time of a marked population (Greenslade 1964b, Nelson 1970; Calkins and Kirk 1973). Thiele (1977) and Southwood (1978) review a number of similar studies.

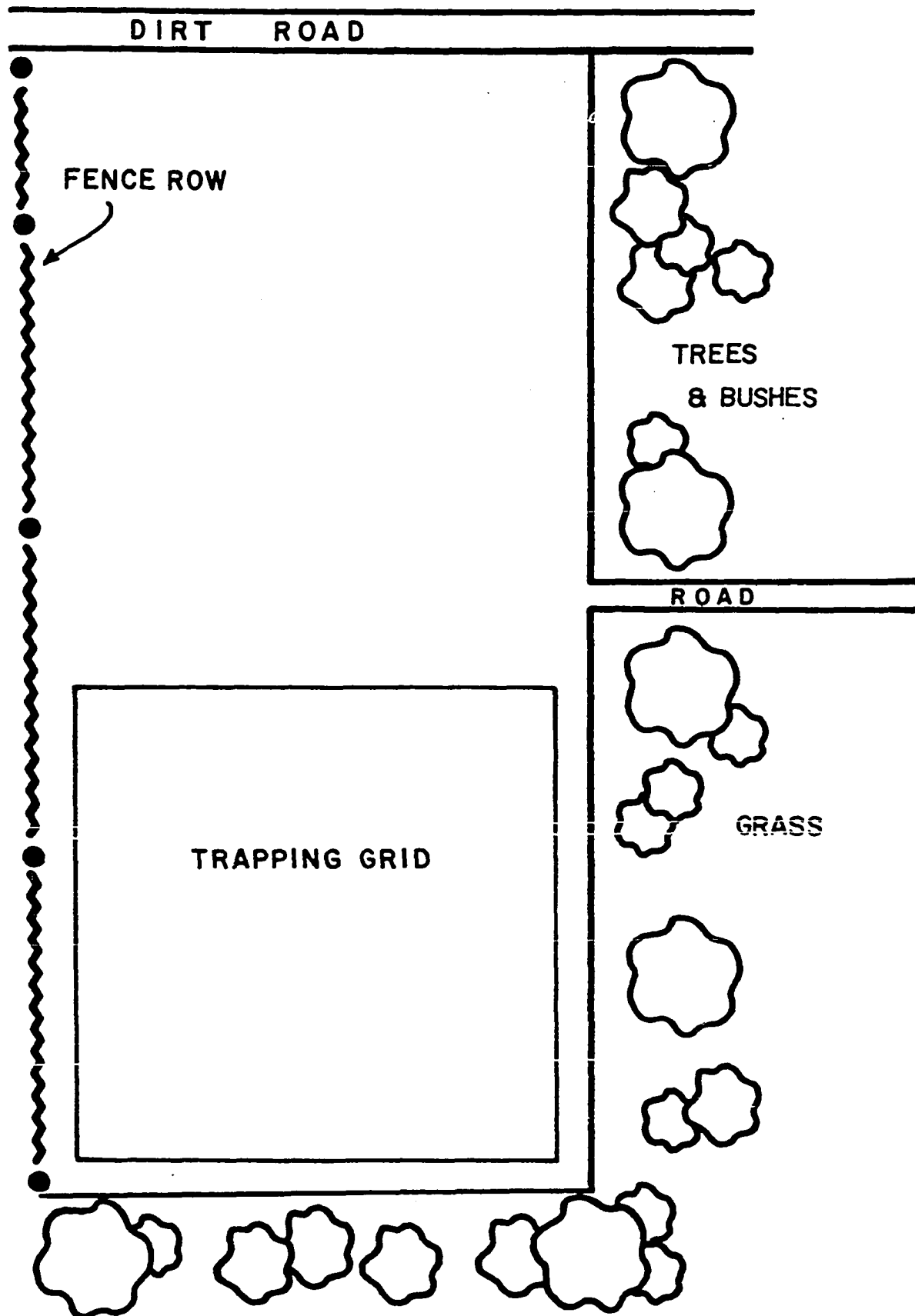
MATERIALS AND METHODS

The study area covered the east $\frac{1}{2}$ of a cornfield near Ames, Iowa. Only $\frac{1}{2}$ of the field was used because the field's length was approximately twice its width and the trapping grid was laid out in a square. The study area is illustrated in Figure 1. The east and north edge of the field were bordered by trees and shrubs. The south edge of the field was a fence row and the west end of the field was bordered by a dirt road (although the west end of the grid was continuous corn).

Three hundred and twenty-four pitfall traps were laid out in a square grid with 18 traps on a side and approximately 9 m between traps. The total area thus sampled was approximately 26,244 m², or 2.6 hectares.

In addition to the 324 traps making up the trapping grid, there were an additional 172 traps around the edge of the grid. These traps were spaced 4.6 m apart and formed a border 18 m from the grid. Along the east and north ends of the field the border traps lay between the cornfield and trees. Along the south end of the field, the border traps lay along the fence row and along the west end of the field the border traps were in the cornfield. These additional traps were to detect movement of beetles out of the grid area. Beetles captured in the border traps, after being recorded, were released at the original point of capture during the next release period. They were not used in calculating population density, dilution rate or survival rates, and were only used as a partial aid in calculating dispersion and dispersal.

Figure 1. Trapping grid in relation to the cornfield and field borders.



Pitfall traps were constructed from 946 ml (32 oz) Solo[®] ¹ plastic cups. A 9 cm plastic petri dish with an approximately 7 cm hole cut out of the center was slipped inside the 946 ml cup. This ring prevented the larger beetles (those species in this study) from climbing out of the trap. The cup was set into another cup of the same size buried in the ground. The cup within a cup arrangement enabled the inner trap to be easily lifted out and its contents emptied.

Each trap was numbered and when emptied, the beetles were placed individually in correspondingly numbered 60 ml (2 oz) plastic cups² and brought to the laboratory for marking.

Marking was accomplished by holding a beetle under a dissecting microscope between thumb and forefinger and etching a pattern of dots on the elytra with a #2 insect pin in a high speed Dremel[®]³ drill. Occasionally, too much elytra material would be scraped off and the wing cover would be punctured. Those beetles were discarded and not used for further calculations. The fact that marked beetles were captured up to 2 mo. after marking indicated that marking per se did not seem to affect vitality or survival.

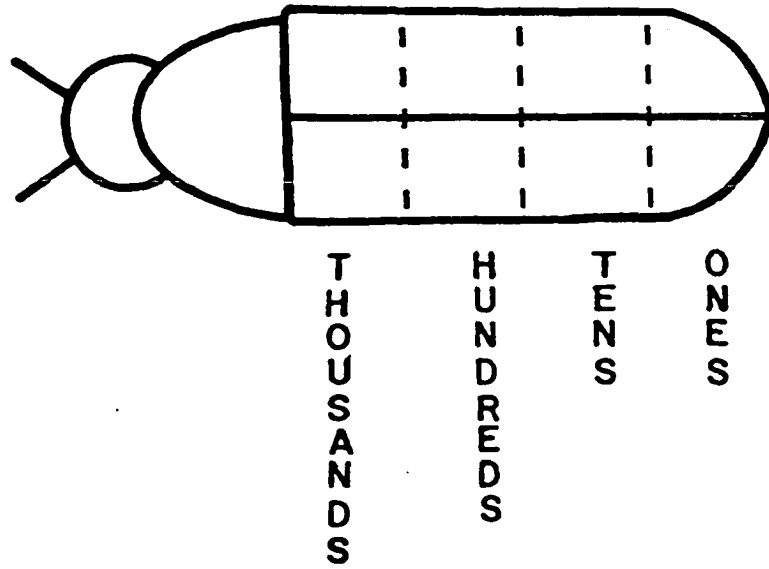
For the purpose of marking, the elytra were mentally divided into quarters (Figure 2). The most posterior quarter was the ones place, while the most anterior quarter was the thousands. Thus the dot pattern

¹Solo Cup Co., P.O. Box 91795, Chicago, Ill., 60693

²Thunderbird Container Corp., 128 Thunderbird Dr., El Paso, Tex., 79901

³Dremel Manufacturing Division, Emerson Electric Co., Racine, Wisc., 53406

Figure 2. Code for marking beetles. (See materials and methods for further explanation).



LINE BETWEEN HALVES OF ELYTRA

1

2

3

4

5

6

7

8

9

0

representing a 3 would be read as a 3 if it were placed in the most posterior quarter but read as 3,000 if it were in the most anterior quarter. With such a system beetles could be individually numbered from 1-9,999.

After marking, the beetles were held in 38 liter aquariums and supplied with food and water until released (usually one or two days later). Release was made at the point of previous capture so that the dispersion and dispersal of beetles would be affected as little as possible.

Traps were emptied and beetles released usually every other day, weather permitting. Unfortunately, at times rain would disrupt the trapping schedule by flooding and dislodging traps. Because of this, there were times when it was several days between successful trappings.

The mark and recapture data were analyzed using Jolly's (1965) stochastic method. With this method, population density, survival rate, and dilution rates as well as the associated variances could be calculated. Calculations using Jolly's formulas are quite tedious, particularly those connected with the variances, so a computer program published by Davies (1971) was used. Apparently there are some misprints in Davies' program and it was necessary to make some slight modifications before it would run. The modified program was checked by using Jolly's (1965) original data and found to be accurate. The changes were as follows:

- 1) Change DO 3I=2, LM to DO 3I=1, LM under the heading of computing R(I).

- 2) Add N3 (LM, LM)=B(LM-1) before DO 10 I=2, LM2 under the heading of computing the lower triangle of matrix N3.
- 3) Change DO 11 J=2, LM2 to DO 11 J=2, LM under the heading of computing the lower triangle of matrix N3.

To represent the dispersion of beetles in the grid area, it was decided to map their distributions based on numbers captured in each trap over time. Only grid traps were actually used in the mapping, although captures in border traps were used to better interpret trends in dispersion of a particular species. Actual mapping of beetle distribution was accomplished by using a computer contour mapping program called SYMAP⁴. The program is very flexible and a number of mapping operations can be easily performed.

After mapping beetle dispersion, the data were analyzed by fitting numbers captured per trap to several mathematical distributions. This was done in order to describe apparent patterns of distributions observed on the SYMAP's statistically. A computer program developed by Gates and Ethridge (1972) was used to fit the data to several mathematical distributions including: Poisson, positive binomial logarithmic with zeros, and negative binomial. A chi square statistic was used to test for significance of fit.

Beetle dispersal was estimated from the distance and direction traveled by marked beetles over time. Maximum and average dispersal were calculated for each species.

⁴Laboratory for Computer Graphics and Spatial Analysis, Graduate School of Design, Harvard University, Cambridge, Mass.

RESULTS

Table 7 lists the recapture rate based on number released and subsequently recaptured for each species of carabid for the entire season's trapping. It should be noted that for both H. pensylvanicus and P. chalcites the number released is higher than the number initially captured. This was because extra beetles captured in parts of the field other than the grid were sometimes released inside the grid.

Toward the end of the season, when the capture rate was very low for P. chalcites, extra beetles were released in hope of increasing the recapture rate. As the recapture rate for P. chalcites did not increase (Table 8) it was suspected that high mortality, low activity or dispersal out of the grid was occurring at this time in the season for this species. Dispersal out of the grid was very strongly suspected as the reason for the low recapture rate for H. pensylvanicus. In spite of the fact that nearly twice as many H. pensylvanicus were released as the other species, the recapture rate remained the lowest (1.69%). Suspected dispersal out of the grid is also supported by the observation that the border traps always captured more H. pensylvanicus than the grid traps (Figure 3).

No correlation was found between numbers of P. chalcites trapped and soil moisture or temperature. Numbers of S. substriatus trapped were negatively correlated to soil moisture ($P \leq .05$) but not correlated to temperature. Numbers of H. pensylvanicus trapped showed a positive correlation to nighttime temperature ($P \leq 0.01$) but were not correlated with either daytime temperature or soil moisture.

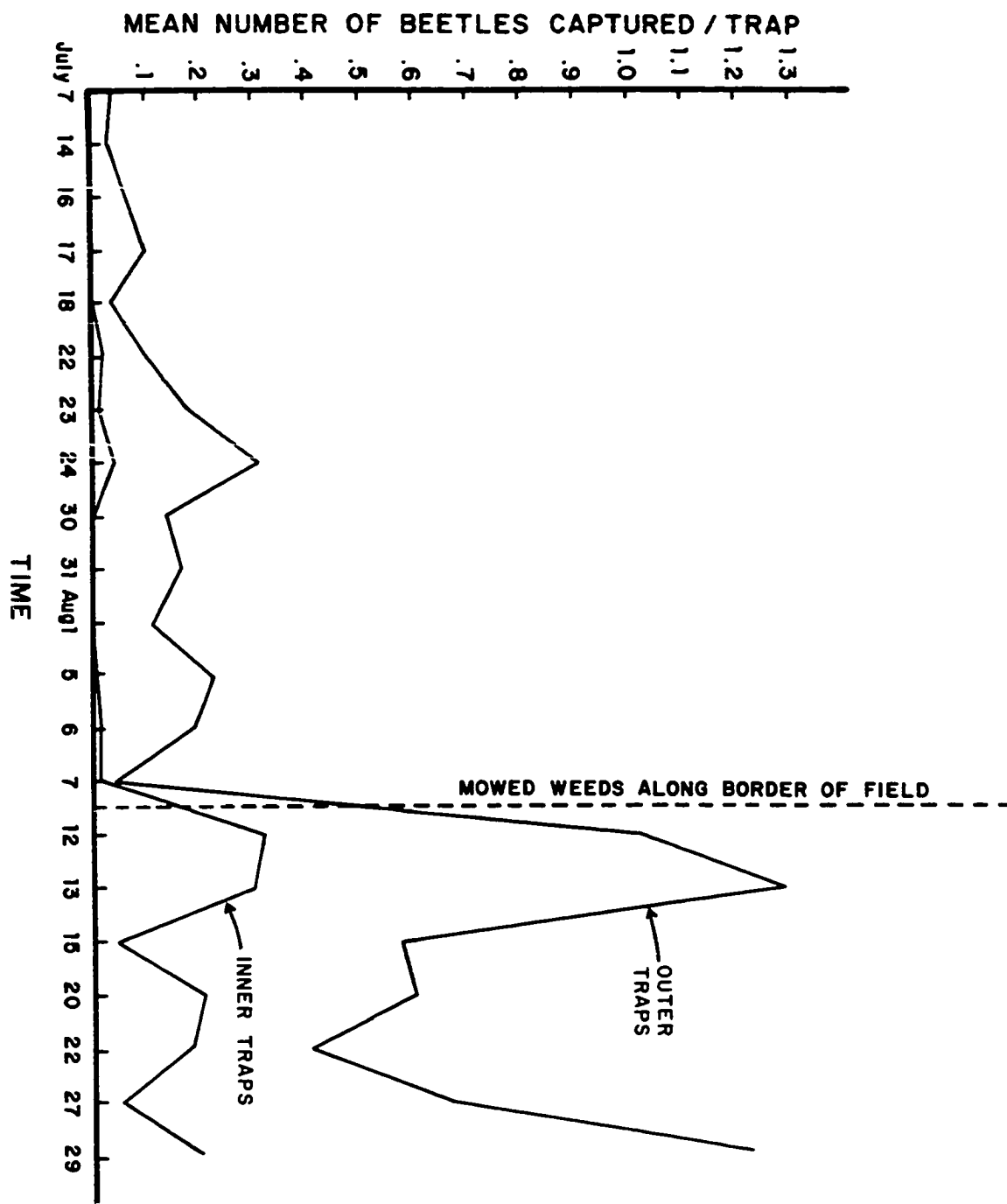
Table 7. Number of captured, marked, released, and recaptured P. chalcites, H. pensylvanicus and S. substriatus during the summer of 1975 from a cornfield in Ames, Iowa.

Captured	Marked Released	Recaptured	Recapture Rate %
<u>P. chalcites</u> ♂			
497	569	41	7.21%
<u>P. chalcites</u> ♀			
584	627	61	9.73%
<u>H. pensylvanicus</u> ♂+ ♀			
321	948	16	1.69%
<u>S. substriatus</u> ♂+ ♀			
424	406	57	14.04%

Table 8. Captures and recaptures of P. chalcites from an Ames, Iowa cornfield during the summer of 1975. n_i = number of captured individuals in the i^{th} sample. s_i = number of marked released individuals from the i^{th} sample. R_i = total number of the individuals subsequently recaptured.

Date of Capture	n_i	s_i	Day when last Captured															
June 3-5	108	108	June 3-5															
June 6-10	61	61	1	June 6-10														
June 11-18	134	123	2	1	June 11-18													
June 19-25	97	96	3	0	2	June 19-25												
June 26-July 2	58	57	0	2	1	1	June 26-July 2											
July 3-6	26	26	1	0	0	1	1	July 3-6										
July 7-10	101	99	1	2	4	2	4	1	July 7-10									
July 11-15	41	41	0	0	1	1	3	1	2	July 11-15								
July 16-17	73	68	1	0	2	0	1	1	4	3	July 16-17							
July 18-22	72	71	0	0	1	2	0	0	5	1	2	July 18-22						
July 23-24	85	85	0	1	0	1	0	1	5	1	3	1	July 23-24					
July 25-30	55	57	0	0	0	1	1	0	1	1	0	2	1	July 25-30				
July 31-Aug. 6	40	199	0	0	0	0	1	0	0	0	0	1	2	1	July 31-Aug. 6			
Aug. 7-12	67	105	0	0	1	0	0	0	0	0	0	0	0	1	4	Aug. 7-12		
Aug. 13-18	63	-	0	0	0	0	0	0	1	0	0	0	0	2	2	4	Aug. 13-18	
R_i			=	9	6	12	9	11	4	18	6	5	4	3	4	6	4	

Figure 3. Number of H. pensylvanicus captured in inner (grid) and outer (border) traps of an Ames, Iowa cornfield from July 7-29, 1975.



One of the objectives of this study was to establish whether there was any significant correlation between absolute population density (as measured by capture-recapture) and relative population density as measured by actual numbers of beetles captured in pitfall traps. As pointed out in the introduction, relative pitfall catches usually give poor estimations of population density. In this study, there was a positive correlation between absolute population density and relative pitfall catches for all three species; however, only in the case of S. substriatus was the correlation significant ($P \leq 0.05$).

Capture-Recapture Population Estimates

Capture-recaptures during the summer of 1975 are tabulated for each species in Tables 8-12. In the case of P. chalcites capture-recaptures were tabulated for males and females separately (Tables 9 and 10) as well as together (Table 8). Because of the possible differences in behavior between males and females, it would have been desirable to analyze the sexes separately for all three species. Low populations and recaptures for the species other than P. chalcites, however, made this impossible. Even in the case of P. chalcites, the recapture rate was too low when the sexes were separated to give very reliable estimates. In the case of H. pensylvanicus (Table 12), the recapture rate was too low even when both sexes were combined to give reliable population estimates.

Total population, survival rate, number of new beetles joining the population, and associated standard errors, as calculated according to Jolly (1965), are listed in Tables 12-17 for each species.

Table 9. Captures and recaptures of ♂ *P. chalcites* in an Ames, Iowa cornfield during the summer of 1975. n_i = number of captured individuals in the i^{th} samples. s_i = number of marked released individuals from the i^{th} sample. R_i = total number of individuals subsequently recaptured.

Date of Capture	n_1	s_1	Day When Last Captured														
June 3-5	36	36	June 3-5														
June 6-10	25	25	1	June 6-10													
June 11-18	83	74	1	1	June 11-18												
June 19-25	8	8	0	0	1	June 19-25											
June 26-July 2	33	33	0	0	1	0	June 26-July 2										
July 3-6	11	11	0	0	0	0	1	July 3-6									
July 7-10	37	37	0	0	2	1	2	0	July 7-10								
July 11-15	21	21	0	0	0	0	1	1	1	July 11-15							
July 16-17	38	34	0	0	1	0	1	1	1	1	July 16-17						
July 18-22	40	40	0	0	1	0	1	0	2	0	1	July 18-22					
July 23-24	47	47	0	1	0	0	0	1	1	1	1	0	July 23-24				
July 25-30	27	27	0	0	0	0	1	0	0	0	0	1	0	July 25-30			
July 31-Aug. 6	27	119	0	0	0	0	0	0	0	0	0	1	1	1	July 31-Aug. 6		
Aug. 7-12	32	57	0	0	1	0	0	0	0	0	0	0	0	0	0	Aug. 7-12	
Aug. 13-18	32	--	0	0	0	0	0	0	0	0	0	0	0	1	1	2	Aug. 13-18
R_1			=2	2	7	1	7	3	5	2	2	2	1	2	1	2	

Table 10. Captures and recaptures of *Q. P. chalcites* in an Ames, Iowa cornfield during the summer of 1975. n_i = number of captured individuals in the i^{th} sample. s_i = number of marked released individuals from the i^{th} sample. R_i = total number of individuals subsequently recaptured.

Date of Capture	n_i	s_i	Day When Last Captured														
June 3-5	72	72	June 3-5														
June 6-10	36	36	1	June 6-10													
June 11-18	51	49	1	0	June 11-18												
June 19-25	89	88	3	0	1	June 19-25											
June 26-July 2	25	24	0	2	0	1	June 26-July 2										
July 3-6	15	15	1	0	0	1	0	July 3-6									
July 7-10	64	62	1	2	2	1	2	1	July 7-10								
July 11-15	20	20	0	0	0	1	2	0	1	July 11-15							
July 16-17	35	34	1	0	1	0	0	0	3	2	July 16-17						
July 18-22	32	31	0	0	0	2	0	0	3	1	1	July 18-22					
July 23-24	38	38	0	0	0	1	0	0	4	0	2	1	July 23-24				
July 25-30	28	30	0	0	0	1	0	0	1	1	0	1	1	July 25-30			
July 31-Aug. 6	13	80	0	0	0	0	1	0	0	0	0	0	1	0	July 31-Aug. 6		
Aug. 7-12	35	48	0	0	1	0	0	0	0	0	0	0	0	1	1	Aug 7-12	
Aug. 13-18	31	--	0	0	0	0	0	0	1	0	0	0	0	1	1	2	Aug. 13-18
$R_i =$			8	4	5	8	5	1	13	4	3	2	2	2	2	2	

Table 11. Captures and recaptures of *S. substriatus* from an Ames, Iowa cornfield during the summer of 1975. n_i = number of captured individuals in the i^{th} sample. s_i = number of marked released individuals from the i^{th} sample. R_i = total number of the individuals subsequently recaptured.

Date of Capture	n_i	s_i	Day When Last Captured																				
June 3-6	100	99	June 3-6																				
June 7-12	39	38	3	June 7-12																			
June 14-18	33	32	2	0	June 14-18																		
June 19-23	25	25	1	1	0	June 19-23																	
June 24-30	37	35	2	1	0	0	June 24-30																
July 1-4	35	34	3	0	1	1	2	July 1-4															
July 5-8	52	51	1	0	1	2	2	1	July 5-8														
July 9-11	30	26	2	1	0	0	0	1	7	July 9-11													
July 12-16	10	10	1	0	0	0	0	0	0	1	July 12-16												
July 17-21	8	7	0	0	1	0	0	0	2	0	0	July 17-21											
July 22-25	15	12	0	0	0	0	0	0	2	1	1	0	July 22-25										
July 26-30	7	7	0	0	0	0	0	0	2	1	0	0	0	July 26-30									
July 31-Aug. 4	5	4	0	0	0	0	0	0	0	0	0	0	2	0	July 31-Aug. 4								
Aug. 5-12	5	4	0	0	0	0	0	0	0	0	0	1	0	0	0	Aug. 5-12							
Aug. 12-18	15	15	0	1	1	0	0	0	0	0	0	0	0	1	0	1	Aug. 12-18						
Aug. 20-25	8	7	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	Aug. 20-25					
$R_i =$			15	5	4	3	4	2	13	3	1	1	2	1	0	2	1						

Table 12. Captures and recaptures of H. pensylvanicus from an Ames, Iowa cornfield during the summer of 1975.

n_i = number of captured individuals in the i^{th} sample. S_i = number of marked released individuals from the i^{th} sample. R_i = total number of individuals subsequently recaptured.

Date of Capture	n_i	s_i	Day When Last Captured					
Aug. 13-14	97	167	Aug. 13-14					
Aug. 15-18	9	376	1	Aug. 15-18				
Aug. 20-21	67	94	2	1	Aug. 20-21			
Aug. 22-25	66	215	1	5	0	Aug. 22-25		
Aug. 27-28	18	105	0	1	0	0	Aug. 27-28	
Aug. 29-31	64	-	0	1	1	2	1	Aug. 29-31
$R_i =$		4	8	1	2	1		

Pterostichus chalcites

The total population of P. chalcites (Table 13) declined in the grid area during the trapping period from a high of approximately 5,000 in early-to mid-June to a low of approximately 1,000-1,500 in late-July to early-August. During its peak, the population density of P. chalcites was estimated to be $0.20/m^2$. The average population density for this species during the trapping period was $0.08/m^2$. When the total population was calculated separately for males and females (Tables 14 and 15), it was observed that during most of June, females appeared to outnumber males by nearly 10 to 1. This may either represent what was naturally occurring in the field or simply be an error resulting from low and erratic recapture rates when the sexes were not combined. Calculated over the entire summer, the sex ratio was 1.2 females to 1.0 male.

Mean survival rate, or probability of surviving over time, for P. chalcites (Table 13) is 0.7993 for the whole period. It should be noted that occasionally the estimated survival rate somewhat exceeded 1.0000 (June 26-July 2, July 7-10, July 11-15, and July 25-30). This is probably due to sampling effects. Overall, there were no obvious changes in survival rate. That is, survival rate apparently did not decrease later in the summer from what it had been earlier. The average survival rate of males, when calculated separately (Table 14), is 0.7420, which compares well with the average survival rate for males and females combined. The average survival rate for females, when calculated separately (Table 15), is much larger (0.9819). The conclusion that females may survive longer than males, however, is a dangerous one to make as survival rate for

Table 13. Capture-recapture analysis of population parameters for *P. chalcites* in an Ames, Iowa cornfield during the summer of 1975, according to Jolly's (1965) model.

Date of Capture	Proportion of recaptures $\hat{\alpha}_i$	Total Marked \hat{m}_i	Total Pop. \hat{n}_i	Survival Rate $\hat{\phi}_i$	# new beetles joining $\hat{\beta}_i$	Standard Errors			Standard errors due to errors in estimation of the parameter itself	
						S.E. (N)	S.E. (ϕ)	S.E. (β)	(N)	(ϕ)
June 3-5	--	0.00	--	0.7623	--	--	0.3884	--	--	0.3862
June 6-10	0.0164	82.33	5022.33	0.8132	1085.84	5566.23	0.3956	5065.24	5566.16	0.3943
June 11-18	0.0224	115.75	5170.16	0.8356	-489.36	3531.92	0.3548	3065.75	3531.73	0.3540
June 19-25	0.0515	197.00	3821.80	0.4277	151.93	2190.33	0.1781	1124.54	2189.95	0.1757
June 26-July 2	0.0690	123.18	1786.14	1.1607	-299.73	1021.56	0.6150	1392.12	1020.95	0.6159
July 3-6	0.1154	204.50	1772.33	0.5692	- 74.62	1281.54	0.2890	591.06	1281.02	0.2872
July 7-10	0.1386	129.50	934.25	1.0249	171.22	327.68	0.4373	433.18	326.35	0.4374
July 11-15	0.1951	219.83	1126.65	1.3922	572.79	569.29	0.7943	787.07	568.51	0.7957
July 16-17	0.1644	352.00	2141.33	0.8536	455.98	1122.83	0.5549	826.14	1122.33	0.5546
July 18-22	0.1528	348.25	2279.46	0.7259	283.72	1334.25	0.5518	697.73	1333.85	0.5514
July 23-24	0.1529	296.33	1937.56	0.2511	240.20	1292.13	0.1923	315.80	1291.74	0.1910
July 25-30	0.1273	92.50	726.79	1.1988	492.98	485.95	0.8249	718.42	485.51	0.8259
July 31-Aug. 6	0.1250	170.83	1366.67	0.3762	958.67	971.40	0.2590	877.99	971.18	0.2577
Aug. 7-12	0.0896	137.25	1532.63	--	--	1127.41	--	--	1127.23	--
Aug. 13-18	0.1429	--	----	--	--	--	--	--	--	--

Table 14. Capture-recapture analysis of population parameters for ♂ *P. chalcites* in an Ames, Iowa cornfield during the summer of 1975, according to Jolly's (1965) model.

Date of Capture	Proportion of Recaptures	Total Marked	Total Pop.	Survival Rate	# new beetles joining	Standard Errors			Standard errors due to errors in estimation of the parameter itself	
	$\hat{\alpha}_i$	\hat{m}_i	\hat{n}_i	$\hat{\phi}_i$	$\hat{\beta}_i$	S.E. (N)	S.E. (ϕ)	S.E. (β)	(N)	(ϕ)
June 3-5	---	0.00	--	0.3750	--	--	0.4158	--	--	0.4079
June 5-10	0.0400	13.50	337.50	0.3352	408.57	485.90	0.3247	502.01	485.81	0.3154
June 11-18	0.0241	12.57	521.71	0.6740	110.44	557.61	0.6696	554.79	557.53	0.6677
June 19-25	0.1250	57.00	456.00	0.5313	879.75	616.12	0.5290	1183.54	616.00	0.5253
June 26-July 2	0.0303	34.00	1122.00	0.7374	-292.00	1204.97	0.4349	980.51	1204.90	0.4315
July 3-6	0.0909	48.67	535.33	1.4727	-149.04	580.95	0.9485	791.94	580.69	0.9548
July 7-10	0.1351	86.40	639.36	1.1782	223.20	397.73	0.9285	626.60	397.37	0.9267
July 11-15	0.1429	139.50	976.50	1.1111	245.00	862.21	1.0682	816.46	862.06	1.0686
July 16-17	0.1316	175.00	1330.00	0.7108	217.50	1114.13	0.6977	645.41	1114.04	0.6970
July 18-22	0.1250	145.00	1160.00	1.0722	570.42	996.90	1.3262	1115.75	996.71	1.3264
July 23-24	0.1064	193.00	1814.20	0.1809	245.65	2096.19	0.2217	460.49	2096.11	0.2203
July 25-30	0.0741	42.50	573.75	0.9259	31.25	613.33	0.8957	491.76	613.10	0.8952
July 31-Aug. 6	0.1111	62.50	562.50	0.3417	264.33	545.32	0.3302	356.21	545.06	0.3283
Aug. 7-12	0.1250	61.00	488.00	--	--	499.50	--	--	499.32	--
Aug. 13-18	0.1250	--	---	--	--	--	--	--	--	--

Table 15. Capture-recapture analysis of population parameters for ♀ *P. chalcites* in an Ames, Iowa cornfield during the summer of 1975, according to Jolly's (1965) model.

Date of Capture	Proportion of Recaptures	Total Marked	Total Pop.	Survival Rate	# new beetles joining	Standard Errors			Standard errors due to errors in estimation of the parameter itself	
	$\hat{\alpha}_i$	\hat{m}_i	\hat{n}_i	$\hat{\phi}_i$	$\hat{\beta}_i$	S.E. (N)	S.E. (ϕ)	S.E. (β)	(N)	(ϕ)
June 3-5	---	0.00	--	0.8889	--	--	0.5184	--	--	0.5171
June 5-10	0.0278	64.00	2304.00	1.0000	2745.00	2622.36	0.6367	5659.85	2622.32	.6367
June 11-18	0.0196	99.00	5049.00	0.8503	-1510.41	5609.77	0.4695	4542.85	5609.75	0.4686
June 19-25	0.0449	125.00	2781.25	0.3818	-396.55	1792.01	0.1969	676.28	1791.79	0.1940
June 26-July 2	0.1200	79.80	665.00	2.8472	261.94	459.06	2.9630	1755.87	458.22	2.9718
July 3-6	0.1333	287.00	2152.50	0.2049	- 3.93	2546.62	0.2045	319.02	2546.07	0.2032
July 7-10	0.1406	61.46	437.06	0.9086	124.70	185.73	0.4549	267.78	184.47	0.4541
July 11-15	0.2000	104.00	520.00	1.6639	133.11	335.29	1.1721	510.70	334.66	1.1761
July 16-17	0.2000	199.67	998.33	0.9199	35.74	665.07	0.8034	442.63	664.62	0.8032
July 18-22	0.2188	208.50	953.14	0.6065	92.32	745.99	0.5911	291.45	745.61	0.5902
July 23-24	0.2105	141.00	669.75	0.3801	109.42	534.09	0.3752	186.57	533.69	0.3734
July 25-30	0.1786	65.00	364.00	1.8000	394.20	315.18	1.8174	810.46	314.83	1.8218
July 31-Aug. 6	0.1538	162.00	1053.00	0.3125	525.00	1120.01	0.3233	692.19	1119.93	0.3219
Aug. 7-12	0.0857	75.00	875.00	--	--	887.55	--	--	887.41	--
Aug. 13-18	0.1613	--	--	--	--	--	--	--	--	--

individual sampling periods is quite variable. In fact, there are several survival rates which are much larger than 1.0000. For example, the survival rate during June 26-July 2 was 2.8472. The fact that this high rate is associated with two very low survival rates (0.3818 during June 19-25 and 0.2049 on July 3-6) suggests that some major error in the estimate exists. The possibility exists that the marks, of one occasion, may have been misread however, the low recapture rate itself probably introduces errors.

The trends in survival rates are correlated with estimates of the number of new beetles joining the population. After decreasing in late-June, the number of new male and female P. chalcites (Table 13) joining the population appears to increase through July into early-August. On the average, 352 beetles, with a range of 172-573, joined the population from one sampling period to the next during the time from July 7-30.

Standard errors are quite high for the estimates of total population, survival rates, and the number of new beetles joining the population (Tables 13-15). In most cases they are approximately the same as the number being estimated. This is somewhat to be expected. A number of authors (e.g. Ericson 1977, Manga 1972, Ettershank and Ettershank 1973) have pointed out that the standard errors associated with Jolly's (1965) estimate are loosely correlated with the number being estimated and that large numbers will have larger standard errors than small numbers such as those published by Jolly (1965).

Scarites substriatus

The total population of S. substriatus (Table 16) remained fairly

Table 16. Capture-recapture analysis of population parameters for *S. substriatus* in an Ames, Iowa cornfield during the summer of 1975, according to Jolly's (1965) model.

Date of Capture	Proportion of recaptures	Total Marked	Total Pop.	Survival Rate	# new beetles joining	Standard Errors			Standard errors due to errors in estimation of the parameter itself	
	\hat{a}_i	\hat{M}_i	\hat{N}_i	$\hat{\phi}_i$	$\hat{\beta}_i$	S.E.(N)	S.E.(ϕ)	S.E.(β)	(N)	(ϕ)
June 3-6	--	0.00	--	0.9515	--	--	0.4575	--	--	0.4570
June 7-12	0.0769	94.20	1224.60	0.9443	857.59	890.31	0.5906	1578.24	890.28	0.5902
June 14-18	0.0606	122.00	2013.00	0.9452	-105.86	1720.02	0.6741	1782.78	1719.99	0.6738
June 19-23	0.0800	144.67	1795.83	0.9105	236.48	1595.38	0.6520	1515.80	1595.32	0.6516
June 24-30	0.0811	151.75	1871.58	1.3333	-1267.78	1404.51	1.1039	1701.34	1404.40	1.1050
July 1-4	0.2000	245.00	1225.00	0.1555	123.90	963.30	0.1132	128.32	963.43	0.1110
July 5-8	0.1346	42.31	314.29	1.2320	- 95.98	141.36	0.7001	161.80	140.82	0.7025
July 9-11	0.3667	106.33	290.00	1.0055	322.43	172.79	1.0899	499.32	172.37	1.0899
July 12-16	0.2000	122.00	610.00	0.5615	-147.87	705.37	0.7330	271.41	705.27	0.7317
July 17-21	0.3750	73.00	194.67	0.5974	56.80	201.54	0.6638	96.08	201.06	0.6614
July 22-25	0.2667	46.00	172.50	0.8333	-36.25	135.60	0.9124	82.82	135.17	0.9110
July 26-31	0.4286	45.00	105.00	0.4490	7.86	108.02	0.5505	36.17	107.54	0.5459
July 31-Aug. 4	0.4000	22.00	55.00	0.8750	57.75	55.87	1.0526	108.53	55.45	1.0505
Aug. 5-15	0.2000	21.00	105.00	1.4167	13.83	132.07	1.8486	141.54	131.91	1.8552
Aug. 12-18	0.2667	34.00	127.50	--	--	142.72	--	--	142.65	--
Aug. 20-25	0.3750	--	--	--	--	--	--	--	--	--

constant during June, averaging 1,726 beetles in the study area. After July 4, the population declined drastically, averaging only 219 in the study area from July 4-August 25. During its peak, the population density of S. substriatus averaged $0.08/\text{m}^2$. During June, the average population density was $0.07/\text{m}^2$, while during July and August the average density was only $0.01/\text{m}^2$.

The survival rate for S. substriatus was very high and relatively constant during June, averaging 1.016, which indicates no mortality. During July and August, the survival rate was only 0.7918 and estimates were far more variable. The few survival rates exceeding 1.0000 are probably due to sampling effects.

Not much can be said about the estimated number of beetles joining the population, other than there seems to be quite a bit of variability over time.

Standard errors for total population and survival rates are somewhat lower for S. substriatus than for P. chalcites, but still relatively high. Standard errors associated with the estimated number of new beetles joining the population are also quite high, preventing conclusions concerning trends for this estimate.

Harpalus pensylvanicus

The estimates of total population, survival rate, and number of new beetles joining the population obtained for H. pensylvanicus (Table 17) show extreme variability. For example, the estimated population from August 15-22 jumped 13-fold from 1,248 to 16,862. Standard errors on all estimates were also extremely large.

Table 17. Capture-recapture analysis of population parameters for *H. pensylvanicus* in an Ames, Iowa cornfield during the summer of 1975, according to Jolly's (1965) model.

Date of Capture	Proportion of recaptures	Total Marked	Total Pop.	Survival Rate	# of new beetles joining	Standard Errors			Standard errors due to errors in estimation of the parameter itself	
	$\hat{\alpha}_1$	\hat{m}_1	\hat{n}_1	$\hat{\phi}_1$	$\hat{\beta}_1$	S.E.(N)	S.E.(ϕ)	S.E.(β)	(N)	(ϕ)
Aug. 13-14	--	0.00	--	0.8301	--	--	0.5526	--	--	0.5518
Aug. 15-18	0.1111	138.63	1247.63	1.4962	14,459.39	1435.83	1.5953	18,020.66	1435.78	1.5957
Aug. 20-22	0.0448	755.00	16,861.66	0.3883	-2944.33	20,102.45	0.5028	4800.49	20,102.50	0.5026
Aug. 22-25	0.0909	328.50	3613.50	0.7833	4631.00	3512.23	0.9688	9086.88	3511.69	0.9687
Aug. 27-28	0.0556	421.00	7578.00	--	--	11,174.59	--	--	11,174.45	--
Aug. 29-31	0.0781	--	--	--	--	--	--	--	--	--

Thus, estimates should be treated with caution. Such large fluctuations are due to an extremely low recapture rate (1.69%) which in turn is probably due to relatively rapid dispersal into and out of the trapping area by this species. Harpalus pensylvanicus evidently preferred the border areas (Figure 3) and was also the most likely species to take flight. Pterostichus chalcites could fly but seldom did and S. substriatus was not capable of flight. In view of this, the only statements concerning the population that can be made is that H. pensylvanicus is the most active and probably the most populous species studied. Population in the study area averaged 7,325 or $0.28/\text{m}^2$ during the last half of August. Even if the estimate of 16,861 is thrown out, this species appears to be fairly abundant.

Distribution

Contour maps showing the distribution or dispersion of each carabid species during the trapping season are shown in Figures 4-13. These maps represent a pooling of trap data over a number of sampling periods. Although individual distribution maps were drawn for each sampling period and for each sex, they were not included here because there was relatively little change over the short sampling periods and there was no obvious differences in the pattern between males and females.

Pterastichus chalcites

Figures 4, 5, and 6 show the distribution of P. chalcites during June 3-30, July 1-31, and August 1-18 respectively. Pooled over the

Figure 4. Contour map for P. chalcites showing the distribution of individuals in an Ames, Iowa cornfield from June 3-30, 1975. Numbers indicate the number of beetles captured within the contour boundaries.

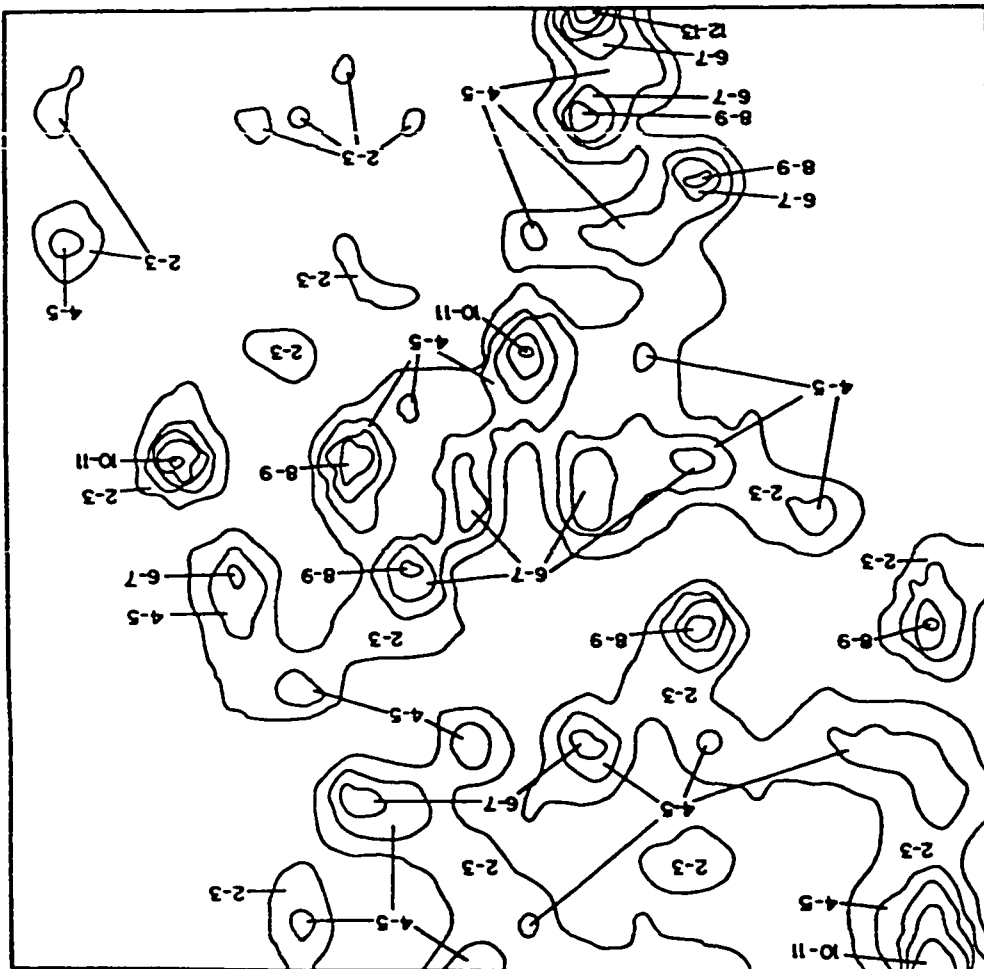


Figure 5. Contour map for P. chalcites showing the distribution of individuals in an Ames, Iowa cornfield from July 1-31, 1975. Numbers indicate the number of beetles captured within the contour boundaries.

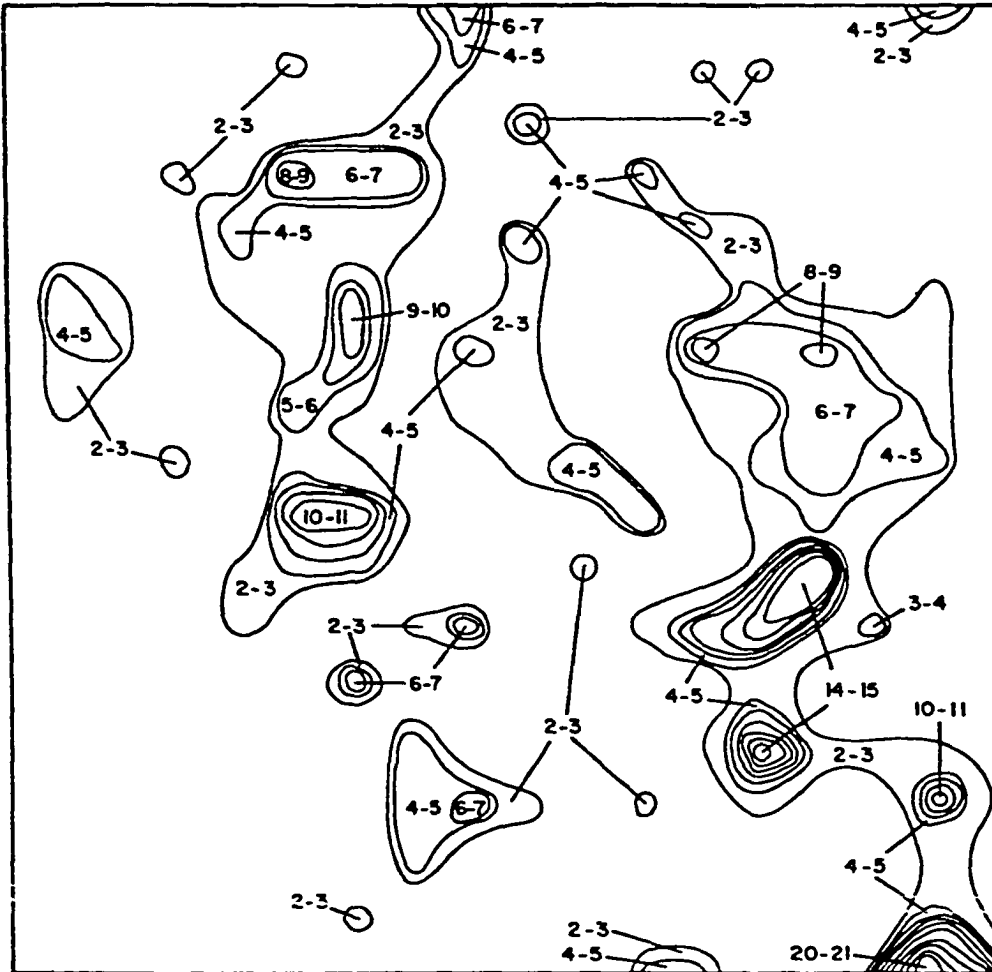
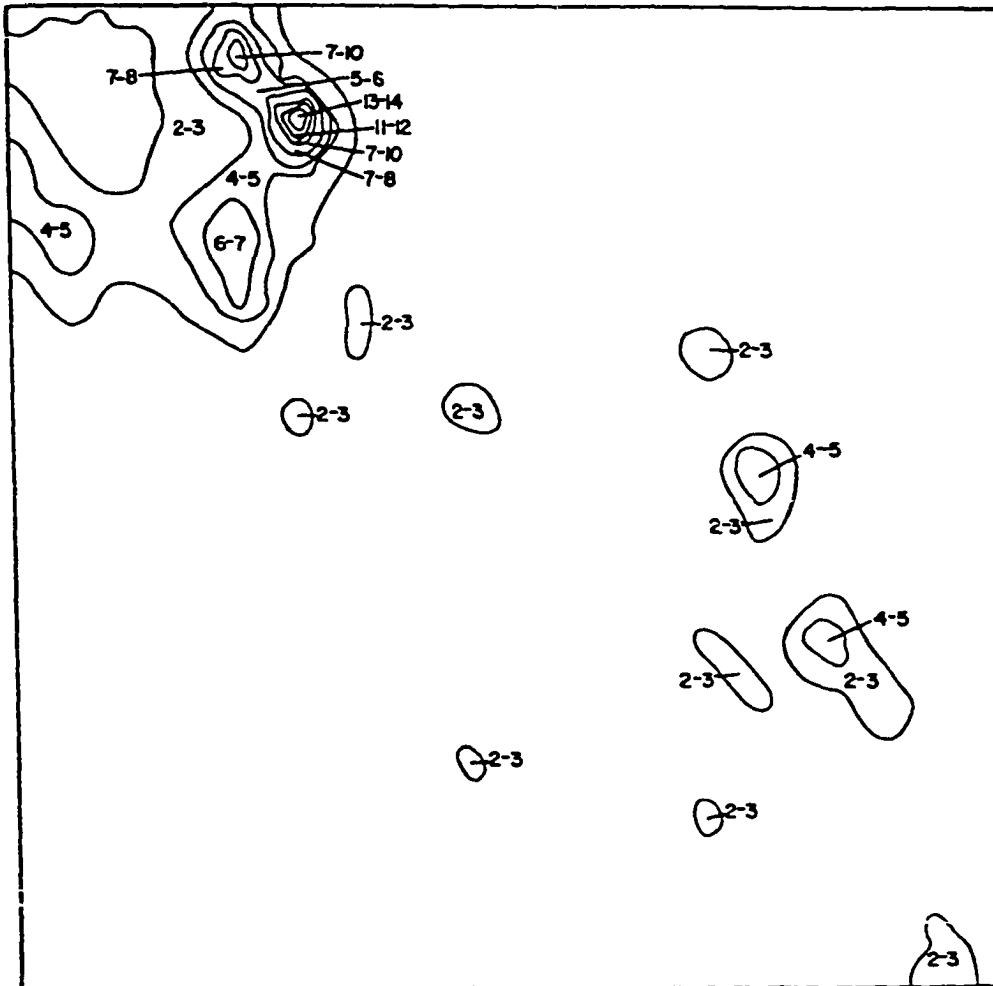


Figure 6. Contour map for P. chalcites showing the distribution of individuals in an Ames, Iowa cornfield from August 1-18, 1975. Numbers indicate the number of beetles captured within the contour boundaries.



month of June, there was a mean of 1.54 P. chalcites captured per trap with a variance of 5.42 and an index of dispersion of 3.53. During July, there was a mean of 1.71 beetles per trap with a variance of 7.29 and an index of dispersion of 4.21, while during August the mean dropped to 0.645 with a variance of 2.06 and an index of dispersion of 3.19.

These data show that during the summer of 1975, this species showed a definite pattern of aggregation over time. In fitting the numbers of P. chalcites captured per trap to several mathematical distributions it was found that the negative binomial gave the best fit for June's and August's data ($P \leq 0.74$ and 0.33 respectively) although logarithmic with zeros may also give a satisfactory fit for August's data ($P = 0.28$). For July's data the logarithmic with zeros gave a better fit than negative binomial ($P \leq 0.77$ and 0.58 respectively). For all three months both Poisson and positive binomial were rejected ($P \leq 0.001$), thus supporting the conclusion that the distribution was aggregated. Aggregation is further suggested in that negative binomial and logarithmic with zeros gave the best fit, while Poisson and positive binomial were rejected when the data were analyzed separately for each sampling period rather than pooled over a whole month.

In addition to noting that the population pattern of P. chalcites is aggregated, it is interesting to note that, whereas some areas of the grid remained as sites of aggregation throughout the summer, other areas changed in respect to beetle aggregation as the summer progressed. For example, the distribution map for August 1-18 (Figure 6) clearly shows an area of aggregation in the southwest corner of the grid which

does not show up on the maps for June (Figure 4) or July (Figure 5).

It is also interesting that during August very few beetles were captured anywhere in the grid other than this southwest corner.

The number of P. chalcites captured in late July and early August declined from what it had been earlier in the season, and the distribution map for August 1-18 (Figure 6) suggests the possibility that this species may have been leaving the grid in search of more favorable areas of the cornfield, or perhaps even leaving the field altogether, moving into the fence row.

Scarites substriatus

Figures 7, 8, and 9 illustrate the distribution of S. substriatus during June 3-30, July 1-31, and August 1-25 respectively. Pooled over the month of June, there was a mean of 0.52 S. substriatus captured per trap with a variance of 0.696 and an index of dispersion of 1.33. During July, there was a mean of 0.49 beetles per trap with a variance of 0.81 and an index of dispersion of 1.67. In August, the mean per trap dropped to 0.10 per trap with a variance of 0.09 and an index of dispersion of 0.97. Although the indexes of dispersion of S. substriatus are much closer to 1 than for P. chalcites, the distribution maps for June and July indicate that the distribution is aggregated. Furthermore, there seems to be a fair degree of consistency between June and July as to where aggregation occurs in the grid. In fitting the numbers of S. substriatus per trap to the same mathematical distributions as were used for P. chalcites, it was found that logarithmic with zeros fit the trap data from June and July the best ($P \leq 0.90$ and 0.97 respectively),

Figure 7. Contour map for S. substriatus showing the distribution of individuals in an Ames, Iowa cornfield from June 3-30, 1975. Numbers indicate the number of beetles captured within the contour boundaries.



Figure 8. Contour map for S. substriatus showing the distribution of individuals in an Ames, Iowa cornfield from July 1-31, 1975. Numbers indicate the number of beetles captured within the contour boundaries.

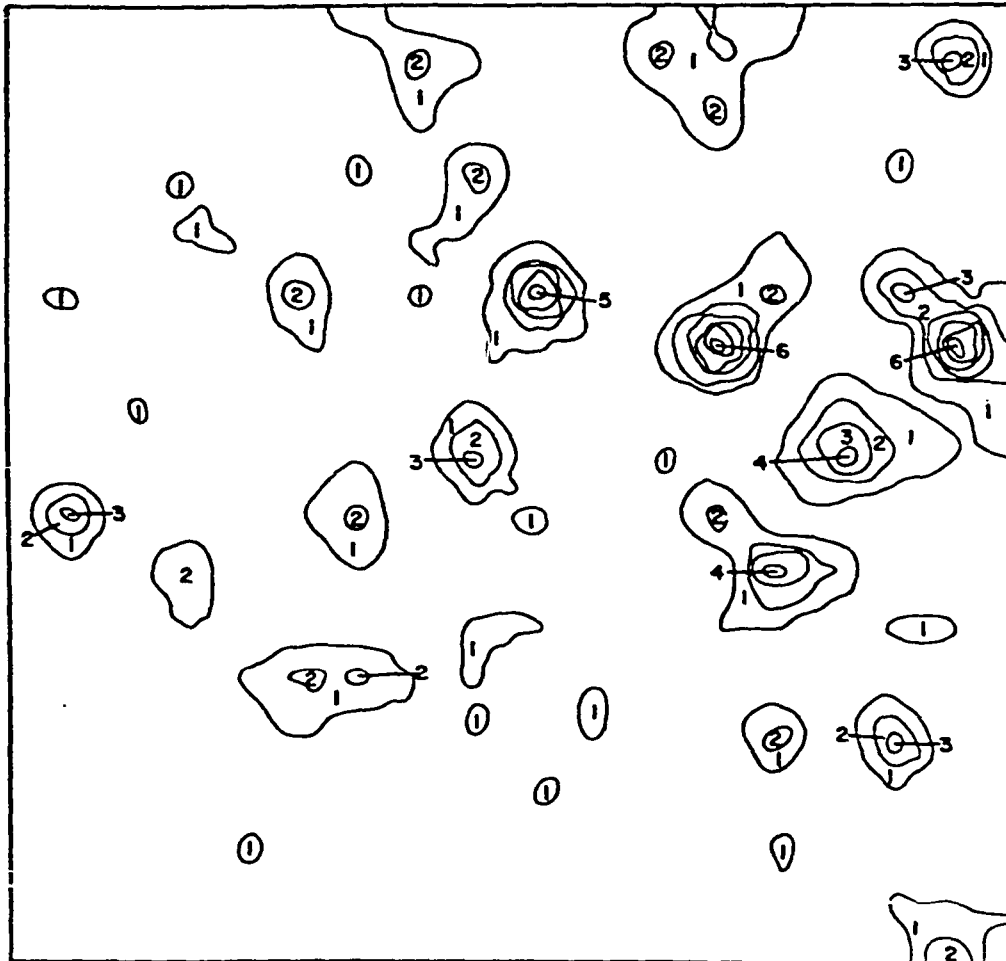


Figure 9. Contour map for S. substriatus showing the distribution of individuals in an Ames, Iowa cornfield from August 1-25, 1975. Numbers indicate the number of beetles captured within the contour boundaries.

although negative binomial gave a satisfactory fit for both months' data ($P \leq 0.62$ for June and $P \leq 0.38$ for July). Both Poisson and positive binomial were rejected ($P \leq 0.01$) for June and July. Poisson and positive binomial were also rejected as acceptable models when the data were analyzed separately for each sampling period rather than pooled over a whole month.

During August, so few beetles were trapped that no distributions were fit to the data. The distribution map for August (Figure 9) gives the impression of a nonaggregated pattern, but this may be due to low numbers captured. One interesting observation is that very few beetles were trapped in the south half of the field. The map for July (Figure 8) also shows a higher concentration of beetles in the north part of the grid than in the south. This may be due to the stunted corn in the south and the southeast part of the field during late summer, resulting in hotter, more sunny ground conditions. The soil in this part of the grid also had a low organic content and was sandier than the rest of the field. In contrast, the north part of the field during this time had normal corn plants, rich soil, and was bordered by an area of trees and grass which was part of an arboretum (Figure 1).

Harpalus pensylvanicus

Because H. pensylvanicus was active only in late summer and because the distribution patterns for this species changed quite a bit over short periods of time, in contrast to those for P. chalcites and S.

substriatus, four maps were used to illustrate the distribution during August (Figures 10-13). All four maps show H. pensylvanicus to be aggregated in its distribution. There was a mean of 1.02 beetles caught per trap from August 10-25 with a variance of 3.55 and an index of dispersion of 3.48. Negative binomial or logarithmic with zeros ($P \leq 0.43$ and 0.51 respectively) fit the data best. Both Poisson and positive binomial were rejected as fitting either the pooled data from August 10-25 or the data from individual sampling periods.

The changes in the distribution pattern of H. pensylvanicus in the cornfield during August is probably due to this species being a transient inhabitant of the field (Figure 3). Its preferred habitat was the field borders and it could disperse rapidly by flight.

Prior to August 7, there were practically no H. pensylvanicus captured in the grid, although this species had been captured in the outer border traps since July 7 (Figure 3). Between August 7 and August 12, the northern and eastern borders of the field were mowed. This corresponded to significantly higher catches in both grid and outer traps, which is probably due to increased beetle activity (Figure 3). The distribution map for August 10-12 (Figure 10) suggests that H. pensylvanicus was dispersing into the field from the northern and eastern sides (the sides mowed). Later in August, it appeared that H. pensylvanicus had dispersed throughout the grid (Figures 11-13), although aggregated into certain areas.

Figure 10. Contour map for H. pensylvanicus showing the distribution of individuals in an Ames, Iowa cornfield from August 10-12, 1975. Numbers indicate the number of beetles captured within the contour boundaries.

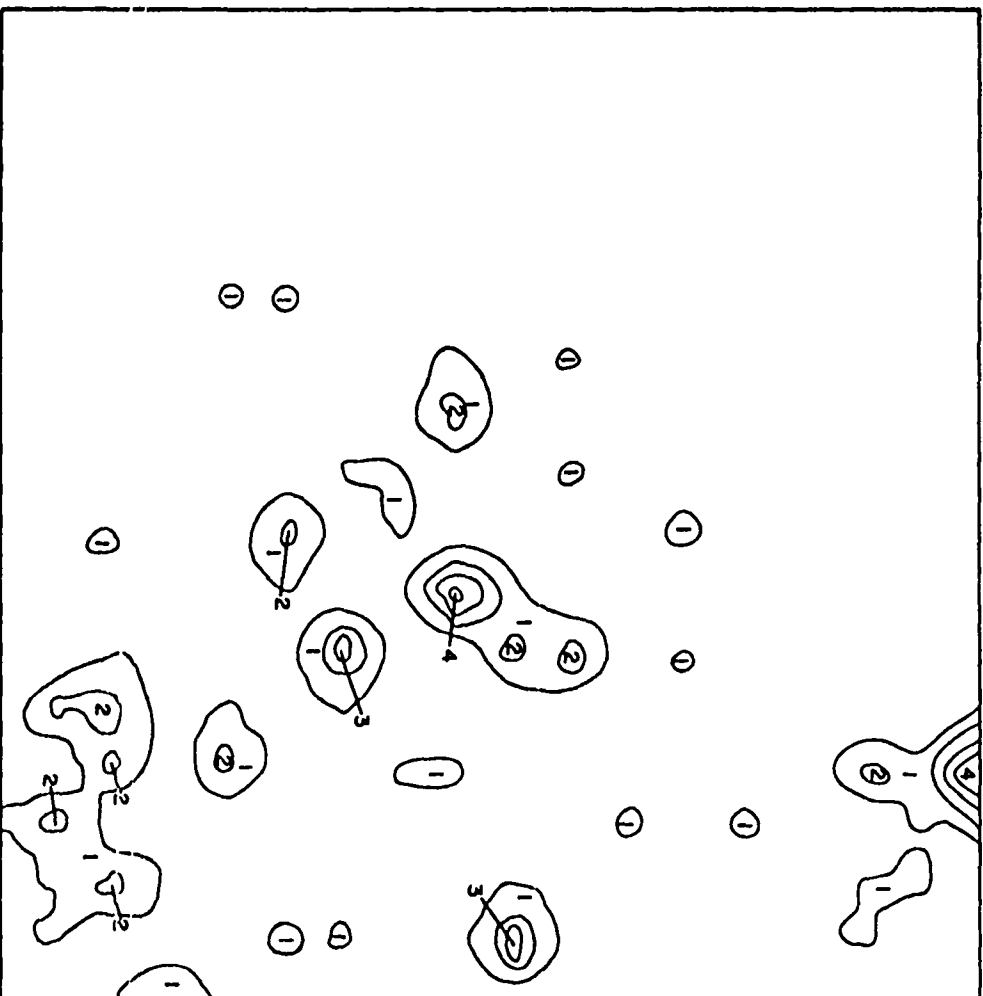


Figure 11. Contour map for H. pensylvanicus showing the distribution of individuals in an Ames, Iowa cornfield from August 13-14, 1975. Numbers indicate the number of beetles captured within the contour boundaries.

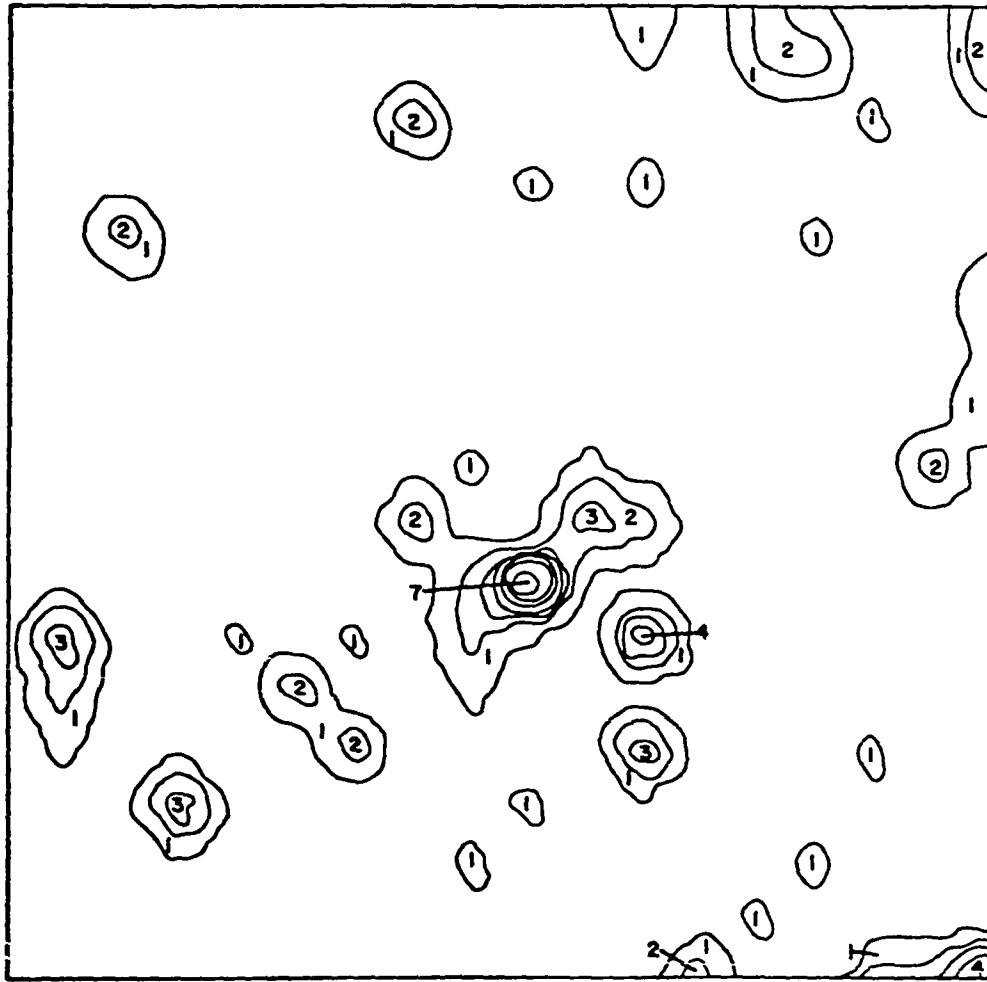


Figure 12. Contour map for H. pensylvanicus showing the distribution of individuals in an Ames, Iowa cornfield from August 15-21, 1975. Numbers indicate the number of beetles captured within the contour boundaries.

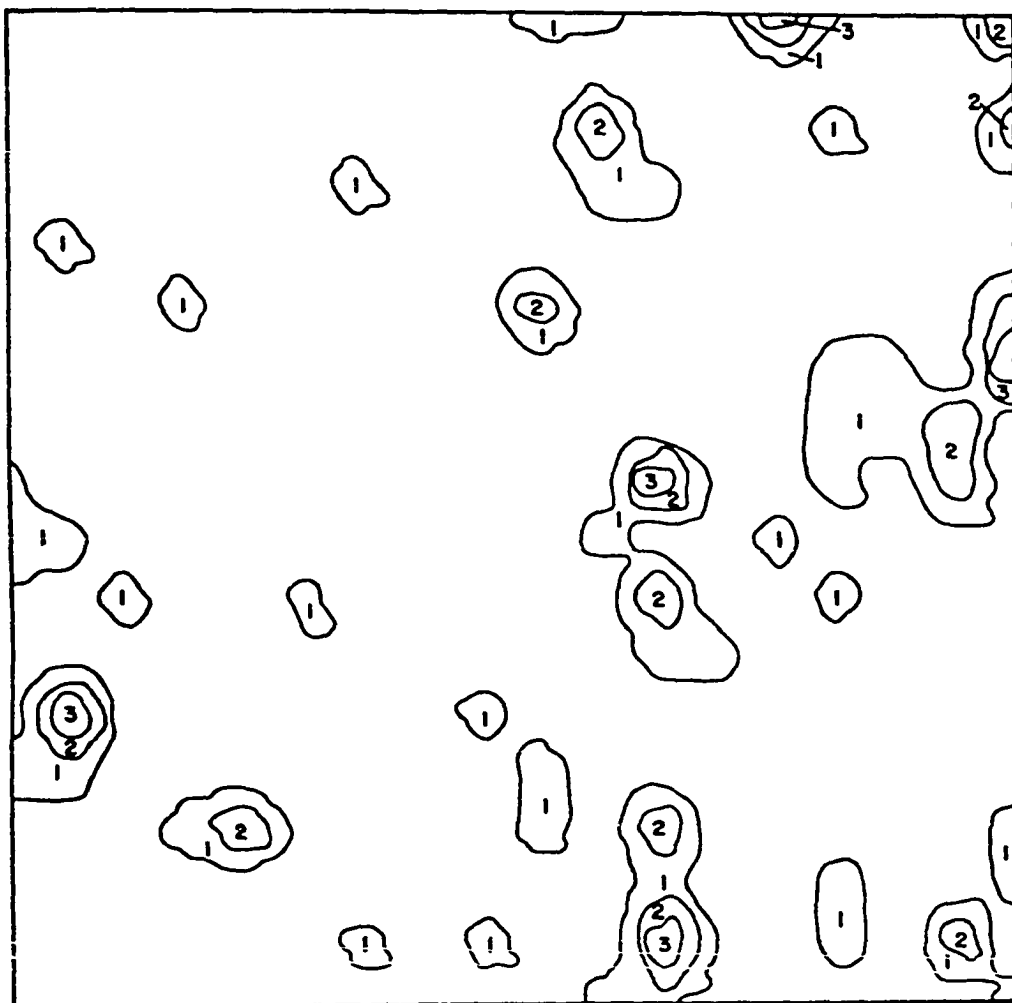
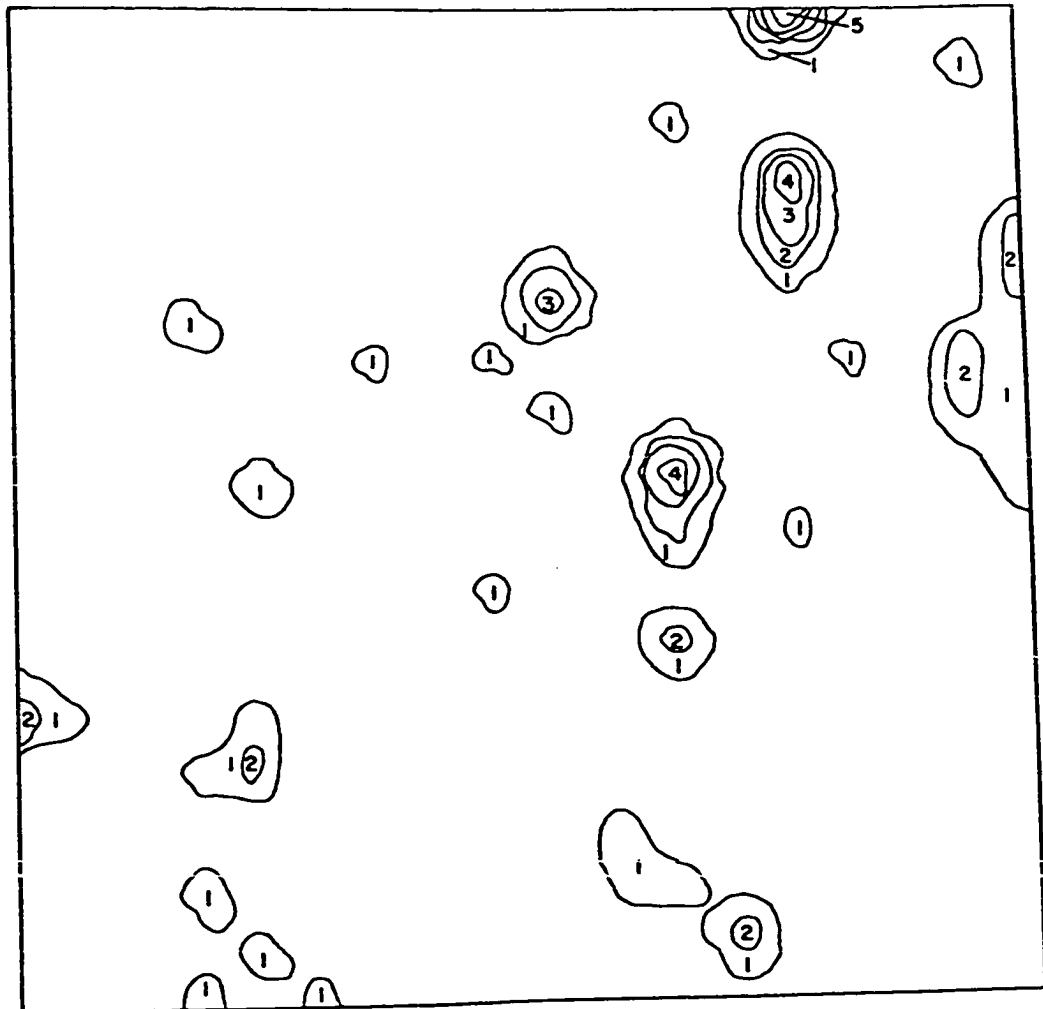


Figure 13. Contour map for H. pensylvanicus showing the distribution of individuals in an Ames, Iowa cornfield from August 22-25, 1975. Numbers indicate the number of beetles captured within the contour boundaries.



Correlations Between Species and Sexes

Pterostichus chalcites and S. substriatus were both prominent members of the corn ecosystem, active at the same time of the summer, and predaceous. Because S. substriatus is more than twice as large as P. chalcites, S. substriatus may occasionally prey on P. chalcites or at least compete with it for food. Thus, it would not be surprising to see differences in distribution between these two species within a cornfield. But distribution maps, however, failed to show obvious differences. This may partially be due to the fact that the data were pooled, because, when numbers of P. chalcites and S. substriatus captured during an individual trapping period were compared statistically, there were significant negative correlations (Table 18). Out of 14 individual trapping periods analyzed, only 2 (June 21-22 and June 23-24) failed to show a significant negative correlation at the 0.01 level.

The seasonal activity of H. pensylvanicus and P. chalcites adults also overlap, although the overlap is not as great as between P. chalcites and S. substriatus. These two species are nearly the same size, although H. pensylvanicus is slightly larger, and probably more herbivorous (Best and Beegle 1977). Comparing the number of beetles captured in each trap per trapping period gave significant ($P \leq 0.01$) negative correlations between the distributions of these two species (Table 19). This may represent a difference in habitat preference which is related to food preference.

Table 18. Correlations of spatial distributions between P. chalcites and S. substriatus over time based on those traps which caught at least one (1) beetle.

Date	Correlation Coefficient	Degrees of Freedom
June 3-4	- 0.362 **	68 d.f.
June 5-6	- 0.582 **	26 d.f.
June 7-10	- 0.573 **	62 d.f.
June 11-12	- 0.415 **	44 d.f.
June 14-16	- 0.471 **	63 d.f.
June 17-18	- 0.480 **	26 d.f.
June 19-20	- 0.607 **	20 d.f.
June 21-22	- 0.240	20 d.f.
June 23-24	- 0.238	34 d.f.
June 25-30	- 0.583 **	38 d.f.
July 1-2	- 0.638 **	34 d.f.
July 4-6	- 0.669 **	28 d.f.
July 7-8	- 0.306 **	78 d.f.
July 9-10	- 0.668 **	32 d.f.
July 11-12	- 1.000 **	18 d.f.
July 14-15	- 0.624 **	35 d.f.

** Significant at the 0.01 level.

Table 19. Correlations of spatial distributions between P. chalcites and H. pensylvanicus over time based on those traps which caught at least one (1) beetle.

Date	Correlation coefficient	Degrees of freedom
Aug. 12	- 0.428 **	95 d.f.
Aug. 13	- 0.428 **	89 d.f.
Aug. 20	- 0.506 **	55 d.f.

** Significant at the 0.01 level.

Although it is not surprising to see negative correlations between species, it was surprising to see that numbers of male and female P. chalcites captured per trap per sampling period were significantly negatively correlated (Table 20). From June 26-July 24, every sampling period showed a significant negative correlation between the number of male and female P. chalcites captured. One explanation for this negative correlation between sexes may be that females may actually repel males to prevent males from consuming eggs at the time of laying as has been observed for a related species, P. lucublandus (Kirk and Dupraz 1972).

Correlations between numbers of male and female H. pensylvanicus captured showed little if any real significance (Table 21). The significant negative correlation on August 29 may simply be the result of sampling errors.

Dispersal

Due to the nature of the design, only a minimum dispersal rate could be recorded. Beetles which dispersed out of the grid were not trapped and this fact necessarily biased the data. Even if traps were placed in such a manner as to record maximum dispersal, there is no way to know whether a beetle traveled in a straight line to the trap or zig-zagged its way several times across the grid. Thus, a dispersal of 100 m may have required 300 m of travel.

Pterostichus chalcites

The maximum distance traveled by P. chalcites was 91 m/day. Most P. chalcites, however, dispersed relatively little. The average, based

Table 20. Correlations of spatial distributions between P. chalcites males and females over time based on those traps which caught at least 1 beetle.

Date	Correlation Coefficient	Degrees of Freedom
June 11-12	0.074	33 d.f.
June 14-16	- 0.378	15 d.f.
June 17-18	- 0.281	24 d.f.
June 19	- 0.295	16 d.f.
June 26	- 0.440 *	27 d.f.
July 7	- 0.331 *	57 d.f.
July 14	- 0.721 **	17 d.f.
July 16	- 0.674 **	25 d.f.
July 17	- 0.649 **	28 d.f.
July 18	- 0.615 **	23 d.f.
July 22	- 0.409 *	25 d.f.
July 23	- 0.828 **	32 d.f.
July 24	- 0.556 **	33 d.f.
July 25	- 0.486	14 d.f.
July 31	- 0.079	13 d.f.
Aug. 6	- 0.064	13 d.f.
Aug. 12	- 0.506 *	22 d.f.
Aug. 13	- 0.277	42 d.f.

* Significant at 0.05 level.

** Significant at 0.01 level.

Table 21. Correlations of spatial distributions between H. pensylvanicus males and females over time based on those traps which caught at least one (1) beetle.

Date	Correlation Coefficient	Degrees of Freedom
Aug. 12	- 0.339 **	70 d.f.
Aug. 13	- 0.117	133 d.f.
Aug. 15	0.206	44 d.f.
Aug. 20	- 0.017	84 d.f.
Aug. 25	- 0.019	71 d.f.
Aug. 27	0.093	56 d.f.
Aug. 29	0.407 **	62 d.f.

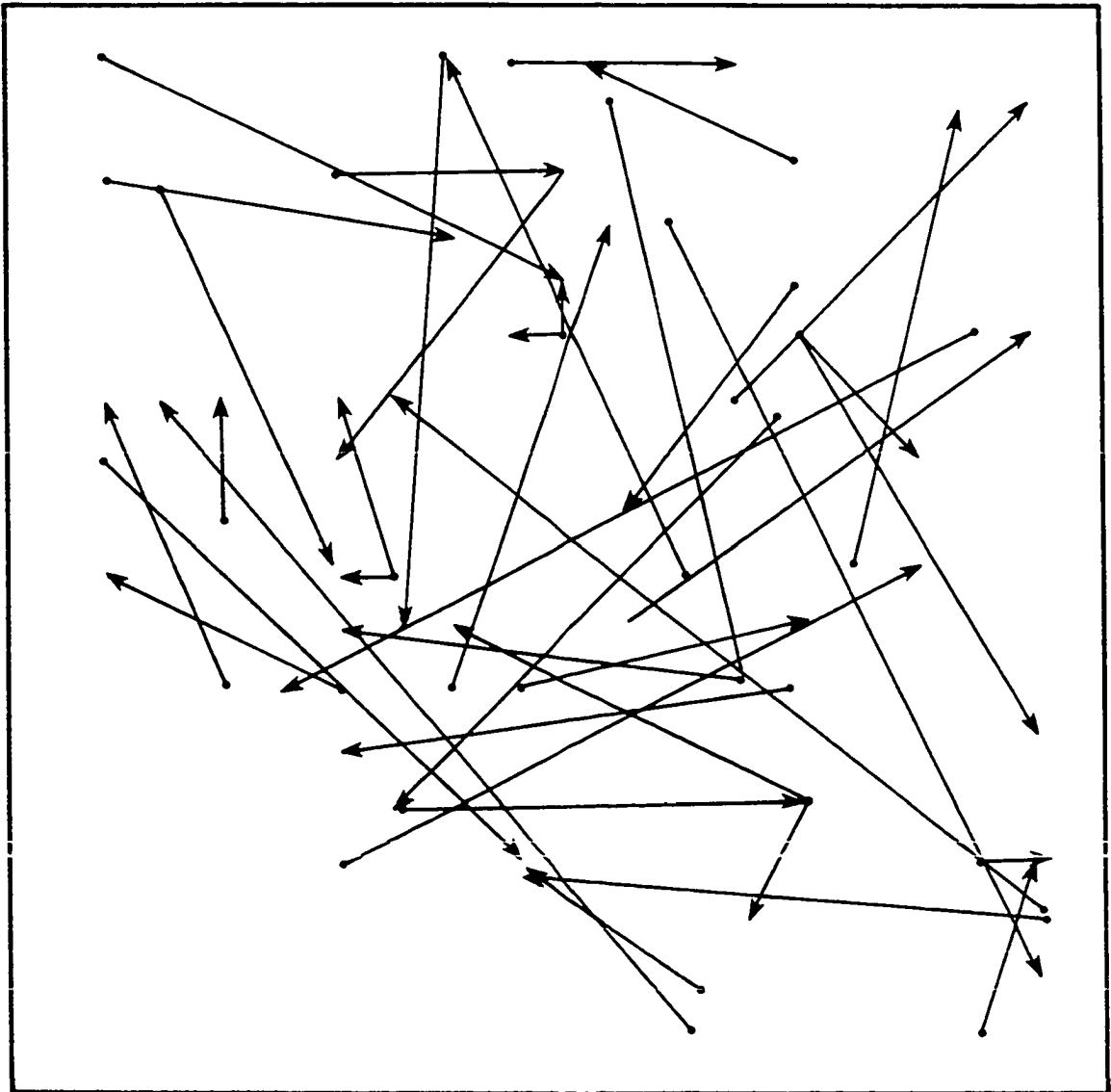
** Significant at the 0.01 level.

on 92 observations, was 8.5 m/day. One beetle dispersed less than 46 m in more than 33 days. Beetles were captured on the average of 14 days after release. However, several beetles were captured more than 40 days after release, and it was not uncommon for beetles to be captured three or four times. This suggests that the population as a whole was fairly stable and that not much dispersal out of the area was occurring. Distribution maps (Figures 4-6), indicate that a slow dispersal out of the grid may have occurred late in the summer. Movement of P. chalcites within the grid seemed to be fairly random. There was no observed tendency to disperse in any particular direction, although beetles apparently avoided the southeast corner after early-to mid-July (Figure 14).

Scarites substriatus

The maximum distance traveled by S. substriatus was 65 m/day, with an average of 12.2 m/day, (63 observations). Many S. substriatus dispersed relatively little, one beetle traveling only 41 m in 62 days, and several beetles were captured up to three times. Beetles were captured on the average of 14 days after release. This suggests that S. substriatus did not readily disperse out of the area. Toward the end of the summer, there may have been some dispersal toward the more favorable northern part of the field and into the area adjoining the arboretum (Figure 9). However, so few beetles were captured during August that it is difficult to determine whether this is the case or not. Dispersal within the grid seemed to be random.

Figure 14. Dispersal pattern for P. chalcites in an Ames, Iowa cornfield
from July 7-25, 1975.



Harpalus pensylvanicus

Based on 19 recaptures, the maximum recorded distance traveled by H. pensylvanicus was 25 m/day. The average dispersal distance was 10.2 m/day. Such low figures may not reflect the true dispersal rate for this species because very few beetles were recaptured, which suggests that they may have left the grid entirely. If this is the case, captures would only reflect random short distance movements within the grid and not true dispersal. Movement within the grid appeared to be random for this species. Distribution maps (Figures 10-13) and border trapping data (Figure 3) suggest that H. pensylvanicus may have dispersed into the grid from border areas.

DISCUSSION

Capture-Recapture Population Estimate

Several authors (Nelson 1970, Manga 1972, Ericson 1977) have used marking methods (branding and scraping of the elytra) which are similar to the method employed in this study. They concluded that such marking had no effect on vitality or survival. The longevity of marked individuals (over 2 mo.) in this study seems to support this conclusion. Cormack (1972) states that if physical damage does occur during marking, then there is consequent reduction in the probability of survival. Although the estimates of population density will not be affected, survival rate will overestimate natural mortality and hence the number of new beetles joining the population will be underestimated.

In the case of S. substriatus and P. chalcites, survival rates seem to be fairly high, indicating that unusual mortality was not occurring. For S. substriatus there was almost no mortality observed in June and only moderate mortality during July and August. During one sampling period, however, (July 5-8) the survival rate was exceedingly low. This may have been the result of excessive mortality due to marking or it may have been due to the misreading of some marks. Estimates of survival for P. chalcites compare favorably with those published for Pterostichus cupreus (L.) and P. melanarius (Ill.) by Ericson (1977). The unusually low survival rate for P. chalcites during July 23-24 may have been the result of excessive mortality due to marking or may have been due to marks being misread. No conclusions

about the survival rate of H. pensylvanicus can be drawn because the data was too incomplete and erratic.

For all three species, there are cases where the survival rate exceeds 1.0000. This is in most cases due to survival rates being greater than 1.0000 due to small sample biases at low sampling intensities (Carothers 1973). In those cases which the survival rate greatly exceeds 1.0000, such as August 5-15, for S. substriatus and August 15-18, for H. pensylvanicus, there may be a more serious error such as marks being misread (Southwood 1978).

Low sampling intensities may also lead to unusually high values for total population (Carothers 1973; Ericson 1977), or the total population may be overestimated due to reimmigration (Ericson 1977). Thomas and Sleeper (1977) state that Jolly's (1965) method may overestimate the population size due to a violation of the equal risk of capture assumption, which Carothers (1973) states, probably never occurs. Although these problems may exist, the population densities of the three species in this study are no greater than population estimates of other carabid species studied. Kirk (1971) visually estimated that there were from 4,000-6,200 H. pensylvanicus per acre in several cornfields in South Dakota. Based on capture-recapture analysis, Ericson (1977) estimated 0.64 Pterosticus cupreus (L.)/m² in 1969 and 2.5/m² in 1970. Manga (1972) estimated populations of Nebria brevicollis (F.) to vary from 0.13-0.39/m⁻² during 1967-68. Thiele (1977) states that, in general for larger carabids, one individual per m² is the rule, while for medium sized carabids, the density is usually a few to less than

10 per m². It would appear from these figures that either the population densities of this study are underestimates or, that these species are not as numerous as some of the other carabids studied.

The rather poor correlation for P. chalcites and H. pensylvanicus between the relative numbers captured (based on simple pitfall trapping) and the absolute estimates of population density (based on capture-recapture) supports the contention that pitfall trapping does not adequately reflect population size.

Standard errors of population estimates in this study are quite large. As was already mentioned in the Results section, standard errors are slightly correlated with the numbers being estimated; thus, larger estimates have larger standard errors. Roff (1973) considers a coefficient of variance of 10% to be the acceptable level of accuracy for a population estimate. Thomas and Sleeper (1977) state, however, "we cannot realistically expect to get estimates this precise for invertebrate populations, and it is desirable to obtain some estimate of population size even if the C. V. may be as great as 100%". Ettershank and Ettershank (1973) state that Jolly's (1965) method gives realistic estimates of standard error, and that when the population size is known, it is found that the standard error associated with excessively large estimates usually encloses the true population value.

Distribution

Moisture, temperature, ground cover, food preferences, food abundance, and competition are some of the factors which determine carabid

distribution. Thiele (1977) states that abiotic factors are probably more important than biotic in determining distribution.

The data in this study indicate that all three species had aggregated distributions. This is evidenced by the distribution maps (Figures 4-13) and by the data's fit to statistical distributions which are characteristically used to describe aggregated biological distributions (i.e. negative binomial and logarithmic with zeros). Overdispersion or aggregation can be caused, however, by true contagion (interaction between like organisms) or by heterogeneity of the environment (interaction with external factors) (Cassie 1962). In the latter case, organisms may aggregate in response to the environment and not even be aware of one another. The species in this study are probably aggregated due to an interaction with the environment rather than true contagion, in that the aggregations observed were never very dense, and they covered fairly large and relatively consistent areas of the grid. Furthermore, at least in the case of P. chalcites, males and females may actually avoid one another during certain times of the year as indicated by the negative correlation between male and female captures (Table 20).

Pterostichus chalcites apparently prefers cornfields to either fence rows or pasture, as Esau and Peters (1975) captured seven times as many of this species in corn as in fence rows, and none in pasture. Kirk (1975) also reported that this species was most numerous in corn, and observed that this species preferred low, poorly drained soil which was not waterlogged.

The results of this study showed that areas of the field which had low organic content, were sandy, hot, dry, and had open-plant cover during mid-to late-summer captured very few P. chalcites. The southeast corner of the grid, in particular, was characterized by these conditions, and as Figures 6 and 14 indicate, very few beetles were present here in mid-to late-summer.

The preferred habitat of S. substriatus apparently is also corn-fields. Esau and Peters (1975) captured more than 10 times as many of this species in corn as in fence rows and 25 times as many in corn as in pasture. In general, there appears no obvious differences in the distribution of S. substriatus and P. chalcites in this study. Apparently S. substriatus, as was the case with P. chalcites, avoided areas of the field such as the southeast corner which were characterized by low organic content, sandy soil, open ground cover, low moisture and high temperatures (Figures 8 and 9). There was, however, a significant negative correlation between S. substriatus and P. chalcites when the number of beetles per trap were analyzed (Table 18). In other words, it appeared that these species occupy the same habitat but avoid making close contact. This may be due to overt competition between these two species, or it may be due to relatively small differences in habitat preference. For example, there was no correlation between soil moisture and number of P. chalcites captured, but there was a significant negative correlation between soil moisture and number of S. substriatus captured. This implies that S. substriatus may prefer slightly drier soil than P. chalcites.

The distribution pattern of H. pensylvanicus was not accurately mapped because the species was predominantly found in the field borders, and borders were not adequately sampled. Esau and Peters (1975) also captured slightly more of this species in fence rows than cornfield. This species preference for borders agrees with what is known about its feeding habits. In addition to feeding on insects, Lund and Turpin (1977a) and Best and Beegle (1977) found that this species readily fed upon certain weed seeds. Pterostichus chalcites did not prefer plant material and was presumed to be more predaceous than H. pensylvanicus (Best and Beegle 1977). Therefore, the negative correlation between numbers of beetles captured per trap for P. chalcites and H. pensylvanicus (Table 19) may be the result of different habitat preference based on different feeding habits.

Dispersal

Summarizing results of several studies, Thiele (1977) states that the average speed of dispersal for larger carabids is a few meters in 24 h. Kirchner, 1960, as cited in Thiele (1977) recorded an average dispersal rate of 3 m in 24 h for Pterostichus vulgaris L. with the maximum being 15 m. Skuhrový, 1957, as cited in Thiele (1977) reported that most of the released Pterostichus cupreus L. were recaptured at the site of release, and the maximum dispersal for P. cupreus was 250 m in 1 mo.

It would appear from these figures that the beetles in this study dispersed more than average. This may partially be due to the fact that open ground (lack of weeds) in agricultural land allows for more rapid dispersal. Results dealing with a pasture inhabiting species (Evarthrus

alternans) however, indicate that some carabids may travel fairly great distances in a short period of time, even though crawling through dense vegetation (Best unpublished).

In spite of relatively great dispersal capabilities, it remains unclear whether beetles actually dispersed into or out of the field or whether the recorded dispersal just reflected random movements within the field. Greenslade (1964b) observed only a random pattern of dispersal for Nebria brevicollis (F.). He also found that this species moved extensively within the study plot but not beyond it. Such random movements within an area, but not out of it, could be due to hungry beetles moving about in search of food. Grüm (1971) noted that satiated carabids were characterized by low mobility, while hungry ones were quite mobile. He concluded that there are areas in a field which present optimal site conditions from the standpoint of environmental factors such as temperature, moisture, and isolation. He further states that the chances for food acquisition, however, ought to be greater outside these areas because of a lower concentration of beetles. This leads to migration into and out of the optimal sites in search of food, according to Grüm. If this is the case, beetles might disperse rapidly over short distances but not be apt to migrate from one field to another. Calkins and Kirk (1973) working with false wireworms, concluded that these species had the capability of travel but appeared to be localized in their movements. They also concluded that movement results from a general reshuffling within a field which allows most preferred sites to be colonized.

There did not appear to be any well-defined direction of movement within the grid for P. chalcites (Figure 14) or for the other species in this study. There did, however, seem to be a drift in the distribution for P. chalcites, H. pensylvanicus, and possibly S. substriatus (Figures 4-13) throughout the season. Whether the change in distribution for P. chalcites and S. substriatus reflects dispersal in late-summer or not remains uncertain. Very few P. chalcites and S. substriatus were captured in the grid during late summer. This may reflect reduced activity or dispersal out of the grid. Dispersal of these species out of the field and into other fields, however, was probably only minimal, particularly during early and mid-summer. There does appear, however, to be rather strong evidence from this study that H. pensylvanicus may have dispersed into the field from the borders. Rivard (1966) also noted that H. pensylvanicus was not abundant near the center of the field until the end of the season.

This brings up the question of how important field borders are in providing sites for dispersal of predators into a cornfield in response to insect pests. Thiele (1977) concluded that hedge rows around fields apparently do not act as reservoirs for carabids. He further stated that those species which are predominant in cultivated fields have little connection with the hedges. Jones (1979), while studying nine species of carabids in a winter wheat field, showed that some carabids migrate into the growing crop or into the stubble after harvest, while others are permanent field residents. Esau and Peters (1975) observed that both P. chalcites and S. substriatus were found primarily in cornfields