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BEST, RICHARD L.

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

A Dissertation Submitted to the Graduate Faculty in Partial Fulfillment of the Requirements for the Degree of DOCTOR OF PHILOSOPHY

Major: Entomology

Approved:

Signature was redacted for privacy.

In Charge of Major Work

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For the Major Department

Signature was redacted for privacy.

For the Graduate College

Iowa State University
Ames, Iowa

1979
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</tbody>
</table>
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 (Bouche) eggs and Frank (1967) reported 40% destruction of healthy Operophtera brummata (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, Evarthus 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 peppercress, 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 bromegrass, 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. substriatu*s 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. substriatu*s, 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*.

<table>
<thead>
<tr>
<th>Food Item</th>
<th>Mean volume consumed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black cutworm larvae</td>
<td>6.00 a</td>
</tr>
<tr>
<td>Smooth dock seeds</td>
<td>3.78 ab</td>
</tr>
<tr>
<td>Barnyard grass seeds</td>
<td>1.75 b</td>
</tr>
<tr>
<td>Yellow foxtail seeds</td>
<td>1.25 b</td>
</tr>
</tbody>
</table>

1. Based on 20 replications.
2. Consumed volume is expressed in peppercress units. One peppercress unit equals the volume of one peppercress 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>
<thead>
<tr>
<th>Host</th>
<th>Mean amount consumed $^{1,2}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dead green cloverworm larva</td>
<td>3.55a $^3$</td>
</tr>
<tr>
<td>Dead black cutworm larva</td>
<td>3.25a</td>
</tr>
<tr>
<td>Live green cloverworm larva</td>
<td>3.20a</td>
</tr>
<tr>
<td>Dead cricket</td>
<td>1.80b</td>
</tr>
<tr>
<td>Live black cutworm larva</td>
<td>0.90bc</td>
</tr>
<tr>
<td>Live angleworm</td>
<td>0.55c</td>
</tr>
<tr>
<td>Dead corn rootworm adult</td>
<td>0.50c</td>
</tr>
<tr>
<td>Dead slug</td>
<td>0.50c</td>
</tr>
<tr>
<td>Dead phalangid</td>
<td>0.30c</td>
</tr>
<tr>
<td>Live slug</td>
<td>0.30c</td>
</tr>
<tr>
<td>Dead tiger moth larva</td>
<td>0.30c</td>
</tr>
<tr>
<td>Live isopod</td>
<td>0.20c</td>
</tr>
<tr>
<td>Dead angleworm</td>
<td>0.20c</td>
</tr>
<tr>
<td>Dead isopod</td>
<td>0.00c</td>
</tr>
<tr>
<td>Live phalangid</td>
<td>0.00c</td>
</tr>
<tr>
<td>Live cricket</td>
<td>0.00c</td>
</tr>
<tr>
<td>Live corn rootworm adult</td>
<td>0.00c</td>
</tr>
<tr>
<td>Live tiger moth larva</td>
<td>0.00c</td>
</tr>
</tbody>
</table>

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 = 1/2 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*.

<table>
<thead>
<tr>
<th>Host</th>
<th>Mean amount consumed&lt;sup&gt;1,2&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dead cricket</td>
<td>3.45&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Dead green cloverworm larva</td>
<td>3.00&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Live black cutworm larva</td>
<td>2.95&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Dead black cutworm larva</td>
<td>2.95&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Live green cloverworm larva</td>
<td>2.55&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Live angleworm</td>
<td>1.15&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Dead tiger moth larva</td>
<td>0.80&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Dead phalangid</td>
<td>0.60&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Live slug</td>
<td>0.60&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Dead isopod</td>
<td>0.35&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Live corn rootworm adult</td>
<td>0.30&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Live cricket</td>
<td>0.30&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Dead slug</td>
<td>0.30&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Dead angleworm</td>
<td>0.20&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Dead corn rootworm adult</td>
<td>0.20&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Live isopod</td>
<td>0.00&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Live tiger moth larva</td>
<td>0.00&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Live phalangid</td>
<td>0.00&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

<sup>1</sup> Means based on 20 replications. Standard error of a mean = 0.174.

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

<sup>3</sup> 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*.

<table>
<thead>
<tr>
<th>Host</th>
<th>Mean amount consumed&lt;sup&gt;1,2&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dead cricket</td>
<td>4.35a&lt;sup&gt;3&lt;/sup&gt;</td>
</tr>
<tr>
<td>Live green cloverworm larva</td>
<td>2.80b</td>
</tr>
<tr>
<td>Dead corn rootworm adult</td>
<td>2.35b</td>
</tr>
<tr>
<td>Live black cutworm larva</td>
<td>2.25bc</td>
</tr>
<tr>
<td>Dead green cloverworm larva</td>
<td>1.45bcd</td>
</tr>
<tr>
<td>Live isopod</td>
<td>0.90cd</td>
</tr>
<tr>
<td>Dead black cutworm larva</td>
<td>0.85cd</td>
</tr>
<tr>
<td>Live angleworm</td>
<td>0.70d</td>
</tr>
<tr>
<td>Dead tiger moth larva</td>
<td>0.55d</td>
</tr>
<tr>
<td>Dead phalangid</td>
<td>0.45d</td>
</tr>
<tr>
<td>Dead angleworm</td>
<td>0.35d</td>
</tr>
<tr>
<td>Live cricket</td>
<td>0.30d</td>
</tr>
<tr>
<td>Dead isopod</td>
<td>0.30d</td>
</tr>
<tr>
<td>Live corn rootworm adult</td>
<td>0.20d</td>
</tr>
<tr>
<td>Live tiger moth larva</td>
<td>0.00d</td>
</tr>
<tr>
<td>Live phalangid</td>
<td>0.00d</td>
</tr>
<tr>
<td>Live slug</td>
<td>0.00d</td>
</tr>
<tr>
<td>Dead slug</td>
<td>0.00d</td>
</tr>
</tbody>
</table>

<sup>1</sup>Means based on 20 replications. Standard error of a mean = 0.217.

<sup>2</sup>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.

<sup>3</sup>Numbers 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*.

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

$^1$ 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 = 1/2 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 substratus adults were tested to determine the number of black cutworm pupae that they could consume. Scarites substratus, 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. substratus* 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 consump­
tions, 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 signifi­
cant 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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean</th>
<th>SD</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>S. substriatus</td>
<td>5.2</td>
<td>1.9</td>
<td>1.5-8.0</td>
</tr>
<tr>
<td>P. chalcites</td>
<td>3.1</td>
<td>1.6</td>
<td>0.5-6.0</td>
</tr>
<tr>
<td>P. lucublandus</td>
<td>2.2</td>
<td>0.8</td>
<td>1.0-3.6</td>
</tr>
<tr>
<td>H. pensylvanicus</td>
<td>2.1</td>
<td>1.2</td>
<td>1.0-4.5</td>
</tr>
</tbody>
</table>

*Based 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 character­
istic. 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-

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 m\(^2\), 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, Wis., 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

THOUSANDS  HUNDREDS  TENS  ONES
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 SYMAP\(^4\). 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.

\(^4\)Laboratory 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. substratus* during the summer of 1975 from a cornfield in Ames, Iowa.

<table>
<thead>
<tr>
<th>Captured</th>
<th>Marked Released</th>
<th>Recaptured</th>
<th>Recapture Rate %</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>P. chalcites ♂</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>497</td>
<td>569</td>
<td>41</td>
<td>7.21%</td>
</tr>
<tr>
<td><strong>P. chalcites ♀</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>584</td>
<td>627</td>
<td>61</td>
<td>9.73%</td>
</tr>
<tr>
<td><strong>H. pensylvanicus ♂ ♀</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>321</td>
<td>948</td>
<td>16</td>
<td>1.69%</td>
</tr>
<tr>
<td><strong>S. substratus ♂ ♀</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>424</td>
<td>406</td>
<td>57</td>
<td>14.04%</td>
</tr>
</tbody>
</table>
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.

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

$R_i = 9 6 12 9 11 4 18 6 5 4 3 4 6 4$
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. substriatu s_ was the correlation significant (P ≤ 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. \( n_1 \) = number of captured individuals in the \( i \)th samples. \( s_1 \) = number of marked released individuals from the \( i \)th sample. \( R_1 \) = total number of individuals subsequently recaptured.

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

\[ R_1 = 2 \ 2 \ 7 \ 1 \ 7 \ 3 \ 5 \ 2 \ 2 \ 2 \ 1 \ 2 \ 1 \ 2 \]
Table 10. Captures and recaptures of *P. chalcites* in an Ames, Iowa cornfield during the summer of 1975. \( n_i \) = number of captured individuals in the \( i^{th} \) sample. \( s_i \) = number of marked released individuals from the \( i^{th} \) sample. \( R_i \) = total number of individuals subsequently recaptured.

<table>
<thead>
<tr>
<th>Date of Capture</th>
<th>( n_i )</th>
<th>( s_i )</th>
<th>Day When Last Captured</th>
</tr>
</thead>
<tbody>
<tr>
<td>June 3-5</td>
<td>72</td>
<td>72</td>
<td>June 3-5</td>
</tr>
<tr>
<td>June 6-10</td>
<td>36</td>
<td>36</td>
<td>1</td>
</tr>
<tr>
<td>June 11-18</td>
<td>51</td>
<td>49</td>
<td>1 0</td>
</tr>
<tr>
<td>June 19-25</td>
<td>89</td>
<td>88</td>
<td>3 0 1</td>
</tr>
<tr>
<td>June 26-July 2</td>
<td>25</td>
<td>24</td>
<td>0 2 0 1</td>
</tr>
<tr>
<td>July 3-6</td>
<td>15</td>
<td>15</td>
<td>1 0 0 1 0</td>
</tr>
<tr>
<td>July 7-10</td>
<td>64</td>
<td>62</td>
<td>1 2 2 1 2 1</td>
</tr>
<tr>
<td>July 11-15</td>
<td>20</td>
<td>20</td>
<td>0 0 0 1 2 0 1</td>
</tr>
<tr>
<td>July 16-17</td>
<td>35</td>
<td>34</td>
<td>1 0 1 0 0 0 3 2</td>
</tr>
<tr>
<td>July 18-22</td>
<td>32</td>
<td>31</td>
<td>0 0 0 2 0 0 3 1 1</td>
</tr>
<tr>
<td>July 23-24</td>
<td>38</td>
<td>38</td>
<td>0 0 0 1 0 0 4 0 2 1</td>
</tr>
<tr>
<td>July 25-30</td>
<td>28</td>
<td>30</td>
<td>0 0 0 1 0 0 1 1 0 1 1</td>
</tr>
<tr>
<td>July 31-Aug. 6</td>
<td>13</td>
<td>80</td>
<td>0 0 0 0 1 0 0 0 0 0 0 1 0</td>
</tr>
<tr>
<td>Aug. 7-12</td>
<td>35</td>
<td>48</td>
<td>0 0 1 0 0 0 0 0 0 0 0 1 1</td>
</tr>
<tr>
<td>Aug. 13-18</td>
<td>31</td>
<td>0</td>
<td>0 0 0 0 0 0 0 1 0 0 0 0 1 1 2</td>
</tr>
</tbody>
</table>

\[
R_i = 8 4 5 8 5 1 13 4 3 2 2 2 2 2
\]
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.

<table>
<thead>
<tr>
<th>Date of Capture</th>
<th>( n_i )</th>
<th>( s_i )</th>
<th>Day When Last Captured</th>
</tr>
</thead>
<tbody>
<tr>
<td>June 3-6</td>
<td>100</td>
<td>99</td>
<td>June 3-6</td>
</tr>
<tr>
<td>June 7-12</td>
<td>39</td>
<td>38</td>
<td>3 June 7-12</td>
</tr>
<tr>
<td>June 14-18</td>
<td>33</td>
<td>32</td>
<td>2 0 June 14-18</td>
</tr>
<tr>
<td>June 19-23</td>
<td>25</td>
<td>25</td>
<td>1 1 0 June 19-23</td>
</tr>
<tr>
<td>June 24-30</td>
<td>37</td>
<td>35</td>
<td>2 1 0 June 24-30</td>
</tr>
<tr>
<td>July 1-4</td>
<td>35</td>
<td>34</td>
<td>3 0 1 1 2 July 1-4</td>
</tr>
<tr>
<td>July 5-8</td>
<td>52</td>
<td>51</td>
<td>1 0 1 2 2 1 July 5-8</td>
</tr>
<tr>
<td>July 9-11</td>
<td>30</td>
<td>26</td>
<td>2 1 0 0 0 1 7 July 9-11</td>
</tr>
<tr>
<td>July 12-16</td>
<td>10</td>
<td>10</td>
<td>1 0 0 0 0 0 0 1 July 12-16</td>
</tr>
<tr>
<td>July 17-21</td>
<td>8</td>
<td>7</td>
<td>0 0 1 0 0 2 0 0 July 17-21</td>
</tr>
<tr>
<td>July 22-25</td>
<td>15</td>
<td>12</td>
<td>0 0 0 0 0 2 1 1 0 July 22-25</td>
</tr>
<tr>
<td>July 26-30</td>
<td>7</td>
<td>7</td>
<td>0 0 0 0 0 2 1 0 0 0 July 26-30</td>
</tr>
<tr>
<td>July 31-Aug. 4</td>
<td>5</td>
<td>4</td>
<td>0 0 0 0 0 0 0 0 2 0 July 31-Aug. 4</td>
</tr>
<tr>
<td>Aug. 5-12</td>
<td>5</td>
<td>4</td>
<td>0 0 0 0 0 0 0 0 1 0 0 0 Aug. 5-12</td>
</tr>
<tr>
<td>Aug. 12-18</td>
<td>15</td>
<td>15</td>
<td>0 1 1 0 0 0 0 0 0 1 0 1 Aug. 12-18</td>
</tr>
<tr>
<td>Aug. 20-25</td>
<td>8</td>
<td>7</td>
<td>0 1 0 0 0 0 0 0 0 0 0 0 1 1 Aug. 20-25</td>
</tr>
</tbody>
</table>

\( R_i = 15 \) 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.

\[ n_1 = \text{number of captured individuals in the } i^{\text{th}} \text{ sample. } S_i = \text{number of marked released individuals from the } i^{\text{th}} \text{ sample. } R_i = \text{total number of individuals subsequently recaptured.} \]

<table>
<thead>
<tr>
<th>Date of Capture</th>
<th>( n_1 )</th>
<th>( s_i )</th>
<th>Day When Last Captured</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aug. 13-14</td>
<td>97</td>
<td>167</td>
<td>Aug. 13-14</td>
</tr>
<tr>
<td>Aug. 15-18</td>
<td>9</td>
<td>376</td>
<td>1</td>
</tr>
<tr>
<td>Aug. 20-21</td>
<td>67</td>
<td>94</td>
<td>2</td>
</tr>
<tr>
<td>Aug. 22-25</td>
<td>66</td>
<td>215</td>
<td>1</td>
</tr>
<tr>
<td>Aug. 27-28</td>
<td>18</td>
<td>105</td>
<td>0</td>
</tr>
<tr>
<td>Aug. 29-31</td>
<td>64</td>
<td>-</td>
<td>0</td>
</tr>
</tbody>
</table>

\[ R_i = 4 \quad 8 \quad 1 \quad 2 \quad 1 \]
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/m². The average population density for this species during the trapping period was 0.08/m². 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.

<table>
<thead>
<tr>
<th>Date of Capture</th>
<th>Proportion of recaptures</th>
<th>Total Marked</th>
<th>Total Pop. Rate</th>
<th>Survival # new</th>
<th>Standard Errors due to errors in estimation of the parameter itself</th>
<th>Standard Errors</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Proportion</td>
<td>Total Marked</td>
<td>Total Pop. Rate</td>
<td>Survival</td>
<td># new</td>
<td>Standard Errors</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 3-5</td>
<td>--</td>
<td>0.00</td>
<td>--</td>
<td>0.7623</td>
<td>--</td>
<td>0.3884</td>
</tr>
<tr>
<td>June 6-10</td>
<td>0.0164</td>
<td>82.33</td>
<td>5022.33</td>
<td>0.8132</td>
<td>1085.84</td>
<td>0.3956</td>
</tr>
<tr>
<td>June 11-18</td>
<td>0.0224</td>
<td>115.75</td>
<td>5170.16</td>
<td>0.8356</td>
<td>-489.36</td>
<td>0.3548</td>
</tr>
<tr>
<td>June 19-25</td>
<td>0.0515</td>
<td>197.00</td>
<td>3821.80</td>
<td>0.4277</td>
<td>151.93</td>
<td>0.1781</td>
</tr>
<tr>
<td>June 26-July 2</td>
<td>0.0690</td>
<td>123.18</td>
<td>1786.14</td>
<td>1.1607</td>
<td>-299.73</td>
<td>0.6150</td>
</tr>
<tr>
<td>July 3-6</td>
<td>0.1154</td>
<td>204.50</td>
<td>1772.33</td>
<td>0.5692</td>
<td>-74.62</td>
<td>0.2890</td>
</tr>
<tr>
<td>July 7-10</td>
<td>0.1386</td>
<td>129.50</td>
<td>934.25</td>
<td>1.0249</td>
<td>171.22</td>
<td>0.4373</td>
</tr>
<tr>
<td>July 11-15</td>
<td>0.1951</td>
<td>219.83</td>
<td>1126.65</td>
<td>1.3922</td>
<td>572.79</td>
<td>0.7943</td>
</tr>
<tr>
<td>July 16-17</td>
<td>0.1644</td>
<td>352.00</td>
<td>2141.33</td>
<td>0.8536</td>
<td>455.98</td>
<td>0.5549</td>
</tr>
<tr>
<td>July 18-22</td>
<td>0.1528</td>
<td>348.25</td>
<td>2279.46</td>
<td>0.7259</td>
<td>283.72</td>
<td>0.5519</td>
</tr>
<tr>
<td>July 23-24</td>
<td>0.1529</td>
<td>296.33</td>
<td>1937.56</td>
<td>0.2511</td>
<td>240.20</td>
<td>0.1923</td>
</tr>
<tr>
<td>July 25-30</td>
<td>0.1273</td>
<td>92.50</td>
<td>726.79</td>
<td>1.1988</td>
<td>492.98</td>
<td>0.8249</td>
</tr>
<tr>
<td>July 31-Aug. 6</td>
<td>0.1250</td>
<td>170.83</td>
<td>1366.67</td>
<td>0.3762</td>
<td>958.07</td>
<td>0.2590</td>
</tr>
<tr>
<td>Aug. 7-12</td>
<td>0.0896</td>
<td>137.25</td>
<td>1532.63</td>
<td>--</td>
<td>--</td>
<td>1127.41</td>
</tr>
<tr>
<td>Aug. 13-18</td>
<td>0.1429</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
</tbody>
</table>
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.

<table>
<thead>
<tr>
<th>Date of Capture</th>
<th>Proportion of Recaptures</th>
<th>Total Marked</th>
<th>Total Pop.</th>
<th>Survival Rate</th>
<th>S.E.(N)</th>
<th>S.E.((\phi))</th>
<th>S.E.((\beta))</th>
<th>Standard Errors due to errors in estimation of the parameter itself</th>
</tr>
</thead>
<tbody>
<tr>
<td>June 3-5</td>
<td>--</td>
<td>0.00</td>
<td>--</td>
<td>0.3750</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>June 5-10</td>
<td>0.0400</td>
<td>13.50</td>
<td>337.50</td>
<td>0.3352</td>
<td>408.57</td>
<td>485.90</td>
<td>0.3247</td>
<td>502.01</td>
</tr>
<tr>
<td>June 11-18</td>
<td>0.0241</td>
<td>12.57</td>
<td>521.71</td>
<td>0.6740</td>
<td>110.44</td>
<td>557.61</td>
<td>0.6696</td>
<td>554.79</td>
</tr>
<tr>
<td>June 19-25</td>
<td>0.1250</td>
<td>57.00</td>
<td>456.00</td>
<td>0.5313</td>
<td>879.75</td>
<td>616.12</td>
<td>0.5290</td>
<td>1183.54</td>
</tr>
<tr>
<td>June 26-July 2</td>
<td>0.0303</td>
<td>34.00</td>
<td>1122.00</td>
<td>0.7374</td>
<td>-292.00</td>
<td>1204.97</td>
<td>0.4349</td>
<td>980.51</td>
</tr>
<tr>
<td>July 3-6</td>
<td>0.0909</td>
<td>48.67</td>
<td>535.33</td>
<td>1.4727</td>
<td>-149.04</td>
<td>580.95</td>
<td>0.9485</td>
<td>791.94</td>
</tr>
<tr>
<td>July 7-10</td>
<td>0.1351</td>
<td>86.40</td>
<td>639.36</td>
<td>1.1782</td>
<td>223.20</td>
<td>397.73</td>
<td>0.9285</td>
<td>626.60</td>
</tr>
<tr>
<td>July 11-15</td>
<td>0.1429</td>
<td>139.50</td>
<td>976.50</td>
<td>1.1111</td>
<td>245.00</td>
<td>862.21</td>
<td>1.0682</td>
<td>816.46</td>
</tr>
<tr>
<td>July 16-17</td>
<td>0.1316</td>
<td>175.00</td>
<td>1330.00</td>
<td>0.7108</td>
<td>217.50</td>
<td>1114.13</td>
<td>0.6977</td>
<td>645.41</td>
</tr>
<tr>
<td>July 18-22</td>
<td>0.1250</td>
<td>145.00</td>
<td>1160.00</td>
<td>1.0722</td>
<td>570.42</td>
<td>996.90</td>
<td>1.3262</td>
<td>1115.75</td>
</tr>
<tr>
<td>July 23-24</td>
<td>0.1064</td>
<td>193.00</td>
<td>1814.20</td>
<td>0.1809</td>
<td>245.65</td>
<td>2096.19</td>
<td>0.2217</td>
<td>460.49</td>
</tr>
<tr>
<td>July 25-30</td>
<td>0.0741</td>
<td>42.50</td>
<td>573.75</td>
<td>0.9259</td>
<td>31.25</td>
<td>613.33</td>
<td>0.8957</td>
<td>491.76</td>
</tr>
<tr>
<td>July 31-Aug. 6</td>
<td>0.1111</td>
<td>62.50</td>
<td>562.50</td>
<td>0.3417</td>
<td>264.33</td>
<td>545.32</td>
<td>0.3302</td>
<td>356.21</td>
</tr>
<tr>
<td>Aug. 7-12</td>
<td>0.1250</td>
<td>61.00</td>
<td>488.00</td>
<td>--</td>
<td>--</td>
<td>499.50</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Aug. 13-18</td>
<td>0.1250</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
</tbody>
</table>
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.

<table>
<thead>
<tr>
<th>Date of Capture</th>
<th>Proportion of Recaptures</th>
<th>Total Marked</th>
<th>Total Pop.</th>
<th>Survival Rate</th>
<th># new beetles joining</th>
<th>Standard Errors</th>
<th>Standard errors due to errors in estimation of the parameter itself</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><em>N</em>&lt;sub&gt;1&lt;/sub&gt;</td>
<td><em>n</em>&lt;sub&gt;1&lt;/sub&gt;</td>
<td><em>N</em>&lt;sub&gt;1&lt;/sub&gt;</td>
<td><em>phi</em>&lt;sub&gt;1&lt;/sub&gt;</td>
<td><em>beta</em>&lt;sub&gt;1&lt;/sub&gt;</td>
<td>S.E.(N)</td>
<td>S.E.(*)</td>
</tr>
<tr>
<td>June 3-5</td>
<td>--</td>
<td>0.00</td>
<td>--</td>
<td>0.8889</td>
<td>--</td>
<td>--</td>
<td>0.5184</td>
</tr>
<tr>
<td>June 5-10</td>
<td>0.0278</td>
<td>64.00</td>
<td>2304.00</td>
<td>1.0000</td>
<td>2745.00</td>
<td>2622.36</td>
<td>0.6367</td>
</tr>
<tr>
<td>June 11-18</td>
<td>0.0196</td>
<td>99.00</td>
<td>5049.00</td>
<td>0.8503</td>
<td>-1510.41</td>
<td>5609.77</td>
<td>0.4695</td>
</tr>
<tr>
<td>June 19-25</td>
<td>0.0449</td>
<td>125.00</td>
<td>2781.25</td>
<td>0.3818</td>
<td>-396.55</td>
<td>1792.01</td>
<td>0.1969</td>
</tr>
<tr>
<td>June 26-July 2</td>
<td>0.1200</td>
<td>79.80</td>
<td>665.00</td>
<td>2.8472</td>
<td>261.94</td>
<td>459.06</td>
<td>2.9630</td>
</tr>
<tr>
<td>July 3-6</td>
<td>0.1333</td>
<td>287.00</td>
<td>2152.50</td>
<td>0.2049</td>
<td>-3.93</td>
<td>2546.62</td>
<td>0.2045</td>
</tr>
<tr>
<td>July 7-10</td>
<td>0.1406</td>
<td>61.46</td>
<td>437.06</td>
<td>0.9086</td>
<td>124.70</td>
<td>185.73</td>
<td>0.4549</td>
</tr>
<tr>
<td>July 11-15</td>
<td>0.2000</td>
<td>104.00</td>
<td>520.00</td>
<td>1.6639</td>
<td>133.11</td>
<td>335.29</td>
<td>1.1721</td>
</tr>
<tr>
<td>July 16-17</td>
<td>0.2000</td>
<td>199.67</td>
<td>998.33</td>
<td>0.9199</td>
<td>35.74</td>
<td>665.07</td>
<td>0.8034</td>
</tr>
<tr>
<td>July 18-22</td>
<td>0.2188</td>
<td>208.50</td>
<td>953.14</td>
<td>0.6065</td>
<td>92.32</td>
<td>745.99</td>
<td>0.5911</td>
</tr>
<tr>
<td>July 23-24</td>
<td>0.2105</td>
<td>141.00</td>
<td>669.75</td>
<td>0.3801</td>
<td>109.42</td>
<td>534.09</td>
<td>0.3752</td>
</tr>
<tr>
<td>July 25-30</td>
<td>0.1786</td>
<td>65.00</td>
<td>364.00</td>
<td>1.8000</td>
<td>394.20</td>
<td>315.18</td>
<td>1.8174</td>
</tr>
<tr>
<td>July 31-Aug. 6</td>
<td>0.1538</td>
<td>162.00</td>
<td>1053.00</td>
<td>0.3125</td>
<td>525.00</td>
<td>1120.01</td>
<td>0.3233</td>
</tr>
<tr>
<td>Aug. 7-12</td>
<td>0.0857</td>
<td>75.00</td>
<td>875.00</td>
<td>--</td>
<td>--</td>
<td>887.55</td>
<td>--</td>
</tr>
<tr>
<td>Aug. 13-18</td>
<td>0.1613</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
</tbody>
</table>
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.

<table>
<thead>
<tr>
<th>Date of Capture</th>
<th>Proportion of recaptures $\hat{N}_1$</th>
<th>Total Marked $\hat{N}_1$</th>
<th>Total Pop. $\hat{N}_1$</th>
<th>Survival Rate $\hat{\phi}_1$</th>
<th># new beetles joining $\hat{\beta}_1$</th>
<th>Standard Errors S.E.(N) S.E.((\phi)) S.E.((\beta)) (N) ((\phi))</th>
</tr>
</thead>
<tbody>
<tr>
<td>June 3-6</td>
<td>-</td>
<td>0.00</td>
<td>0.9515</td>
<td>-</td>
<td>0.4575</td>
<td>-</td>
</tr>
<tr>
<td>June 7-12</td>
<td>0.0769</td>
<td>94.20</td>
<td>1224.60</td>
<td>857.59</td>
<td>890.31</td>
<td>0.5906 (0.4575) 1578.24 890.28 0.5902</td>
</tr>
<tr>
<td>June 14-18</td>
<td>0.0606</td>
<td>122.00</td>
<td>2013.00</td>
<td>0.9452</td>
<td>-105.86</td>
<td>857.59 (0.4575) 1578.24 890.28 0.5902</td>
</tr>
<tr>
<td>June 19-23</td>
<td>0.0800</td>
<td>144.67</td>
<td>1795.83</td>
<td>0.9105</td>
<td>236.48</td>
<td>1595.38 (0.6520) 1515.80 1595.32 0.6516</td>
</tr>
<tr>
<td>June 24-30</td>
<td>0.0811</td>
<td>151.75</td>
<td>1871.58</td>
<td>1.3333</td>
<td>-1267.78</td>
<td>1404.51 (1.1039) 1701.34 1404.40 1.1050</td>
</tr>
<tr>
<td>July 1-4</td>
<td>0.2000</td>
<td>245.00</td>
<td>1225.00</td>
<td>0.1555</td>
<td>123.90</td>
<td>963.30 (0.1132) 128.32 963.43 0.1110</td>
</tr>
<tr>
<td>July 5-8</td>
<td>0.1346</td>
<td>42.31</td>
<td>314.29</td>
<td>1.2320</td>
<td>-95.98</td>
<td>141.36 (0.7001) 161.80 140.82 0.7025</td>
</tr>
<tr>
<td>July 9-11</td>
<td>0.3667</td>
<td>106.33</td>
<td>290.00</td>
<td>1.0055</td>
<td>322.43</td>
<td>172.79 (1.0899) 499.32 172.37 1.0899</td>
</tr>
<tr>
<td>July 12-16</td>
<td>0.2000</td>
<td>122.00</td>
<td>610.00</td>
<td>0.5615</td>
<td>-147.87</td>
<td>705.37 (0.7330) 271.41 705.27 0.7317</td>
</tr>
<tr>
<td>July 17-21</td>
<td>0.3750</td>
<td>73.00</td>
<td>194.67</td>
<td>0.5974</td>
<td>56.80</td>
<td>201.54 (0.6638) 96.08 201.06 0.6614</td>
</tr>
<tr>
<td>July 22-25</td>
<td>0.2667</td>
<td>46.00</td>
<td>172.50</td>
<td>0.8333</td>
<td>-36.25</td>
<td>135.60 (0.9124) 82.82 135.17 0.9110</td>
</tr>
<tr>
<td>July 26-31</td>
<td>0.4286</td>
<td>45.00</td>
<td>105.00</td>
<td>0.4490</td>
<td>7.86</td>
<td>108.02 (0.5505) 36.17 107.54 0.5459</td>
</tr>
<tr>
<td>July 31-Aug. 4</td>
<td>0.4000</td>
<td>22.00</td>
<td>55.00</td>
<td>0.8750</td>
<td>57.75</td>
<td>55.87 (1.0526) 108.53 55.45 1.0505</td>
</tr>
<tr>
<td>Aug. 5-15</td>
<td>0.2000</td>
<td>21.00</td>
<td>105.00</td>
<td>1.4167</td>
<td>13.83</td>
<td>132.07 (1.8486) 141.54 131.91 1.8552</td>
</tr>
<tr>
<td>Aug. 12-18</td>
<td>0.2667</td>
<td>34.00</td>
<td>127.50</td>
<td>-</td>
<td>142.72</td>
<td>-</td>
</tr>
<tr>
<td>Aug. 20-25</td>
<td>0.3750</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
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 den-
sity of *S. substriatus* averaged 0.08/m\(^2\). During June, the average
population density was 0.07/m\(^2\), while during July and August the average
density was only 0.01/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 con­
cerning 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.

<table>
<thead>
<tr>
<th>Date of Capture</th>
<th>Proportion of Marked recaptures</th>
<th>Total Marked</th>
<th>Total Pop.</th>
<th>Survival Rate</th>
<th># of new beetles joining</th>
<th>Standard Errors</th>
<th>Standard errors due to errors in estimation of the parameter itself</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( \hat{N}_1 )</td>
<td>( \hat{m}_1 )</td>
<td>( \hat{n}_1 )</td>
<td>( \hat{\phi}_1 )</td>
<td>( \hat{\beta}_1 )</td>
<td>S.E.(N)</td>
<td>S.E.(( \phi ))</td>
</tr>
<tr>
<td>Aug. 13-14</td>
<td>--</td>
<td>0.00</td>
<td>--</td>
<td>0.8301</td>
<td>--</td>
<td>--</td>
<td>0.5526</td>
</tr>
<tr>
<td>Aug. 15-18</td>
<td>0.1111</td>
<td>138.63</td>
<td>1247.63</td>
<td>1.4962</td>
<td>14459.39</td>
<td>1435.83</td>
<td>1.5953</td>
</tr>
<tr>
<td>Aug. 20-22</td>
<td>0.0448</td>
<td>755.00</td>
<td>16861.66</td>
<td>0.3883</td>
<td>-2944.33</td>
<td>20102.45</td>
<td>0.5028</td>
</tr>
<tr>
<td>Aug. 22-25</td>
<td>0.0909</td>
<td>328.50</td>
<td>3613.50</td>
<td>0.7833</td>
<td>4631.00</td>
<td>3512.23</td>
<td>0.9688</td>
</tr>
<tr>
<td>Aug. 27-28</td>
<td>0.0556</td>
<td>421.00</td>
<td>7578.00</td>
<td>--</td>
<td>--</td>
<td>11174.59</td>
<td>--</td>
</tr>
<tr>
<td>Aug. 29-31</td>
<td>0.0781</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
</tbody>
</table>
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/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 ≤ 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 ≤ 0.77 and 0.58 respectively). For all three months both Poisson and positive binomial were rejected (P ≤ 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 < 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* ≤ 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 < 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.

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

** 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.

<table>
<thead>
<tr>
<th>Date</th>
<th>Correlation coefficient</th>
<th>Degrees of freedom</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aug. 12</td>
<td>- 0.428 **</td>
<td>95 d.f.</td>
</tr>
<tr>
<td>Aug. 13</td>
<td>- 0.428 **</td>
<td>89 d.f.</td>
</tr>
<tr>
<td>Aug. 20</td>
<td>- 0.506 **</td>
<td>55 d.f.</td>
</tr>
</tbody>
</table>

** 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 zigzagged 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.

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

* 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.

<table>
<thead>
<tr>
<th>Date</th>
<th>Correlation Coefficient</th>
<th>Degrees of Freedom</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aug. 12</td>
<td>-0.339 **</td>
<td>70 d.f.</td>
</tr>
<tr>
<td>Aug. 13</td>
<td>-0.117</td>
<td>133 d.f.</td>
</tr>
<tr>
<td>Aug. 15</td>
<td>0.206</td>
<td>44 d.f.</td>
</tr>
<tr>
<td>Aug. 20</td>
<td>-0.017</td>
<td>84 d.f.</td>
</tr>
<tr>
<td>Aug. 25</td>
<td>-0.019</td>
<td>71 d.f.</td>
</tr>
<tr>
<td>Aug. 27</td>
<td>0.093</td>
<td>56 d.f.</td>
</tr>
<tr>
<td>Aug. 29</td>
<td>0.407 **</td>
<td>62 d.f.</td>
</tr>
</tbody>
</table>

** 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/m² 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 popu-
lation 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 inver-
tebrate 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 *Pterostichus 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 cornfields. 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. Skuhravý, 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 (*Evarthus*
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. substratiatus* (Figures 4–13) throughout the season. Whether the change in distribution for *P. chalcites* and *S. substratiatus* reflects dispersal in late-summer or not remains uncertain. Very few *P. chalcites* and *S. substratiatus* 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. substratiatus* were found primarily in cornfields...