AN ABSTRACT OF THE THESIS OF

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Title: THE BIONOMICS OF THE CABBAGE FLEA BEETLE, *PHYLLOTRETA CRUCIFERAE* (GOEZE), IN WESTERN OREGON

Abstract approved: Redacted for privacy
H. H. Crowell

The cabbage flea beetle, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae) was introduced into the United States from Europe during the 1920's and 1930's. It was described as a new species, *P. columbiana*, native to North America by F. H. Chittenden in 1927. This synonymic situation was discovered in 1953 after *P. cruciferae* had become established as an economically important pest of crucifers in northeastern and northwestern United States.

The immature stages (egg, three larval stages, prepupal and pupal stage) are soil inhabitants. The adult is bluish black and two to three millimeters in length.

P. cruciferae was found to be univoltine in western Oregon, with the adults of the annual generation apparently overwintering in a state of reproductive diapause. Grass sod appeared to be the favored overwintering site.

Circumstances indicated that darkness was a factor influencing oviposition. Oviposition was not observed, but the probable oviposition period occurred from June to the middle of July. The preoviposition period was found to be about three and one half days. The females laid about 37 eggs per mating. Field sampling indicated a 1:1 ratio of males to females existed.

The major attack, which causes the greatest economic loss, arises from the overwintered generation feeding on spring-planted crucifers. The larvae feed externally on the roots of crucifers.

One natural enemy, tentatively identified as *Microctonus vittatae* Muesebeck (Hymenoptera:Braconidae) was found parasitizing ten percent of *P. cruciferae* in the field.

The Bionomics of the Cabbage Flea Beetle, *Phyllotreta cruciferae* (Goeze), in Western Oregon

by

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INTRODUCTION

The cabbage flea beetle, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae), is widely distributed, causing damage to crucifers in both the Eastern and Western Hemispheres. El-Sawaf, Hammad, and Abdelfattah (1965) reported *P. cruciferae* as being one of the most important pests of crucifers in Egypt. Varma (1961) affirmed that *P. cruciferae* is a serious pest of cultivated crucifers in India. Newton (1928) remarked that the injury caused by the cabbage flea beetle to crucifers represents a great loss financially to England's agriculture.

Chittenden's systematic study of the genus *Phyllotreta* (1927) contains the first mention of *P. cruciferae* (incorrectly cited as *P. columbiana*) in North America. The species was evidently introduced from Europe to the Pacific Northwest of the United States during the early 1920's (Milliron, 1953). Later records show *P. cruciferae* very abundant along the northern east coast, where it was apparently introduced into the United States a second time during the late 1930's or early 1940's (Milliron, 1953). Gentry (1969) asserts that *P. cruciferae* is distributed as an economically important pest in the northeastern states (Vermont, New York, Pennsylvania, New Jersey, Maryland, Delaware, Virginia, Ohio) and the

Pacific Northwest (Washington, Oregon, Idaho, Utah).

During World War II, the growing of crucifers for seed became a notable part of western Oregon's agriculture. The importance of the cabbage flea beetle as a crucifer pest was first recognized when flea beetles were found attacking the bolting crucifer plants, causing damage to the reproductive parts of the plants and lowering yields.

During the 1950's, emphasis changed from crucifer seed production to raising crucifers for vegetables. Broccoli, turnip, radish, Brussels sprouts, cauliflower, and rutabaga became important vegetable crops in the Willamette Valley. The cabbage flea beetle has established itself successfully in this crucifer growing region, causing considerable damage when crops are not protected.

Europeans have studied the biology of *Phyllotreta* species, finding that the immature stages of *P. cruciferae* are soil borne and feed on the roots of crucifer plants. The reported number of generations of *P. cruciferae* per year is inconsistent. Little information is known about its reproductive habits. A search of the literature revealed no published information on the biology of *P. cruciferae* in North America. Since reports on the number of generations of *P. cruciferae* were contradictory and information relating to the reproductive activities of the beetle was limited, a study was initiated on the bionomics of *P. cruciferae* in western Oregon to alleviate the lack of biological data from the United States.

IDENTITY AND NOMENCLATURE

The currently accepted scientific name for the cabbage flea beetle is *Phyllotreta cruciferae* (Goeze). The species was first described by Goeze in 1777 as *Chrysomela cruciferae*, but was transferred to the genus *Phyllotreta* in 1876 (Junk, 1924). The synonymy of the species prior to 1924 is discussed in Junk's *Coleopterorum Catalogus*. In addition, *P. columbiana* (Chittenden, 1927) was placed as a synonym of *P. cruciferae* by Milliron (1953). According to Milliron, this synonymous relationship was recognized as early as 1945 by H. S. Barber, but Barber's conclusions were not published. Consequently, only until an examination of the material in the United States National Museum from both North America and Europe had been completed in 1952, did the synonymy become established (Milliron, 1953).

While investigating the synonymy of *P. cruciferae*, the writer found that confusion existed as to whom the credit for authorship of *Phyllotreta* should be given. Horn (1889) and Leng, Mutchler, Blackwelder (1920) credited Foudras with the authorship of *Phyllotreta*; Junk (1924) in *Coleopterorum Catalogus* credited Stephens; Chittenden (1927) reported Dejean; and Blackwelder (1946) indicated Chevrolat as the author of *Phyllotreta*.

According to Chittenden (1927) the generic name *Phyllotreta* was used by Chevrolat in 1833, presumably as a manuscript name in Dejean's *Catalogue Coleoptera*. Foudras defined the genus *Phyllotreta* in 1859, and he should be credited if the previous citations by Chevrolat, Dejean, and Stephens are invalid.

White (1969) confirmed Blackwelder's conclusion that Chevrolat is the correct author of *Phyllotreta*. The generic name *Phyllotreta* was first used by Chevrolat in Dejean's *Catalogue Coleoptera*, which was published in 1836.

PROCEDURES

Field experiments, sampling, and observations, together with laboratory investigations, constituted the approaches utilized in studying the bionomics of P. cruciferae.

The immature developmental stages of P. cruciferae were reared in the laboratory by incubating the eggs between pieces of damp filter paper and supplying the larvae with young turnip roots. Larvae were also reared on live Brussels sprouts seedlings.

The seasonal occurrence of P. cruciferae immature stages was studied by taking random root and soil samples from host plants and floating the immature stages from the soil with water. Adult P. cruciferae populations were studied by taking three to six samples at intervals; a sample consisted of 20 sweeps with a 15-inch wide circular sweeping net.

Early investigations of the overwintering habits of P. cruciferae consisted of collecting samples of standard volume from grass sod, leaf litter, and other suspected overwintering habitats. The samples were examined using Berlese funnels. Later studies involved caging beetles over the most promising habitats during the fall of the year, followed by sampling of these habitats during the winter using the flotation method.

Voltinism of P. cruciferae was determined by investigating the possibilities of the occurrence of an early spring generation or late summer generation. Also a sexual maturation study was performed to determine if the reproductive system of females was maturing the same season as emergence.

Studies of the reproductive activities of *P. cruciferae* entailed field observations of mating, field experiments exposing beetles to various sizes of plants for oviposition, and field sampling of adults to determine the sex ratio. Oviposition, preoviposition, and fecundity were studied in the laboratory by caging mated pairs of beetles in small vials containing crucifer seedlings.

A field experiment was designed to study the larval feeding habits. Potted crucifer plants were buried randomly among field turnips and the crucifer roots in three pots were examined weekly for larval entrance holes or other signs of larval activity.

Adult feeding preferences were investigated by planting crucifers in a randomized block experiment and evaluating flea beetle injury. The flea beetles' feeding preference was based on the severity of the injury to different plant species.

Field observations, identification, and rearing of parasites or predators constituted the approaches for the study of the natural enemies of *P. cruciferae*.

DESCRIPTION OF LIFE STAGES

The immature stages of the cabbage flea beetle develop in the soil. The eggs are laid around the bases of crucifer plants and the larvae feed on the roots. The third and last larval instar develops into a prepupa, which prepares an earthen cell for the ensuing pupa. In about two weeks the adult beetle emerges from the pupal stage. The immature developmental stages are shown in Figure 1 and the duration of various stadia in Figure 2.

Egg

The eggs are pale yellow, elongate oval, one-half millimeter in length, with breadth half the length. Shell sculpturing shows an even pattern of fine pits at 90X magnification. Following oviposition, embryonic differentiation begins with the translucent egg contents changing to a gray granular state within 48-72 hours. Prior to hatching, the "C" shaped form of the young first instar larva can be seen through the egg shell.

In these studies eggs were incubated between two pieces of damp filter paper in plastic petri dishes. The eggs were examined every 24 hours for development and hatching. The length of the incubation period ranged from five to ten days with 75% of the eggs hatching in seven days (Table 1). Temperature and humidity conditions in

Figure 1. Immature developmental stages of
P. cruciferae (6X magnification).

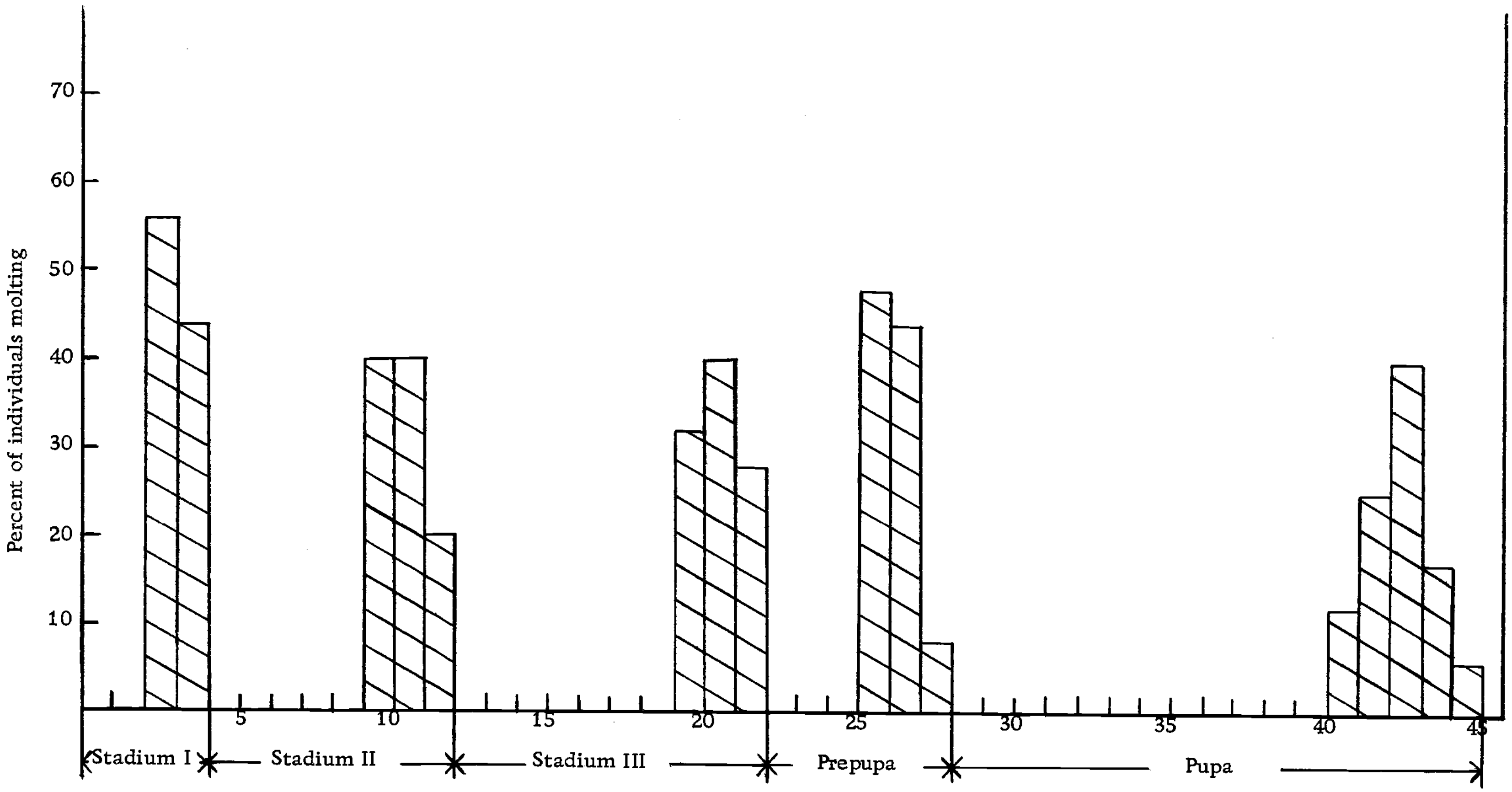

Figure 2. Duration of stadia in days following eclosion under laboratory conditions.

Table 1. Number of days required for *P. cruciferae* eggs to hatch.

No. of eggs per trial	Number hatched per day										
	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	*
27	0	0	0	0	5	10	7	1	1	1	2
23	0	0	0	0	2	5	10	2	1	1	2
29	0	0	0	0	6	5	11	2	1	1	3
25	0	0	0	0	5	5	9	3	2	0	1
31	0	0	0	0	3	9	10	2	3	0	3
20	0	0	0	0	4	6	6	4	0	0	0
24	0	0	0	1	4	5	9	1	2	0	2
25	0	0	0	0	3	7	9	2	2	1	1
Percent per day	0	0	0	.5	16	25	35	8.3	6	2	
Accumulative percent	0	0	0	.5	16.5	41.5	76.5	84.8	90.8	92.8	

*Failed to hatch.

the laboratory for all rearing experiments were not controlled, but followed normal daily variations.

Larvae

The newly hatched larvae are about one millimeter in length, almost transparent, with the head and anal plates appearing large in proportion to the remaining parts of the body. They are very delicate, being highly susceptible to injury and desiccation. After 48 hours, the head and anal plates become sclerotized, enabling the larvae to feed for about 24-48 hours before molting to the second instar. The length of the first stadium is three to four days (Figure 2).

Some of the larvae were reared to adults between two pieces of damp filter paper in petri dishes stored in the dark. The larvae were fed fresh, clean, young turnip roots every 24 hours. Five larvae per dish were incubated in a total of 30 dishes. Because of larval mortality, only in five dishes were all larvae reared to adults. In determining the length of the stadia, accurate records of ecdyses were maintained. The presence of exuviae indicated the larvae had molted. The period of time between molts was recorded as the length of each stadium.

Other larvae were reared on live Brussels sprouts seedlings in order to compare the rates of development of the two rearing techniques, and to observe the habits of the larvae in their natural soil habitat. Plastic petri dishes were half-filled with sandy clay loam soil and small openings were cut in the lids so that the seedlings could be positioned with their roots in the soil and leafy portions exposed to light. Water was added to the dishes through cotton packing around the seedling stems. Periodic examinations of the dishes showed that the rates of development of the larvae under the conditions of the two techniques were parallel.

Newly molted second stage larvae are white with brown head and anal plates. They are about two millimeters in length and one-half millimeter in width. The body can be differentiated into distinct head, thoracic, and abdominal regions. Six to eight days are required for the second stadium (Figure 2).

The mature third instar larvae are semi-arcuate in shape, white, and measure five to six millimeters in length and one in width. The head is strongly sclerotized, narrower than the prothorax, longer than broad, and directed obliquely downward and forward. The terga of the first three thoracic and ninth abdominal segments are slightly more chitinized than the remaining terga. The third larval instar lasts from eight to ten days (Figure 2).

Prepupa

Toward the end of the third stadium, the mature larvae stop feeding and become shorter and thicker. Later, the whole body becomes arcuate, with the head and thorax bent ventrally. As the larvae complete the transition to the prepupal stage, they construct pupal cells in the soil by repeated contortions of their bodies (Figure 3). Four to six days are required for transformation to the prepupal stage and construction of the pupal cells (Figure 2). Pupation occurs shortly thereafter.

Pupa

The pupae are white, measuring about three millimeters in length and one in width. Development within the pupal cell takes place with the pupa ventral side upward. The pupae pass through a series of color changes beginning with a red tinge of the eyes on about the fifth day. By the ninth day the eyes are reddish brown with the pupa evincing gray pigmentation. As pigmentation and sclerotization progress, the pupa becomes brown or brownish black. The beetles emerge from the soil in 12-16 days (Figure 2) as callow adults, requiring a few additional days to complete the hardening and pigmentation processes.

Adult

The adults are bluish black, often with a greenish tint, and two to three millimeters in length. They are elongate, narrowed anteriorly, but gradually broadening posteriorly and rounding at the

Figure 3. Pupal cell of P. cruciferae showing adult for size comparison (6X magnification).

apex. The head is finely punctate, with the dorsal surface slightly convex, and the antennae extending beyond the middle of the elytra. The ventral side is covered with fine, minute, whitish hairs. El-Sawaf, Hammad, and Abdelfattah (1965) may be consulted for a detailed description of *P. cruciferae*.

SEASONAL HISTORY

Adults of *P. cruciferae* begin to emerge the second half of July, and continue emerging for about one month (Figures 4 and 5). The beetles feed heavily on maturing crucifer plants during the month of August. Toward the end of August and early in September, the beetles seek overwintering sites, resulting in an abrupt drop in field populations. During the winter, on moderately warm sunny days, a few *P. cruciferae* may be found on crucifer plants, but the majority of the beetles remain in diapause. In the spring a few days of warm weather will bring the beetles from their overwintering sites in large numbers. They prefer to feed on young cultivated crucifers, but will feed on maturing wild crucifers until cultivated seedlings are available. Mating and oviposition begin around the first of June and continue to the middle of July. By this time, the overwintered flea beetles have completed their reproductive functions and their numbers begin to decline.

Seasonal Occurrence of Life Stages

Sampling of cultivated turnip plants for immature stages of *P. cruciferae* was started the first week in June 1968, and continued through September. Ten samples were examined each week by floating the immature stages from the soil with water. Each random sample consisted of a core of soil and roots taken from a turnip row using a six inch diameter soil sampler inserted to a depth of six inches. Numbers of larvae, prepupae, and pupae per ten samples were recorded weekly. Eggs were not found in the field.[1]

The imago was found to be the overwintering form and would be expected to be present in the field the following season since pupae or other immature stages were not found after August 15. Information concerning the specific time of year the adult beetles begin to emerge was determined by a dissection study.[2]

Based on field sampling and observations, the writer estimated the seasonal occurrence of each life stage to be as shown in Figure 4.

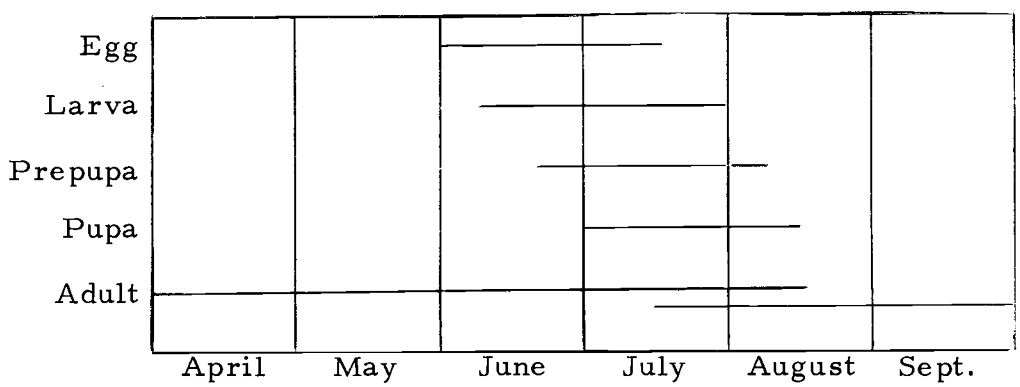

Figure 4. Seasonal occurrence of the life stages of *P. cruciferae* in western Oregon during 1968.

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[1] The estimated occurrence of their presence in the field is discussed in a later chapter titled "Reproduction" on page 35.

[2] The dissection study involved determining the sexual maturity of the reproductive system of females. Details of the study are discussed on page 29.

Adult Population Studies

At the Oregon State University Entomology Farm, sweep net samples were taken 35 times at varying intervals between November 20, 1967, and April 28, 1968, on cultivated turnips left in the field for flea beetles studies. Since the winter was mild, the turnips remained in a state of vegetative growth suitable for sweeping purposes. Beetles were found on ten different occasions from December to March whenever temperatures were above 60° F. In April, following a few days of temperatures in the high 60's and low 70's, climaxed by an 87° F recording on April 28, beetles appeared on turnips and from then into the summer they were present in the field despite subsequent periods of cool weather.

During the summers of 1967 and 1968, sweep net samples of P. curciferae were collected to determine population trends of the beetles. In 1967, rutabagas were sampled at the Oregon State University Vegetable Crops Farm until they were destroyed for winter cover crop seed bed preparation. Sampling was then transferred to the Oregon State University Entomology Farm where a slightly larger population of flea beetles was present. In 1968, the entire population study was performed at the Oregon State University Entomology Farm using turnips as host plants for the beetles. A sample consisted of 20 sweeps, with three to six samples taken per sampling date. The mean numbers of flea beetles per sweep were calculated for July, August, and September of the two summers (Figures 5 and 6).

General sampling of flea beetle populations revealed that population levels may vary with the time of day samples are taken (Table 2) and with unseasonal environmental conditions (Figure 6). Table 2 illustrates the approximate population of flea beetles present on cultivated turnips at hourly intervals during periods in July of 1967 and 1968.

Table 2. Daily occurrence of *P. cruciferae* on turnip foliage.

	Mean no. of flea beetles per sweep[1]	
Time of day	July 23-24, 1967[2]	July 1968[2]
7:00 AM		.40 a
8:00 AM	.24 a	.50 a
9:00 AM	.63 b	1.10 b
10:00 AM	1.02 c	1.71 c
11:00 AM	1.73 d	2.24 d
12:00 Noon	2.02 e	2.91 d
1:00 PM	2.11 e	2.83 d
2:00 PM	1.92 e	2.90 d
3:00 PM	2.23 e	3.00 d
4:00 PM	2.14 e	2.88 d
5:00 PM	1.94 e	2.02 c
6:00 PM	1.12 c	1.43 b
7:00 PM		1.16 b

[1] Three 20-sweep samples were taken at each hour indicated.

[2] Numbers in the same column followed by the same letter are not significantly different from each other at the 95% level of confidence (Duncan's Multiple Range Test).

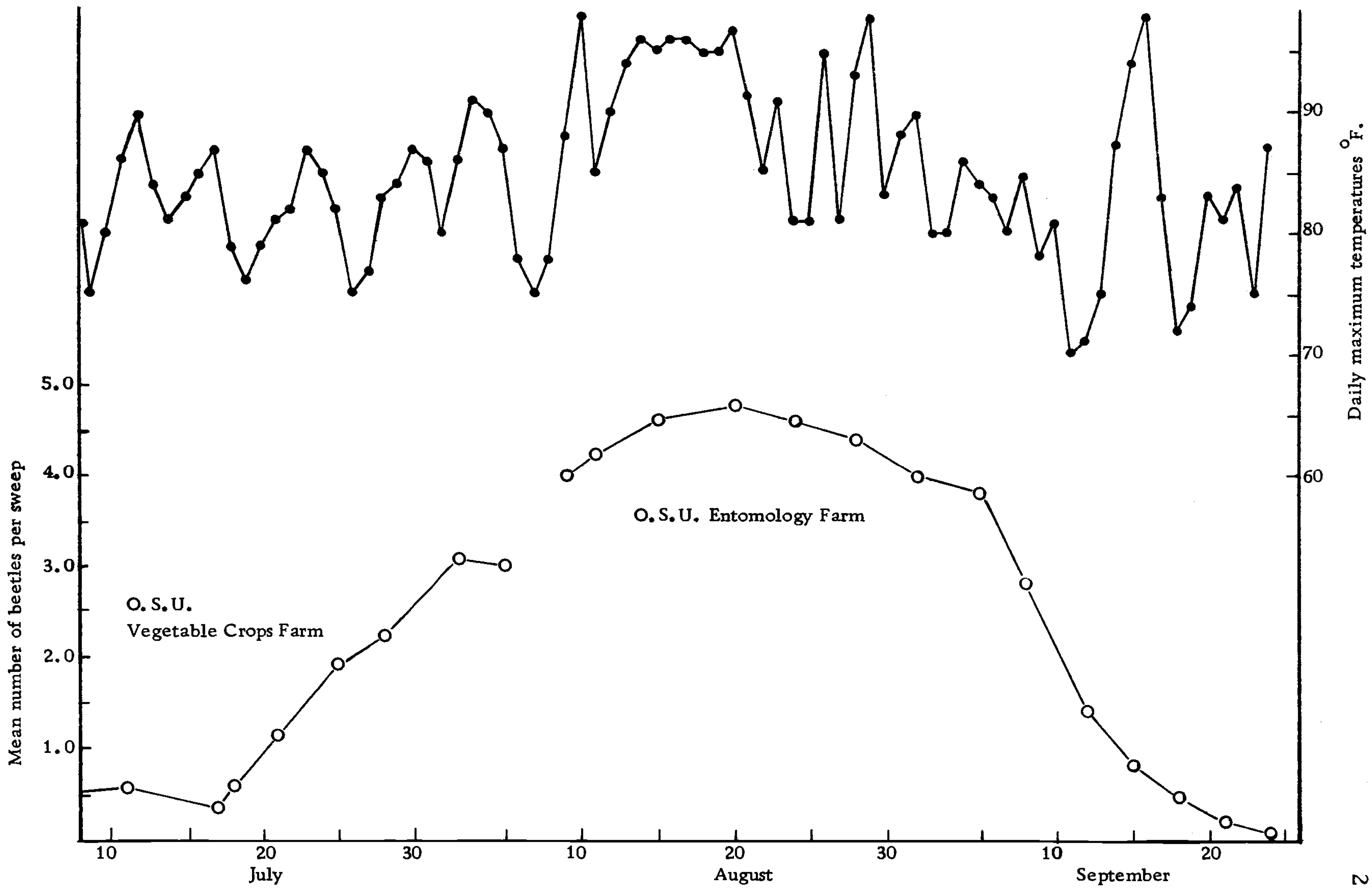

Figure 5. Seasonal abundance of adult P. cruciferae population in 1967.

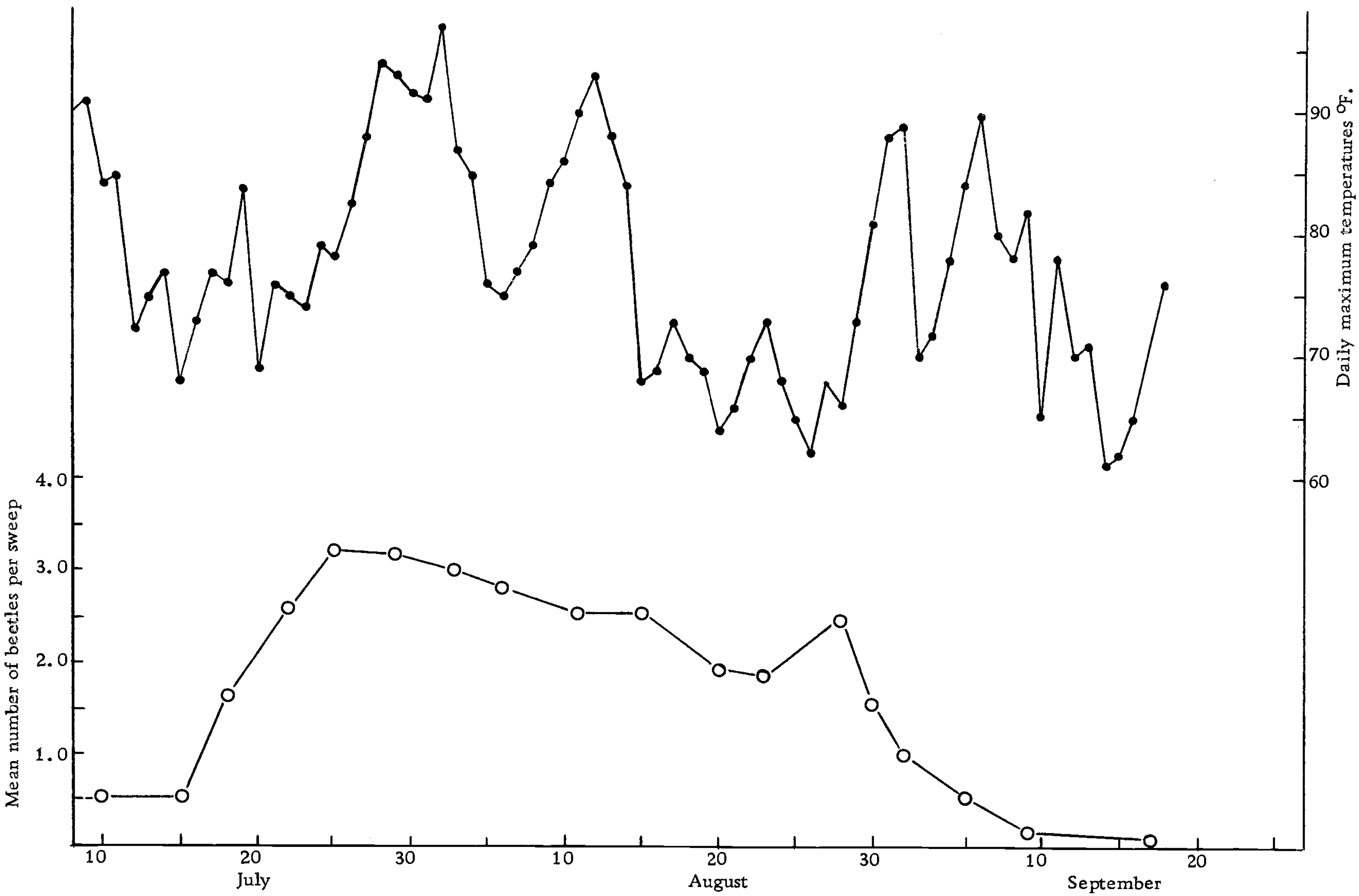

Figure 6. Seasonal abundance of adult P. cruciferae population in 1968.

Largest numbers of cabbage flea beetles were collected between 12:00 noon and 4:00 PM, indicating optimum conditions for activity occurred during the afternoon hours. At night as the temperature dropped, the beetles sought cover at the bases of crucifer plants or just below the soil surface around the bases of the plants. As the temperature rose the next day, the beetles returned to the foliage where they were readily collected in net samples. Samples collected during the morning hours would not accurately estimate the flea beetle population.

Unseasonal environmental conditions may cause variation in numbers of beetles collected. The seasonal populations of P. cruciferae for the summer of 1967 (Figure 5) were possibly normal for western Oregon. Unseasonably cool wet weather during August of 1968 (Figure 6) suppressed the activities of the flea beetles as indicated by the low population numbers recorded during that period.

Overwintering

The cabbage flea beetle overwinters in the adult stage. The beetles survive the winter probably in a state of "reproductive diapause" (Beck, 1968; Bonnemaison, 1965), which is the suppression of reproductive development accompanied by reduced metabolic and behavioral functions. Dissections of beetles collected in late summer of 1968 revealed that the reproductive systems of the new generation females were not maturing and fat reserves were no accumulating.

Beck (1968) defines diapause as a genetically determined state of suppressed development, beginning before the onset of unfavorable ecological conditions. Photoperiodism has been postulated as the major factor controlling the induction and termination of diapause in insects (Beck, 1968). Photoperiodic control has been clearly demonstrated in three genera of chrysomelid beetles: Chrysomela, Haltica, and Leptinotarsa (Danilevskii, 1961).

P. cruciferae began migrating from crucifer fields to overwintering sites around the first of September (Figures 5 and 6). Since temperatures were favorable for normal summer behavior, some other environmental factor, possibly photoperiod, may have been responsible for initiating their migration to overwintering sites.

According to Newton (1928), Phyllotreta species may be found in protective areas not far from the scene of their summer activities, e.g., hedgerows, grassy field borders, leaf litter, and debris.

During the winter months of November 1967 through February 1968, samples from suspected overwintering habitats were collected from the Oregon State University Entomology Farm and examined using Berlese funnels. Samples consisted of soil and roots from field turnip rows, corn stubble residues, leaf litter, sawdust mulch, and grass sod. Only three P. cruciferae were found, and they were in the leaf litter samples.

Early in the spring before the flea beetles became active, emergence cages were set up over turnip plants to detect the possible presence of *P. cruciferae.* A few cabbage flea beetles were found in the cages, which leads to the inference that a small percentage of the beetles were overwintering around host turnip plants. These preliminary investigations indicated that a revision of sampling methods and techniques was necessary to determine accurately where the beetles were overwintering.

Late in August of 1968, habitats were selected representing the three most promising overwintering sites in the vicinity of the Oregon State University Entomology Farm; leaf litter, grass sod, and turnip plants. Three screen cages (4' x 2' x 3') were placed over sections of turnip rows; grass sod and leaf litter were added so that each cage included the three habitat types. Turnip foliage was swept until 400-500 flea beetles had been collected for placement in each of the three cage replicates.

During the middle of January 1969, after 20 days of temperatures of 32° F or lower, including a low of 14° F late in December 1968 (Oregon State University Weather Bureau), samples from each cage were immersed in water and the numbers of beetles found floating were recorded with the results shown in Table 3.

Table 3. *P. cruciferae* found in three habitat types.

Cage No.	Leaf litter Number	Leaf litter Percent	Turnip plants Number	Turnip plants Percent	Grass sod Number	Grass sod Percent
1	0	0	64	39	100	61
2	8	11	8	11	56	78
3	0	0	12	21	44	79
Mean percent		3.6		24		72.4

The results of this experiment indicated that *P. cruciferae* overwintered in all of the three habitat types provided, but favored grass sod for an overwintering site.

VOLTINISM

Much literature exists concerning the number of generations of *P. cruciferae*. Estimates range from a single generation to 11 generations per year.

Varma (1961) stated that seven to eight generations of *P. cruciferae* per year were common in New Delhi, India. Bonnemaison (1965) confirmed Varma's report by indicating the occurrence of 7-11 generations of *P. cruciferae* in Bengal, India.

Pyatakava (1928) reported that *P. cruciferae* has three generations per year in southern Russia. The overwintering adults resume their activities toward the middle of April, producing the imagoes of the first generation in mid-June. The second generation appears by mid-July, and the third by the end of August.

In the United States, Milliron (1951) affirmed that two complete overlapping generations of *P. cruciferae* occur in Delaware. The first generation of adults appear in mid-June, followed by the second generation in early August.

Taylor (1918) and Newton (1928) in England and H. Blunck (as cited by Jourdheuil, 1960) in Germany performed ecological studies, the results of which indicated that only one generation of *P. cruciferae* occurs annually. Jourdheuil (1960) in France performed weekly dissections of the reproductive systems of *P. cruciferae* to determine sexual maturity. Jourdheuil's results indicated a partial second generation, but due to a low percentage of female beetles in a state of reproduction and unfavorable conditions for the developing larvae, only a single generation occurs successfully.

Because of the conflicting evidence concerning the number of generations of P. cruciferae, efforts were made to determine accurately the number of generations of P. cruciferae occurring under western Oregon conditions.

Possible Early Spring Generation

Since there are many wild crucifer plants available as potential early spring hosts in western Oregon, it is conceivable that an early generation of flea beetles could be completed on wild crucifers before the normal annual summer generation occurs on cultivated crucifers. If P. cruciferae were utilizing wild crucifers for hosts, two complete generations might be occurring. Some of the wild crucifer plants available as hosts are jointed charlock, Raphanus raphanistrum; Shepherd's Purse, Capsella Bursa-pastoris; black mustard, Brassica niger; and wild turnip, Brassica campestris, of which the latter is the most abundant.

Flea beetles on wild crucifers were carefully observed on repeated occasions in the early spring of 1968, but no reproductive activity was noted. On April 20 and May 19, samples of roots and soil from wild crucifer plants, mainly wild turnip, were examined for the immature stages of P. cruciferae.[3] Failure to find the immature stages indicated the non-existence of an early spring generation.

Possible Late Summer Generation

Under irrigated conditions in western Oregon, Diabrotica species (Coleoptera:Chrysomelidae) are able to complete a second generation and perhaps a partial third. The possibility of this phenomenon occurring in P. cruciferae was investigated late in the summer of 1968 by supplementing rainfall with sprinkler irrigations. In a previous experiment[4] it was noted that female flea beetles favored small seedlings for oviposition. Cultivated turnips were planted early in August to furnish an attractive host for oviposition. The seedlings were observed for flea beetle mating and oviposition. Mating and oviposition were not observed, nor were any immature stages found.[5]

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[3] Sampling for the immature stages of P. cruciferae was performed as described on page 16.

[4] Various stages of crucifers plants were exposed to flea beetles for oviposition. Details of the experiment are discussed on page 37.

[5] Sampling for the immature stages of P. cruciferae was performed as described on page 16.

Sexual Maturation of Female *P. cruciferae*

A study was performed during the summer of 1968 to follow the development of sexual maturity in female flea beetles. A study of this nature would indicate whether or not the female reproductive system of the new generation matured the same season as emergence. The study was initiated in July so that the reproductive systems of the overwintered beetles could be compared with those of the new generation.

Adult beetles were collected at approximately five day intervals and preserved in 95% alcohol for dissection. Varma's paper (1963) was consulted for information concerning the morphology of chrysomelid reproductive systems. Females were used in the study because of the relative ease in determining sexual maturity. Sexually mature (overwintered) females could be distinguished from immature (new generation) females on the basis of their enlarged oviducts and vagina, or through the occurrence of oögenesis. Fifty female beetles were examined from each sample. The percentages of sexually mature versus sexually immature beetles are presented in Figure 7. The period from July 15 to August 15 represents the approximate time when the two populations overlap. The new generation began emerging around July 15 and by August 15 had dominated the flea beetle population. At the same time, the percentage of sexually mature

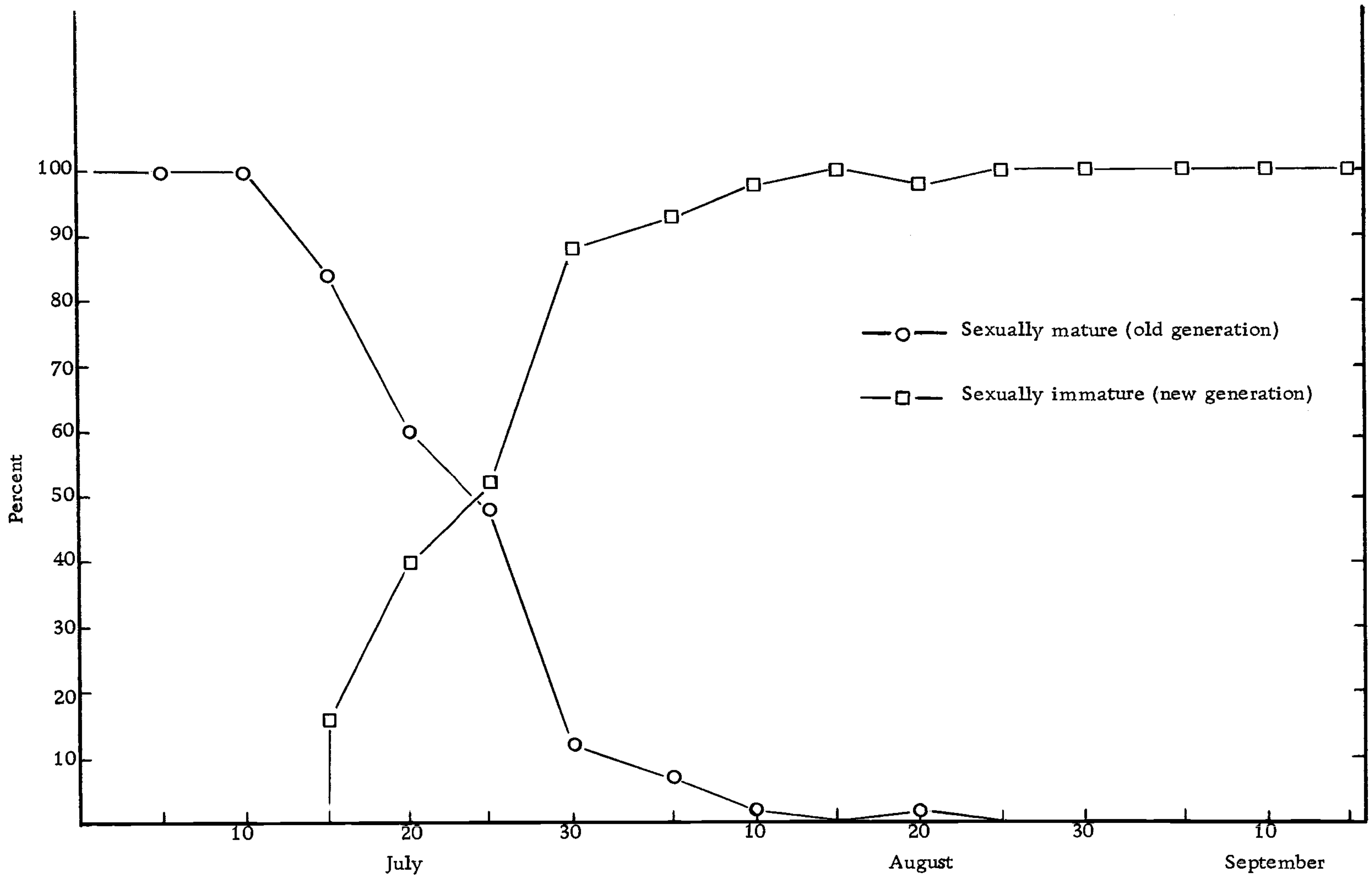

Figure 7. Seasonal occurrence of overwintered and new generations of *P. cruciferae* based on sexual maturity of females.

overwintered beetles began decreasing and was practically non-existent in the population by August 15. Sweep sampling was continued through September and into October. During October, only a single sample of cabbage flea beetles containing 16 females could be collected. Dissections indicated that the reproductive systems of these females were immature.

Based on the following evidence, the writer concluded that *P. cruciferae* was univoltine in western Oregon. Seasonal history studies indicated that each life stage occurred only once during the year. Attempts to find the developmental stages early in the spring and late in the summer were unsuccessful. Adult beetle population studies inferred that a single generation emerged during July and August. Sexual maturation studies showed that the reproductive system of the female beetle did not mature the same year as emergence. If the reproductive system had matured, at least a partial second generation could have occurred.

Beck (1968) discusses the role of critical daylength in relation to voltinism of a geographically widespread insect species. Northern forms tend to have a longer critical daylength for diapause induction than southern forms of the same species. The phenomenon of latitudinal adaptation has been reported for many insect species (Danileviskii, 1961). In western Oregon where *P. cruciferae* is univoltine, migration to overwintering sites begins around September 1, and the overwintering phase of the life cycle terminates sometime in April. Varma (1961) reports that *P. cruciferae* overwinters only during the months of November, December, and January.

Comparing the reports of the number of generations of *P. cruciferae* on a latitudinal basis, there is a geographical progression from a univoltine population around 45° latitude to a multivoltine population at 20° latitude. Taylor (1918) and Newton (1928) in England, and Jourdheuil (1960) in France, all reported only one generation of *P. cruciferae* at about 45° latitude. Pyatakava (1928) reported that three generations of *P. cruciferae* occurred in the southern province of Russia, which is about 37° latitude. Varma (1961) and Bonnemaison (1965) reported that 7-11 generations of *P. cruciferae* occurred seasonally in parts of India at about 20° latitude.

Apparently the critical daylength and the gradual lengthening of the growing season as one progresses toward the equator are factors involved in determining voltinism of *P. cruciferae*. A thorough investigation of these factors would be required before final statements could be made.

REPRODUCTION

The reproductive activities of the cabbage flea beetle were difficult to study because of the beetles' small size and elusiveness in the field. Nevertheless, most of their reproductive activities were studied.

Oviposition--Time of Day

Oviposition was not observed in the field nor were eggs found, so attempts were made to obtain the eggs of *P. cruciferae* in the laboratory. A few eggs obtained in a preliminary trial led to a successful technique for egg collecting.

In the partially successful attempt, eight to ten beetles were selected randomly from field collected samples and caged in 5-inch high shell vials. The vials were filled one-third full of plaster of Paris, dampened, an inch of soil added, and a small Brussels sprouts seedling transplanted into the soil. In all previous oviposition studies, the laboratory lights had been left on day and night in order to grow crucifer plants for another experiment. During this attempt to induce oviposition, the lights were not on at night and two days later eggs were found in two of the 15 vials. Circumstances indicated that low light intensity or darkness might be a requirement for oviposition.

In the field, *P. cruciferae* have been observed moving down toward the bases of turnip plants as night approached. At dawn and during early morning hours, numerous cabbage flea beetles have been found under clods around the bases of turnip plants suggesting that oviposition probably was occurring from dusk to dawn, and explaining why no one has reported actually observing oviposition.

Following the discovery that darkness was a factor influencing oviposition, eggs were successfully obtained in the laboratory by collecting copulating pairs of P. cruciferae in the field and caging the beetles in shell vials as previously described. Five to six mated pairs of beetles were caged in each vial. During the period from June 15 to July 15 of 1968, a total of 200 pairs of beetles were collected and exposed to normal night and day light conditions at ambient temperatures. Eggs were found in some of the vials as early as 60 hours and in all the vials by 84 hours, indicating the preoviposition period of P. cruciferae was two and one-half to three and one-half days (Table 4).

Table 4. Preoviposition time requirements for P. cruciferae following mating.

Dates	No. of vials	Number of vials containing eggs after 24 hrs.	48 hrs.	60 hrs.	72 hrs.	84 hrs.
June 15-22	12	0	0	2	2	12
June 23-29	10	0	0	1	1	10
July 2-8	11	0	0	1	1	11
July 9-15	7	0	0	0	0	7
Totals		0	0	4	4	40
Percent		0	0	10	10	100

Oviposition--Time of Year

Oviposition probably began during the first week of June and continued well into July of 1968. Because actual oviposition was not observed, the indicated oviposition interval was based on the relative factors of mating observation dates and known lengths of the preoviposition period, incubation period of the egg, and larval stadia.

Numerous matings of flea beetles were first observed in early June. The length of the preoviposition period was determined to be three and one-half days. The length of the incubation period of the egg was six to seven days while the length of the first larval stadium was three to four days.[6] Thus, the total calculated developmental time from copulation to second instar larvae was determined as 13-14 days. Second instar larvae were first found around the roots of turnip plants on June 17. Fourteen days previous to the date of finding the first larvae coincided closely with the time mating was first observed, indicating that oviposition began during the first week in June.

Mating of the flea beetles was observed occurring from June until mid-July. Because of the short preoviposition period, oviposition was probably occurring during the same period as mating.

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[6] These periods of time for the incubation period and larval stadia are from the "Description of Life Stages" study on page 7.

Larval, prepupal, and pupal stages have been found existing simultaneously in the soil around host plants, also indicating that oviposition was occurring over a long period of time.

Oviposition--Egg Deposition in the Laboratory

The females of *P. cruciferae* attached their eggs to soil particles in the near vicinity of the plant and occasionally on the plant stems near the ground. Most of the eggs found in this study were in the top one-fourth inch of soil and infrequently on the soil surface. Eggs were usually deposited singly--rarely two, three, or four together.

Fecundity

Eggs from the oviposition experiment were counted. Results indicated that females laid an average of 37 eggs per mating with a range of 22-49 eggs as shown in Table 5.

Table 5. Fecundity of *P. cruciferae* in the laboratory.

Date	No. of females	Total no. of eggs	No. of eggs per female
June 16	5	175	35
19	5	110	22
22	5	245	49
23	5	183	36
28	5	220	44
July 1	5	151	30
7	5	125	25
9	5	232	46
14	5	191	38
15	5	205	41

Average number of eggs per female = 36.6

Stage of Plant Selected for Oviposition

Soon after the flea beetles emerged from diapause in the spring of 1968, turnips (variety Purple Top Globe) were planted at intervals to serve as hosts for the beetles. Observations indicated mating pairs of flea beetles were found most frequently on the youngest crucifer plants in the field. An experiment was designed to determine if a particular stage of plant development was favored for oviposition by the female cabbage flea beetle.

Three different sizes of cabbage plants (variety Danish Ballhead) were grown under greenhouse conditions and transferred to the field the second week of July. The three stages of plants were: (1) young seedlings, seven days old; (2) plants with five to seven true leaves, 20 days old; and (3) plants of transplanting size, 40 days old. The plants for each stage were grown in ten six-inch pots with three plants per pot. The 30 pots of cabbage plants were buried randomly in the field so that the top of the pot was level with the soil surface. The potted plants were left in the field exposed to the flea beetles for one week. Varma (1961) stated that eggs were counted by floating them from the soil with water, but despite repeated trials using his technique, eggs could not be found. Actual tests showed the eggs would not float in water. Because of the lack of a suitable technique for egg recovery, an alternate approach based on the numbers of larvae found per pot was utilized. Potted plants were transferred to the laboratory where they were maintained for one month before examining the soil for developing larvae. The results are shown in Table 6.

Table 6. Mean number of flea beetle larvae found for each plant stage and percentage of pots containing larvae.

Stage of plant	Mean no. of larvae per pot[1]	Percent of pots containing larvae
Young seedlings	3.6 a	80
Plants with 5-7 true leaves	1.3 b	40
Transplants	.4 c	10

[1] Means followed by a common letter are not significantly different at the 99% level of confidence (Duncan's Multiple Range Test).

Since there was a 30 day interval from oviposition to larval recovery, it cannot be stated definitely that young seedlings were preferred for oviposition. However, results showed that the largest number of larvae found were in pots containing young seedlings.

Mating

Mating was observed occurring on the leaves of young crucifer plants. On numerous occasions the males and females touched their antennae together momentarily before the male mounted the female. During copulation the female passively accepted the male. Toward the end of copulation, which was usually completed within five to seven minutes, the female became restive, striving to dislodge the male. In some cases the female removed the male by scraping him off with the edge of a leaf.

Observations indicated the males were polygamous, since on one occasion in the field a male was seen to mate with several different females. Efforts to determine whether or not females were polyandrous were not conclusive.

Sex Ratio

The sexes of the cabbage flea beetle can be easily distinguished by the external genital segments. The last ventral abdominal segment of the male has a decided median concavity, a definitely impressed median longitudinal line, and the sides turn inwardly posteriorly to a median lobe. The last ventral abdominal segment of the female is convex and tapers normally to the apex of the abdomen.

Ten samples of 50 or more beetles were collected from the field during 1968 in early spring, midsummer, and fall to determine the ratio of males to females. In all cases, sampling indicated a close approximation of a 1:1 ratio of males to females as shown in Table 7.

Table 7. Ratio of males to females from field collected specimens in 1968.

Date	Mean no. of males	Mean no. of females	Ratio
May 4	80	76	1.05:1.0
June 22	48	52	.92:1.0
August 17	136	128	1.06:1.0

LARVAL AND ADULT FEEDING HABITS

Feeding Habits of the Larvae

The larvae of *P. cruciferae* are soil inhabitants, feeding on the roots of crucifers. I. Bedel (as cited by Newton, 1928) found the larvae of *P. cruciferae* around the roots of eight commonly cultivated crucifers. A survey conducted during the summer of 1967 in western Oregon on two common weed species, *Amaranthus retroflexus* (pigweed) and *Senecio vulgare* (groundsel), together with species in the families Cucurbitaceae and Cruciferae, revealed that larvae of *P. cruciferae* were present only on cultivated crucifers. The second and third instar larvae were easily found by searching through the soil around cultivated crucifer plants in the field. The depth at which they live depends on the depth of the root system and moisture content of the soil. They are negatively phototrophic, moving actively away from light by peculiar snake-like movements.

In reference to the feeding habits of the larvae, the evidence in the literature is inconsistent. Varma (1961) ascertained that all larval stages of *P. cruciferae* feed within the crucifer roots. Newton (1928) stated that the larval stages feed externally on crucifer roots. A field study was conducted during June and July of 1968 at the Oregon State University Entomology Farm. Turnip plants were transplanted from the field into 24 metal pots six inches in diameter and eight inches deep, containing half sand and half clay loam soil. The roots were washed clean of field soil before transplanting. After the turnip plants had recovered from the shock of transplanting, the pots were returned to the field and buried randomly in rows of field turnips. The examination of turnip roots was performed after carefully removing the roots from the friable potting soil with the least amount of disturbance possible. The roots were inspected for larval entrance holes or any other signs of larval activity. After the external inspection, the roots were split open and examined for the presence of larvae or evidences of root mining. Three pots per week were examined during an eight week period with the first pots being examined after they had been in the field for ten days. The results of the study are shown in Table 8.

Table 8. Number of larvae found feeding on turnip roots.

Dates	Total no. of larvae per 3-pot sample	Number of larvae feeding	
		Internally	Externally
June 17-21	18	0	18
24-28	36	2*	34
July 1- 5	25	1*	24
8-12	15	0	15
15-19	8	0	8
22-26	2	0	2
29- 2	0	0	0
Aug. 5- 9	0	0	0

*With each of these three larvae, the original entrance into the root was made by a cabbage maggot, *Hylemya brassica*.

Evidence from the field study clearly indicated that the larval stages of the cabbage flea beetle do not mine within turnip roots. Evidence of external feeding was present, but it was difficult to determine whether the damage noted was due to flea beetle larvae or other soil inhabiting herbivores.

Because several flea beetle larvae were found feeding within the turnip roots, a study was designed to determine if cabbage maggot tunneling increased the incidence of root mining by flea beetle larvae. The experiment consisted of two treatments and ten replications. Flea beetle larvae were allowed to feed on healthy four-week-old turnip roots in one treatment and maggot-tunneled roots in the other treatment. Replicates consisted of plastic petri dishes containing four flea beetle larvae with one turnip root of each of the above mentioned treatments. Turnip roots and larvae were placed in a one-quarter inch layer of damp sand between layers of moistened black filter paper and incubated in the dark for 72 hours before examination. The results are illustrated in Table 9.

Table 9. Mean number of flea beetle larvae feeding on turnip roots.

	Mean number of larvae feeding	
Condition of roots	Internally	Externally
Healthy	0	40
Maggot-tunneled	14	26

Cabbage maggot tunneling of turnip roots apparently increased the incidence of root mining by flea beetle larvae with the tunnels providing an entrance for the larvae into the roots. Feeding damage on the healthy roots consisted of small surface depressions and in no case were mines formed.

While growing crucifer crops in the field during the course of research, there were no major indications of larval feeding being deleterious to the growth of plants. Newton (1928) stated that the damage caused to crucifer plants by larval feeding was minor and of little economic importance. Consequently, experiments were not designed to determine the direct affects of larval feeding on plants.

Feeding Habits of the Adult

Seedling crucifers attacked by flea beetles are either killed or stunted depending on the extent of cotyledon damage. Death may be caused by the complete destruction of cotyledons or desiccation following extensive epidermal feeding (Figures 8 and 9).

Newton (1928) describes an "underground" attack which occurs while the young seedlings are emerging from the soil. The flea beetles gain access to the young cotyledons through the broken crust of soil being pushed up by the crucifer seedlings. This type of attack is extremely dangerous because it occurs beneath the ground level concealed from the grower's attention. The "underground"

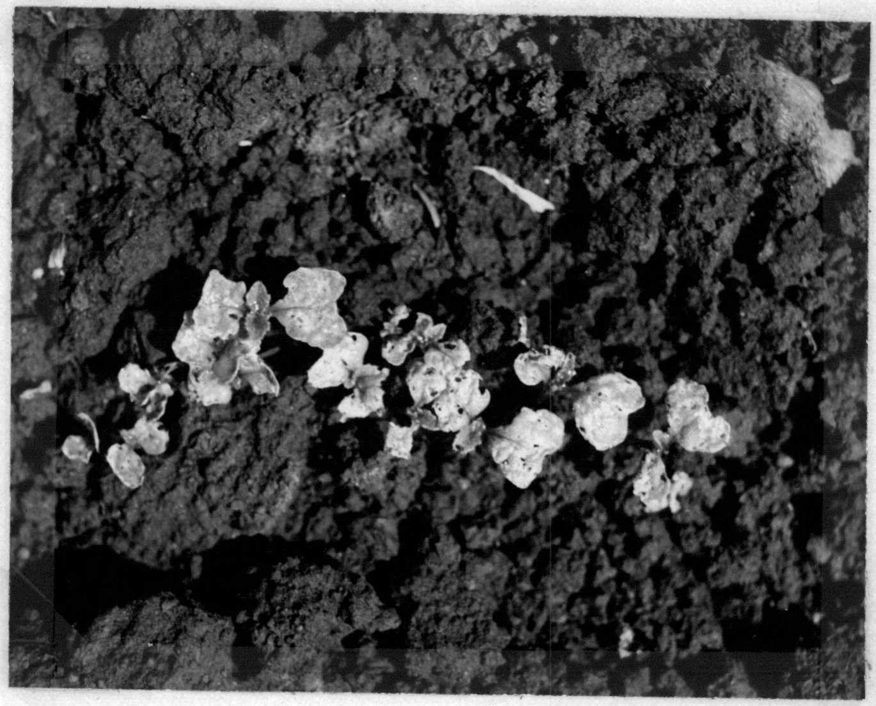

Figure 8. P. cruciferae injury to cultivated turnips resulting in death of plants.

Figure 9. P. cruciferae injury to cultivated turnips resulting in stunting of plants.

attack was not observed in western Oregon.

Injury to mature plants varies according to the nature of the vegetation attacked. Feeding injury on cole crops having thin leaves is characterized by a "shot hole" appearance (Figure 10). Cole crops having thick leaves, such as broccoli and cabbage, are damaged by the beetles eating small pits in the leaves.

The major attack, which causes the greatest economic loss, is from the overwintered generation of flea beetles feeding on spring planted crucifer seedlings. There is a tendency for the beetles to be gregarious, resulting in a spotted pattern of destruction. Margins of fields are most frequently damaged in the initial stages of attack. The suddenness of beetle attack, along with their large numbers, can result in the destruction of a large portion of a seedling stand in a short time. If considerable injury has occurred, the grower will have to replant, increasing the expense of production and delaying the establishment of the crucifer crop.

Crucifers grown for seed are also subject to attack by the overwintered generation of beetles. Schudel (1952) states that uncontrolled flea beetle populations will lower crucifer seed yields considerably.

Around the first of August, the mass appearance of the new generation marks the second period of attack. The new generation feeds on mature crucifer plants which are now usually able to support

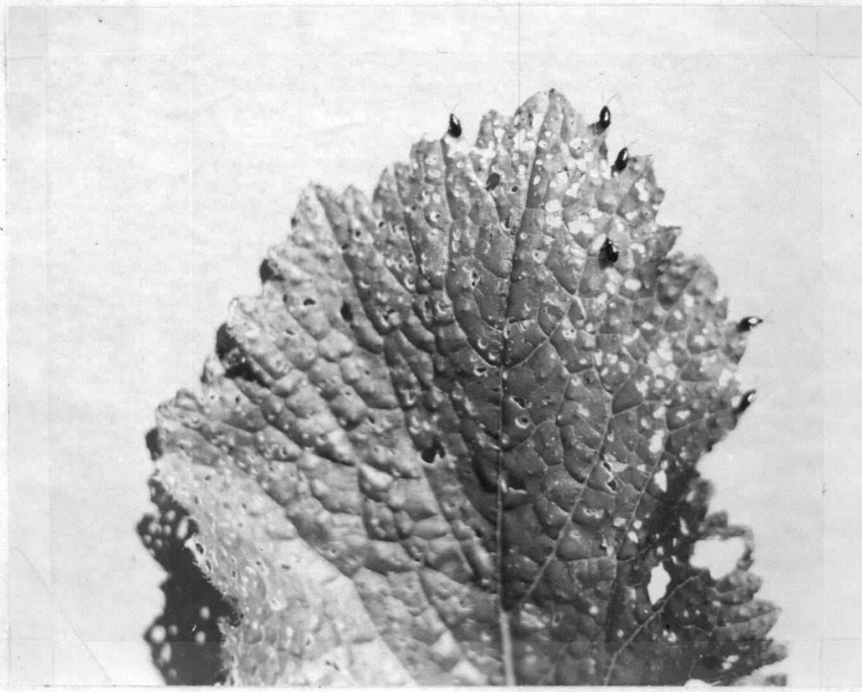

Figure 10. P. cruciferae injury to mature cultivated turnips.

the flea beetle population without serious loss. Only occasionally do flea beetle populations reach abnormally high levels causing considerable damage to the foliage of mature plants. The leaves become riddled with small holes, resulting in premature defoliation.

Adult Host Preference

During the summer of 1967, cabbage flea beetles were often found feeding in large numbers on turnips rather than equally distributed on all crucifer crops present in the field. Based on this observation, an experiment was designed to determine if particular plant species in the family Cruciferae were preferred by adult *P. cruciferae* for feeding. Seeds of seven commonly grown cole crops, one crucifer weed, and a legume were planted on June 12, 1968, for this test. The garden pea, *Pisum sativum*, was included because the cabbage flea beetle was found feeding heavily on this legume in the summer of 1967 as shown in Figure 11. The following plant species (Bailey, 1942) were included in the experiment:

1.	Broccoli	*Brassica oleracea* var. *botrytis*
2.	Brussels sprouts	*Brassica oleracea* var. *gemmifera*
3.	Cabbage	*Brassica oleracea* var. *capitata*
4.	Cauliflower	*Brassica oleracea* var. *botrytis*
5.	Wild turnip	*Brassica campestris*
6.	Rutabaga	*Brassica campestris* var. *Napo-Brassica*
7.	Turnip	*Brassica rapa*

Figure 11. P. cruciferae feeding on Pisum sativum.

8. Radish — _Rhaphanus sativus_
9. Garden pea — _Pisum sativum_

Evaluation of the cabbage flea beetles' feeding preference was based on the amount of injury to each plant species. Injury ratings were based on the scoring of 25 leaves selected at random from each of four plots with four categories of damage established: clean--no flea beetle feeding injuries, value of zero; slight--one to four injuries, value of one; moderate--four to ten injuries, value of two; heavy--ten or more injuries, value of four.

Within the family Cruciferae, much variation exists between the plant species. For example, rutabaga and cultivated turnips are both biennial root crops in the genus _Brassica_, but the thickness of the leaves of the plants is variable. Cultivated turnip, radish, and wild turnip leaves are thin in comparison with the leaves of rutabaga. Rutabaga leaves possess a heavy waxy cuticle and tend to be thick and leathery. Cauliflower, Brussels sprouts, broccoli, and cabbage are all varieties of _Brassica oleracea_, and possess leaves similar to rutabaga.

The cabbage flea beetle infestation was light while the plants were in the seedling stage, so the first crop preference rating for flea beetle injury was delayed until June 29. Approximately one month later the second crop preference rating was evaluated after a portion of the new generation of beetles had emerged. By this time, the majority of the crucifers were approaching maturity. The results of the injury ratings are shown in Table 10.

Table 10. Crop preference ratings of flea beetle injury.[1]

Crop	Mean ratings of flea beetle injury[2] June 29		Crop	July 30	
Wild turnip	56	a	Wild turnip	100	a
Cultivated turnip	53	a	Cultivated turnip	84	b
Radish	47	b	Radish	13	c
Cauliflower	33	c	Rutabaga	11	cd
Rutabaga	32	c	Cauliflower	7	d
Brussels sprouts	31	c	Brussels sprouts	6	d
Broccoli	31	c	Broccoli	5	d
Cabbage	27	c	Cabbage	5	d
Garden pea	0	d	Garden pea	0	e

[1] The highest rating possible in 100, indicating that plants are damaged heavily.

[2] Numbers in the same column followed by the same letter are not significantly different from each other at the 95% level of confidence (Duncan's Multiple Range Test).

Results of the June 29 injury rating evaluation indicated that wild turnip and cultivated turnip were the preferred plants for beetle feeding. Radish was intermediate, while the remaining crucifer plants were the least attractive. In the July 30 injury rating, wild turnip and cultivated turnip plants were undoubtedly preferred for feeding to the other crucifer plants (Figures 12 and 13).

A correlation exists between the cabbage flea beetles' preference for certain crucifer plants and the thickness of the crucifer plant leaves (Table 10). Based on the groupings of the injury ratings

Figure 12. P. cruciferae feeding on wild turnip, B. campestris.

Figure 13. P. cruciferae feeding on wild turnip in preference to cauliflower, B. oleracea var. botrytis.

and observations, the thin-leaved plants were chosen in preference to the thick-leaved plants for feeding. The heavy waxy cuticle of the thick-leaved plants may offer some morphological resistance, discouraging the feeding activities of the flea beetles. The cabbage flea beetles' preference for radish was peculiar, with radish being intermediately attractive on June 29, and least attractive by July 30. The reasons may be that radish belongs to a different genus, *Rhaphanus*, and more importantly, radish is an early maturing crop (25 days) while the other crucifers are later maturing crops (60-90 days). By July 30, the radish plants were senescent, and had progressively formed a heavier cuticle.

As shown in Table 10, garden peas were not selected for feeding where various crucifers were available. The observation of *P. cruciferae* feeding on peas during the summer of 1967 was probably due to the occurrence of a high population of cabbage flea beetles along with the absence of available crucifer plants for food.

NATURAL ENEMIES

Oldham (1933) found a nematode parasite, Howardula phyllotretae Oldham, attacking P. cruciferae. He concluded that H. phyllotretae was insignificant in suppressing P. cruciferae populations since only seven percent of the beetles were infested. Pyatakava (1928) reported that 17% of P. cruciferae populations were infected and killed by an unidentified fungus in southern Russia.

The only insect parasite of P. cruciferae found during these studies was a small braconid parasite in the genus Microctonus, tentatively identified as M. vittatae Muesebeck, a parasite of striped flea beetles (Phyllotreta species). Positive identification of specimens sent to the Systematic Entomology Laboratory of the United States Department of Agriculture has not yet been received.

Parasites were first noted in the field the last week in June 1968, but not until the first week in August were large numbers of parasites observed ovipositing on flea beetles. In one instance on cultivated turnips, a single parasite was observed ovipositing on 53 beetles during a 30 minute period. The parasite oviposited in the lateral region of the thorax or anterior abdominal region of the adult beetle. The parasite approached the beetle from the side, bent its abdomen anteriorly between its legs, and quickly darted its ovipositor forward inserting it into the beetle's body cavity. The beetle reacted by immediately jumping away. It is not known what percent of the oviposition attempts were successful.

When performing the dissections for the sexual maturation study, the numbers of beetles parasitized by M. vittatae were recorded. Over 1,000 P. cruciferae collected between July 1 and September 15 were dissected, and ten percent of the beetles were found to contain the immature stages of M. vittatae. Immature forms were recognized from descriptions by Smith (1952).

A study conducted by Smith and Peterson (1950) revealed that M. vittatae was a key factor in preventing the build-up of large populations of striped flea beetles in the northern United States. Percent parasitism averaged 46% over a three year period. Loan (1967) presented evidence indicating that populations of P. cruciferae near Ottawa, Canada, were being parasitized by M. vittatae and suggested that the parasite may be utilizing unicolored Phyllotreta species as hosts. Loan (1967) also discovered a hyperparasite (Hymenoptera: Ichneumonidae) Mesochorus phyllotretae Jourdheuil, which he believed to be of considerable importance in depressing the parasitic effect of M. vittatae on Phyllotreta species.

Investigations of the biology of the parasite were limited because of the late discovery of the parasite during the course of the study. Flea beetle dissection studies revealed that M. vittatae immature stages were present in P. cruciferae as the beetles entered diapause, suggesting that the parasite overwinters in the adult flea beetle. A sample of 30 beetles from those collected in January 1969, during the overwintering studies of the beetle, were dissected; five of the beetles were found to contain the larvae of *M. vittatae*. In his study of the biology of *M. vittatae*, Smith (1952) noted that the immature stages of the parasite overwintered in the flea beetles.

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