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TB 1581 (1978)

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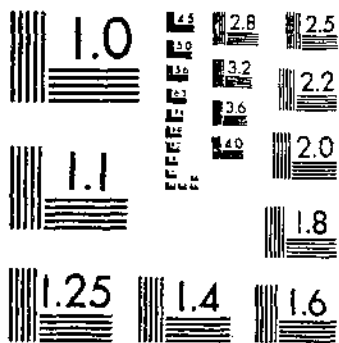
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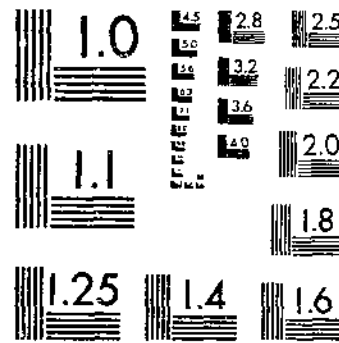
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IMPACT OF PERILLUS BIOCULATUS ON THE COLORADO POTATO BEETLE AND PLANT DAMAGE

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On January 24, 1978, four USDA agencies—Agricultural Research Service (ARC), Cooperative State Research Service (CSRS), Extension Service (ES), and the National Agricultural Library (NAL)—merged to become a new organization, the Science and Education Administration (SEA), U.S. Department of Agriculture.

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ABSTRACT

George Tamaki and B. A. Butt. Impact of *Perillus Bioculatus* on the Colorado Potato Beetle and Plant Damage. U.S. Department of Agriculture, Technical Bulletin 1581, 11 pp. 1978

The potential impact of *Perillus bioculatus*, a pentatomid predator, on the Colorado potato beetle, *Leptinotarsa decemlineata*, was evaluated by studying the biology, constructing life tables, and determining the feeding potential of different life stages of the predator on the eggs and larval stages of the defoliator. At average temperatures of 24° C, the developmental time of the egg of *P. bioculatus* was about 8 days and for the nymphal stage, about 17 days. Predator nymphs consumed up to 39 eggs or 0.6 of a large larva of *L. decemlineata* per day. The potential replacement rate was 46 daughters per generation. The population of *P. bioculatus* is able to double its size in 8½ days, and the generation time is 47 days.

In laboratory studies, *L. decemlineata* on potato foliage consumed 2,710 mm² of potato leaf area during its larval development at 24° ± 7° C. The fourth stage of the beetle consumed an average of 538 mm² and the adults, 687 mm² of foliage per day. Field census of all stages of the beetle on potatoes and the total leaf areas of potato plants were measured at different times of the year. For instance, the field population of an average of 26.4 larvae and adult beetles per plant on July 14 consumed 14,037 mm² of leaf area per plant and can completely defoliate a medium-size plant in 11 days.

Given the number and life stages of the predators and defoliators, we predicted the amount of predation and defoliation. Knowing the size of the potato plants, we predicted the percentage of defoliation resulting from the predator-prey-plant interaction. Moreover, knowing the percentage of defoliation of a plant, we estimated the yield loss.

KEYWORDS: *Perillus bioculatus*, Colorado potato beetle, *Leptinotarsa decemlineata*, pest management, biological control, crop damage, predators, potato pest, modeling, twospotted stink bug, *Solanum tuberosum*.

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IMPACT OF PERILLUS BIOCULATUS ON THE COLORADO POTATO BEETLE AND PLANT DAMAGE

By GEORGE TAMAKI and B.A. BUTT, *research entomologists*¹

INTRODUCTION

In North America, Gibson et al. (7)² intensively studied the Colorado potato beetle, *Leptinotarsa decemlineata* (Say); however, for the last 50 years, most of the literature on *L. decemlineata* is from research done in Europe, and much of the very recent published work stems from eastern European countries (10). This indicates the Colorado potato beetle is a more serious pest in Europe than in North America, probably because *L. decemlineata* is native to North America and was accidentally introduced and established in Europe without its natural enemies. In addition, resistance of the Colorado potato beetle to insecticides is more pronounced in Europe than in the United States. For instance, in the United States, Cutkomp et al. (2) reported a sevenfold to ninefold increase of DDT³ in LD₅₀ for resistant population compared with a susceptible population, whereas in Poland, Lakocy (15) reported up to 123-fold increase in LD₅₀'s for resistant pests compared with susceptible populations.

Knight (13) reported on the life history and

biology of a pentatomid predator, the twospotted stink bug, *Perillus bioculatus* (Fabricius), and found it to be an important predator of the *L. decemlineata*. Since the late 1920's, many attempts have been made to establish and to study this predator in France (24), West Germany (5), Poland (25), Czechoslovakia (11), Hungary (12), Russia (17), and Italy (23). In 1967, Szmidt and Wegorek (20) reported that when *P. bioculatus* was introduced in many countries it did not become established. Permanent mass rearing and annual releases are necessary if the predator is to be used in the program.

In this study, biological and ecological studies were conducted to evaluate the impact of a natural control against *P. bioculatus* on the pest or prey population, *L. decemlineata*. However, more importantly, we emphasized the total approach in evaluating the impact of the natural enemies not only against the pest but to predict their impact in preventing plant damage and as a deterrent to loss in yield.

PREDATOR—*PERILLUS BIOCULATUS*

Materials and Methods

In biology and life-table studies, adults and nymphs of *P. bioculatus* were held individually in

237-ml waxed ice-cream cartons with clear plastic lids. Water was provided in a 1-dr vial with a cotton plug slanted downward so gravity flow would keep the plug wet. A 3-cm² piece of Styrofoam was used to prevent the vial from rolling. The photoperiod (light:dark = L:D) was 16:8 hours per day. Two temperature ranges were used, 22° ± 1.5° C for biological and life-table studies and 24° ± 7° for biological studies.

In most cases, the immature stages of *P.*

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²Italic numbers in parentheses refer to Literature Cited, p. 11.

³1,1,1-trichloro-2,2-bis(p-chlorophenyl)ethane.

bioculatus were either fed larvae or eggs of *L. decemlineata* throughout their nymphal stages. In a few experiments, the first- and second-stage nymphs were fed eggs and then switched to larvae. Nymphs were never given eggs and larvae at the same time. The number of eggs or larvae consumed was determined daily. The amount of food provided always exceeded the amount consumed by the predator.

The incubation period for eggs of *P. bioculatus* was studied in tests conducted in 1975 and 1976. The eggs were held at $22^{\circ} \pm 1.5^{\circ}$ C and at 23° (range, 18° to 30°) with a 16:8-hour photoperiod. Eggs laid on the same day by one female were placed into a 29 cm³ jelly cup and checked daily for mortality and hatching.

Results and Discussion

EGGS

The eggs of *P. bioculatus* reared at a constant temperature of 22° C had an incubation period of $7.76 \pm .02$ standard error (S.E.) days. Eggs incubated at a temperature of 23° hatched in 7.51 days $\pm .03$ S.E. (table 1). From a total of 1,926 eggs, the average hatching time was 7.64 days $\pm .02$ S.E.; therefore, for most calculations, egg hatch was rounded to 8 days.

The eggs are barrel shaped and laid in batches. In the field, the eggs are laid on potato leaflets and, at times, on the petioles of the leaves. When first laid, the eggs are bright green, and in a few hours they turn shiny black. The newly hatched nymphs emerge from a circular hole on top of the eggs. The emerging nymphs are gregarious.

In one of our biology studies in the laboratory, nymphs were fed eggs and adults were fed larvae of *L. decemlineata*. The surviving 19 reproductive

TABLE 1.—Incubation period for eggs of *Perillus bioculatus* held at constant and variable temperatures

Days post-oviposition	Eggs hatched	
	$22^{\circ} \pm 1.5^{\circ}$ C	23° C (19° to 32°)
	-----Number-----	
5	0	11
6	10	117
7	225	382
8	603	392
9	26	146
10	6	8

females laid 127 egg clusters with an average of $17.8 \pm .6$ S.E. eggs per cluster.

IMMATURE STAGE

The developmental time and the rates of consumption of the predator were emphasized based on diets of either eggs or larvae of *L. decemlineata*. In comparing the developmental and consumption rate of *P. bioculatus* fed on eggs at the mean temperatures of 22° and 24° C—except for the first and second stages, which had almost equal developmental time—those reared at the lower temperature had a longer developmental period for each nymphal stage. Each additional stage had increased its developmental time by 1.0, and 1.9 days for the fourth and fifth stages, respectively, when reared at the higher temperature of 24° . The nymphs took 18.2 days to complete their development at 24° compared with 20.7 days when reared at 22° (table 2).

Franz (4), Knight (13), and Landis (14) have observed that the nymphs of the first-instar stage of *P. bioculatus* do not feed. In the course of our study, it was apparent that the first nymphal stage did not need food to complete its stadium, and mortality can be kept at a minimum with an available moisture source such as a potato leaf.

TABLE 2.—Developmental and consumption rates of nymphal stages of *Perillus bioculatus* on eggs of *Leptinotarsa decemlineata*

Stage	Replications	Days to develop \pm S.E.	Eggs consumed	
			Per instar	Per day
-----22° ± 1.5° C-----				
-----Number-----				
1	52	$2.29 \pm .08$	0.1	0.05
2	43	$3.44 \pm .11$	10.0	3.00
3	42	$3.33 \pm .13$	20.0	6.00
4	42	$4.14 \pm .12$	54.0	13.00
5	41	$7.54 \pm .09$	204.0	27.00
-----24° C (19° to 32°)-----				
1	44	$2.18 \pm .07$.3	.12
2	80	$3.33 \pm .07$	9.0	3.00
3	51	$3.92 \pm .10$	21.0	7.00
4	51	$3.11 \pm .08$	61.0	20.00
5	47	$5.68 \pm .15$	222.0	39.00

TABLE 3.—Developmental and consumption rates of nymphal stages of *Perillus bioculatus* feeding on 3d and 4th instar larvae of *Leptinotarsa decemlineata* at temperatures of 24° C (range: 18°–32°)

Predator stage	Number of predators	Number days to develop ± S.E.	Average number of 3d and 4th stage larvae consumed per instar	Average number of larvae consumed per day
1	43	2.16 ± .07	0	0
2	26	5.42 ± .42	.537	.098
3	47	3.53 ± .20	.369	.104
4	41	4.00 ± .18	.952	.238
5	34	5.79 ± .17	1.205	.208

However, our studies did show that, occasionally, the first instar will feed on eggs, but the amount consumed is negligible—less than 0.1 percent of the total food consumed during the entire nymphal development (table 2).

At both temperature ranges, the percentage of eggs consumed during each nymphal instar was similar (table 2). For instance, starting with the second-nymphal stage at 22° C, each succeeding nymphal stage consumed 3.4, 7.0, 18.8, and 70.8 percent, whereas at 24°, 2.9, 6.8, 19.4, and 70.9 percent of the eggs were consumed. Likewise, the average number of eggs consumed during each stage was similar. Therefore, the different lengths of developmental time had only a slight change in the amount of food consumed during each stage. At 22° the number of eggs consumed per day definitely decreased, and at 24° the developmental times were shorter with more eggs consumed per day.

When predators were fed larvae instead of eggs, the greatest difference occurred during the second nymphal stadium with an extended developmental period of 2 days. We hypothesize that the extended second instar developmental period was due to the lack of nourishment because of the difficulty encountered by a young, small predator attempting to prey on a much larger third or fourth larval stage of *L. decemlineata*. We have observed the small predator actually being tumbled over or walked upon by larger prey, but the more successful attackers actually rode on top of the abdomen of the larvae while feeding.

The first-stage nymphs of *P. bioculatus* showed no difference in developmental time in the presence of eggs or larvae of *L. decemlineata*. The second, third, and fourth nymphal stages showed the greatest extension of developmental time when fed larvae instead of eggs (table 3). Likewise, the fifth-stage nymph showed little difference in de-

velopmental time when fed either eggs or larvae. Therefore, the large or nearly mature predators can easily attack the larvae of *L. decemlineata* and acquire necessary nutrients for normal development. Apparently, the late-stage nymphs of the predator are not inhibited by the need to attack and capture moving prey.

The rate of consumption for each nymphal instar on larvae of *L. decemlineata* was erratic when compared with that found in feeding studies using eggs of *L. decemlineata*. For example, starting with the second instar, each succeeding nymphal instar consumed 3, 7, 19, and 71 percent of the eggs. This progressive rate of increase in percentage of consumption was accurate because the distended eggs due to predation were easily identified. In the consumption of larvae of *L. decemlineata*, the second to fifth nymphal instars consumed 17, 12, 31, and 39 percent of the larvae, respectively. The erratic data on the consumption of larvae can be explained as follows: (1) The data did not indicate the amount of food consumed but the number of larvae killed; (2) dead larvae were counted but moribund larvae were not included; and (3) all larvae were not the same size, whereas all the eggs were the same size.

To estimate the nymphal consumption rate of the larvae more accurately, we used the point value method of assessing predator feeding of different size prey (6). Because nymphal predation on eggs was assumed to be the most accurate consumption rate, this feeding rate was used as the basic rate. As shown in table 4, the third and fourth nymphal instars' consumption of larvae

TABLE 4.—Calculation of consumption rate of nymphal stages of *Perillus bioculatus* on the 3d and 4th larval stage of *Leptinotarsa decemlineata* based on the number of eggs consumed¹

Predator stage	Eggs consumed per instar at 24° C	Observed larvae consumed	Calculated larvae	
			Consumed ²	Consumed per day ³
			-----Number-----	
1	0.3	0	0.004	0.002
2	9.0	.537	.151	.028
3	21.0	.369	.351	.099
4	61.0	.952	1.004	.251
5	222.0	1.205	3.672	.634

$$^1 \text{Selected point value } X = \frac{0.369}{21} + \frac{0.952}{61} / 2 = 0.0165.$$

² $Y_n = (X)$ (column 2 minus number of eggs consumed in each nymphal stage).

³ $Z_n = (Y_n)/\text{Days to develop on larvae food in each nymphal stage (table 3, column 3)}.$

was selected to calculate the point value or equivalent value of a larva to one egg consumed. The point value, X , is calculated for the formula

$$X = \frac{\left[\begin{array}{c} L_3 \\ E_3 \end{array} + \begin{array}{c} L_4 \\ E_4 \end{array} \right]}{2}$$

L_3, L_4 = the number of larvae consumed during the third and fourth nymphal stage of *P. bioculatus*, respectively.

E_3, E_4 = the number of eggs consumed during the third and fourth nymphal stage of *P. bioculatus*, respectively.

The reasons for selecting only the third and fourth nymphal stages are as follows: (1) The consumption rate of the first-instar nymphs was omitted because larvae of *L. decemlineata* are not attacked, (2) the consumption of the second-instar nymphs was not included because of the discrepancy of high larvae consumption when repeated observation indicated that the small size of the predator made it difficult to successfully attack large moving prey, (3) third and fourth nymphal stages were large enough to attack and consume the larvae, and (4) the large fifth instar was eliminated because their daily larval consumption rate was less than that of the smaller fourth instar.

Next, the calculated number of larvae consumed per nymphal stage is Y_n where

$$Y_n = (X)(E_n)$$

E_n = the consumption rate of each nymphal stage of *P. bioculatus* feeding on eggs of *L. decemlineata*.

The formula for the calculation of the daily consumption rate is

$$Z_n = Y_n / D_n$$

D_n = Developmental time of each nymphal stage of *P. bioculatus* preying on larvae of *L. decemlineata* (table 3).

ADULTS AND POPULATIONS

An age-specific life table was constructed for the predation of *P. bioculatus* (table 5). The first column is the age interval column (X), which begins at the mean age (30 days) of all females reaching adult eclosion. The experiment was terminated at 103 days because of the lack of food for the lone surviving female. The l_x column is the survival rate of the 25 females of the original 50 predators of mixed sexes, and, at 30 days, the 76-percent survival represents only the female survival rate.

The m_x column is the expected number of daughters produced by a female still alive at age x . As shown in table 5, the first eggs were laid on the 37th day, and the last egg was laid on the 96th

TABLE 5.—Age-specific life table of *Perillus bioculatus*

Pivotal days (x)	Survival rate (l_x)	Fecundity rate (m_x)	($l_x m_x$)	Number dying during age interval \times (d_x)	Mortality rate (1,000 q_x)	Mean expected life (e_x)
30	0.76	0	0	0	0	35.68
31	.76	0	0	0	0	34.68
32	.76	0	0	0	0	33.68
33	.76	0	0	0	0	32.68
34	.76	0	0	0	0	31.68
35	.76	0	0	0	0	30.68
36	.76	0	0	0	0	29.68
37	.76	1.75	1.33	0	0	28.68
38	.76	.58	.44	0	0	27.68
39	.76	1.61	1.22	0	0	26.68
40	.76	1.08	.82	0	0	25.68
41	.76	3.47	2.63	0	0	24.68
42	.76	.61	.46	0	0	23.68
43	.76	3.80	2.88	0	0	22.68
44	.76	2.56	1.94	0	0	21.68
45	.76	4.06	3.08	0	0	20.68
46	.76	3.31	2.51	0	0	19.68
47	.76	4.03	3.06	.04	52.63	18.68
48	.72	3.21	2.31	.04	55.55	18.69
49	.68	3.56	2.42	.04	58.82	18.76
50	.64	4.4	2.81	.04	62.50	18.90
51	.60	2.43	1.45	0	0	19.13
52	.60	1.17	.70	0	0	18.13
53	.60	3.87	2.32	.04	66.66	17.13
54	.56	3.14	1.75	.04	71.42	17.32
55	.52	1.27	.66	.04	76.92	17.61
56	.48	3.91	1.87	.12	250.00	18.04
57	.36	1.56	.56	.04	111.11	22.88
58	.32	3.50	1.12	0	0	24.68
59	.32	1.75	.56	0	0	23.68
60	.32	3.50	1.12	0	0	22.68
61	.32	1.00	.32	0	0	21.68
62	.32	0	0	0	0	20.68
63	.32	2.12	.67	0	0	19.68
64	.32	2.00	.64	.04	125.00	18.68
65	.28	1.07	.29	0	0	20.28
66	.28	1.21	.33	0	0	19.28
67	.28	.71	.19	0	0	18.28
68	.28	1.21	.33	0	0	17.28
69	.28	0	0	.04	142.85	16.28
70	.24	2.75	.66	0	0	17.91
71	.24	0	0	0	0	16.91
72	.24	.58	.13	0	0	15.91
73	.24	2.16	.51	0	0	14.91
74	.24	0	0	0	0	13.91
75	.24	1.50	.36	.08	333.33	12.91
76	.16	3.37	.53	0	0	18.12
77	.16	0	0	0	0	17.12
78	.16	0	0	0	0	16.12
79	.16	0	0	0	0	15.12
80	.16	0	0	0	0	14.12
81	.16	0	0	0	0	13.12
82	.16	0	0	.04	250.00	12.12
83	.12	0	0	0	0	15.00
84	.12	2.66	.31	0	0	14.00
85	.12	0	0	0	0	13.00

TABLE 5.—Age-specific life table of *Perillus bioculatus*—Continued

Pivotal days (<i>t</i>)	Survival rate (<i>l_x</i>)	Fecundity rate (<i>m_x</i>)	<i>l_xm_x</i>	Number dying during age interval <i>x</i> (<i>d_x</i>)	Mortality rate (1,000 <i>q_x</i>)	Mean expected life (<i>e_x</i>)
86	.12	0	0	0	0	12.00
87	.12	0	0	0	0	11.00
88	.12	0	0	0	0	10.00
89	.12	0	0	0	0	9.00
90	.12	0	0	0	0	8.00
91	.12	0	0	0	0	7.00
92	.12	0	0	0	0	6.00
93	.12	0	0	.04	333.33	5.00
94	.08	0	0	0	0	6.25
95	.08	0	0	0	0	5.25
96	.08	2.00	.16	0	0	4.25
97	.08	0	0	.04	500.00	3.25
98	.04	0	0	0	0	5.00
99	.04	0	0	0	0	4.00
100	.04	0	0	0	0	3.00
101	.04	0	0	0	0	2.00
102	.04	0	0	0	0	1.00
103	.04	0	0	0	0	0

day. The preoviposition period was 7 days, and the oviposition period was 60 days. The sum of the *m_x* column is the gross reproductive rate, or the total number of births produced by the female in her lifetime.

The *l_xm_x* column is the product of the number of surviving at each age interval multiplied by the number of expected daughters. The sum of the *l_xm_x* column is *R₀*, defined as the net replacement rate, which is the number of daughters produced by the average female in a generation. Of course, a stable population will have an *R₀* = 1.

The *d_x* column represents the number dying at age interval *x* and the *q_x* column represents the mortality for age *x*. The *e_x* column is the number of days remaining that the predators are expected to live at age *x*. For example, table 5 reads as follows: At the pivotal age of 53 days, 60 percent of the original female population is alive and 3.87 daughters were laid by the female. The replacement rate for the 53d day was 2.32 daughters; 0.4 female died in the interval, and the mortality rate times 1,000 was 66.66. The female predators that are alive at the end of 53 days are expected to live 17.13 more days.

A graphic representation of the survival rate curve (*l_x*) and the fecundity curve (*m_x*) is shown in figure 1. There are two periods of steep rate of mortality. The first heavy mortality takes place during the first and second stages, and the other mortality period takes place 17 to 28 days into adulthood. Visual estimates of the area under the *m_x* curve indicate that most ovipositions took place during the 13 to 20 days into adulthood.

The intrinsic rate of increase (*r_m*) is probably the most important parameter of the population obtained from the construction of a life table. The approximate *r_m* was calculated from the following formulas presented in Birch (1). First the approximate generation time (*T*) is defined as follows:

$$T = \frac{\sum x l_x m_x}{\sum l_x m_x}$$

Then *r_m* can be approximated from the formula as follows:

$$r_m = \frac{\log_e R_0}{T}$$

With the approximate *r* value, a computer program starting with two provisional *r* values greater and less than the approximated *r* value was entered into the formula as follows:

$$\sum e^{7-rx} l_x m_x = 1,097$$

Using the iterative process, the different provisional *r*'s were entered until the *r* value converged to the sum of 1,097. At that point, the accurate *r_m* was established at 0.080.

The population growth statistics of *P. bioculatus* are given in table 6. The intrinsic rate of increase is considered a characteristic of the species and is affected by changes in the environment. Therefore, the *r_m* of 0.080 is the innate or intrinsic rate of increase of *P. bioculatus* at 22° C (± 1.5°) under near optimal conditions of food, space, and density. For example, excess food was given daily to predators caged singly in a 0.47-liter cage. The finite rate of increase is the antilog of *r_m*, or *e_{r_m}*, or for every one individual in day 1 there will be 1.083 individuals in day 2. The doubling time of 8.7 days is the number of days required for the population to double itself. The *T* value in table 6 is the more accurate estimation of generation time and represents the mean period of time elapsing between the birth of parents and the birth of the offspring.

PEST—LEPTINOTARSA DECEMLINEATA

Materials and Methods

In 1976, an experiment was designed to meas-

ure the amount of leaf area consumed by the different life stages of the Colorado potato beetle. The photoperiod was 16:8 hours per day and the

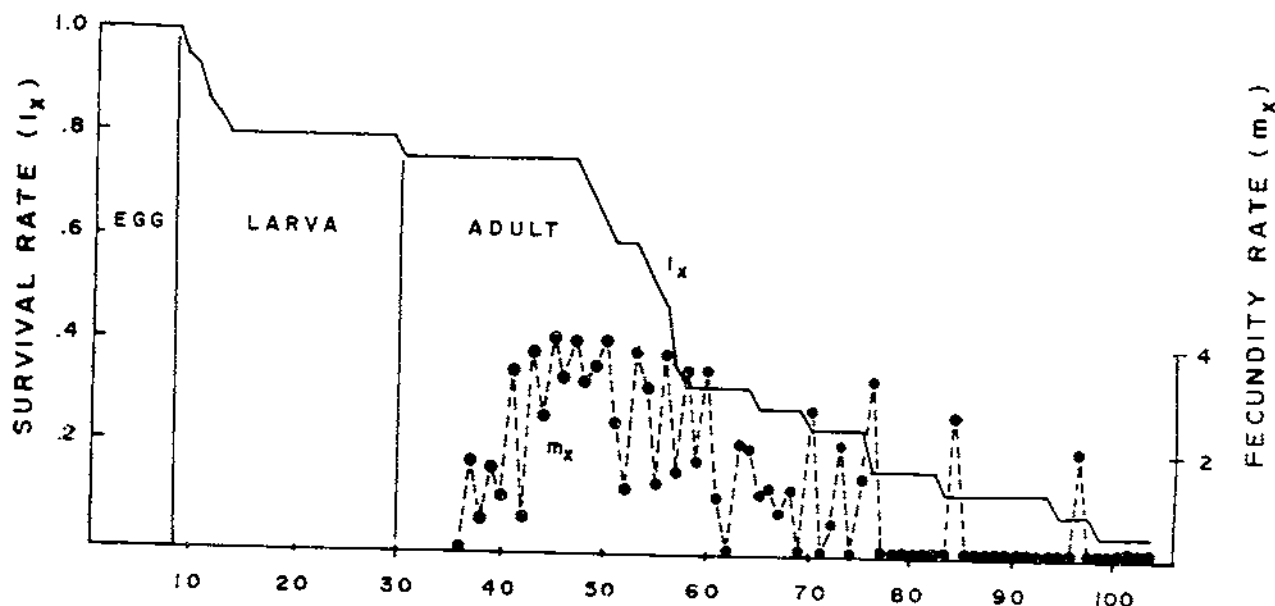


FIGURE 1.—Survival and age-specific fecundity of *Perillus bioculatus* reared on eggs and larvae of *Leptinotarsa decemlineata*.

TABLE 6.—Population growth statistics of *Perillus bioculatus*

Item	Source	Value
Gross reproduction rate (GRR)	(m_x)	88.47
Net reproduction rate (R_0)	$(l_x m_x)$	45.61
Intrinsic rate r_m	Graph	0.080
Finite rate of increase (λ)	Antilog r_m	1.083
Generation time in days	$T = \log_e R_0 / r_m$	47.75
Doubling time	$DT = \log_e 2 / r_m$	8.66

temperature range was $24^\circ \pm 7^\circ$ C. Initially, one newly hatched larva was placed individually in a 0.47-liter ice-cream carton that had a rubber sheath with a hole the right size to hold the neck of the leaf bouquet bottle as shown in Tamaki and Butt (22).

The cages were checked daily for survivors, stage of growth, and maintenance. The leaves of the potato plants were measured daily to determine the amount of area consumed. During the first larval stage, the leaves were changed every other day, but in later nymphal stages the leaves were changed daily. Although optical planimeter and portable area meter were available, the amount consumed was best measured by manual measurement. An optical planimeter (16) is not designed to measure small areas of a few square millimeters. The portable area meter and the op-

tical planimeter require a tare measurement of leaf area taken before the leaf is fed upon; however, there is a substantial leaf area shrinkage of leaves held in a leaf bouquet that interferes with an accurate estimate of the amount of leaf area consumed. The size of the feeding area was often irregular, but different size patterns on millimeter grid paper were used to approximate the consumed area.

Another study was designed to estimate the amount of potato leaves consumed by adults of *L. decemlineata*. On June 23, 1976, 100 last-instar larvae of the Colorado potato beetles were collected in the field and placed in a pan 17 cm deep by 40 cm wide filled to a depth of 10 cm with soil. Potato foliage was added daily until all the larvae entered the soil to pupate. When the 38 adults emerged, they were placed singly into 0.47-liter cages with a leaf bouquet. Leaves were changed daily, and the amount of leaf eaten was measured with millimeter grid paper.

Field census of the different life stages of *L. decemlineata* was taken by randomly selecting potato plants and inspecting every leaf of the plant. At 2-week intervals from June 7 to July 14, 50 to 100 plants were inspected in a potato field 30 by 90 m. In a portion of the same field, two portable Saran cloth field cages, 3.6 by 4.8 by 2.1 m high, (3) were placed in the field in late May to protect some potato plants from beetle defoliation. On August 3, when the uncaged plants were almost totally defoliated, the cages were removed to expose the protected plants to the beetle and to extend the time to study the field population of beetles.

Results and Discussion

The developmental periods for the first three larval stadia were very similar with no more than 0.37 day separating the stages (table 7). The last larval stadium was substantially longer by about three-fourths to more than a full day longer than the earlier stages. The first instar consumed less than 2 percent; the second, 6 percent; the third, 19 percent; and the fourth, 73 percent of the total leaf area consumed by the larval stages. Based on the consumption rate of the leaf area consumed per day, the fourth larval stages consumed two-thirds more food than all other larval stages combined.

In the adult consumption studied, the 38 newly emerged adults of *L. decemlineata* were followed for the first 10 days (table 8). The greatest consumption of leaves occurred during the 2 to 6 days after emergence. After 7 days, the feeding rate substantially declined. The average rate for a 10-day period was 687 mm² of leaf area per day.

TABLE 7.—*Developmental and consumption rates of the Leptinotarsa decemlineata reared on potato leaves at 24° ± 7°C*

Instar	Number	Average days to develop ± S.E.	Average leaf area consumed—	
			Per instar	Per day per instar
			Square millimeters	
1	70	2.89 ± .05	65	23
2	65	2.52 ± .09	161	64
3	63	2.84 ± .08	517	182
4	62	3.66 ± .11	1,967	538

TABLE 8.—*Consumption rate of adults of Leptinotarsa decemlineata during the first 10 days after emergence based on 38 insects*

Days after emergence	Average amount of foliage consumed per adult (± S.E.)
	Square millimeters
1	624 ± 43
2	949 ± 44
3	1,228 ± 66
4	959 ± 45
5	895 ± 50
6	989 ± 59
7	594 ± 53
8	339 ± 36
9	164 ± 23
10	130 ± 21

Our first field inspection on June 7 showed that the overwintering adults of *L. decemlineata* had begun ovipositing, and some eggs had already hatched as indicated by the presence of the first-instar nymphs (table 9). By June 21, all life stages of the *L. decemlineata* were found on the potato plants. The population of beetles rapidly declined because they had completely defoliated the potato plants by August 3. The counts made on potato plants previously protected by large portable field cages indicated the beetles quickly moved onto the potato plants as shown in counts on August 3 and 16 (table 9).

The estimated consumption rate of the field population of *L. decemlineata* as shown in table 10

TABLE 9.—*Field populations of Leptinotarsa decemlineata on potatoes at different sampling dates*

Date	Number of plants	Egg	Larvae				Adult
			1	2	3	4	
June 7	100	58.6	1.6	0	0	0	0.9
16	100	88.9	1.8	.8	.5	0	1.4
21	50	98.4	20.4	5.4	2.8	2.7	.5
28	50	87.2	7.3	8.1	5.1	9.0	.6
July 8	50	37.3	2.5	5.3	6.1	15.5	.7
14	50	9.4	.2	1.2	3.6	9.4	12.0
Aug. 3	50	(¹)	(¹)	(¹)	(¹)	(¹)	4.5
3 ²	10	54.6	0	0	0	0	13.5
16 ²	50	45.8	16.8	20.4	23.9	30.0	1.3

¹ Plants defoliated.

² Potato plants in same field plot protected by two 3.6 by 4.8 by 2.1 m cages covered by Saran cloth until last week of July.

TABLE 10.—*The consumption potential of field populations of Leptinotarsa decemlineata on potato leaves based on feeding capacities of each life stage developed in laboratory studies*

Date	Amount of leaf area consumed for each of the following stages				
	Larvae				
	1	2	3	4	Adult
	Square millimeters				
June 7	36	0	0	0	618
16	41	51	91	0	962
21	463	345	510	1,453	344
28	166	517	929	4,842	412
July 8	57	338	1,111	3,339	481
14	5	77	656	5,057	8,244

was calculated by using the consumption rate based on laboratory studies in tables 7 and 8. On June 7, the only immature stage was the small, first instar, which consumed an estimated 6 percent of the total food consumed; the overwintering adults consumed the rest of the food. From June 21 to July 28, the immature stages consumed over 89 percent of the foliage. The highest larval consumption took place on July 8 when most of the immature stages were in the late third and fourth larval stages. On July 14, the heaviest defoliation

took place, 59 percent of which was attributed to the adult stage.

The estimated number of days required to defoliate a plant of average size measured from field samples on June 16, July 1, July 14, and August 2 was based on the unchanging age distribution of populations of *L. decemlineata* sampled biweekly as shown in table 11. For example, it would take 11 days to defoliate an average size potato plant of 154,900 mm² measured on June 16 (table 11) by the population size of *L. decemlineata* sampled on June 14.

TABLE 11.—Estimated number of days required for the field population of *Leptinotarsa decemlineata* to completely defoliate different size potatoes as measured in the field at biweekly intervals

Date sampled	Size of plants Cm ² ± S.E.	Number of days to completely defoliate based on population of <i>L. decemlineata</i>					
		June 7	June 16	June 21	June 28	July 8	July 14
June 16	1,549 ± 142	236	135	49	22	15	11
July 1	3,208 ± 310	490	280	103	46	31	22
July 14	3,793 ± 256	579	331	121	55	36	27
Aug. 2	6,265 ± 402	957	547	201	91	60	44

PLANT—*SOLANUM TUBEROSUM*

Materials and Methods

At 2-week intervals starting from June 16, 10 to 20 potato plants were removed from our field plots. To insure that each plant represented a hill started from one seed piece, all the roots were exposed and shoots from a common seed piece were considered a single plant. The leaf area of each plant was measured by placing the leaves between two glass plates to flatten the leaves, and the leaf area was measured by a photoplanimeter. Plants were measured from June 16 to August 2, 1976. Measurements were not continued after

August 2 because even the insecticide-protected plants soon were damaged by the large beetle population moving off the untreated defoliated potato plants.

Results and Discussion

The average foliage area of potato plants taken from the field is given in table 11. From June 16 to August 2, the foliage area size increased four-fold. These biweekly foliage measurements will be used to determine the impact of *L. decemlineata* feeding on the total plant.

PREDATOR-PREY-PLANT-YIELD INTERACTION

Predator-Prey

An attempt can now be made to integrate the available information of the ecology, biology, and the feeding rates of the predator *P. bioculatus* on the pest *L. decemlineata* to predict the amount of predators required to reduce a known number of pests. For example, the numbers of individuals of different life stages of *L. decemlineata*, based on field samples taken on June 21, are given in table 12. Also included is the laboratory consumption

rate of *P. bioculatus* on different life stages of *L. decemlineata*. Table 12 shows the estimated number of fifth-instar larvae of predators required to reduce the pest population to zero. For instance, to reduce 98.4 eggs in one day would require 2.52 predators per plant, and to reduce the total pest population to zero would require 10.56 predators per plant. Such a high predator population of 10 predators per plant has not been observed. High populations of predators would probably be less than 0.5 predators per plant.

TABLE 12.—The estimated number of 5th-instar nymphs of *Perillus bioculatus* necessary to reduce a given number of *Leptinotarsa decemlineata* in each stage to zero in 1, 3, and 7 days

Stage	Field census of <i>L. decemlineata</i> taken on June 21		Fifth-instar nymphs required to reduce pest to zero in—		
	Number	Consumption rate of <i>P. bioculatus</i>	1 day	3 days	7 days
Eggs	98.4	39.1	2.52	0.84	0.36
1st	20.4	15.85	1.29	.43	.18
2d	5.4	5.28	1.02	.34	.15
3d	2.8	1.86	1.51	.50	.22
4th	2.7	.63	4.22	1.41	.60
Total	---	---	10.56	3.52	1.51

Thus, to reduce the pest population to zero in 7 days would require a population of 1.51 per plant, which is still much higher than populations of predators found in potato fields; however, 100-percent mortality of *L. decemlineata* is unnecessary to avoid economic damage.

Predator-Prey-Foliage

In addition to *P. bioculatus* causing direct mortality to *L. decemlineata*, the impact of the predators on the prevention of defoliation was determined by calculating the presence and absence of the predator on the defoliation potential of *L. decemlineata*. For instance, in table 13, the field population of *L. decemlineata* on June 16 defoliated 5,725 mm² in absence of predation; whereas, the addition of 0.5 predators per plant reduced the defoliation by 3,160 mm² or 45 per-

cent reduction in leaf area consumption. High consumption rates by large populations of *L. decemlineata* without predators on June 28 and July 14 were evident in table 13. The addition of 0.5, 1.0, or 2.0 predators per plant to the system did not reduce the consumption of these beetles as it did the smaller *L. decemlineata* population of June 16.

Predator-Prey-Plant

Up to now, no attempt has been made to correlate the amount of defoliation based on total plant size. Table 14 shows the percentage of defoliation estimated in the absence and presence of different numbers of predators per plant based on the field population of *L. decemlineata* on June 16, June 28, and July 14. Thus, the larger the population of *L. decemlineata*, the greater is the amount of defoliation, and the addition of the same number of predators per plant will have less of an impact on reducing defoliation of larger populations of *L. decemlineata* than will smaller ones.

Predator-Prey-Yield

The impact of artificially defoliating potato plants to estimate hail damage was conducted in the neighboring State of Idaho (21, 19). Figure 2 is a graphic representation of this study by Sparks and Woodbury (18). Their data are correlated with the height of plants, but in their earliest publication (Takatori et al., 21), they gave the corresponding dates of 15.2 cm height on June 23 to 26, 30.6 cm height on July 14 to 16, and plants near maturity on July 26 to August 7, which allowed us to relate the dates of our sampling periods.

Loss in yield on U.S. No. 1 potatoes can be estimated by using figure 2 and the percentage of defoliation given in table 14. For example, on July 14 (estimated 12-inch growth stage), 18.5-percent defoliation, as shown in table 14, is esti-

TABLE 13.—The estimated amount of leaf area consumed and the percent reduction of foliage by *Leptinotarsa decemlineata* in absence and presence of different number of predators

Number of 5th-instar <i>Perillus</i> per plant	Leaf area consumed in 5 days by pest population			Reduction in leaf area consumed		
	June 16	June 28	July 14	June 16	June 28	July 14
	---Square millimeters---			-----Percent-----		
0	5,725	34,325	70,190	--	--	--
.5	3,160	31,760	67,625	45	7.5	3.7
1.0	610	20,210	65,075	90	15.0	7.4
2.0	--	24,095	59,960	--	30.0	15.0

TABLE 14.—The percentage of leaf area defoliated in 5 days in the absence and presence of predators from plants on 3 different dates

Number of 5th-instar <i>Perillus</i> per plant	Leaf area defoliated		
	June 16	June 28	July 14
	-----Percent-----		
0.0	3.7	10.7	18.5
.5	2.04	9.9	17.8
1.0	.39	9.1	17.2
2.0	--	7.5	15.8

ated to cause 9-percent loss in yield (fig. 2). By adding two fifth-instar larvae of the predators per plant, the calculated defoliation is reduced to 15.8 percent and the loss of yield is reduced to 8 per-

cent. Thus, little loss is prevented by the addition of two predators into the system having a large initial population of Colorado potato beetles.

P. bioculatus can apparently decrease the rate of defoliation when populations of *L. decemlineata* are small, but as the population of *L. decemlineata* increases, the effectiveness of the predator to decrease the rate of defoliation is diminished. Thus, in central Washington, we determined that *P. bioculatus* is ineffective in preventing the depletion of the food supply and subsequent starvation of *L. decemlineata*. This agrees with the findings of Harcourt (8) and Harcourt and LeRoux (9) in Canada.

As stated earlier, the major purpose of this study was to demonstrate experimental procedures that expand the research in biological control from the impact on the pest to its ability to sufficiently reduce foliage loss and plant damage and deter losses in yield. The interaction of *P. bioculatus*, *L. decemlineata*, and plant yield serves as an example of such a model.

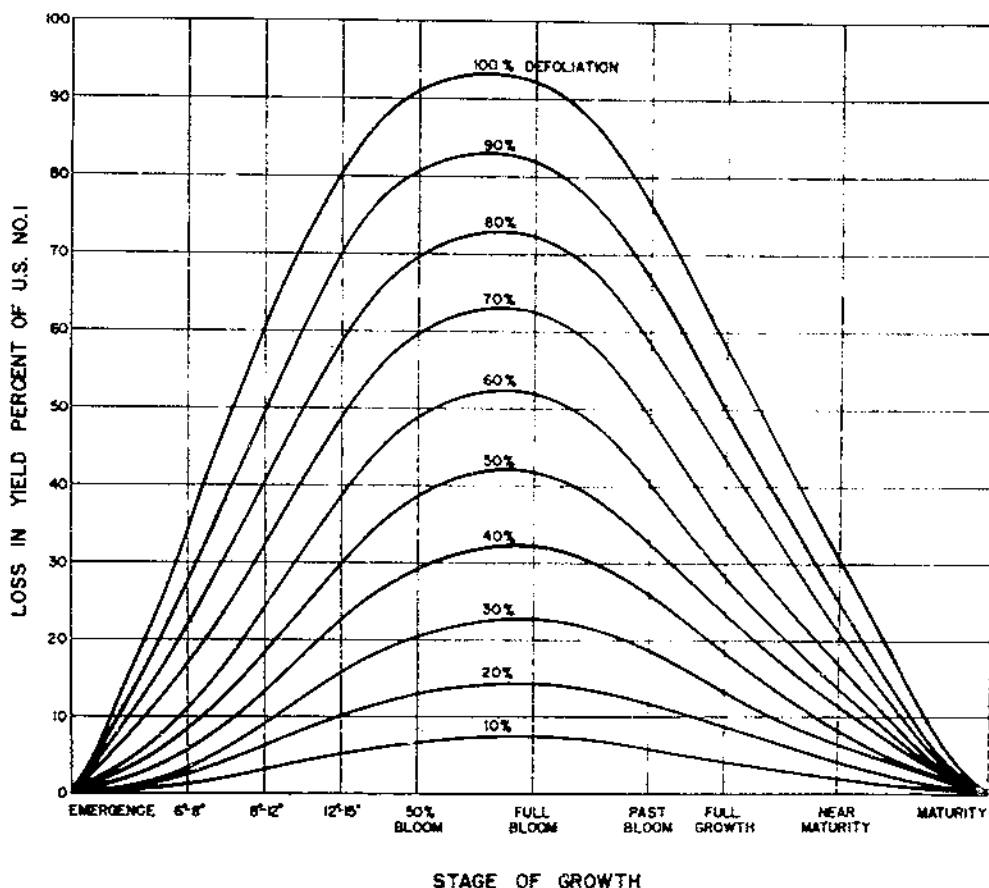


FIGURE 2.—A method of estimating yield loss when percentage of defoliation and stage of growth are known (18).

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