Life Tables and Larval Dispersal of Mexican Bean Beetle (Coleoptera: Coccinellidae) on Dry Bean in the High Plains

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ABSTRACT Survivorship of experimental cohorts of Mexican bean beetle, *Epilachna varivestis* Mulsant, was studied in three commercial dry bean (*Phaseolus vulgaris* L.) fields in 1995 and 1996 near Scottsbluff, NE. Mexican bean beetle survival was relatively low in 1995 but higher in 1996. In 1995, ~50% of the egg masses did not hatch. The high egg mortality observed was likely related to drought stress of the host plants, because stressed plants turn their leaves over and expose eggs to sunlight. In 1996, environmental conditions were mild compared with 1995, and egg hatch was greater. Mortality of young larvae was lower than it was in the last two larval stages. The cumulative mortality ranged from 92.1 to 95.8% in 1995 and from 60.9 to 75.6% in 1996. No parasitized or diseased larvae were observed in the study fields or in those held for parasitism tests. Larvae from the same cohort (egg mass) were found distributed throughout a maximum range of 3.6 row-meter.

KEY WORDS Epilachna varivestis, life tables, survivorship, dry bean

THE MEXICAN BEAN beetle, Epilachna varivestis Mulsant, injures dry beans (Phaseolus vulgaris L.) in several production areas of the United States. In Nebraska, as in other western states, the insect can be a serious problem and recent outbreaks occurred in 1994 and 1995. Mexican bean beetles overwinter as adults in and around bean fields (Hagen 1986). Emergence of the overwintering beetles depends on the weather. Adult beetles emerge late in the spring after prolonged warm temperatures. Precipitation has a direct influence on beetle emergence, and the percentage emerging is directly influenced by the temperature during the period of rainfall (Douglass 1928), whereas dry weather delays emergence from hibernation sites (Howard 1931). Winters with high snowfall contribute to increased overwintering adult survival (Douglass 1933). Also, beetle population dynamics are highly dependent on availability of beans (*Phaseolus* spp.) or soybean (*Glycine max* (L.) Merrill) (Stinner et al. 1982). Mexican bean beetles generally have two generations on soybeans although a third generation has been frequently observed in some locations (Stevens et al. 1975).

Only one full generation and a partial second generation occurs in western Nebraska (Hagen 1986). Mexican bean beetle larval populations generally reach their peak during late July to early August, coinciding with bean flowering and pod filling, the most susceptible stages to defoliation injury (Schaafsma and Ablett 1994). Although the biology and ecology of the Mexican bean beetle and the factors affecting its population dynamics have not been studied in the western high plains, there are many studies of beetle biology from other regions of the United States on soybean. Abiotic factors, such as drought, have long been recognized as important factors affecting Mexican bean beetle population dynamics and pest status (Marcovitch and Stanley 1930, Miller 1930, Howard 1931) and play an important role in geographic distribution (Sweetman 1932). Recent studies have established the sensitivity of Mexican bean beetle eggs and larvae to humidity and temperature (Kitayama et al. 1979). However, the precise causes of outbreaks may also be related to other abiotic and biotic factors that potentially affect beetle survival.

The list of natural enemies of the Mexican bean beetle is considerable, but early workers found little influence on Mexican bean beetle population dynamics (Howard and English 1924, Howard and Landis 1936). Despite some positive results using the parasite *Pediobius foveolatus* (Crawford) (Angalet al. 1968), the parasites could not survive the winter in the field, and maintenance in laboratory was required during the winter (Stevens et al. 1975). *P. foveolatus* has been used in an ongoing biological control program for Mexican bean beetle in some soybean growing regions of the eastern United States (Edwards et al. 1994). Various potential predators of Mexican bean beetle also have been recognized in soybean (Howard and English 1924, Barry 1973, Shepard et al. 1974).

Because we have only limited information available on factors influencing Mexican bean beetle survivorship on dry bean, development of pest management programs for the insect also has been limited. Identifying key natural enemies and vulnerable life stages of Mexican bean beetle are essential for possible biolog-

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ical control efforts and for developing practical management programs. Also, characterizing stage-specific survivorship can be important for reflecting the impact of natural enemies in economic thresholds (Pedigo 1997). Life table analysis of Mexican bean beetle would provide the necessary information to meet all these needs.

Currently, economic thresholds for the Mexican bean beetle on dry bean are calculated based on the percentage of defoliation injury (Schaafsma and Ablett 1994) or on number of larvae per plant (Michels and Burkhardt 1981). However, integrated pest management adoption in dry bean is limited by the lack of an adequate sampling procedure. Estimation of defoliation in the field is difficult and often inaccurate, especially when the plant canopy becomes continuous (Bellinger et al. 1981). Also sampling for Mexican bean beetle larvae is costly and time consuming. For example, to sample a one m section of soybean row at R3 and R6 stages and counting all Mexican bean beetle instars, requires an average of 8 min to complete each sample (Turnipseed and Shepard 1980).

An alternative to avoid these sampling problems is to establish economic thresholds based on numbers of eggs, rather than larval numbers or levels of defoliation. Because eggs are not the injurious stage, the prediction of injury can be highly affected by environmental and biological factors. In using egg numbers for decision making regarding late-stage larvae, which produce the most injury, adjustments should be made to account for natural mortality to avoid grossly overestimating potential injury. Also, it is important to determine larval dispersal patterns, so that these can be incorporated in sampling programs as appropriate.

Consequently, we report here results of 2 yr of life table studies on Mexican bean beetle in western Nebraska. Additionally, we describe larval dispersal patterns. These data provide important information on the basic biology of Mexican bean beetle and offer a foundation for work on Mexican bean beetle biological control and pest management programs for this insect.

Materials and Methods

Field studies were conducted during 1995 and 1996 in Scottsbluff, Scottsbluff County, NE. Three locations per year were selected from commercial bean fields grown in annual rotation with corn and sugarbeets. Different fields were used in each year. In both years, fields were planted the first week of June, with 0.76 row-meter spacing. Conventional tillage and preplant incorporated herbicides were used. No insecticides or fungicides were applied in the experimental area. Postemergence weeds were eliminated by cultivation. All fields were furrow irrigated, except one in 1996 (variety 'Tara'), which was irrigated with overhead irrigation. Because water was applied in alternate rows, inspections could be made even when plants were being irrigated by walking in the row that was not receiving water.

The study was initiated each year at the flowering stage to correspond with natural timing of infestation. In 1995, 15 plants, naturally infested with a single egg mass, were randomly selected and tagged. All other naturally occurring egg masses were removed by hand from sample plants and from plants on 3 m on either side of the sample plant. Naturally occurring egg masses were also removed from adjacent plants (6 row-meter) of both border rows. In 1996, infestations were made by confining five gravid females on a caged field plant giving them 3-4 d to oviposit. When at least one egg mass had been deposited, both cage and beetles were removed. The plant containing the chosen egg mass was marked with a flag, and the leaf with attached egg mass was tagged. All other egg masses on the same plant and on all other plants within 3 rowmeter were eliminated. Because beetle populations were high in 1995, inspections for additional natural infestations were made twice a week during the first 2 wk of the study and on a weekly basis thereafter. The varieties used were Tara (2 fields in 1995 and one field in 1996) and 'Marquis' (one field in 1995 and two fields in 1996).

After infestation, plants were inspected daily to determine if eggs hatched. If eggs hatched, the larval census was begun. After hatching, larvae remained clumped, attached to each other on the eggshells for \approx 6–8 h before starting to feed and disperse. At that time it was difficult to determine their precise numbers without disturbing them. We believed that attempting to count larvae at that time would disturb larvae and induce unnatural mortality. Instead, when larvae were found clumped on an egg mass that had not hatched completely, we waited until larvae started to move from the eggshells and to spread on the leaflet to make the first count. With this procedure, we accounted for the fate of every egg, either as unhatched or as a first stage larva. Subsequently, we followed the fate of each individual larva that hatched from each egg. Inspections began on 13 July in 1995 and on 15 July in 1996. During the first 2 wk, larval counts were made every other day. After 2 wk, larval counts were made every 3-4 d. Any larvae that dropped to the ground when disturbed were collected and returned to the leaves. As the bean canopy size increased, more time was required to inspect plots. An average of eight to 12 h was usually spent to evaluate one field when larvae had already dispersed in the bean canopy. Therefore, inspections were not possible at shorter time intervals.

During sampling, all stems and leaflets of each plant in the three row-meter around an egg mass were inspected for larvae. Also, the presence of predators was recorded. The number of surviving larvae was recorded for all four larval stages on all infested plants. Causes of larval mortality, when identified, were recorded, and any dead or missing larvae were noted.

Because Mexican bean beetle eggs are large enough to be counted in the field without help of a magnifier, the initial population (lx) could be established based on the observations in situ. Individuals originated from the same egg cohort were followed throughout their



Fig. 1. Mexican bean beetle larval dispersal from the same egg cohort along (forward and backward) the bean row, Scottsbluff, NE, 1995.

complete life cycle. For our experimental approach to be sound, we had to use great care to identify each individual in a cohort and to provide an adequate indication of cause of death. The relatively low percentage of missing individuals points to the precision of the monitoring procedure. Fortunately, egg masses and cadavers remained on plants for many days; therefore, our estimates were not confounded by many missing individuals. In assigning cause of death, we used objective criteria where possible. In particular, deaths assigned to desiccation were based on visual recognition of a desiccated cadaver-a larva without signs of parasitism, predation, or disease, which appeared identical to larvae that had died from desiccation in the greenhouse (where we knew the cause of death with certainty). In many instances, we observed desiccated first instars only partially emerged from eggs. We looked for evidence of predation, parasitism, and disease in cadavers but found few or no examples of these during our study. We also conducted visual surveys for predators during sampling, to provide an estimate of potential predators in the study sites.

Beyond looking for evidence with cadavers, parasitization also was evaluated from eggs, fourth instars, and pupae collected in adjacent areas of each study field. The egg masses or larvae were isolated in plastic cups (30-ml capacity) until larvae hatched from eggs or adults emerged from pupae. One hundred egg masses, 100 fourth instars, and 100 pupae were collected from each field in each year (600 egg masses, 600 larvae, and 600 pupae in total) to evaluate parasitization.

When all Mexican bean beetle larvae had pupated, pupae were "marked" using a red strip of plastic stapled in the plant part where the pupa was fixed. This was used to determine adult emergence and the distance larvae moved from where the egg mass was laid. Marking the pupa was possible because all pupation occurred underneath the lower leaves and on stems. Plants were inspected for adults 1 wk after pupation.



Fig. 2. Mexican bean beetle larval dispersal from the same egg cohort along (forward and backward) the bean row, Scottsbluff, NE, 1996.

x (stage)	lx (no. at beginning of each stage)	dxF (factor of mortality)	dx (no. dying during each x)	100qx (dx as % of lx)	100rx (cumulative in relation to initial lx)
Eggs/egg mass Larva	54.74 ± 1.24	Never hatched	33.87 ± 5.91	61.87	61.87
1st instar	20.87 ± 5.61	Desiccation	13.54 ± 4.92	64.88	86.61
		Unknown	1.53 ± 0.68	7.33	89.40
			15.07	72.21	
2nd instar	5.8 ± 2.81	Desiccation	0.93 ± 0.6	16.03	91.1
			0.93	16.03	
3rd instar	4.87 ± 2.37	Unknown	0.40 ± 0.33	8.21	91.83
			0.40	8.21	
4th instar	4.47 ± 2.27	_	0.00	0.00	91.83
Pupa	4.47 ± 2.27	Desiccation	0.13 ± 0.13	2.91	92.07
			0.13	2.91	
Adult	4.34 ± 2.22	—	—	—	92.07

Table 1. Life table for Mexican bean beetle (*E. varivestis* Mulsant) on dry beans (*P. vulgaris* L.) Marquis, at Scottsbluff, NE (26 July to 4 September 1995), based on averages from 15 cohorts (egg masses)

Adult emergence was determined by inspecting pupae on the marked plant.

Observations of larval dispersal in the row of beans were made at each study site when inspecting the mortality factors throughout the larval life cycle. Distance and direction of the larval movement from the initial egg mass, were recorded at pupation. Starting from the plant where the egg mass was laid, flags were set in the row at a 0.3-m interval. Numbers of larvae in each interval were recorded. Data were used to construct histograms to show how far larvae from the same egg cohort were distributed in the bean row.

Meteorological data were collected from an official Automated Weather Data Network Station located in Scottsbluff. Data were condensed into life tables following method described by Harcourt (1969), with the last column representing the cumulative mortality of successive developmental stages, in percent (100rx) instead of the survival rate within x (Sx).

Results and Discussion

Larval Dispersal. In the first 2 d after hatching, larvae fed on the same leaf where they hatched and only later spread into the canopy. Although some larvae were found feeding nearby on the same plant or even on the same branch of the plant, there was no evidence for aggregation. Larvae from the same egg cohort were found distributed throughout a maximum range of 3.6 row-meter (i.e., 1.8 m in either direction from the egg mass). In 1995, 40, 35, and 14% of the larvae pupated in a 0.6 m range from the point where the egg mass was laid, respectively, in fields 1, 2, and 3 (Fig. 1). Larvae were more clumped in 1996, when 69, 37, and 50% of the larvae pupated in a 0.6-m range from the point where the egg mass was laid, respectively, in fields 1, 2, and 3 (Fig. 2).

In 1995, larvae were more dispersed in the row probably because plants were more water stressed and larvae may have been forced to move to cooler locations. In 1996, plants were less stressed, and larvae remained near where eggs hatched. The differences in larval dispersal between the two years may reflect differences in environmental conditions between 1995 and 1996. However, the important observation for developing sampling programs is that in both years larvae did not disperse widely and were relatively close to the oviposition site throughout larval development and pupation.

Mexican Bean Beetle Life Tables and Survivorship. Survivorship data are summarized in six life tables (Tables 1-6). In 1995, the greatest mortality occurred during the egg stage (Tables 1–3), with mortality ranging from 62 to 82%. The high mortality observed is likely related to high temperatures associated with significant drought stress on the plants. Fig. 3 summarizes the temperatures (minims and maxims) and the relative humidity observed during the experiments. During the hottest part of the day, leaves turned over exposing the egg masses and young larvae to the sun. This also increased the potential for a higher temperature and lower humidity, factors responsible for egg mortality. Howard (1931) suggested that low relative humidity reduced egg survival in the field. A high reduction in egg survival when average daily maximum temperatures exceeded 38°C in the field was observed by Sprenkel and Rabb (1981). Under laboratory conditions, Mellors and Allegro (1984) observed that egg development was greatly affected by high temperatures even when relative humidity was high. Sprenkel and Rabb (1981) found that at 38°C and 74% RH, percentage of egg hatch was only 4.8%. In 1996, however, the stress at which bean plants were submitted was mild compared with 1995, allowing greater egg hatch (Tables 4-6) with mortality in the egg stage of only 7.8 and 8.9%.

Environmental conditions had a similarly important influence on mortality of young larvae. In 1995, the observed mortality from dessication in the first larval stage, ranged from 49.8 to 66.3% within the stage. In 1996, the first-instar mortality was less though still substantial at 40.7 and 45.2% within the stage. These estimates are from direct counts of desiccated cadavers. It is likely some of the deaths in the missing

x (stage)	lx (no. at beginning of each stage)	dxF (factor of mortality)	dx (no. dying during each x)	100qx (dx as % of lx)	100rx (cumulative in relation to initial lx)
Eggs/egg mass Larva	55.25 ± 1.77	Never hatched	45.25 ± 3.41	81.90	81.90
1st instar	10.00 ± 3.52	Desiccation	6.63 ± 2.74	66.30	93.90
		Unknown	0.56 ± 0.33	5.60	94.91
			7.19	71.9	
2nd instar	2.81 ± 1.36	Desiccation	0.31 ± 0.31	11.03	95.48
			0.31	11.03	
3rd instar	2.50 ± 1.220	Unknown	0.06 ± 0.06	2.40	95.58
			0.06	2.40	
4th instar	2.44 ± 1.22	Unknown	0.01 ± 0.01	0.53	95.61
			0.01	0.53	
Pupa	2.43 ± 1.21	_	0.00	0.00	95.61
Adult	2.43 ± 1.21	_	_	_	95.61

Table 2. Life table for Mexican bean beetle (*E. varivestis* Mulsant) on dry beans (*P. vulgaris* L.) Tara, field 1, at Scottsbluff, NE (13 July to 23 August 1995), based on averages from 16 cohorts (egg masses)

category may also be from desiccation. Water stress of host plants immediately after egg hatching, likely accounted for the mortality in first and second larval stages. Mortality in the second instar was reduced compared with that of first instars, but still greater than that in later stages. The greater mobility of larvae at third and fourth stages allows them to move to a cooler place in the canopy, which reduces the chances of desiccation. In Scottsbluff, as in much of the High Plains, bean fields suffer drought stress because of delays in irrigation. The problem is aggravated in some years when early season soil moisture is low because irrigation water usually is not provided to farmers until early July, which coincides with the Mexican bean beetle oviposition peak.

Mortality levels decreased as larval stage increased. Compared with all other larval stages, young larvae had higher mortality, independently of the year. The observed mortality in the third and fourth stages was very low. In 1995, the contribution of these two stages to the total mortality ranged from 0.7 to 1.8% in 1995 (Tables 1–3) and 1.8–8.9 in 1996 (Tables 4–6). The

mortality observed in the pupal stage was insignificant. Larvae usually pupate beneath leaves and on stems located at the lower part of bean plants, so they are less likely to be exposed to direct sunlight reducing the chance of desiccation and the effect of high temperatures. Miller (1930) studied the influence of temperature, relative humidity, and sunlight on Mexican bean beetle fourth-stage larvae and pupae. Single exposures of adults, larvae, and pupae to 37.5°C for 3 h did not affect survival of individuals at any stage, independent of the relative humidity imposed (0, 30.72, 56.18, 73.14, and 100%). However, for a one degree rise in temperature, there was a marked increase in death below 60% and above 80% RH. For temperatures of 39.5, 40.0, and 41.5°C, results were very similar with a lower percent of survival for each increase of one degree of temperature. For a temperature of 42.5°C there was an almost complete kill at all relative humidities tested. Across all temperatures, the optimum humidity was 73%. Howard (1931) suggested that fluctuations in canopy microclimatological factors above or below

Table 3. Life table for Mexican bean beetle (E. varivestis Mulsant) on dry beans (P. vulgaris L.) Tara, field 2, at Scottsbluff, NE (24 July to 28 August 1995), based on averages from 14 cohorts (egg masses)

x (stage)	lx (no. at beginning of each stage)	dxF (factor of mortality)	dx (no. dying during each x)	100qx (dx as % of lx)	100rx (cumulative in relation to initial lx)
Eggs/egg mass Larva	56.21 ± 0.98	Never hatched	39.57 ± 5.22	70.40	70.40
1st instar	16.64 ± 5.18	Desiccation Unknown	7.86 ± 2.75 0.43 ± 0.43	47.24 2.58	84.38 85.14
2nd instar	8.35 ± 3.04	Desiccation	$\begin{array}{c} 8.29\\ 3.14\pm1.64\end{array}$	49.82 37.6	90.73
3rd instar	5.21 ± 1.86	Unknown	$3.14 \\ 0.78 \pm 0.44 \\ 0.78$	37.6 14.97 14.97	92.12
4th instar	4.43 ± 1.64	Unknown	0.21 ± 0.15	4.74	92.49
			0.21	4.74	
Pupa Adult	$\begin{array}{c} 4.22 \pm 1.58 \\ 4.22 \pm 1.25 \end{array}$	_	0.00	0.00	92.49 92.49

x (stage)	lx (no. at beginning of each stage)	dxF (factor of mortality)	dx (no. dying during each x)	100qx (dx as % of lx)	100rx (cumulative in relation to initial lx)
Eggs/egg mass Larva	51.58 ± 2.41	Never hatched	8.75 ± 2.53	16.96	16.96
1st instar	42.83 ± 3.47	Desiccation	24.00 ± 3.60	56.03	63.49
		Unknown	0.58 ± 0.42	1.35	64.62
			24.58	57.35	
2nd instar	18.25 ± 2.92	Desiccation	4.75 ± 1.61	26.03	73.83
			4.75	26.03	
3rd instar	13.5 ± 2.61	Unknown	0.42 ± 0.26	3.11	74.64
			0.42	3.11	
4th instar	13.08 ± 2.6	Unknown	0.50 ± 0.26	3.82	75.61
			0.50	3.82	
Pupa	12.58 ± 2.53	_	0.00	0.00	75.61
Adult	12.58 ± 2.53	_	_	_	75.61

Table 4. Life table for Mexican bean beetle (*E. varivestis* Mulsant) on dry beans (*P. vulgaris* L.) Marquis, field 1, at Scottsbluff, NE (13 July to 23 August 1996), based on averages from 12 cohorts (egg masses)

tolerance limits are of major importance in Mexican bean beetle population dynamics.

The cumulative mortality ranged from 92.1 to 95.8%, in 1995 and from 60.9 to 75.6% in 1996 (Tables 1–6). In comparing the tables, it can be seen that there was a great difference in mortality between the two years. Varieties seemed to have no influence on larval survival. However, under laboratory conditions, Flanders (1984), found significant differences in larval and pupal survivorship when Mexican bean beetle were raised on different varieties of snap beans.

Overall, Mexican bean beetle sustained a high mortality during the egg and the first two larval stages. Desiccation was the most important mortality factor (Table 7). Even though there was a great difference in mortality between the two years, the survivorship curves would have the same form, with the greatest mortality occurring especially in the egg and first larval stages (Figs. 4 and 5).

No parasitism was observed for any stage in either year. In 1995, no predators were found in the study

fields, but in 1996 damsel bugs (Nabis sp.) were present. Although the damsel bugs were not seen feeding on Mexican bean beetle larvae, a few dead larvae with signs of predation or scavenging (partially consumed tissue) were found in the surrounding study field. We suspect that predation may have had some effect on mortality and may be included in the missing category. No diseased larvae were seen in the study fields nor in those held for parasitization tests. The absence of natural enemies was not a complete surprise because none of the introduced or naturally occurring enemies of the Mexican bean beetle in the United States has shown high potential for reducing the beetle population (Angalet et al. 1968, Barry 1973, Stevens et al. 1975). Also, the harsh summer environment of the western Nebraska high plains may be unfavorable for many pathogens or parasitoids.

Implications for Pest Management. Altogether, the data indicate that the population of the Mexican bean beetle on dry bean in western Nebraska is governed by a few factors. All are related to variation of weather

Table 5. Life table for Mexican bean beetle (*E. varivestis* Mulsant) on dry beans (*P. vulgaris* L.) Marquis, field 2, at Scottsbluff, NE (23 July to 25 August 1996), based on averages from 9 cohorts (egg masses)

x (stage)	lx (no. at beginning of each stage)	dxF (factor of mortality)	dx (no. dying during each x)	100qx (dx as % of lx)	100rx (cumulative in relation to initial lx)
Eggs/egg mass Larva	55.22 ± 1.73	Never hatched	4.33 ± 0.83	7.84	7.84
1st instar	50.89 ± 1.99	Desiccation Unknown	$\begin{array}{c} 23.00 \pm 3.17 \\ 0.11 \pm 0.11 \end{array}$	45.2 0.22	49.49 49.69
2nd instar	27.78 ± 3.64	Desiccation Unknown	$\begin{array}{c} 23.11 \\ 3.56 \pm 1.04 \\ 0.11 \pm 0.11 \end{array}$	45.42 12.81 0.4	56.14 56.34
3rd instar	24.11 ± 3.14	Unknown	$\begin{array}{c} 3.67\\ 3.78\pm1.6\end{array}$	13.21 15.68	63.18
4th instar	20.33 ± 2.92	Unknown	$3.78 \\ 1.00 \pm 0.67 \\ 0.11 \pm 0.11$	$15.68 \\ 4.92 \\ 0.54$	64.99 65.19
Pupa Adult	$\begin{array}{c} 19.22 \pm 3.26 \\ 19.22 \pm 3.26 \end{array}$		1.11 0.00 —	5.46 0.00 —	65.19 65.19

x (stage)	lx (no. at beginning of each stage)	dxF (factor of mortality)	dx (no. dying during each x)	100qx (dx as % of lx)	100rx (cumulative in relation to initial lx)
Eggs/egg mass Larva	54.33 ± 1.04	Never hatched	4.83 ± 1.08	8.89	8.89
1st instar	495 ± 128	Desiccated	20.17 ± 1.87	40.75	46.02
15t mota	1010 = 1120	Unknown	0.08 ± 0.08	0.16	46.16
			20.25	40.91	
2nd instar	29.25 ± 2.01	Desiccated	7.08 ± 1.28	24.21	59.19
		Unknown	0.17 ± 0.11	0.58	59.51
			4.75	24.79	
3rd instar	22.0 ± 1.86	Desiccated	0.25 ± 0.18	1.14	59.97
		Unknown	0.17 ± 0.11	0.77	60.28
			22.17	1.91	
4th instar	21.58 ± 1.89	Unknown	0.33 ± 0.1	1.53	60.89
			0.33	1.53	
Pupa	21.58 ± 2.53	_	0.00	0.00	60.89
Adult	21.58 ± 2.53	—	_	_	60.89

Table 6. Life table for Mexican bean beetle (*E. varivestis* Mulsant) on dry beans (*P. vulgaris* L.) Tara, at Scottsbluff, NE (25 July to 4 September, 1996), based on averages from 12 cohorts (egg masses)

components, which result in changes in the microclimate within the bean canopy. The great influence of abiotic factors, particularly desiccation, on mortality of eggs and early instars is not unexpected, given the dry, hot summer climate of the High Plains. It is somewhat surprising, however, that natural enemies had so little influence in this system. Perhaps Mexican bean beetles represent too transient a resource for generalist predators, at least at common beetle population densities. The lack of evidence for disease or parasitism also may be associated with host phenology and population densities, but barriers from the hot, dry climate seem a more likely explanation. These findings suggest that conventional biological control efforts are not likely to be successful for Mexican bean beetle in this region. In particular, the egg parasitoid, *P. foveolatus*, which has been used in biological control efforts against Mexican bean beetle in the eastern United States, would be a poor choice in western dry bean systems where eggs are so subject to desiccation.



Fig. 3. Temperature (°C) and relative humidity (%) registered during the experiments.

Table 7. Contributing mortality factors for life stages of *E. varivestis*, Scottsbluff, NE 1995–1996

Life Stage	Contributing Factor(s)	% Mortality	
		1995	1996
Eggs	Desiccation and Infertility	71.39	11.23
Larvae			
1st instar	Desiccation	18.42	42.26
2nd instar	Desiccation	2.61	9.73
3rd instar	Unknown	0.74	2.81
4th instar	Unknown	0.20	1.20
Pupa	_	0.08	0.00
Total	_	93.44	67.23

The economic importance of Mexican bean beetle to soybean in the eastern United States has diminished in recent years, although it remains an important occasional pest (Edwards et al. 1994, Way 1994). Although life table data are not available from soybean in the eastern United States, natural enemies have an important influence on beetle populations in this region (Edwards et al. 1994). Consequently, a detailed survivorship (life table) study of Mexican bean beetle in the eastern United States would provide an invaluable opportunity to examine how variable environments may alter the influence of biotic and abiotic factors on an insect population.

Variation in levels of mortality observed in these studies can greatly affect economic thresholds. Kabissa and Fronk (1986) reported that 87% of the leaf area consumed by Mexican bean beetle larvae occurred during the third and fourth stages. Consequently, population estimates for economic thresholds



Fig. 4. Survival of Mexican bean beetle eggs, larvae, and pupae in three dry bean fields, Scottsbluff, NE, 1995.



Fig. 5. Survival of Mexican bean beetle eggs, larvae, and pupae in three dry bean fields, Scottsbluff, NE, 1996.

should focus on these life stages, rather than on earlier stages in which negligible injury occurs. Adequately incorporating Mexican bean beetle survivorship in egg mass sampling plans and economic thresholds is essential to avoid overestimating injury from Mexican bean beetle. This study provides the survivorship data necessary for threshold development.

References Cited

- Angalet, G. W., L. W. Coles, and J. A. Stewart. 1968. Two potential parasites of the Mexican bean beetle from India. J. Econ. Entomol. 61: 1073–1075.
- Barry, R. M. 1973. A note on the species composition of predators in Missouri soybeans. J. Georgia Entomol. Soc. 8: 284–286.
- Bellinger, R. G., G. P. Dively II, and L. W. Douglass. 1981. Spatial distribution and sequential sampling of Mexican bean beetle defoliation on soybeans. Environ. Entomol. 10: 835–841.
- Douglass, J. R. 1928. Precipitation as a factor in the emergence of *Epilachna corrupta* from hibernation. J. Econ. Entomol. 21: 203–213.
- Douglass, J. R. 1933. Habits, life history, and control of the Mexican bean beetle in New Mexico. U.S. Dep. Agric. Tech. Bull. 376.
- Edwards, C. R., D. A. Herbert, Jr., and J. W. Van Duyn. 1994. Mexican bean beetle. In L.G. Higley and D. J. Boethel. Handbook of soybean insect pests. Entomol. Soc. Amer., Lanham, MD.
- Flanders, R. V. 1984. Comparisons of bean varieties currently being used to culture the Mexican bean beetle (Coleoptera: Coccinellidae). Environ. Entomol. 13: 995– 999.
- Hagen, A. 1986. Dry bean insects in Nebraska. University of Nebraska Coop. Extn. Pub., G86–786.

- Harcourt, D. G. 1969. The development and use of life tables in the study of natural insect populations. Annu. Rev. Entomol. 14: 175–196.
- Howard, N. F. 1931. The effect of the 1930 drought on the Mexican bean beetle. J. Econ. Entomol. 24: 660–662.
- Howard, N. F., and L. L. English. 1924. Studies on Mexican bean beetle in southeast. U.S. Dep. Agric. Dep. Bull. 1243.
- Howard, N. F., and B. J. Landis. 1936. Parasites and predators of the Mexican bean beetle in the United States. U.S. Dep. Agric. Agric. Circ. 418.
- Kabissa, J., and W. D. Fronk. 1986. Bean foliage consumption by Mexican bean beetle (Coleoptera: Coccinellidae) and its effect on yield. J. Kans. Entomol. Soc. 59: 275–279.
- Kitayama, K., R. E. Stinner, and R. L. Rabb. 1979. Effects of temperature, humidity, and soybean maturity on longevity and fecundity of the adult Mexican bean beetle, *Epilachna varivestis*. Environ. Entomol. 8: 458–464.
- Marcovitch, S., and W. W. Stanley. 1930. The climatic limitations of Mexican bean beetle. Ann. Entomol. Soc. Am. 23: 666–686.
- Mellors, W. K., and A. Allegro. 1984. Comparison of constant and alternating temperatures for determining developmental rates of Mexican bean beetle eggs and pupae. Ann. Entomol. Soc. Am. 77: 6–10.
- Michels, G. J., and C. C. Burkhardt. 1981. Economic threshold levels of the Mexican bean beetle on pinto beans in Wyoming. J. Econ. Entomol. 74: 5–6.
- Miller, D. F. 1930. The effect of temperature, relative humidity and exposure to sunlight upon the Mexican bean beetle. J. Econ. Entomol. 23: 945–954.
- Pedigo, L. P. 1997. General models for economic thresholds, pp. 41–57. In L. G. Higley and L. P. Pedigo [eds.], Economic thresholds for integrated pest management. University of Nebraska Press, Lincoln, NE.

- Schaafsma, A. W., and G. R. Ablett. 1994. Yield loss response of Navy-bean to partial or total defoliation. J. Prod. Agric. 7: 202–205.
- Shepard, M., G. R. Carner, and S. G. Turnipseed. 1974. Seasonal abundance of predaceous arthropods in soybeans. Environ. Entomol. 3: 985–988.
- Sprenkel, R. K., and Rabb, R. L. 1981. Effects of micrometeorological conditions on survival and fecundity of the Mexican bean beetle in soybean fields. Environ. Entomol. 10: 219–221.
- Stevens, L. M., A. L. Steinhauer, and J. R. Coulson. 1975. Suppression of Mexican bean beetle on soybeans with annual inoculative releases of *Pediobius foveolatus*. Environ. Entomol. 4: 947–952.
- Stinner, R. E., J. Regniere, and K. Wilson. 1982. Differential effects of agroecosystem structure on dynamics of three soybean herbivores. Environ. Entomol. 11: 538–543.
- Sweetman, H. L. 1932. The effects of temperature and moisture on the distribution of the Mexican bean beetle *Epilachna corrupta* Muls. Ann. Entomol. Soc. Am. 25: 224– 240.
- Turnipseed, S. G., and M. Shepard. 1980. Sampling Mexican bean beetle on soybean, pp. 189–200. In M. Kogan and D. C. Herzog [eds.], Sampling methods in soybean entomology. Springer, Berlin.
- Way, M. O. 1994. Status of soybean insect pests in the United States. *In L. G. Higley and D. J. Boethel* [eds.], Handbook of soybean insect pests. Entomological Society of America, Lanham, MD.

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