Chapter 3

Population dynamics and mortality of the alfalfa weevil in Virginia

For decades, biological control has kept the alfalfa weevil, *Hypera postica* Gyllenhal (Coleoptera: Curculionidae), below damaging levels in the northeastern U.S. (Day 1981, Kingsley et al. 1993). At least six different Hymenopteran species contribute to this biological control including two adult parasitoids, *Microctonus colesi* Drea (Braconidae) and *M. aethiopoides* Loan, an egg parasitoid, *Anaphes luna* (Girault) (Mymaridae), and three larval parasitoids, *Bathyplectes anurus* (Thomson), *B. curculionis* (Thomson) (Ichneumonidae), and *Oomyzus incertus* Ratzburg (Eulophidae) (Brunson and Coles 1968, Bryan et al. 1993, Radcliffe and Flanders 1998). In addition, an entomopathogenic fungus, *Zoophthora phytonomi* (Arthur) (Zygomycetes: Entomophthorales), also kills a high percentage of alfalfa weevil larvae, particularly under warm and humid conditions (Harcourt et al. 1977, Los and Allen 1983).

Prior to the occurrence of these natural enemies in Maryland, virtually all alfalfa fields required insecticide applications to protect the crop against serious alfalfa weevil feeding damage (Manglitz and App 1957). By the mid-1980's, after the release and establishment of several of the alfalfa weevil parasitoids, less than 15% of Maryland alfalfa fields exceeded the economic threshold for weevil (Lamp et al. 1990). Reported cases of alfalfa weevil damage are rare today in Maryland and other Mid-Atlantic states (W. H. Day, *personal communication*).

In Virginia, the alfalfa weevil persists as a major pest, despite numerous parasitoid releases (Bryan et al. 1993) and the occurrence of *Z. phytonomi* (Los and Allen 1983). The severity of pest pressure also appears to vary with geography in the state (Chapter 2). The objectives of this study were to investigate the population dynamics and mortality factors of the alfalfa weevil at three geographic locations in Virginia to determine why this insect remains a serious pest in the state.

Materials and methods

Field locations. Alfalfa weevil populations were sampled in nine different alfalfa fields in Virginia. Three of the fields were located near the town of Rustburg (79°10'W 37°20'N; elevation ≈ 200 m) and represented the Piedmont region. Another three fields were located near Fairfield (79°31'W 37°78'N; elevation ≈ 500 m) in the southern tip of the Shenandoah Valley. The remaining three fields were located in Blacksburg (80°25'W 37°14'N; elevation ≈ 640 m) and represented the southwestern region of the state. Alfalfa fields were 2- to 5-year old commercial stands, which were maintained according to standard agronomic practices including a final late-fall (October or November) harvest. No insecticides were applied to any of the fields for alfalfa weevil control in the spring.

Temperature monitoring. Daily max-min temperature data were recorded hourly at each of the field sites using hygrothermograph recorders (Omega Engineering, Inc.) in 1997-98 and Hobo Pro Series® data loggers (Onset Computer Corp., Pocasset, MA) in 1998-99. Degree-days for alfalfa weevil egg and larval development were calculated using a minimum developmental temperature of 9˚C (Harcourt 1981). Degree-days for weevil oviposition were calculated using a minimum adult activity threshold of 1.7°C (Hsieh and Armbrust 1974).

Sampling alfalfa weevil adult populations. Alfalfa weevil adults become active in Virginia in late-fall (Pamanes and Pienkowski 1965). Oviposition occurs in late-October or November and continues through the winter and spring (Woodside et al. 1968, Hilburn 1985). Alfalfa weevil adults were sampled in all fields in November, January, and March during the 1997-98 season and in November, December, January, and March the following season. Twenty 0.05-m^2 samples of soil and litter were collected from each field using a soil sampling device developed by Hilburn (1985). Live and dead adult weevils were extracted from the soil and litter by washing the material through two sieves (USA standard series 5 and 14). Overwintering survival of adults was estimated by regressing the density of live adults over time (Blickenstaff 1967). Adult alfalfa weevils that were collected by Hilburn sampling, plus additional adults collected

via sweep-netting in March and April were assessed for parasitism by rearing the insects individually or by dissecting the insects under water (Brunson and Coles 1968, Hilburn 1985).

Sampling egg populations. Alfalfa weevil egg density was estimated every 10-15 days from November to May. Samples of plant material were collected from each field using 20 arbitrary tosses of a 0.02-m^2 sampling frame. All live and dead stems from within the frame at each toss were clipped near the soil surface and placed in a plastic bag. Alfalfa weevil eggs were extracted from the plant material using a blender-flotation method (Pass and VanMeter 1966). Eggs were counted and categorized as yellow, brown, or black-head stage based on their development (Roberts et al. 1970). The total number of eggs deposited over time was estimated by summing the sample means of egg density at approximately 100 degree-day intervals before and after the population peak as described by Stark et al. (1994). Estimations of alfalfa weevil fecundity were made by dividing the total number of eggs produced by the starting density of adult females.

Egg viability and parasitism were checked at each sampling period throughout the season. A sub-sample of 50 to 100 eggs was incubated on moist filter paper at room temperature (25 ± 5°C) for 15 days. An egg was considered viable if it reached the blackhead stage of development or hatched. Parasitism by *A. luna* was confirmed by the red-eyed stage of parasitoid development, which was easily observed through the egg chorion.

Sampling larval populations. Alfalfa weevil larval density was estimated every 10-15 days from late-February to mid-May (first alfalfa harvest). Twenty samples of 10 alfalfa stems were shaken into a bucket to expose alfalfa weevil larvae for counting (Legg et al. 1985). Larvae were classified as period-one (1^{st} and 2^{nd} instars) or period-two (3^{rd} and 4^{th} instars) according to their head capsule size (Bartell and Roberts 1974). A sub-sample of 20 shakened stems was placed in a modified Berlese funnel to estimate the proportion of larvae remaining on stems after the bucket-shake method (Higgins et al. 1991). Alfalfa stem density was measured in each field to convert larvae per stem values to larvae per square meter. Period-one larvae require ≈100 DD to

complete their development (Hsieh et al. 1974). Thus, the total number of larvae produced over the season was estimated by summing sample means at approximately 100 degree-day intervals before and after the population peak.

Subsamples of 50 or more period-two larvae were collected from each field and reared in the laboratory on alfalfa bouquets at room temperature (21 ± 5°C; ~20% RH). Parasitism by *B. anurus*, *B. curculionis*, or other species was determined by identifying the parasitoid cocoons and any emerged adults (Brunson and Coles 1968, Bryan et al. 1993). All larvae that died before reaching the adult stage were assessed for fungal infection. Presence of live conidia or resting spores of the entomopathogenic fungus, *Z. phytonomi*, were confirmed by the KOH-visual technique described by Los and Allen (1982). Percentage larval mortality from each of the natural enemy species was calculated using the "recruitment method" of van Driesche et al. (1991).

Preparation of life tables. The construction and analysis of life tables can be an effective method for evaluating insect population dynamics and mortality factors (Varley and Gradwell 1970, Bellows et al. 1992). Using the alfalfa weevil population and mortality data collected, a total of 18 life tables were developed, representing 6 field-years from each of the three locations. Life table columns were those used by Morris and Miller (1954), where x represents the different life stage intervals, l_x represents the number of individuals entering x over an entire generation, d_x represents the number dying from various mortality factors, and $100q_x$ represents percentage mortality of l_x.

Life tables included five alfalfa weevil stage intervals (x): potential fecundity, observed eggs, period-one larvae, period-two larvae, and pupae. The l_x value for potential fecundity was calculated from a temperature-based oviposition model, which incorporated average daily temperature, starting adult density, and a temperature-based egg-laying function derived from LeCato and Pienkowski (1970). The model is described by the following function:

$$\sum_{s=1}^{165}[a(2.6022+1.1423t_s)] \qquad [1]$$

where, a = adult female density, s = days after 1 November, and t_s = average temperature for day = s. Duration for the egg-laying model = 150 days (1 November to 15 April), which represented a normal oviposition period for alfalfa weevil, based on preliminary results collected in 1996-97 (T.P.K, *unpublished data*) and other studies conducted in Virginia (Evans 1959, Woodside et al. 1968). The mortality value (d_x) for "eggs not laid" reflects the extent to which females returning to alfalfa fields failed to lay their expected compliment of eggs. This was calculated as the difference between expected eggs based on the model and the actual number of eggs laid.

Key factor analysis. To determine the relative contribution made by the individual mortality factors to the population dynamics of *H. postica,* mortalities were expressed as k values, the difference between the logarithms of l_x before and after the action of the mortality factor (Varley and Gradwell 1960). Total mortality (K) equaled the summation of submortalities (individual k values) as follows:

$$\text{Total mortality} = K = k_1 + k_2,...,k_5,$$

where k_1 = eggs not laid

k_2 = egg mortality

k_3 = period-one larval mortality

k_4 = *Z. phytonomi* infection

k_5 = larval parasitism

To determine which of the components contributed the most to variation in K, plots of each individual k_i over the field-years were compared to the plot of K over the field-years. The k_i plot that followed a similar fluctuating course as K was considered to be a key factor in the population dynamics (Varley and Gradwell 1970). In addition, a series of linear regressions were made of individual k values on the y-axis against K on the x-axis. The individual k value

that gave the greatest slope, while maintaining a significant correlation coefficient (r) was recognized as the key factor (Podoler and Rogers 1975, Southwood 1978). Significant r–values were determined using Snedecor's (1946) table of significant values of r.

Data analysis. Alfalfa weevil population and mortality data were analyzed separately by year. Weevil densities were normalized using a square root transformation and all proportion mortality data were normalized using an arcsine square root transformation prior to analysis (Ott 1984). Differences in alfalfa weevil population and mortality levels among the three Virginia locations were analyzed separately by year using analysis of variance (ANOVA) procedures. Means were separated with Fisher's protected least significant difference (LSD) at the 0.05 level of significance. Differences in survivorship among locations were analyzed using chi-square "goodness of fit" tests with a = 0.05.

Results

1997-98 alfalfa weevil populations. All six alfalfa fields located in Fairfield and Blacksburg had alfalfa weevil populations that were noneconomic based on current guidelines used in Virginia. According to these guidelines, the economic threshold for alfalfa weevil is 1 larva per stem on 30-cm tall alfalfa and 2 larvae per stem on 40-cm alfalfa (Luna 1986). In contrast, all three fields located in Rustburg exceeded the economic threshold for alfalfa weevil. Alfalfa weevil peak adult densities ($F = 8.46$; df = 2, 6; $P < 0.05$), total egg densities ($F = 13.91$; df = 2, 6; $P < 0.01$), period-one larval densities ($F = 18.16$; df = 2, 6; $P < 0.005$), and period-two larval densities ($F = 12.34$; df = 2, 6; $P < 0.01$) differed among the sample locations (Table 3.1). Peak adult density at Rustburg averaged 3 times more than Fairfield and 5 times more than Blacksburg. Concomitant egg and larval densities were 8 to 15 times greater in Rustburg compared with Fairfield and Blacksburg, which indicated potential differences in alfalfa weevil reproduction among the locations.

Alfalfa weevil fecundity differed significantly among the locations (F = 6.67; df = 2, 6; P < 0.05). Rustburg females deposited a mean (± SEM) of 1020.2 ± 17.9 eggs each over the season, which was significantly greater than females located in Fairfield (402.2 ± 220.2) and Blacksburg (402.1 ± 92.1) (P < 0.05).

One factor that impacted alfalfa weevil fecundity was winter climate. Average daily temperatures in Rustburg were approximately 2°C warmer than Fairfield and 3.3°C warmer than Blacksburg from 1 November to 15 April (Table 3.2). This resulted in the accumulation of 1,001 oviposition degree-days (ODD) (base 1.7°C) at Rustburg compared with 692 ODD at Fairfield and 642 ODD at Blacksburg (Table 3.2).

To determine if temperature alone accounted for the differences in fecundity among locations, predicted egg-laying values were calculated for each field using the temperature-based oviposition model [1] and compared with observed egg numbers obtained from sampling. Results showed that a substantial percentage of the potential eggs were not laid at all three locations (Table 3.3). This suggests that other factors in addition to temperature reduced alfalfa weevil fecundity.

1998-99 alfalfa weevil populations. Weevil population levels were lower in all fields compared with the previous season (Table 3.4). Nonetheless, all of the alfalfa fields located in Rustburg exceeded the economic threshold for alfalfa weevil, whereas none of the fields located in Fairfield and Blacksburg exceeded threshold. Alfalfa weevil peak adult densities (F = 155.22; df = 2, 6; P < 0.001), egg densities (F = 410.01; df = 2, 6; P < 0.001), period-one larval densities (F = 5.55; df = 2, 6; P < 0.05), and period-two larval densities (F = 6.96; df = 2, 6; P < 0.05) differed significantly among locations. Peak adult density, total egg density, and period-one larval density at Rustburg, respectively, were 2.3, 5.1, and 4.5 times greater than Fairfield, and 4.7, 8.6, and 4.3 times greater than Blacksburg (Table 3.4).

Alfalfa weevil fecundity levels were similar to the previous season and again differed among locations (F = 75.55; df = 2, 6; P < 0.001). Rustburg females deposited more (mean ± SEM =

1048.3 ± 47.04) eggs each over the season than females in Fairfield (480.40 ± 33.03) and Blacksburg (566.66 ± 20.38) ($P < 0.001$).

Average daily temperatures in Rustburg were approximately 2°C warmer than Fairfield and 3.8°C warmer than Blacksburg from 1 November to 15 April, which resulted in the accumulation of 1,084 ODD at Rustburg compared with 844 ODD at Fairfield and 798 ODD at Blacksburg (Table 3.5). Similar to the 1997-98 season, observed egg numbers were substantially lower than those predicted by the temperature model at all locations (Table 3.6).

Adult mortality. Based on my samples, alfalfa weevil adult density was highest in November and declined over the winter months. The rate of adult population decline was similar in both years ($\chi^2 = 7.942$; df = 35; $P > 0.05$). Adult population decline also was not different between Rustburg and Fairfield ($\chi^2 = 3.687$; df = 20; $P > 0.05$) and Rustburg and Blacksburg ($\chi^2 = 6.061$; df = 17; $P > 0.05$). Overwintering adult survival combined for locations and years fit the regression equation: $y = -0.0054x + .9491$; $r^2 = 0.82$ ($F = 45.71$; df = 1, 58; $P < 0.001$); where y = proportion of adults surviving and x = number of days after 1 November (Fig. 3.1). Adult weevils were attacked by the fungal pathogen, *Beauveria bassiana* (Balsamo) Vuillemin (Deuteromycetes), and two insect parasitoids, *M. aethiopoides* and *Hyalomyodes triangulifera* (Loew) (Diptera: Tachinidae). Infection by *B. bassiana* was relatively low, ranging from 2.8 to 13.2% and was not significantly different among the locations in 1997-98 ($F = 2.25$; df = 2, 6; $P = 0.168$) or 1998-99 ($F = 0.961$; df = 2, 6; $P = 0.4436$) (Table 3.7). *Microctonus aethiopoides* was the primary parasitoid species recovered from adult alfalfa weevils. In 1997-98, differences in parasitization among locations were significant at the 0.08 level ($F = 3.53$; df = 2, 6; $P = 0.080$). Parasitization at Rustburg averaged (mean ± SEM) 1.8 ± 0.7%, which was significantly lower than Fairfield (24.02 ± 6.6%; $P < 0.05$) and Blacksburg (21.4 ± 9.2%; $P < 0.05$) (Table 3.8). In 1998-99, *M. aethiopoides* parasitization rates were relatively low in all fields, but still differed among locations ($F = 15.77$; df = 2, 5; $P < 0.05$). Mean parasitization in Blacksburg was higher than Rustburg ($P < 0.01$), but not Fairfield ($P = 0.09$; Table 3.8). *Hyalomyodes*

triangulifera, was only found in 3 adult weevils out of a total of 883 examined over the two years, therefore, percent parasitization by this species was not analyzed.

Egg mortality. In 1997-98, total egg mortality, as measured by the difference between egg density and period one larval density, was similar among locations (F = 0.655; df = 2, 6; P = 0.5531) and ranged from 33.8 to 54.9%. The percentage of eggs hatching over the winter months averaged 84.8 ± 3.7% in Rustburg, 75.2 ± 4.5% in Fairfield, and 71.9 ± 4.1% in Blacksburg. The location by months interaction was not significant for egg viability (F = 2.129; df = 6, 9; P = 0.148), nor was the main effect of location (F = 3.087; df = 2, 3; P = 0.1870).

In 1998-99, total egg mortality again was similar among locations (F = 3.383; df = 2, 6; P = 0.1038) and ranged from 45.2 to 71.9%. Viability of eggs over the winter months averaged 66.4 ± 5.2% in Rustburg, 68.2 ± 6.9% in Fairfield, and 64.4 ± 7.4% in Blacksburg. Again, there was no significant location by months interaction (F = 0.584; df = 8, 24; P = 0.781), and egg viability did not differ by locations (F = 0.082; df = 2, 6; P = 0.922).

Egg parasitism was not an important factor contributing to alfalfa weevil egg mortality. The mymarid parasitoid, *A. luna*, was found in a few weevil eggs, but parasitization levels were very low (<1%) in all fields. No other egg parasitoid species was detected.

Larval mortality. Death of early instars can be an important mortality factor of alfalfa weevil populations. This factor is referred to as period-one larval mortality and calculated as the difference between period-one and period-two larval densities. In 1997-98, period-one larval mortality differed significantly among locations (F = 5.637; df = 2, 6; $P < 0.05$). In Blacksburg, period-one larval mortality averaged (mean ± SEM) 49.2 ± 5.0%, which was higher than Fairfield (17.9 ± 11.4%) ($P < 0.05$) and Rustburg (13.7 ± 0.68%) ($P < 0.05$). In 1998-99, period-one larval mortality was not different among locations (F = 0.010; df = 2, 8; P = 0.9902), and ranged from 27.3 to 34.6%.

Three natural enemy species were found attacking period-two alfalfa weevil larvae, the fungus, *Z. phytonomi*, and the parasitoids, *B. anurus* and *B. curculionis* (Table 3.9). Locations

differed significantly in *Z. phytonomi* infection in 1997-98 (F = 23.978; df = 2, 6; $P < 0.01$). The percentage of larvae infected with *Z. phytonomi* was higher in Blacksburg than Fairfield ($P < 0.01$) or Rustburg ($P < 0.01$; Table 3.9). The following season, *Z. phytonomi* infection was not different among locations (F = 3.158; df = 2, 6; P = 0.116), and ranged from 1.0 ± 1.0% in Blacksburg to 19.1 ± 9.3% in Rustburg.

Bathyplectes anurus accounted for 92.3% of all parasitoids emerging from alfalfa weevil larvae. *Bathyplectes curculionis* (diapausing and non-diapausing strains) accounted for all other larval parasitoids. Locations differed significantly in total larval parasitization in 1997-98 (F = 6.720; df = 2, 6; $P < 0.05$) and 1998-99 (F = 286.98; df = 2, 6; $P < 0.001$). In both years, parasitization was higher in Fairfield than the other locations ($P < 0.05$; Table 3.9). In 1998-99, larval parasitization was higher at Blacksburg than Rustburg ($P < 0.05$).

Lifetables. Partial life tables of *H. postica*, representing a composite mean of 6 field-years for each location are presented in Table 3.10. Total mortality from egg to pupal stage was high at all locations, ranging from 92.1% at Rustburg to 98.6% at Fairfield. Eggs not laid (k_1), egg mortality (k_2), and larval parasitism (k_5) accounted for most (77 to 93%) of the total alfalfa weevil mortality (K). For Rustburg, egg mortality (k_2) was a key factor contributing to alfalfa weevil population dynamics. In the graphical analysis method, k_2 mortality fluctuations were the most similar in magnitude and direction to the total within-generation mortality, K (Fig. 3.2). Also, k_2 regressed against K gave the slope closest to unity (b = 0.7857), with a significant r = 0.92; df = 5, $P < 0.05$ (Table 3.11).

For Fairfield, larval parasitism (k_5) rivaled k_2 as the key factor. Both mortality factors followed the fluctuations in K over the field-years, but k_5 was greater in magnitude (Fig. 3.3). Moreover, k_5 regressed against K had the slope closest to unity (b = 0.7059), with a significant r = 0.95; df = 5, $P < 0.05$ (Table 3.11). For Blacksburg, period-one larval mortality (k_3) most followed the fluctuations in K (Fig. 3.4). The regression slope of k_3 against K was b = 0.5647 with a significant r = 0.92; df = 5, $P < 0.05$ (Table 3.11).

Discussion

Alfalfa weevil population levels varied with geographic location in Virginia. Higher densities of all life stages of alfalfa weevil were found at Rustburg (elevation = 200 m) in the Piedmont region compared with Fairfield in the Shenandoah Valley (elevation = 500 m) or Blacksburg in the southwestern region of the state (elevation = 640 m). Winter temperatures were 2 to 4˚C warmer at Rustburg than the other locations, which allowed for greater oviposition. Alfalfa weevil females at the Rustburg location laid ≈1000 eggs each, which was higher than females at Fairfield and Blacksburg (400 to 600 eggs per female). Under optimal environmental conditions, alfalfa weevil females can deposit an average of 3650 eggs each (Coles and Day 1977). This rate decreases substantially at lower temperatures (LeCato and Pienkowski 1970, Hsieh and Armbrust (1974).

In the northern U.S., above 40 degrees latitude, winter temperatures frequently drop below –15°C, or remain below freezing for extended periods, which causes mortality of alfalfa weevil eggs that are present (Morrison and Pass 1974, Shade and Hintz 1983). As a result, fall and winter-laid alfalfa weevil eggs contribute very little to spring larval populations in the northern U.S. (Townsend and Yendol 1968, Blickenstaff et al. 1972). In Virginia, this does not appear to be the case. Viability of alfalfa weevil eggs was relatively high (60 to 70%) during the winter months at all three Virginia locations, and total egg mortality averaged roughly 50 to 60%. Very few eggs (<1%) were parasitized by *A. luna*. This parasitoid appears to be declining in importance in other regions of the U.S. as well (DeGooyer et al. 1995, Radcliffe and Flanders 1998).

Mortality of alfalfa weevil adults also was similar among the three locations in Virginia. By spring, adult alfalfa weevil populations were reduced to approximately 20 to 30% of their early winter peaks. Alfalfa weevil adults are cold hardy and can survive temperatures as low as -18°C (Armbrust et al. 1969). Moreover, adult weevils burrow through litter and soil to insulate

themselves against harsh weather (Tysowsky and Dorsey 1970). Thus, it is not surprising that the differences in winter climate exhibited among the Virginia locations did not affect survival of adults. Overwintering survival of alfalfa weevil adults in Virginia was similar to that reported in New York by Helgesen and Cooley (1976) and in Maryland by Blickenstaff et al. (1972).

Parasitism of adults by *M. aethiopoides* is a critical factor in reducing alfalfa weevil populations in the northeastern and north central U.S. (Day 1981, Kingsley et al. 1993). Parasitization of overwintering adult weevils generally exceeds 50% in these regions with levels of 70 to 90% not uncommon (Brunson and Coles 1968, Abu and Ellis 1976, van Driesche and Gyrisco 1979). In Virginia, adult parasitization was low (1 to 25%) at all locations. This contributes to higher weevil fecundity rates because adult parasitism by *M. aethiopoides* sterilizes adult weevils and removes them from the egg-laying population (Drea 1968). Low parasitism results in greater alfalfa weevil oviposition (van Driesche and Gyrisco 1979).

Harcourt et al. (1977) reported that 26% of alfalfa weevil larvae in Ontario were killed during establishment in their feeding sites. Similar results were found at the three Virginia locations; period-one larval mortality ranged from 13 to 49%. Causes of period-one larval death mr locinclude: freezing temperatures (Shade and Hintz 1983, Stark et al. 1994), disease (Harcourt et al. 1977), predation (DeGooyer et al. 1995), and parasitism trauma by *Bathyplectes* spp. (Duodu and Davis 1974).

Zoophthora phytonomi can be the primary mortality factor of alfalfa weevil, killing up to 90% of larval populationsa tion environmental conditionss (; Table 3.9). In 1998-99, larval (Harcourt et al. 1977, Los and Allen 1983, DeGooyer et al. 1995). In the two years of my study, fungal epizootics did not occur and alfalfa weevil mortality caused by *Z. phytonomi* was generally low. Low fungal infection benefits larval parasitoids, such as *B. anurus* and *B. curculionis*, because *Z. phytonomi* kills parasitized alfalfa weevil larvae as well (Harcourt et al. 1990). Parasitization of alfalfa weevil larvae was generally high (36.0 to 92.4%) at all Virginia locations and was comparable, if not higher than rates reported in the northeastern U.S. (Day

1981, Kingsley et al. 1993). The primary larval parasitoid species was *B. anurus*, accounting for 92% of all parasitoids emerging from alfalfa weevil.

Partial life-table studies of the alfalfa weevil have been conducted in Ontario, Canada (Harcourt et al. 1977), Kentucky (Latheef et al. 1979), and Iowa (DeGooyer et al. 1995). Still, ecological information obtained on this pest in one state may not pertain to other states because of the ecological complexities of alfalfa weevil and the variability in biological control across the U.S. (Armbrust 1978, Radcliffe and Flanders 1998). My study presents current life tables of alfalfa weevil populations at three elevations in Virginia. These life tables should be more applicable to southern states than those of Harcourt et al. (1977) and DeGooyer et al. (1995) because they account for fall- and winter-laid alfalfa weevil eggs. These life tables also are current and account for a number of natural enemy species that have become established since the study by Latheef et al. (1979) in Kentucky. Analysis of the life-table data in the present study, revealed that egg mortality was a key factor explaining alfalfa weevil population dynamics at the Rustburg location. This may have been the result of a higher oviposition rate at this location, particularly in the fall and winter. Egg mortality was relatively high because an abundance of eggs were laid. At Fairfield, larval parasitism was shown to be a key factor. Larval parasitization was highest at this location and ranged from 69.3 to 92.4%. At Rustburg, period-one larval mortality was a key factor. This may have been the result of freezing temperatures occurring in late March, after a number of eggs had hatched. Alfalfa weevil larvae are not as cold tolerant as the egg and adult stage (Armbrust et al. 1969), and late-season frosts can cause substantial larval mortality (Stark et al. 1994).

Table 3.1. Alfalfa weevil population levels at three locations in Virginia, 1997-98

	Mean ± SEM (per m^2)			
Location	Peak Adults	Total Eggs	Period 1 larvae	Period 2 larvae
Rustburg (n = 3 fields)	9.7 ± 2.3a	4903.7 ± 1150.2a	2063.1 ± 418.7a	1808.8 ± 464.7a
Fairfield (n = 3 fields)	3.3 ± 0.9b	530.0 ± 172.8b	258.0 ± 25.0b	214.3 ± 25.9b
Blacksburg (n = 3 fields)	2.0 + 0.6b	454.6 ± 215.0b	237.7 ± 74.3b	122.2 ± 44.5b

Means within columns followed by the same letter are not significantly different (Fisher's protected LSD; $P > 0.05$)

Table 3.2. Average monthly temperatures and alfalfa weevil oviposition degree-day (ODD) accumulations[1] at three locations in Virginia, 1997-98

	Rustburg	Fairfield	Blacksburg
Month	Avg. Temp. °C (ODD)	Avg. Temp. °C (ODD)	Avg. Temp. °C (ODD)
Nov	7.4 (173)	5.9 (149)	3.5 (111)
Dec	5.4 (158)	1.5 (69)	1.1 (75)
Jan	5.1 (125)	2.6 (73)	2.0 (87)
Feb	6.7 (147)	5.2 (111)	2.7 (84)
March	8.8 (224)	6.7 (161)	5.8 (153)
April (1-15th)	13.3 (174)	12.6 (129)	11.9 (132)
Seasonal avg. temp (Total ODD)	7.8 (1001)	5.8 (692)	4.5 (642)

[1]Oviposition degree days were calculated using 1.7°C as the minimum threshold for adult activity (Hsieh and Armbrust 1974)

Table 3.3. Comparison of predicted alfalfa weevil egg numbers according to a temperature-based oviposition function[1] and observed egg numbers at three Virginia locations, 1997-98

Location (n = 3 fields)	Predicted eggs based on adult female density and temperature[1] (mean ± SEM per m^2)	Observed eggs (mean ± SEM per m^2)	% of eggs not laid
Rustburg	8503 ± 2053	4904 ± 1150	42.3 %
Fairfield	2161 ± 571	530 ± 173	75.7 %
Blacksburg	1056 ± 305	455 ± 215	56.9 %

[1]Calculated from an oviposition model [1] using average daily temperature from 1 Nov to 15 April, adult alfalfa weevil density, and a temperature-based egg-laying function.

Table 3.4. Alfalfa weevil population levels at three locations in Virginia, 1998-99

	Mean ± SEM (per m^2)			
Location	Peak Adults	Total Eggs	Period 1 larvae	Period 2 larvae
Rustburg (n = 3 fields)	4.7 ± 0.3a	2431.8 ± 95.5a	679.0 ± 220.7a	469.8 ± 125.3a
Rustburg (n = 3 fields)	2.0 ± 0.0b	480.4 ± 33.0b	150.0 ± 19.7b	99.6 ± 18.8b
Rustburg (n = 3 fields)	1.0 + 0.0c	283.3 ± 10.2b	156.7 ± 25.9b	117.7 ± 52.1b

Means within columns followed by the same letter are not significantly different (Fisher's protected LSD; $P > 0.05$)

Table 3.5. Average monthly temperatures and alfalfa weevil oviposition degree-day (ODD) accumulations[1] at three locations in Virginia, 1998-99

	Rustburg	Fairfield	Blacksburg
Month	Avg. Temp. °C (ODD)	Avg. Temp. °C (ODD)	Avg. Temp. °C (ODD)
Nov	10.1 (228)	8.3 (179)	6.3 (181)
Dec	7.7 (175)	5.1 (129)	3.5 (134)
Jan	5.6 (149)	3.2 (96)	1.7 (110)
Feb	6.1 (149)	4.7 (114)	2.3 (106)
March	7.3 (179)	5.4 (133)	3.0 (96)
April (1-15th)	15.3 (204)	14.6 (193)	13.1 (171)
Seasonal avg. temp (Total ODD)	8.7 (1084)	6.8 (844)	4.9 (798)

[1]Oviposition degree days were calculated using 1.7°C as the minimum threshold for adult activity (Hsieh and Armbrust 1974)

Table 3.6. Comparison of predicted alfalfa weevil egg numbers according to a temperature-based oviposition function[1] versus observed egg numbers at three Virginia locations, 1998-99

Location (n = 3 fields)	Predicted eggs based on adult female density and temperature[1] (mean ± SEM per m^2)	Observed eggs (mean ± SEM per m^2)	% of eggs not laid
Rustburg	4516 ± 323	2432 ± 96	46.2 %
Fairfield	1580 ± 0	481 ± 33	69.6 %
Blacksburg	613 ± 0	283 ± 10	53.8 %

[1]Calculated from an oviposition model [1] using average daily temperature from 1 Nov to 15 April, adult alfalfa weevil density, and a temperature-based egg-laying function.

Table 3.7. *Beauveria bassiana* infection of alfalfa weevil adults at three locations in Virginia

	1997-98		1998-99	
Location	Number of adult weevils examined	% infection	Number of adult weevils examined	% infection
Rustburg	302	3.6 ± 1.3a	74	4.9 ± 2.5a
Fairfield	110	8.9 ± 2.0a	47	13.2 ± 1.1a
Blacksburg	134	2.8 ± 1.8a	26	6.5 ± 3.6a

Means within columns followed by the same letter are not significantly different (Fisher's protected LSD; $P > 0.05$)

Table 3.8. *Microctonus aethiopoides* parasitization of alfalfa weevil adults at three locations in Virginia

	1997-98		1998-99	
Location	Number of adult weevils examined	% parasitization	Number of adult weevils examined	% parasitization
Rustburg	302	1.8 ± 0.7a	227	5.1 ± 1.1a
Fairfield	110	24.0 ± 6.6b	69	8.8 ± 0.3ab
Blacksburg	134	21.4 ± 9.2b	41	12.4 ± 0.9b

Means within columns followed by the same letter are not significantly different (Fisher's protected LSD; $P > 0.05$)

Table 3.9. *Zoophthora phytonomi* infection and *Bathyplectes* spp. parasitization of alfalfa weevil larvae at three locations in Virginia

	% of larvae infected by *Z. phytonomi* (mean ± SEM)		% of larvae parasitized by *Bathyplectes* spp. (mean ± SEM)	
Location (*n* = 3 fields)	1997-98	1998-99	1997-98	1998-99
Rustburg	4.8 ± 1.9a	19.1 ± 9.3a	49.5 ± 4.7a	36.0 ± 1.5a
Fairfield	2.8 ± 2.1a	2.9 ± 0.7a	69.3 ± 4.1b	92.4 ± 1.6b
Blacksburg	36.5 ± 3.8b	1.0 ± 1.0a	49.0 ± 4.5a	75.1 ± 0.6c

Means within columns followed by the same letter are not significantly different (Fisher's protected LSD; $P > 0.05$)

Table 3.10. Partial composite lifetables[a] of *H. postica* at Rustburg (a), Fairfield (b), and Blacksburg (c), Virginia.

(a) Rustburg (elevation = 200 m)

x	l_x[b]	d_xF	d_x	$100q_x$	k
Potential fecundity	6510	Eggs not laid	2842	43.7	0.574
Observed Eggs	3668	Egg mortality	2297	62.6	0.984
		Pd.1 Larval			
Pd.1 Larvae	1371	Mortality	232	16.9	0.185
Pd.2 Larvae	1139	*Z. phytonomi*	136	11.9	0.127
		Parasitism	487	42.8	0.518
Pupae	516				
Total			5993	92.1	2.387

(b) Fairfield (elevation = 500 m)

x	l_x[b]	d_xF	d_x	$100q_x$	k
Potential fecundity	1871	Eggs not laid	1365	73.0	1.309
Observed Eggs	505	Egg mortality	301	59.6	0.907
		Pd.1 Larval			
Pd.1 Larvae	204	Mortality	47	23.1	0.263
Pd.2 Larvae	157	*Z. phytonomi*	4	2.8	0.029
		Parasitism	127	80.8	1.449
Pupae	26				
Total			1845	98.6	3.956

(c) Blacksburg (elevation = 640 m)

x	l_x[b]	d_xF	d_x	$100q_x$	k
Potential fecundity	835	Eggs not laid	466	55.8	0.816
Observed Eggs	369	Egg mortality	172	46.5	0.625
		Pd.1 Larval			
Pd.1 Larvae	198	Mortality	78	39.2	0.498
Pd.2 Larvae	120	*Z. phytonomi*	23	18.8	0.208
		Parasitism	75	62.1	0.931
Pupae	22				
Total			812	97.2	3.078

[a] Mean of 6 field-years encompassing 1997-99.
[b] Number per square meter.

Table 3.11. Linear regression of individual submortalities (*k*-values) against total mortality (*K*) of *H. postica* at three locations in Virginia, 1997-99.

	Rustburg		Fairfield		Blacksburg	
Submortality	*b*	r	*b*	r	*b*	r
k_1 (eggs not laid)	0.0576	0.53	-0.1649	0.31	0.0543	0.10
k_2 (egg mortality	0.7857	0.92*	0.3363	0.75	0.3393	0.54
k_3 (Pd. 1 larval mortality	0.0917	0.31	0.1042	0.37	0.5647	0.92*
k_4 (*Z. phytonomi*)	0.1308	0.50	0.0023	0.11	0.0600	0.12
k_5 (larval parasitism)	-0.0660	0.21	0.7059	0.96*	0.0028	0.00

* indicates significant r value according to Snedecor (1946)

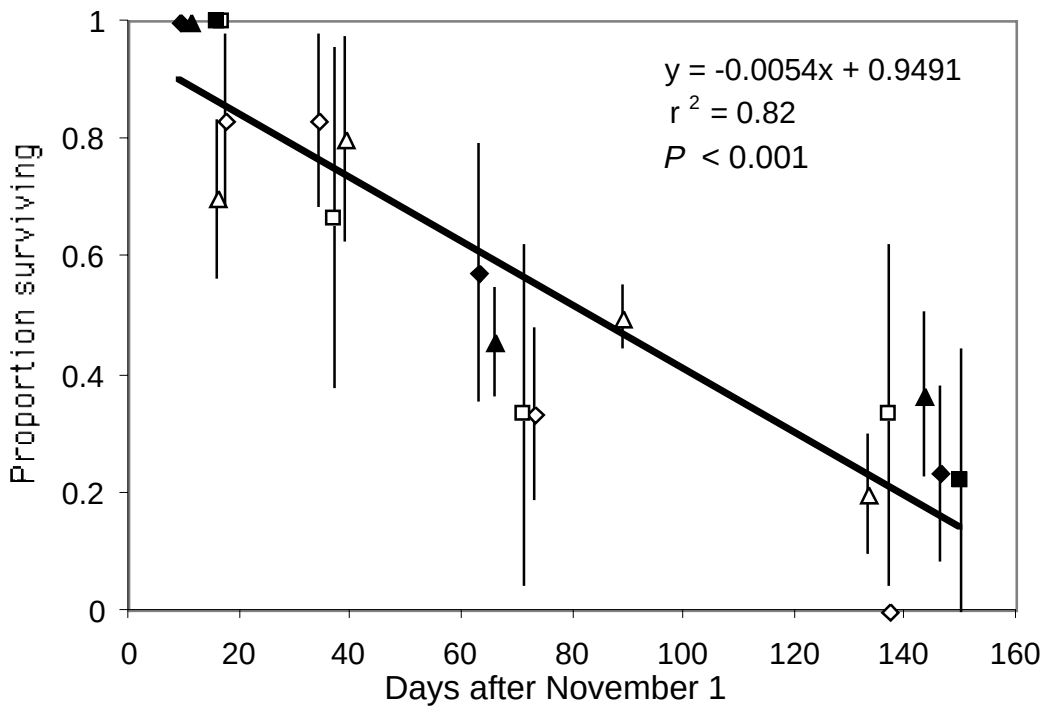

Fig. 3.1. Overwintering survival of alfalfa weevil adults in Virginia. Data points represent the mean (± SEM) of the proportion of adult population from 3 fields. Triangles represent Rustburg, diamonds represent Fairfield, and squares represent Blacksburg. Black represents the 1997-98 season and white represents 1998-99.

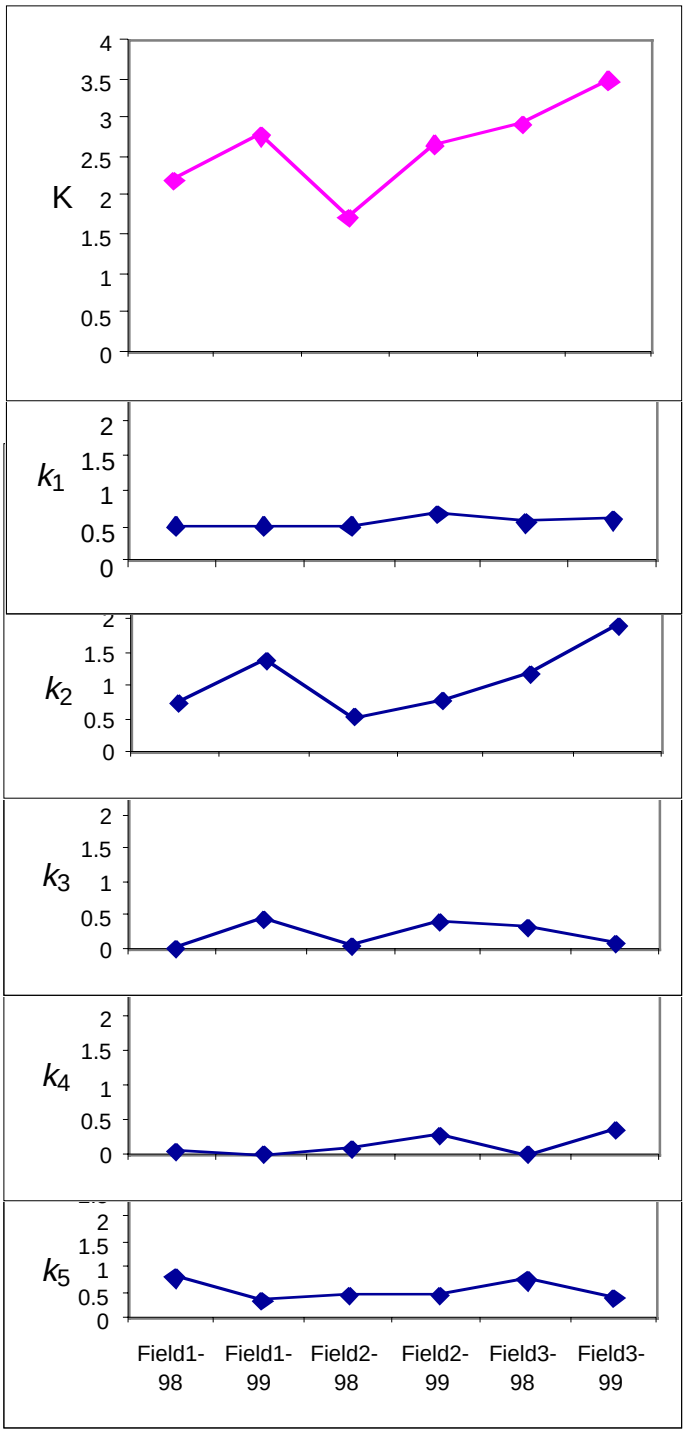

Fig. 3.2. Fluctuations in individual mortalities (*k*- values) with total mortality (*K*) of *H. postica* over 6 field-years at Rustburg, Virginia; k_1 = eggs not laid, k_2 = egg mortality, k_3 = period-one larval mortality, k_4 = *Z. phytonomi*, k_5 = larval parasitism.

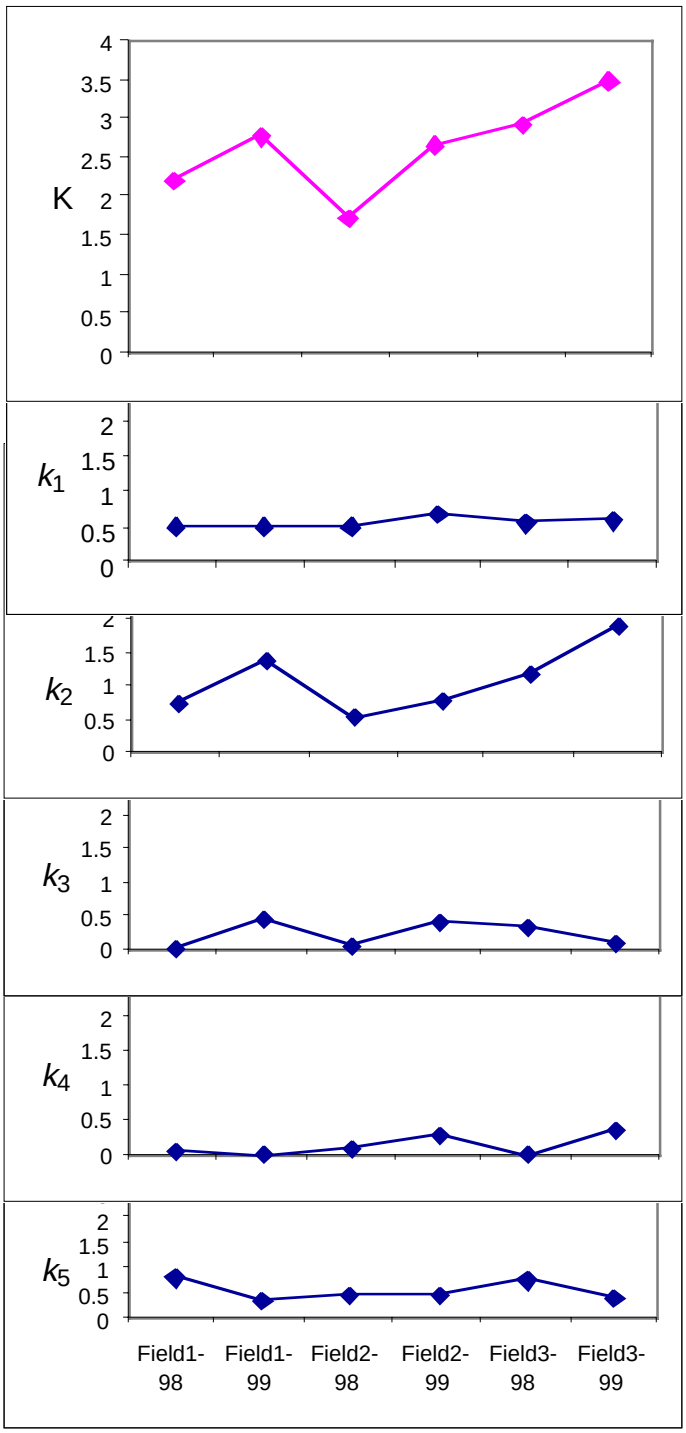

Fig. 3.3. Fluctuations in individual mortalities (*k*- values) with total mortality (*K*) of *H. postica* over 6 field-years at Fairfield, Virginia; k_1 = eggs not laid, k_2 = egg mortality, k_3 = period-one larval mortality, k_4 = *Z. phytonomi*, k_5 = larval parasitism.

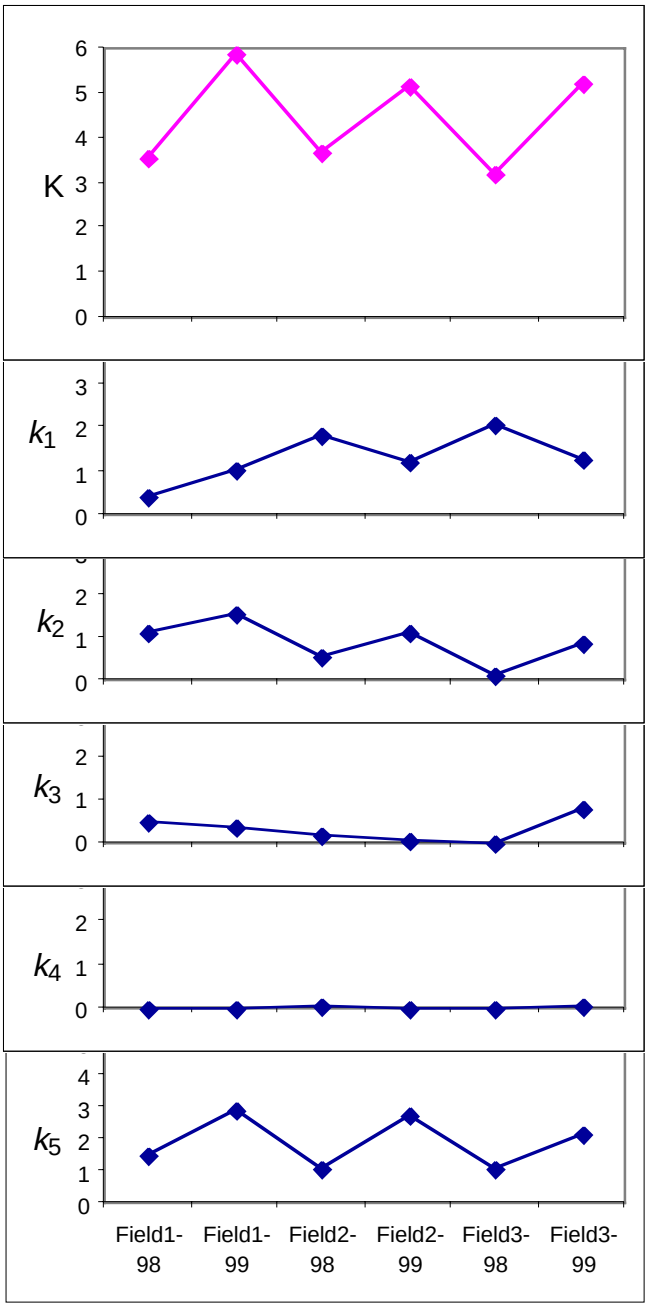

Fig. 3.4. Fluctuations in individual mortalities (*k*- values) with total mortality (*K*) of *H. postica* over 6 field-years at Blacksburg, Virginia; k_1 = eggs not laid, k_2 = egg mortality, k_3 = period-one larval mortality, k_4 = *Z. phytonomi*, k_5 = larval parasitism.