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Population dynamics of tef epilachna (*Chnootriba similis* Thunberg) (Coleoptera, Coccinellidae) in Ethiopia

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Abstract

Studies on the population dynamics of *Chnootriba similis* Thunberg, were carried out in Southern Ethiopia, in Wolaita Zone for 2 years (2004 and 2005) at three locations, Boloso Sore, Damot Gale and Sodo Zuria.

Mortality of eggs and early larval stages was higher at all locations when compared to the later stages. The highest rate of mortality on the eggs was caused mainly by the egg parsitoid, *Oaencyrtus epulus* (Encyrtidae). The parasitoids, *Pediobius foveolatus* (Eulophidae) and *Mesopolobus* spp. (Pteromalidae), were the main causes of the pupal mortality. The mortality of the larval stages was supposed to be due mainly to the many predators present, namely as *Chlaenius* sp. (Carabidae), ladybird beetles (Coccinellidae), larvae of hoverflies (Syrphidae) and green lacewings (Chrysopidae), assassin bugs (Reduviidae), earwigs and spiders. A fungal entomopathogen (*Beauveria* spp.) was also found on adults.

The egg parasitoid *O. epulus* and the pupal parasitism caused by the *P. foveolatus* and *Mesopolobus* spp. were the key mortality factors in the population dynamics of the *C. similis.* The egg and pupal parasitism were density dependant at two and one locality, respectively.

Keywords: *Chnootriba similis*; Life tables; Mortality; Predation; Parasitoides; Entomopathogen

1. Introduction

The herbivorous ladybird beetle, tef epilachna (*Chnootriba similis* Thunberg, Coleoptera, Coccinellidae), is a pest of cereal crops and distributed in many African countries and Yemen. In Ethiopia, it was reported as a pest of tef (*Eragrostis tef*) and other small cereals in different parts of the country (Wale, 1998; Haile and Ali, 1985; Crowe and Shitaye, 1977; Hill, 1966). It has also been considered as a pest of maize, rice, sugarcane and other graminaceous plants in the West, East and Southern African countries (Schmutterer, 1971, 1969) and cereal crops in Yemen (Moharram et al., 1996). During the process of feeding on the leaf tissue, it transmits one of the most economically damaging diseases of rice in sub-Saharan Africa, the rice yellow mottle virus (RYMV), (Abo et al., 2001; Nwilene, 1999).

Although, this insect was known to cause damage on different cereal crops in many countries including Ethiopia, little attention has been given to develop integrated pest management (IPM) to reduce its damage. An important aspect of IPM is the extent to which biological control with a range of natural enemies, including insect parasitoids, predators and pathogens can affect the tef epilachna population. Mortality due to natural enemies varies depending on the target insects and may be severe enough to cause extinction of local populations (Lei and Hanski, 1997; Eber and Brandl, 1994; Washburn and Cornell, 1981), or be very trivial (Price and Craig, 1984; Embree, 1965). Therefore, the natural enemies of tef epilachna and their effect on its mortality need to be identified. Life table studies provide information required to identify these

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factors and can be an effective method for evaluating insect population dynamics and mortality factors (Bellows et al., 1992; Varley and Gradwell, 1970). Once mortality agents are identified, numerical and functional responses of agents, or group of agents, to changes in pest densities may be determined.

Serious outbreaks of *C. similis,* formerly known as *E. similis,* have occurred on wheat in the Rift Valley of Ethiopia (Wale, 1998), in barley in Chencha (A. Agena, pers. commun.) and Wolaita, South Ethiopia (Beyene et al., 2006) and possibly in other areas within the country and other tropical places in Africa. Until recently these outbreaks on cereal crops have not been controlled in Ethiopia due to unavailability of pest management options. Study on the biotic mortality factors and overall population dynamics of tef epilachna, therefore, would be essential contribution for developing sustainable crop protection strategies, and for safeguarding the health of agricultural environments.

2. Materials and materials

In 2003, during both the short and main rainy seasons, preliminary studies were conducted to assess the presence of natural enemies (parasitoids and entomopathogens) on the different stages of the tef epilachna (*C. similis*). Egg, larval and pupal specimens were collected from farmer's barley fields in Southern Ethiopia, Wolaita Zone. The collected specimens were reared in Petri dishes at the crop protection laboratory of the College of Agriculture, University of Hawassa. The emerged parasitoids were recorded and samples were preserved for identification.

In 2004 and 2005, data on population density and mortality factors of the tef epilachna were collected on barley fields in three locations namely, Damot Gale (37°49′56.5″ East and 6°55′36.2″ North, altitude 2136 m.a.s.l.), Sodo Zuria (37°49′10.1″ East and (6°54′16.9″ North, altitude 2213 m.a.s.l.) and Boloso Sore (37°41′17.8″ East and 7°04′24.0″ North, altitude 1722 m.a.s.l.) Woredas (Districts) in Southern Ethiopia, Wolaita Zone, over four seasons (two short and another two main growing seasons). These sites were within a distance of about 40 km.

The population densities of the different developmental stages of *C. similis* were estimated by sampling from insecticide free barley fields in the three locations, each more than 1600 m^2. Sampling of tef epilachna was started within the first week of the barley germination and continued weekly until crop maturity. Ten completely random samples throughout the field were taken using a 0.25 m^2 (0.5 m × 0.5 m) quadrate per plot from each barley field that was divided into four equal size plots. Average population density per quadrate from the total sum of the weekly counts (40 quadrates/week), converted to per 1 m^2 was calculated to estimate recruitment of the insects entering each life stage for the purpose of the life table analysis.

All arthropods found within the quadrates during sampling were assessed and recorded with samples preserved for identification. The number of egg batches, early larvae (1st and 2nd instars), late larvae (3rd and 4th instars), pupae and adults found within the quadrates were counted and recorded every week. The early and late larval instars are identified by their body size and colour. The early larval instars are dark in colour and become whitish at later stages.

Rearing of the developmental stages of the insect was undertaken in the crop protection laboratory of the University of Hawassa. The egg batches were sampled every week and reared in the laboratory separately using Petri dishes to assess the rate of parasitism (Southwood, 1966) and fertility. Eggs, which were not hatched, were checked under a dissecting microscope to detect whether they were unfertilised (empty eggs). When the eggs were darker they were dissected to detect either dead larvae or a parasitoid. Their spines or bristles on their body assisted identification of *C. similis* larvae. Samples of larvae were reared in Petri dishes individually to observe parasitism and/or pathogen development. Larvae were fed barley leaves until pupation. Pupae collected from the field were also kept in Petri dishes separately and were observed for the rate of parasitism. The parasitoids found during rearing in the laboratory were preserved for identification. The aggregate losses in the population to a specific factor were calculated from the losses in each sampling interval during the study.

2.1. Life table preparation

Data on the population density of the tef epilachna was classified into egg, early larvae (1st and 2nd instars), late larvae (3rd and 4th larval instars), pupae and adults. Based on the population density data and mortality of the tef epilachna, a total of six life tables representing three locations and 2 years of study (total 12 field generations) were prepared. The different stage intervals of the insect were organised into life tables as described by Harcourt (1969) and Morris and Miller (1954), where the different stage intervals were denoted by x, while l_x represents the number of individuals entering x over an entire generation. The number dying from different mortality factors and percentage mortality of l_x were represented by d_x and 100 q_x, respectively.

The estimates of the numbers entering successive stages were obtained by measuring the recruitment to each stage interval of the insect, the recruitment approach, (Van Driesche and Bellows, 1988; Van Driesche, 1988; Southwood, 1978). This approach provides direct assessment of the processes, which contributes to stage densities, and thus permits intermediate construction of the life table without recourse to stage-frequency analysis (Bellows and Van Driesche, 1999). The total numbers entering the stages were found by adding together the recruitments for all time periods during the sampling of generations. Population

density of adults, on the other hand, was estimated as the difference between the recruited and parasitized pupal population density, because the recruitment method applies for relatively immobile stages (Southwood, 1978).

The stage-specific marginal rates of mortality for each mortality factor were estimated from the observed (i.e., apparent) stage-specific mortalities based on the concepts proposed by Royama (1981), and later elaborated by Elkinton et al. (1992) and Buonaccorsi and Elkinton (1990). To estimate the over all effect of the mortality factors on a generation and to compare the role of population factors within the same generation real mortality, the ratio of the number dying in a stage (d_x) to the number initially entering the first stage in a life table (l_0) d_x/l_0 (Southwood, 1978), was calculated.

2.2. Key factor analysis

The relative contributions made by the individual mortality factors to the population dynamics of *C. similis* were determined by expressing mortalities as k values, the difference between the logarithms of l_x before and after the action of the mortality factor (Varley and Gradwell, 1960). The summation of sub-mortalities (individual k values) equalled total mortality (K): Total mortality $= K = k_1 + k_2 + k_3 + k_4$, where k_1 = egg mortality (k_{1a} = infertility of the eggs; k_{1b} = parasitism; k_{1c} = disappearance); k_2 = early larval mortality; k_3 = late larval mortality; k_4 = pupal parasitism.

Plots of each individual k_i over the generation were compared to the plot of K over the same generation to determine which of the components contributed the most to variation in K. The k_i plot that followed a similar fluctuating course as K was considered to be a key factor in the population dynamics (Varley et al., 1973; 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 for quantitative evaluation of the roles of each factor (k). The individual k value that gave the greatest slope, while maintaining a significant correlation coefficient (r) or coefficient of determination (r^2) was recognised as the key factor (Southwood, 1978; Podoler and Rogers, 1975).

Linear regression analysis was performed on the various sub-mortality factors (k-values) to test them for direct-density dependence by plotting each of them against the number of insects of a given cohort entering the stage (age interval) on which it acts. Significance of regression was used to suspect the presence of density dependence (Southwood, 1966).

Average population density per 2.5 m^2 or 10 quadrates (n = four sampling plots) of the total sum of the weekly counts of the life stages entering each stage (recruitment) and mortality data were analysed separately by location, four generations per 2 years (2004 and 2005) in one location each using linear regression analysis and ANOVA procedures of MINITAB Statistical Software 14 (Minitab Inc., 2003).

3. Results

The preliminary studies in 2003 discovered that the egg and pupal stages were attacked by different insect parasitoids. In addition to the parasitoids, some predators such as ladybird beetles, assassin bugs, spiders and other predatory beetles were also found in cereal fields attacked by *C. similis*. These results helped design further more detailed studies on the identification and significance of the natural enemies on the population dynamics of the insect pest.

The studies at the three locations in 2004 and 2005 showed that the population density of the different stages (egg, early larvae, late larvae and pupae) of *C. similis* varied depending on the season (Table 1). The population density of the first generation was significantly higher than the second generation at all locations throughout the study period. Variations in population density of the first generation were not observed at all the study areas except in one (Boloso Sore), where the population densities of all stages were significantly higher in 2004. Similarly, in the second generation but, the population densities of the larval and pupal stages at Boloso Sore were significantly lower in 2005 than in 2004.

3.1. Mortality and life tables

3.1.1. Egg mortality

In 2004, the egg mortality, the difference between the total number of egg and early larval population recruitments, of the first generation was between 53% and 56% with the average of 54.3%, while that of the second

Table 1
Chnootriba similis population mean (number of insects/2.5 m^2 ± S.D.; n = 4 sample plots) at three locations in Southern Ethiopia, 2004 and 2005

Location	Eggs	Early larvae	Late larvae	Pupae
Year 2004				
1st generation				
Boloso Sore	2293 ± 121a	1069 ± 22a	542 ± 24a	421 ± 39a
Damot Gale	2004 ± 130b	883 ± 54b	427 ± 41b	281 ± 15bc
Sodo Zuria	1870 ± 133b	867 ± 50b	376 ± 30b	293 ± 34bc
2nd generation				
Boloso Sore	1045 ± 72c	619 ± 72c	362 ± 25b	295 ± 35bc
Damot Gale	818 ± 24d	361 ± 50d	291 ± 40cd	242 ± 21cd
Sodo Zuria	739 ± 50d	399 ± 11d	208 ± 25d	165 ± 19e
Year 2005				
1st generation				
Boloso Sore	1944 ± 91b	867 ± 16b	429 ± 31b	342 ± 31b
Damot Gale	1937 ± 142b	852 ± 46b	409 ± 21b	329 ± 31b
Sodo Zuria	1810 ± 158b	813 ± 62b	408 ± 21b	319 ± 24b
2nd generation				
Boloso Sore	646 ± 45d	225 ± 28e	117 ± 18e	92 ± 14f
Damot Gale	787 ± 14d	367 ± 33d	236 ± 24c	192 ± 15de
Sodo Zuria	796 ± 80d	432 ± 30d	239 ± 28c	174 ± 19e

Means within columns followed by the same letter are not significantly different (Tukey's test; $P > 0.05$).

Table 2
Partial life table for *C. similis* in barley at Boloso Sore in 2004

x	l_x	d_x	d_xf	$100q_x$	s_x
Generation I					
Egg	917	45	Infertility	4.90	0.47
		432	Parasitism	47.10	
		12	Disappearance	1.33	
		489	Total	53.33	
Early larvae	428	211	Disappearance	49.30	0.51
Late larvae	217	49	Disappearance	22.58	0.77
Total larvae				60.75	0.39
Pupae	168	119	Parasitism	70.75	0.29
Adult[a]	49				
Population trend index[b] = 0.46					
Generation II					
Egg	418	16	Infertility	3.80	0.59
		143	Parasitism	34.30	
		11	Disappearance	2.57	
		170	Total	40.67	
Early larvae	248	103	Disappearance	41.53	0.58
Late larvae	145	27	Disappearance	18.62	0.81
Total larvae				52.42	0.48
Pupae	118	30	Parasitism	25.26	0.75
Adult[a]	88				
Population trend index[b] = 1.86					

Note: x = stage; l_x = number entering stage x; d_x = number dying during the stage; $100q_x$ = apparent generation mortality; d_xf = Mortality factor; s_x = survival rate of stage x.
Values for l_x and d_x are number of individuals per 1 m^2.
[a]Adult population density, estimated as total pupal recruitment less parasitized pupal hosts (not a direct recruitment measure like the other stages).
[b]Number of new generation egg divided by number of old generation eggs.

Table 3
Partial life table for *C. similis* in barley at Boloso Sore in 2005

x	l_x	d_x	d_xf	$100q_x$	s_x
Generation I					
Egg	778	29	Infertility	3.70	0.45
		376	Parasitism	48.30	
		26	Disappearance	3.40	
		431	Total	55.40	
Early larvae	347	175	Disappearance	50.43	0.50
Late larvae	172	35	Disappearance	20.35	0.80
Total larvae				60.52	0.39
Pupae	137	79	Parasitism	57.43	0.43
Adult[a]	58				
Population trend index[b] = 0.33					
Generation II					
Egg	258	21	Infertility	8.20	0.35
		96	Parasitism	37.30	
		51	Disappearance	19.62	
		168	Total	65.12	
Early larvae	90	43	Disappearance	47.78	0.52
Late larvae	47	10	Disappearance	21.28	0.79
Total larvae				58.89	0.41
Pupae	37	13	Parasitism	34.87	0.65
Adult[a]	24				
Population trend index[b] = 3.11					

Note: x = stage; l_x = number entering stage x; d_x = number dying during the stage; $100q_x$ = apparent generation mortality; d_xf = Mortality factor; s_x = survival rate of stage x.
Values for l_x and d_x are number of individuals per 1 m^2.
[a]Adult population density, estimated as total pupal recruitment less parasitized pupal hosts (not a direct recruitment measure like the other stages).
[b]Number of new generation egg divided by number of old generation eggs.

generation was between 40% and 56% with the average of 47.5% in the three locations. In 2005, the range of the egg mortality in the first generation was very narrow with the average of 55.5% as compared in the second generation where it was between 45% and 65% (average 54.7%) in the three locations (Tables 2–7). The egg mortality was very high in all locations throughout the study period and therefore contributed much to the population dynamics of the insect.

The mortality of the egg population of *C. similis* was caused by infertility of the eggs (k_{1a}), parasitism (k_{1b}), and disappearance (k_{1c}) due to unknown mortality factors. The egg parasitism was the major cause of the mortality and it was identified as *Ooencyrtus epulus* Annecke (Encyrtidae). Some predators might have caused the disappearance of the eggs.

3.1.2. Early larval mortality (k2)

In 2004, the mortality of early larvae, the difference between the population recruitment of early and late larval stages, of the first generation was from 49% to 56%, average 52.5% while of the second generation it was between 19% and 49% with the average of 36.4% in the three study locations. During the next year the record of the first generation mortality was between 50% and 52%, average 50.7% while it was from 36% and 48% with the average of 42.8% (Tables 2–7). The contribution of the early larval stage mortality to the changes in the density of the late larval stage was very high.

3.1.3. Late larval mortality (k3)

Mortality of the late larval stage (the difference between the late larval and pupal stages) was generally lower than the early larvae and it was between 23% and 35% with the average of 26.5% in the first generation while it was from 17% to 20%, average 17.7% in the three locations of the study in 2004. Similarly it was lower in 2005, too. The first generation had a mortality of 20–22% with average of 20.9% while in the second generation it was between 18% and 28% with average of 22.5% in all study areas (Tables 2–7).

The mortality of the larval stages (early and late larval stages) was recorded as disappearance. This disappearance might have been caused by different predators, which were found in the study sites. Insect predators, adults and larvae of ladybird beetles (Coccinallidae), assassin bugs (Reduviidae), larvae of hover flies (Syrphidae) and green lacewings (Chrysopidae), *Chlaenius* sp.

Table 4
Partial life table for *C. similis* in barley at Damot Gale 2004

x	l_x	d_x	d_xf	$100q_x$	s_x
Generation I					
Egg	802	26	Infertility	3.20	0.44
		417	Parasitism	52.00	
		6	Disappearance	0.79	
		449	Total	55.99	
Early larvae	353	182	Disappearance	51.56	0.48
Late larvae	171	59	Disappearance	34.50	0.65
Total larvae				68.27	0.32
Pupae	112	60	Parasitism	53.29	0.47
Adult[a]	52				
Population trend index[b] = 0.41					
Generation II					
Egg	327	11	Infertility	3.50	0.44
		106	Parasitism	32.50	
		65	Disappearance	19.96	
		183	Total	55.96	
Early larvae	144	27	Disappearance	18.75	0.81
Late larvae	117	20	Disappearance	17.09	0.83
Total larvae				32.64	0.67
Pupae	97	27	Parasitism	28.34	0.72
Adult[a]	70				
Population trend index[b] = 2.37					

Note: x = stage; l_x = number entering stage x; d_x = number dying during the stage; $100q_x$ = apparent generation mortality; d_xf = Mortality factor; s_x = survival rate of stage x.
Values for l_x and d_x are number of individuals per 1 m^2.
[a]Adult population density, estimated as total pupal recruitment less parasitized pupal hosts (not a direct recruitment measure like the other stages).
[b]Number of new generation egg divided by number of old generation eggs.

Table 5
Partial life table for *C. similis* in barley at Damot Gale 2005

x	l_x	d_x	d_xf	$100q_x$	s_x
Generation I					
Egg	775	18	Infertility	2.30	0.44
		398	Parasitism	51.30	
		19	Disappearance	2.40	
		434	Total	56.00	
Early larvae	341	177	Disappearance	51.91	0.48
Late larvae	164	33	Disappearance	20.12	0.80
Total larvae				61.58	0.38
Pupae	131	82	Parasitism	62.91	0.37
Adult[a]	49				
Population trend index[b] = 0.41					
Generation II					
Egg	315	11	Infertility	3.50	0.47
		116	Parasitism	36.70	
		41	Disappearance	13.13	
		168	Total	53.33	
Early larvae	147	53	Disappearance	36.05	0.64
Late larvae	94	17	Disappearance	18.09	0.82
Total larvae				47.62	0.52
Pupae	77	21	Parasitism	27.82	0.72
Adult[a]	56				
Population trend index[b] = 2.37					

Note: x = stage; l_x = number entering stage x; d_x = number dying during the stage; $100q_x$ = apparent generation mortality; d_xf = Mortality factor; s_x = survival rate of stage x.
Values for l_x and d_x are number of individuals per 1 m^2.
[a]Adult population density, estimated as total pupal recruitment less parasitized pupal hosts (not a direct recruitment measure like the other stages).
[b]Number of new generation egg divided by number of old generation eggs.

(Carabidae) larvae, earwigs and spiders were recorded during the study.

3.1.4. Pupal mortality (percent pupal parasitism, K4)

The percent mortality of the first generation pupal stage in 2004 was between 51% and 71% with average of 58.2% while it was lower in the second generation, which was between 25% and 31% with the average of 28.3%. The extent of the pupal mortality in 2005 was almost comparable to the 2004. It was from 57% to 63% with the average of 59.8% in the first generation and 28% and 35% with the average of 30.8% in the second generation (Tables 2–7).

Though insignificant percentage of pupal disappearance due to unknown mortality factors were recorded parasitism, parasitism was the main cause of the mortality. The pupal parasitoids were identified as *Mesopolobus* spp. (Pteromalidae) and *Pediobius foveolatus* Crawford (Eulophidae).

3.1.5. Fungus as mortality factor

Other than the natural enemies recorded on eggs, larval and pupal stages, the entomopathogenic fungus (*Beauveria* spp.) was found on adults. In 2004, between July and August a total of 383 adults tef epilachna were collected and most of them (218 adults) were died in pots of barley seedlings within 3–4 days of collection. Out of the dead adults 61 were developed white substances ('white bloom') on their body and this white mass of spores (conidia) was identified as *Beauveria* sp. fungus. The percent mortality was 56.92, however, the white masses of the spores were developed only on 15.93% of the adults and the cause could be the fungus.

3.1.6. Total mortality

Out of the deposited egg of *C. similis* more than 78% were lost before the adult stage and this was attributed to many mortality factors. The highest population reduction of 91% to nearly 95% (real mortality) was recorded from the first generation as compared to the 78% to nearly 85% (real mortality) from the second generation in all locations throughout the study period (Tables 8–10).

Although the real mortality on the larval stages especially on the early larval stage was significantly higher, the main mortality factor was not known as different factors might have been acted in a contemporaneous fashion.

The main mortality factors on the egg and pupal population were insect parasitoids. The graphical method

Table 6
Partial life table for *C. similis* in barley at Sodo Zuria 2004

x	l_x	d_x	d_xf	$100q_x$	s_x
Generation I					
Egg	748	58	Infertility	7.70	0.46
		341	Parasitism	45.60	
		2	Disappearance	0.31	
		401	Total	53.61	
Early larvae	347	196	Disappearance	56.48	0.44
Late larvae	151	34	Disappearance	22.52	0.77
Total larvae				66.28	0.34
Pupae	117	59	Parasitism	50.50	0.50
Adult[a]	58				
Population trend index[b] = 0.40					
Generation II					
Egg	296	20	Infertility	6.80	0.54
		109	Parasitism	36.90	
		7	Disappearance	2.25	
		136	Total	45.95	
Early larvae	160	77	Disappearance	48.13	0.52
Late larvae	83	17	Disappearance	20.48	0.80
Total larvae				58.75	0.41
Pupae	66	21	Parasitism	31.15	0.69
Adult[a]	45				
Population trend index[b] = 2.45					

Note: x = stage; l_x = number entering stage x; d_x = number dying during the stage; $100q_x$ = apparent generation mortality; d_xf = Mortality factor; s_x = survival rate of stage x.
Values for l_x and d_x are number of individuals per 1 m^2.
[a]Adult population density, estimated as total pupal recruitment less parasitized pupal hosts (not a direct recruitment measure like the other stages).
[b]Number of new generation egg divided by number of old generation eggs.

Table 7
Partial life table for *C. similis* in barley fieldat Sodo Zuria 2005

x	l_x	d_x	d_xf	$100q_x$	s_x
Generation I					
Egg	724	28	Infertility	3.80	0.45
		363	Parasitism	50.10	
		9	Disappearance	1.21	
		399	Total	55.11	
Early larvae	325	162	Disappearance	49.85	0.50
Late larvae	163	36	Disappearance	22.09	0.78
Total larvae				60.92	0.39
Pupae	127	75	Parasitism	58.97	0.41
Adult[a]	52				
Population trend index[b] = 0.44					
Generation II					
Egg	318	16	Infertility	4.90	0.54
		113	Parasitism	35.60	
		16	Disappearance	5.10	
		145	Total	45.60	
Early larvae	173	77	Disappearance	44.51	0.55
Late larvae	96	27	Disappearance	28.13	0.72
Total larvae				60.12	0.40
Pupae	69	21	Parasitism	29.74	0.70
Adult[a]	48				

Note: x = stage; l_x = number entering stage x; d_x = number dying during the stage; $100q_x$ = apparent generation mortality; d_xf = Mortality factor; s_x = survival rate of stage x.
Values for l_x and d_x are number of individuals per 1 m^2.
[a]Adult population density, estimated as total pupal recruitment less parasitized pupal hosts (not a direct recruitment measure like the other stages).
[b]Number of new generation egg divided by number of old generation eggs.

(Fig. 1–3) and the regression analysis (Table 11) confirmed that the egg parasitoid and the pupal parasitism were key factors in all locations throughout the study period. With the exception of the egg parasitoid at Boloso Sore which had a slope of 0.226, $r^2 = 86.9\%$ and significant at 90% probability, the egg mortality due to *O. epulus* and the pupal parasitism were highly significant at 95% probability (Table 11) for key mortality factor analysis.

The analysis for direct density dependence demonstrated that the egg parasitoid in Damot Gale and Sodo Zuria was direct density dependant factor with the slope of 0.000297, $r^2 = 97.8\%$ and 0.000237, $r^2 = 95.1\%$, respectively and they were significant at 95% probability (Table 12). In Sodo Zuria, however, it did not show significant values for density dependence though it had similar trend with a slope of $b = 000157$ and $r^2 = 73.5\%$. The pupal parasitism was significant at 95% probability for its population density dependence only at SodoZuria with the slope of 0.00333 and $r^2 = 96.0\%$ (Table 12).

4. Discussion

In this study, variation in seasonal population density was observed in Southern Ethiopia, Wolaita Zone.

Table 8
Real mortality ($100r_x$) per 1 m^2 of the 1st and 2nd generations of *C. similis* in barley field at Boloso Sore, 2004 and 2005

Stage	2004		2005		Mean	Mean ± S.D.
	1st	2nd	1st	2nd		
Egg	53.33	40.67	55.40	65.12	53.63	53.63 ± 10.05
Early larvae	23.01	24.64	22.49	16.67	21.70	21.70 ± 3.48
Late larvae	5.34	6.46	4.50	3.88	5.04	5.04 ± 1.12
Pupae	12.96	7.13	10.11	5.00	8.80	8.80 ± 3.48
Generation mortality	94.64	78.90	92.50	90.66	89.18	89.18 ± 7.04

S.D. = standard deviation.

Similarly, population density variations were also reported from earlier studies (Beyene et al., 2006).

Mortality of eggs was higher and the main cause was the insect parasitoid *O. epulus*. The egg parasitism was one of the two key mortality factors in the population dynamics of *C similis*. In this study, infertility of the eggs and disappearance, probably due to predators, were also recorded. Research reports show that other parasitoids were found in different places parasitizing on eggs of *C. similis*. *Goencyrtus epulus* (Agyen-Sampong, 1980) and *Paralitomastix polyphaga* (Descamps, 1956) were reported

Table 9
Real mortality ($100r_x$) per 1 m^2 of the 1st and 2nd generations of C. *similis* in barley field at Damot Gale, 2004 and 2005

Stage	2004		2005		Mean	Mean ± S.D.
	1st	2nd	1st	2nd		
Egg	55.99	55.96	56.00	53.33	55.32	55.32 ± 1.32
Early larvae	22.69	8.26	22.84	16.83	17.65	17.65 ± 6.86
Late larvae	7.36	6.12	4.26	5.40	5.78	5.78 ± 1.30
Pupae	7.44	8.41	10.63	6.80	8.32	8.38 ± 1.68
Generation mortality	93.48	78.74	93.73	82.36	87.08	87.08 ± 7.68

S.D. = standard deviation.

Table 10
Real mortality ($100r_x$) per 1 m^2 of the 1st and 2nd generations of *C. similis* in barley field at Sodo Zuria, 2004 and 2005

Stage	2004		2005		Mean	Mean ± S.D.
	1st	2nd	1st	2nd		
Egg	53.61	45.95	55.11	45.60	50.07	50.07 ± 5.00
Early larvae	26.20	26.01	22.38	24.21	24.70	24.70 ± 1.79
Late larvae	4.55	5.74	4.97	8.49	5.94	5.94 ± 1.77
Pupae	7.90	6.95	10.34	6.45	7.91	7.91 ± 1.73
Total Generation mortality	92.26	84.65	92.80	84.75	88.62	88.62 ± 4.53

S.D. = standard deviation.

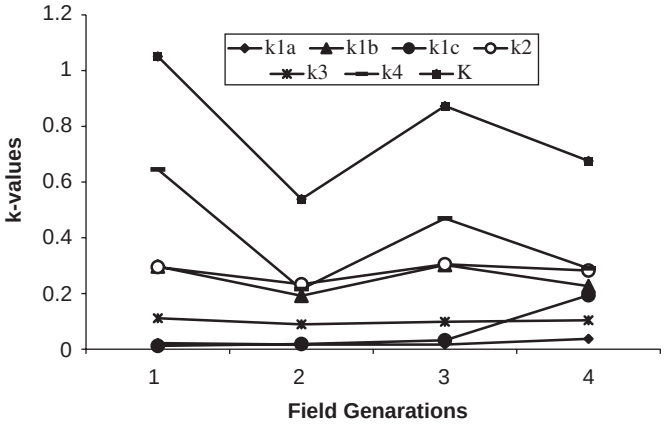

Fig. 1. Individual mortality fluctuations versus total mortality (*K*-value) over four field generations of *C. similis* at Boloso Sore, South Ethiopia in 2004 and 2005, where k_1 = egg mortality (k_{1a} = infertility of the eggs; k_{1b} = parasitism; k_{1c} = disappearance); k_2 = early larval mortality; k_3 = late larval mortality; k_4 = pupal parasitism.

as egg parasitoids of *C. similis* in Sierra Leone and Cameroon, respectively. In Ghana, two parasitoids, (*Coccidencyrthus* sp. and *Ooencyrtus* sp.) were reared from eggs (Scheibelreiter and Inyang, 1974). To the authors' knowledge, *O. epulus* is now reported for the first time in Ethiopia as egg parasitoid of *C. similis*.

Population density dependence of the egg parsitoid, *O. epulus* was observed in two locations in South Ethiopia.

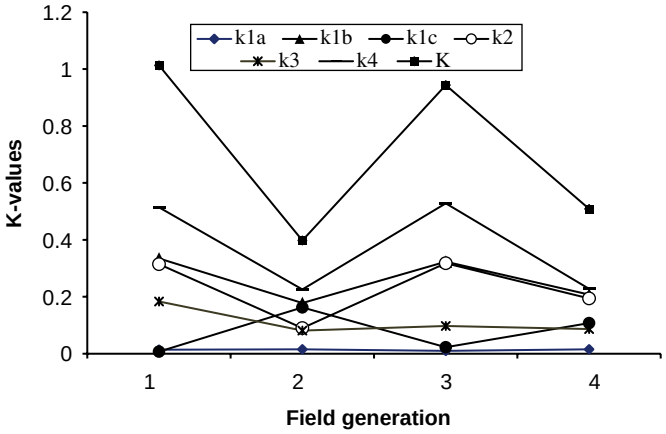

Fig. 2. Individual mortality fluctuations versus total mortality (*K*-value) over four field generations of *C. similis* at Damot Gale, South Ethiopia in 2004 and 2005, where k_1 = egg mortality (k_{1a} = infertility of the eggs; k_{1b} = parasitism; k_{1c} = disappearance); k_2 = early larval mortality; k_3 = late larval mortality; k_4 = pupal parasitism.

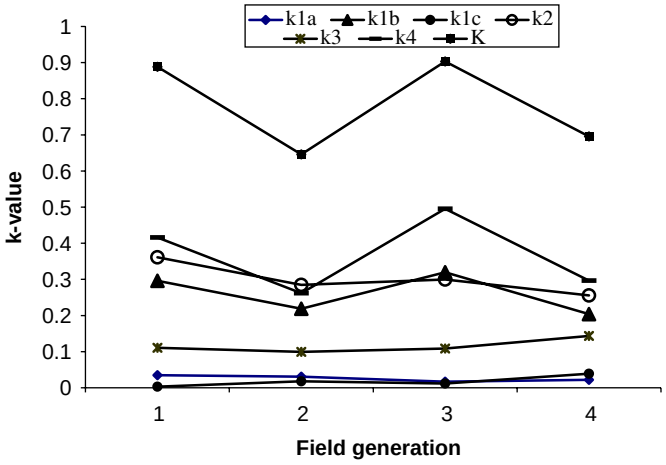

Fig. 3. Individual mortality fluctuations versus total mortality (*K*-value) over four field generations of *C. similis* at Sodo Zuria, South Ethiopia in 2004 and 2005, where k_1 = egg mortality (k_{1a} = infertility of the eggs; k_{1b} = parasitism; k_{1c} = disappearance); k_2 = early larval mortality; k_3 = late larval mortality; k_4 = pupal parasitism.

All the other mortality factors were acting in a density independent fashion except in one location (Sodo Zuria) where the second key mortality factor (pupal parasitism) was population dependant. This may suggest that the effect of the mortality factors was disturbance, which leads to a sporadic change in population density and implies that prediction of population density changes will be difficult Earlier reports also showed that *C. similis* had occasional outbreaks and seasonal variations in population density in different parts of Ethiopia (Beyene et al., 2006; Wale, 1998). However, due to the contemporaneous action of the mortality factors observed in this experiment, it is reasonable to predict that unnoticed density dependant relationship may exist.

Table 11
Linear regression of individual sub-mortalities (k-values) versus total mortality (K) over four field generations of *C. similis* at three locations in South Ethiopia in 2004 and 2005, where k_1 = egg mortality (k_{1a} = infertility of the eggs; k_{1b} = parasitism; k_{1c} = disappearance); k_2 = early larval mortality; k_3 = late larval mortality; k_4 = pupal parasitism

Location	Boloso Sore		Damot Gale		Sodo Zuria	
Sub-mortality	b	r^2 (%)	b	r^2 (%)	b	r^2 (%)
K_{1a}	−0.0061	2.0	−0.00571	47.98	−0.0085	1.9
K_{1b}	0.226	86.9[a]	0.258	99.9[b]	0.414	1.7[b]
K_{1c}	−0.129	11.1	−0.234	97.4	−0.234	97.4
K_2	0.116	66.7	0.342	92.8	0.238	49.3
K_3	0.0333	67.3	0.116	55.3	0.031	4.5
K_4	0.851	98.9[b]	0.542	96.4[b]	0.793	93.5[b]

b = slope; r^2 = coefficient of determination.
[a]r^2 = value at α level of 0.10.
[b]r^2 = value at α level of 0.05.

Table 12
Linear regression of individual sub-mortalities (k-values) against the number of insects entering the stage (age interval) on which it acts over four field generations of *C. similis* per site in three locations in South Ethiopia in 2004 and 2005

Location	Boloso Sore		Damot Gale		Sodo Zuria	
Sub-mortality	b	r^2 (%)	b	r^2 (%)	b	r^2 (%)
K_{1a}	−0.000019	34.7	−0.000007	54.2	−0.000000	0.0
K_{1b}	0.000157	73.5	0.000297	97.8[a]	0.000237	95.1[a]
K_{1c}	−0.0000546	68.5	−0.000715	83.8	−0.000121	56.18
K_2	0.000078	12.8	0.000866	85.4	0.00367	66.0
K_3	0.000025	3.8	0.000908	49.1	−0.000113	5.4
K_4	0.0024	48.8	0.000653	77.4	0.00333	96.0[a]

b = slope; r^2 = coefficient of determination.
[a]Indicates significant r^2 value at an α level of 0.05.

Mortality of the exophytic leaf-eating early and late larval stages of *C. similis* was estimated as a residual mortality caused by probably predators and some other biotic as well as abiotic factors because during this study there was no any record of a parasitoid or an entomopathogen, though, *Pleurotropis mediopunctata* and *Tetrastichus cydoniae* were reported as larval parasitioids in Cameroon (Descamps, 1956). The real mortality of the early larval stage was second highest following egg mortality, which validated the mortality, was higher at the early immature stages pertinent to the type IV survivorship curve described by Southwood (1978, 1966). Cornell and Hawkins (1995) also indicated that in exophytic herbivore insects generally, mortality is highest in early immature stages (egg and small larvae) and decrease with increasing age. Many predators were recorded during this study and estimating mortality due to predation is difficult because hosts that are preyed upon usually disappear from the system. In many life tables, mortality due to diseases and parasites is calculated, and predation is assumed to be the residual mortality that is unaccounted for other factors (Bellows et al., 1992). In fact this technique may underestimate the importance of predation because predation may be contemporaneous with other factors. Alternatively, predation effects may be overestimated if mortality rates due to abiotic, physiological, or unknown factors are high.

Pupal mortality was calculated and found to be very high with high contribution to the population change in the adult stages of the first and second generation. The main mortality factors for the pupal mortality were two insect parasitoids namely *Mesopolobus* sp. and *P. foveolatus*. *Mesopolobus* spp. is a moderately large, virtually cosmopolitan genus that includes a little over 100 described species. Most species are associated with gall-forming insects, but a few have been recorded as parasitoids of eggs and pupae of insects. No described species has been recorded from the pupa of a Coleopteran, although at least two species have been recorded as pupal parasitoids of Lepidoptera, e.g. Tortricidae. Species of the genus can be difficult to identify with certainty, but the present species is probably undescribed and is close to *M. fasciiventris* known only from Europe and the USA and which is associated with galls of Cynipidae (Noyes, 2005, pers. commun.). The second pupal parasitoid, *P. foveolatus*, on the other hand has a circumtropical distribution and is a well-known primary parasitoid of Epilachninae, Coccinellidae. It has been recorded from every stage except adult. It suppresses Mexican Bean Beetle (*Epilachna varivestis* Mulsant (Coccinellidae)) in soybean (Hooker and Barrows, 1989; Angalet et al., 1968) and being produced commercially for biological control. In Ethiopia, though the types of the parasitiods were not identified, pupal parasitism was reported on *C. similis* (Wale, 1998). In Ghana, *Pedibius amaurocoelus* was also reported as a pupal parasitoid (Scheibelreiter and Inyang, 1974).

Although, the adult mortality was not investigated thoroughly, entomopathogenic fungus was recorded, probably for the first time, on this insects and it was identified as *Beauveria* sp. Further studies on this natural enemy is important as it is known for its efficacy in management of different insect pests and it is available commercially. It is with a cosmopolitan distribution and a broad host range. It has been isolated from more than 200 hosts (Feng et al., 1994). Especially, *Beauveria bassiana* has been used in biological control of grasshoppers, scarab beetles and other insects (Hajek and Butler, 2000).

The present study shows that the egg and pupal parasitisms were key mortality factors in the population dynamics of *C. similis;* however, the egg parasitism was not enough to reduce the larval population to a tolerable level considering the damage it has been caused on cereal crops and the mortality of the larval stage, especially the late larval stage was not high. Besides, the larval mortality factors were not key factors. According to Beyene et al. (2006) and Scheibelreiter and Inyang (1974) late larval

stages cause the main leaf scarification. These conditions entail the need of pest management methods to reduce the population density of the larval stage to below economic injury level so that minimise the damage of on the crops. If the pest management targets the early larval stage right after hatching, the effect would help achieve early control results before the leaf injury has occurred.

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References

Abo, M.E., Alegbijo, M.D., Sy, A.A., Misari, S.M., 2001. An overview of the mode of transmission, host plants and methods of detection of rice yellow mottle virus. J. Sustain. Agric. 17, 19–36.

Agyen-Sampong, M., 1980. Parasites of rice pests of mangrove swamps in northern Sierra Leone. WARDA Tech. Newslett. 2, 1–3.

Angalet, G.W., Coles, L.W., Stewart, J.A., 1968. Two potential parasites of the Mexican bean beetle from India. J. Econ. Entomol. 61, 1073–1075.

Bellows, T.S., Van Driesche, R.G., 1999. Construction and analysis of life tables in the evaluation of biological control agents. In: Fisher, T.W., Bellows, Jr., T.S. (Eds.), Handbook of Biological Control: Principles and Applications. Academic Press, San Diego, CA.

Bellows, T.S., Van Driesche, R.G., Elkinton, J.S., 1992. Life-table construction and analysis in the evaluation of natural enemies. Ann. Rev. Entomol. 37, 587–614.

Beyene, Y., Hofsvang, T., Azerefegne, F., Berg, T., 2006. Geographical distribution, abundance and host plants of tef epilachna (*Chnootriba similis* Thunberg, Coleoptera, Coccinellidae) in Ethiopia. Int. J. Trop. Insect Sci. 26, 183–189.

Buonaccorsi, J.P., Elkinton, J.S., 1990. Estimation of contemporaneous mortality factors. Res. Popul. Ecol. 32, 151–171.

Cornell, H.V., Hawkins, B.A., 1995. Survival patterns and mortality sources of herbivorous insects: some demographic trends. Am. Nat. 145, 563–593.

Crowe, T.J., Shitaye, G.M., 1977. Crop Pest Handbook, third ed. Institute of Agricultural Research, Addis Ababa.

Descamps, M., 1956. Insectes nuisibles du riz dans le nord Cameroun. Agron. Trop. 11, 732–755.

Eber, S., Brandl, R., 1994. Ecological and genetic spatial patterns of *Urophora cardui* (Diptera: Tephritidae) as evidence for population structure and biogeographical processes. J. Anim. Ecol. 63, 187–199.

Elkinton, J.S., Buonaccorsi, J.P., Bellows, T.S., Van Driesche, R.G., 1992. Marginal attack rate, *k*-values and density dependence in the analysis of contemporaneous mortality factors. Res. Popul. Ecol. 34, 29–44.

Embree, D.G., 1965. The population dynamics of the winter moth in Nova Scotia, 1954–1962. Mem. Entomol. Soc. Can. 46, 3–74.

Feng, M.G., Poprawski, T.J., Khachatourians, G.G., 1994. Production, formulation and application of the entomopathogenic fungus *Beauveria bassiana* for insect control: current status. Biocontrol Sci. Technol. 4, 3–34.

Haile, A., Ali, K., 1985. A review of research on control of insect pests of small cereals in Ethiopia. In: Abate, T. (Ed.), Review of Crop Protection Research in Ethiopia. Proceeding of the First Ethiopian Crop Protection Symposium, 4–7 February 1985, IAR, Addis Ababa, Ethiopia. United Printers, Addis Ababa, pp. 57–77.

Hajek, A.E., Butler, L., 2000. Predicting the host range of entomopathogenic fungi. In: Follet, P.A., Duan, J.J. (Eds.), Non-target Effects of Biological Control. Kluwer Academic Publishers, Boston, pp. 263–276.

Harcourt, D.G., 1969. The development and use of life tables in the study of natural populations. Ann. Rev. Entomol. 14, 175–196.

Hill, B.G., 1966. Insects of cultivated and wild plants, Harar Province, Ethiopia. 1960–1964. Bull. Entomol. Res. 56, 659–670.

Hooker, M.E., Barrows, E.M., 1989. Clutch sizes and sex ratios in *Pediobius foveolatus* (Hymenoptera: Eulophidae), primary parasites of *Epilachna varivestris* (Coleoptera: Coccinellidae). Ann. Entomol. Soc. Am. 82, 460–465.

Lei, G., Hanski, I., 1997. Metapopulation structure of *Cotesia melitaearum*, a specialist parasitoid of the butterfly *Melitaea cinxia*. Oikos 78, 91–100.

Minitab Inc., 2003. MINITAB Statistical Software, Release 14 for Windows, State College, Pennsylvania. MINITAB® is a registered trademark of Minitab Inc.

Moharram, I.A., Al-Gasahem, M.Y., Morshed, A.E., Al-Mezgage, M., 1996. Collection and classification of insects and their natural enemies on cereal crops in Yemen. Arab. J. Plant Prot. 14, 47–53.

Morris, R.F., Miller, C.A., 1954. The development of life tables for the spruce budworm. Can. J. Zool. 32, 283–301.

Nwilene, F.E., 1999. Current status and management of insect vectors of rice yellow mottle virus (RYMV) in Africa. Insect Sci. Appl. 19, 179–185.

Podoler, H., Rogers, D., 1975. A new method for the identification of key factors from life-table data. J. Anim. Ecol. 44, 85–114.

Price, P.W., Craig, T.P., 1984. Life history, phenology, and survivorship of a stem galling sawfly, *Euura lasiolepis* (Hymenoptera: Tenthredinidae) on the arroyo willow, *Salix lasiolepis*, in northern Arizona. Ann. Entomol. Soc. Am. 77, 712–719.

Royama, T., 1981. Fundamental concepts and methodology for the analysis of animal population dynamics, with particular reference to univoltine species. Ecol. Monogr. 51, 473–493.

Scheibelreiter, G., Inyang, P., 1974. *Epilachna similis* Muls. (Coleoptera, Coccinellidae), a minor pest on maize in Ghana. Ghana J. Agric. Sci. 7, 75–79.

Schmutterer, H., 1969. Pests of Crops in Northeast and Central Africa with Particular Reference to the Sudan. Gustav Fisher Verlag, Stuttgart.

Schmutterer, H., 1971. Contribution to the knowledge of the crop pest fauna in Ethiopia. Z. Angew. Entomol. 67, 371–389.

Southwood, T.R.E., 1966. Ecological Methods, with Particular Reference to the Study of Insect Populations. Methuen & Co Ltd., London.

Southwood, T.R.E., 1978. Ecological Methods, with Particular Reference to the Study of Insect Populations, second ed. Chapman & Hall, London and New York.

Van Driesche, R.G., 1988. Measurement of population recruitment of *Apanteles glomeratus* (L.) (Hymenoptera: Braconidae), a parasitoid of *Pieris rapae* (L.) (Lepidoptera: Pieridae), and factors influencing adult parasitoid foraging success in kale. Bull. Entomol. Res. 78, 199–208.

Van Driesche, R.G., Bellows, T.S., 1988. Host and parasitoid recruitment for quantifying losses from parasitism, with reference to *Pieris rapae* and *Cotesia glomerata*. Ecol. Entomol. 13, 215–222.

Varley, G.C., Gradwell, G.R., 1960. Key factors in population studies. J. Anim. Ecol. 29, 399–401.

Varley, G.C., Gradwell, G.R., 1970. Recent advances in insect population dynamics. Annu. Rev. Entomol. 15, 1–24.

Varley, G.C., Gradwell, G.R., Hassell, M.P., 1973. Insect Population Ecology: An Analytical Approach. Blackwell Scientific Publications, London.

Wale, M., 1998. Outbreaks of tef epilachna (*Epilachna similis*) in wheat in the central Rift Valley of Ethiopia. Rachis 17, 65.

Washburn, J.O., Cornell, H.V., 1981. Parasitoids, patches, and phenology: their possible role in the local extinction of a cynipid gall wasp population. Ecology 62, 597–1607.