The Field Biology of Sorghum Chafer: its Temporal Occurrence and Overseasoning Habits

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Abstract

The investigation was initiated to study the temporal occurrence of the different life stages and inter-seasonal habits of sorghum chafer (*Pachnoda interrupta* Olivier) at three major outbreak areas located in the northeastern part of Central Ethiopia. Adult flight was monitored by trapping while events such as behavior over the dry season, oviposition, and larval occurrence were studied by regular soil sampling and field observations. *P. interrupta* is a univoltine insect; but the adults had two flight periods. The first flight period was September/October and the second June/July. The size of the beetle population in flight in both occasions had no significant correlation with rainfall and temperature. Adult *P. interrupta* stayed in diapause in the soil for 7–8 months from November to the following June/July. Eggs, larvae and pupae were recovered from July to the beginning of October. The mortality rate among adults was generally low during the dry season (October–June). Two parasitoids, *Adapsilia latipennis* (Walker) (Diptera: Pyrgotidae) and *Eutrixopsis* sp. (Diptera: Tachnidae), were identified attacking adult *P. interrupta*. Entomopathogenic fungi *Beauveria* sp. and *Metarrhizium* sp. were isolated from both adults and larvae. Unidentified bacterial/viral pathogens were also causing severe mortality in the larva. Total mortality as high as 96% was observed among larvae collected from one of the study sites, Werer.

Key words: sorghum chafer, *P. interrupta,* flight periods, aestivation, temporal occurrence

Introduction

Sorghum chafer, (*Pachnoda interrupta* Olivier) is a scarab beetle, which belongs to the Cetoniinae, which includes beetles whose adults are commonly associated with flowers and fruits of various plants. The larvae of Cetoniinae are commonly found in cattle manure and compost heaps (Donaldson 1984). Cetoniinae larvae also live in decaying vegetable matter, rotten wood, and in the nests of ants, bees, termites and even sometimes birds (Krikken 1984). *P. interrupta* was known in Ethiopia since the 1960s and reappeared in 1993 in the central region of Ethiopia (North Shewa) as a serious agricultural pest causing considerable damage to sorghum and maize (Clark and Crowe 1978, Hiwot et. al. 1999). Over the last ten years the beetle has become increasingly serious pest in field crops such as sorghum, maize and cotton. The genus Pachnoda comprises over 130 species (Grunshaw 1992), and in Ethiopia 9 species of Pachnoda were recorded (Clark and Crowe 1978). The range of activity and distribution of the beetle lies mainly between 530 and 2190 m and the, pest has seriously affected sorghum production in more than 49 woredas in the major growing areas of Amhara, Afar, Oromia, Tigray and Somali regional states, and the Dire Dawa Administrative Council. Studies indicate that the sorghum chafer situation is complex and challenging and it has been one of the major causes to the enormous yield reduction in sorghum. During extreme outbreaks, a total yield loss could occur in sorghum. The yield loss of sorghum during seasons of high infestation is estimated to be 80% (Yitbarek and Hiwot 2000). The damage caused by the pest on other crops like maize, wheat, sesame and noug is also high. Furthermore, the pest is known to cause serious damage to Acacia trees, the pods of which serve as a major feed for goats and camels of pastoralists in the Afar region.

Generally all Cetoniinae including *P. interrupta* prefer nectar, sap or juice of ripening fruits and vegetables; hence they are common visitors of flowers, where they feed on nectar and pollen or seeds at the milk stage. Sorghum chafer is a gregarious pest and the larvae feed on humus or litter. Studies on related species showed that beetles respond to a wide variety of plants, and when a beetle locates and feeds on an acceptable host, the volatiles are released from the damaged leaves (Harari et al., 1994). Additional beetles are attracted to these volatiles, which enable them to locate host plants more efficiently, the volatiles causing the beetles to aggregate in the vicinity of the host plant.

However, beetles in the genus Pachnoda appear to use both sight and floral scent for locating a food source (Clark and Crowe 1978). The adult *P. interrupta* requires a long period of time to become sexually mature and lay eggs. It usually spends in the soil over the dry season becoming sexually mature after this aestivation period. However, little was known about their activity.

Laboratory study on the biology of *P. interrupta* by Seneshaw and Mulugeta (2002) reported the estimated rate of oviposition as 12.6 eggs per week. Grunshaw (1992) in Mali observed that a single female laid upto 24 eggs per day. Seneshaw and Mulugeta (2002) reported that the duration of adult emergence under laboratory conditions varied considerably and ranged from two to three. The time required to complete development from egg to larva is about two months under similar conditions. When the larva pupates, it makes an oval pupal cell by cementing the soil with larval saliva. Pupal development is completed in about 20 days.

The appearance of adult *P. interrupta* in the field is known from the conspicuous outbreaks and the damage to the crops it infests. But little is known about the temporal occurrence of other life stages of the beetle in the field and the activity of the beetles during the dry season. The current study was made to give a complete picture of the beetles' habits and the temporal occurrence of the different life stages in relation to the seasons and the crop phenology in the field.

Materials and Methods

The study was conducted in three major outbreak sites — Rassa (Sefiberet and Merye), Aroge Minjar and Werer. Rassa and Aroge Minjar are sites in Kewet and Shenkora-Minjar Woreda of the Amhara National Regional State, respectively, while Werer is located in the Amibara Woreda of the Afar National Regional State. These sites are located in the east-central Rift Valley areas of Ethiopia and receive an annual rainfall of 350–750 mm. The annual average temperature of these areas varies between 24 °C and 30 °C. The altitude ranges from 750 to 1560 m. The areas are dominated by Acacia woodland and at the intermediate altitudes these areas are interspersed by small-scale farms. The separate biological events and stages such as emergence and presence of overseasoning adults, mating, oviposition and larval occurrence of *P. interrupta* was monitored by trapping, series of soil sampling and direct field observations.

Adult monitoring

The flight adult beetle was monitored using traps that were deployed throughout the year. The Japanese beetle traps (JBT) containing the floral attractant Phenethyl propionate/eugenol/geraniol 3:7:3 and banana was used. Preliminary observations confirmed that both lures (floral attractant and banana) attract the insect with statistically similar efficiency. The JBT was chosen because it was found to be effective in attracting other Scarabaeid beetle species (Donaldson et al. 1986, Harari et al. 1998) and was more effective than locally-made traps (unpubl. data). About 15 traps in Rassa (Sefiberet), 10 in Aroge Minjar and 20 in Werer were deployed in uncultivated bushland where *P. interrupta* was overseasoning. In Werer the traps were positioned in fruit crops (papaya, orange) adjacent to Acacia woodland at a height of 3 m from the ground. Beetles were physically trapped. The number and sex of beetles caught by the trap were recorded weekly during periods of low beetle flight activity in June and August, and daily when beetle populations were high in July and October. The relationship of beetles flight activity to some environmental factors such as rainfall and temperature was assessed. The monthly beetle catch in traps was used to investigate if it had any correlation with monthly rainfall amount and distribution and mean monthly maximum and minimum temperature.

Diapausing adults were also monitored by collecting soil samples weekly from beetle resting sites at Werer throughout the year. Field observations were made on mating and other behavior patterns during field visits in June/July. Males were distinguished from females by the shallow groove on the underside of the abdomen (Clarke and Crowe 1978). Females collected during the September/October flight were dissected to determine ovarial development (sexual maturity) to confirm whether they were from the same or different generations. The sex ratio of the beetles in flight was analyzed using Chi-square.

Monitoring for eggs and larvae

Surveys were conducted weekly where possible by sampling 30 cm x 30 cm x 30 cm plots in the soil, searching for eggs and larvae under the available vegetation. The number of grubs (categorized as small, < 1 cm; medium, 1-2 cm; and large, > 2 cm) were recorded on each sampling date. Soil samples were sieved to separate eggs from the coarser soil particles. Larvae collected at all sites were taken, together with some of the sampled media, to the laboratory, where they were reared to adulthood and species confirmed. Weekly soil samples were consistently taken throughout the year only at Werer. Sampling for pupae was not done as pupation took place deep in the soil profile, making regular sampling very inconvenient. In addition, other Cetoniinae make similar earthen cocoons and are very difficult to distinguish from *P. interrupta* at the pupal stage. Since the temporal occurrence of other life stages was known, the period during which pupation occurred was defined by extrapolation.

Observations on overseasoning P. interrupta

To ascertain beetles activity at aestivation sites over the dry season, 10 bushes at Meriye, 7 at Aroge Minjar and 10 plots (1 m x 20 cm soil) at Werer were marked. Each bush or digging spot was considered as a sample plot. The plots were sampled by digging to confirm the presence of beetles in the ground. Plots were marked only when enough beetles were found after digging. Plots with one or no beetles were discarded. The plots yielded varying numbers of beetles. Each plot was assigned a locality code and plot number, and the number of beetles recovered was recorded. The beetles were also sexed, and in case of Aroge Minjar and Werer they were marked before they were returned to the soil. All sampled beetles were returned to the soil. A needle was used to mark the dorsal side of the beetles, on the elytra, with a small drop of white synthetic enamel paint. The mark on the beetles was allowed to air-dry before replacing the insects in the soil near major roots and branches. Beetles at Meriye were not marked. A Chi-square analysis was done to confirm the sex

Figure 1 The flight periods of *P. interrupta* at Rassa, Sefiberet, in 2002 and 2003

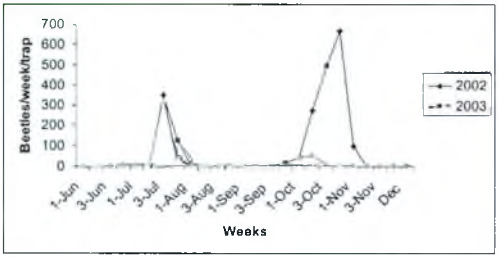
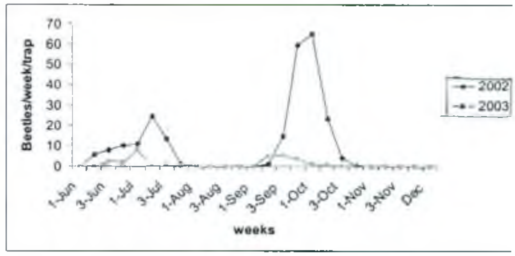


Figure 2 The flight periods of *P. interrupta* at Werer, 2002 and 2003



ratio of the beetles. A search was made at various soil depths in crop fields (cultivated land) adjacent to the plots (uncultivated land) to determine whether beetles aestivated at these sites. Farmers were asked to look out for beetles while plowing their fields; their observations were then communicated to the authors.

From the end of January to July, the marked beetles and the unmarked beetles in the case of Meriye were sampled on a monthly basis. Data were taken on the number, sex, and mortality of the sampled beetles. The position and movement of the beetles in the ground were noted when they were dug out. At the time of sampling, soil temperature and moisture at a depth most beetles were found in (15–30 cm) were recorded.

A soil Moisture Meter manufactured by Lincoln Irrigation (USA), with readings "0" to "10" was used and the soil moisture was measured by inserting the probe into the soil at each sampling plot. The moisture meter readings 0–1, 2–4, 5–6, 7–9 and 10 were designated as dry, average dry, average, average wet and wet (saturated), respectively. A monthly recovery line was plotted to indicate movement or activity of the beetles in the soil during the diapause period. Compost heaps that were 5–8 years old were surveyed in Amibara and Telalak Woreda, Afar Region ,for presence of adult *P. interrupta* during the dry (mid–May) and rainy (end of July) seasons.

Weight of overseasoning P. interrupta

Beetles recovered from Sefiberet, Meriye, Aroge Minjar and Werer were measured monthly from mid–February to the end of June 2003. Since the beetles begin to fly and feed in June after spending the long dry season in the soil, they were not weighed after June. A total of 40 beetles in groups of ten were weighed from each locality every month. The percentage weight loss was calculated from the mean weight of each group for each of the consecutive months. Weights were compared using ANOVA (SAS 1999) to determine whether differences were significant.

Results

Adults

According to the beetle counts from the trap catch, there were two peaks in adult activity and populations during 2002 and 2003 (figures 1 and 2). The second peak occurred during the second half of July (figures 1 and 2), which coincided with flowering and seed formation of wild hosts such as Acacia. The beetle is extremely polyphagous and although it was observed hovering and feeding on the flowers of several wild hosts, Acacia seemed to be the primary host plant. Mating males and females were observed in June/July, frequently coupled on the host plants with the male holding on to the back of the female for more than five minutes. After mating, the females returned to the soil for egg laying.

The first peak of the emerging beetle population occurred around mid–October (figures 1 and 2) and coincided with flowering and seed-set in early-planted sorghum and maize. There was no significant relationship between the size of beetle populations in flight and the amount and distribution of monthly rainfall and monthly mean minimum and maximum temperature (tables 1 and 2).

Most of the beetles maintained in the laboratory stayed alive for more than a year. The September/October beetle population was of mixed age, consisting of individuals from the generation that spent the long dry season in the ground from November to June/July and their progeny. Out of the dissected females, three of them were found with few unlaid eggs in their reproductive system and very little fat tissue around the gut and the reproductive structures. High levels of adult mortality were observed in August and September in the field, the dead might had been primarily composed of individuals from the population emerging from soil in June/July other than their younger offspring (figure 6). The mortality rate during the remaining portion of the dry season was

Figure 3.The oviposition period of *P. interrupta* in relation to soil moisture level at Werer

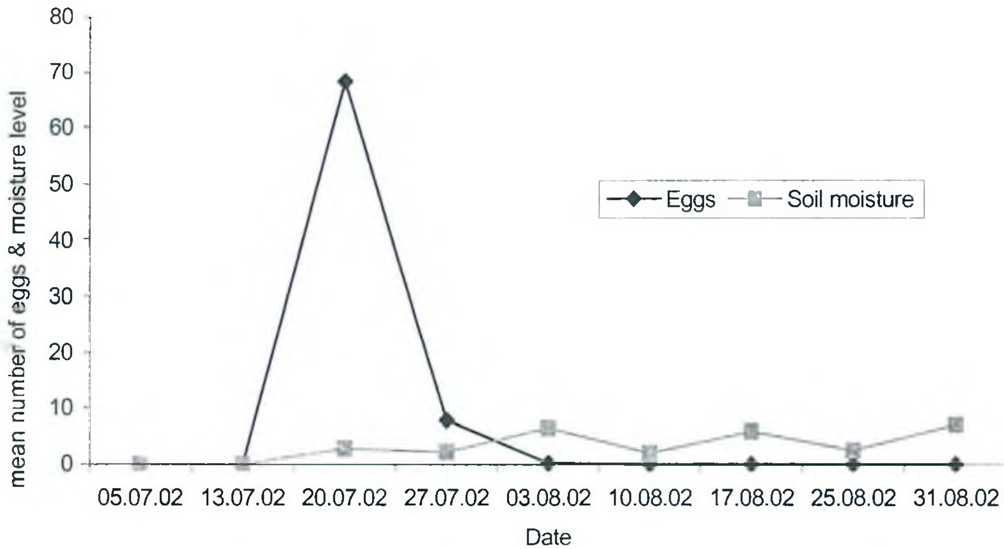
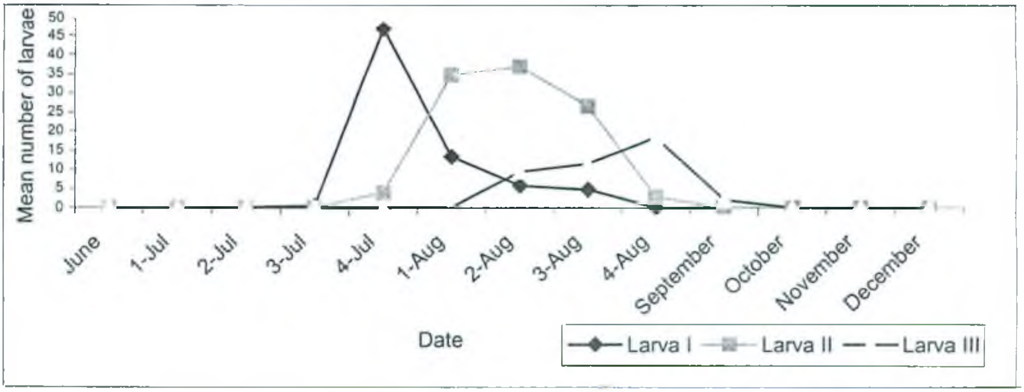


Figure 4. Seasonal distribution of larvae of *P. interrupta* at Werer, 2002



relatively low (figures 7, 8, and 9). Two parasitoids, *Adapsilia latipennis* (Walker) (Diptera: Pyrgotidae) and *Eutrixopsis* sp. (Diptera: Tachnidae), of adult *P. interrupta* were recovered. Entomopathogenic fungi *Beauveria* sp. and *Metarhizium* sp were isolated causing mortality in both adults and larvae.

Eggs and larvae

In the field, eggs and larvae were generally found in areas with high organic matter such as litter and plant debris. Field observations showed that aestivation sites were seen to be preferred oviposition sites for *P. interrupta*. The eggs were found to be spherical and white and darkened towards hatching. The egg-laying period coincided with the start of the rains and increased soil moisture in July (Figure 3). The egg-laying period was from early-mid July to the first week of August. Most of the eggs were laid at a very shallow depth (2–5 cm) and were often recovered together with early instars. The larval period extended from mid July to early October (Figure 4). The larvae were typical grubs with three pairs of legs on the thorax. It wriggled on its back with the legs upwards. Both larvae and eggs were found at similar depths in the soil. The early larval instars are largely inactive whereas the later instars move easily when disturbed. The larvae fed on organic matter in the soil. From the temporal occurrence of the eggs and the larvae we assume that the pupal period occurs during August and September.

Entomopathogenic fungi were significant mortality factors in the larval population. Of 509 *P. interrupta* larvae collected from Werer in July/August 2003, 488 died as a result of fungal infections. Most of the fungi isolated were *Metarhizium* and *Beauveria* spp. But *Asperigillus* and *Fusarium* spp. were also isolated from a few dead larvae. Unidentified bacterial/viral pathogens also appeared to be important mortality factors.

Fate of adult P. interrupta during the dry season

During the dry season from November to the following June/July, adult *P. interrupta* were found in the soil (Figure 5). They aestivated in soils beneath wild bushes and at the edges of streams or other waterways at the beginning of the dry season, sites where soil moisture levels are generally higher than in the surrounding 'open' areas. Preferred overseasoning sites comprised of light soils, usually containing high levels of organic matter under dense vegetation or bush cover. The beetles rested close to the plant roots in

Table 1. The relationship of some environmental factors with *P. interrupta* population in flight at Rassa, Sefiberet and Werer 2002 and 2003

Environmental factor	Rassa(sefiberet)			Werer		
	Mean ± SD	Correlation coefficient	Significance level	Mean ± SD	Correlation coefficient	Significance level
Total no. of monthly rainy days	3. 75 ± 3.14	0.23	ns	4.17 ± 4.26	0.04	ns
Monthly cumulative rainfall	59.2 ± 77.58	0.01	ns	30 ± 38.77	0.21	ns
Monthly mean maximum T (°C)	32.83 ± 0.84	-0.27	ns	35.09 ± 5.14	0.13	ns
Monthly mean minimum T(°C)	14.55 ± 2.20	-0.35	ns	4.17 ± 4.26	0.04	ns

Table 2. Compost heaps core temperature, and soil temperature and moisture status at which sorghum chafer was overseasoning, 2003

	Meriye soil	Minjar soil	Werer soil	Compost heaps core in May 2003
Mean T (^{0}C)	23.1	22.8	25.5	51
Range T (^{0}C)	18 – 28	18 – 27	25 –26	50 – 52
Moisture	dry (0 – 1.5)	dry (0 – 1)	dry (0 —2)	NA*

* NA, not applicable

heavily shaded areas. The bushes under which the beetles shelter were of mixed species. They include, *Acacia* spp., *Securinega virosa*, *Euphorbia* spp, *Opuntia ficus-indica*, *Carissa edulis*, *Grewia tenax*, *Euclea schimperi* and *Pithecolobium dulce*. When emerging from diapause, the beetles fed on all of these plants. The beetles preferred humus-covered soils close to the networks of roots of vegetation growing especially on the sides of gorges, streams or temporary waterways. Overseasoning sites were found to be at the edge of crop fields, but not in crop fields. According to observations made in the present study, *P. interrupta* neither overseasoned nor oviposited in cultivated land. Examination of compost heaps in Amibara and Telalak woredas of Afar Region in mid-May and at the end of July 2003 did not reveal any *P. interrupta*. On both occasions, only the citrus chafer *Rhabdotis*, adults (May) and larvae (July) were recovered. The mean temperature measured in 10 compost heaps in Amibara in mid-May was 51 °C while the mean soil temperatures where adult *P. interrupta* were found during the dry season (November–June) ranged from 18 °C to 28 °C (Table 2); indicating that *P. interrupta* prefers cooler sites.

In the trials where *P. interrupta* adults were buried and repeatedly dug up from the soil, beetles did not move very much in the soil once they had found and occupied a suitable niche in the ground as similar number of beetles were recovered from marked placement in the soil (figures 7, 8 and 9). At

Figure 5. The distribution of the different life stages throughout the year at Werer, 2002

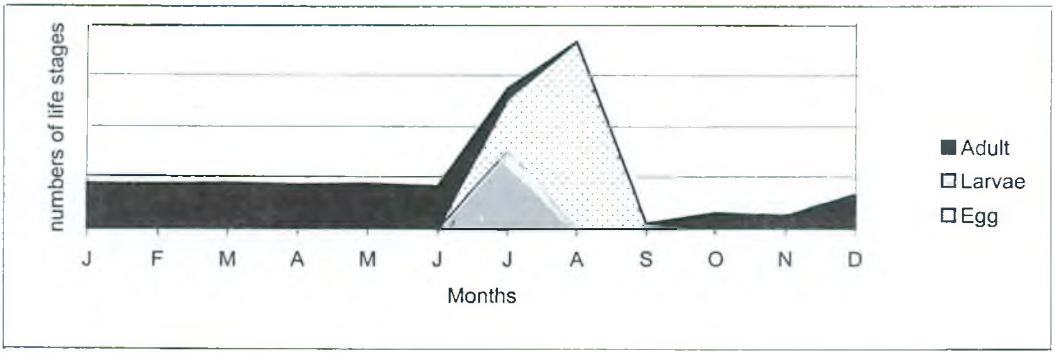
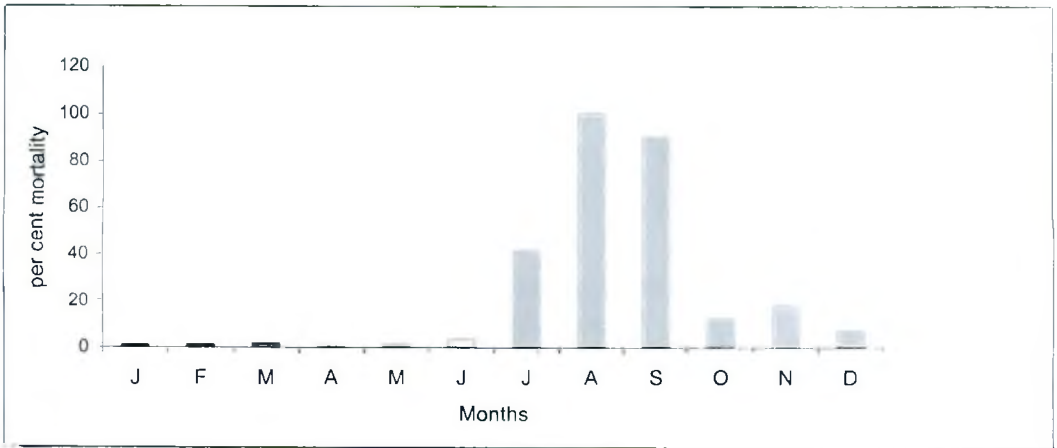


Figure 6. The seasonal distribution of mortality of adult *P. interrupta* at Werer, 2002/3



the Aroge Minjar sites, beetles were found as deep as 45 cm in the ground in soils with less organic matter. At aestivation sites where soils contained high levels of organic matter (decomposed litter, humus) in all localities, beetles were found at shallow depth (10–15 cm), occupying a position close to the roots of the shelter plants.

Observations made in Meriye, Aroge Minjar and Werer showed that overseasoning beetles were inactive. *P. interrupta* diapaused as adults in the soil for 7 to 8 months (November to June/July). Almost all beetles were recovered from approximately the same spots in which they had been placed in the preceding month. Some of the marked beetles were inadvertently injured during their recovery from the soil. In addition, a few were never recovered on each sampling date. The marked beetles were found within the previously dug soil horizon, essentially in the place they were buried the previous month.

The observation at Werer showed that more than 50% of the diapausing beetles did not emerge from the soil even by the last quarter of June (Figure 9). Mortality was moderate, about 21% during the beginning of the dry season (October/November) and was primarily caused by parasitization by *A. latipennis,* and became low (about 2%) as the season progressed.

Weight of overseasoning P. interrupta

Results indicated that beetles highly lost significantly more weight after April than in the preceding months (Figure 10). This trend was consistent across all sites; however, the rate of weight loss was not uniform for beetles collected from different sites.

Discussion

P. interrupta is a univoltine insect with a male–female ratio of 1:1 and has two flight periods per year (Figure 5). The activity of beetles strongly synchronized with the phenology of their host plants rather than weather-related factors such as temperature and rainfall. Mating, feeding and oviposition occured during the June/July flight period whereas adults in flight during September/October only fed to accumulate food reserves for the following dry season. A

Figure 7. Regular monthly recovery of overseasoning *P. interrupta* beetles from the soil at Meriye, 2003

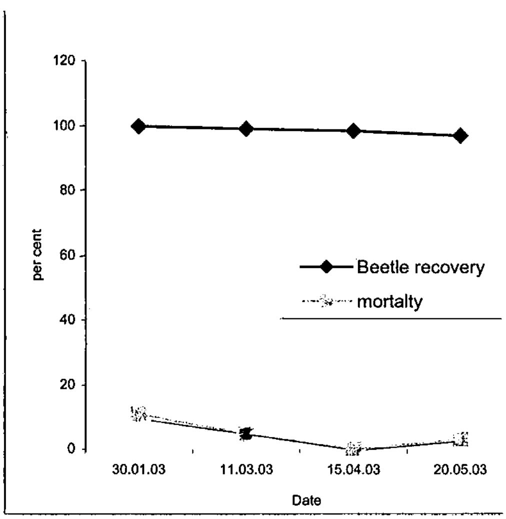
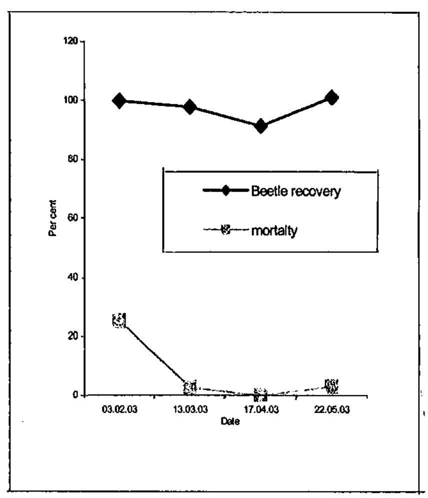


Figure 8. Regular monthly recovery of overseasoning *P. interrupta* beetles from the soil at Aroge, Minjar, 2003



long period of adult diapause/aestivation occurred between the two flight periods. There was very little beetle flight in August; at that time most of the beetles were either in the soil or might have died. The high level of adult mortality following the second peak of flight activity in August and September substantiates the latter view. Clarke and Crowe (1978) stated that beetles die in large numbers after completing egg laying. However, most of the adult mortality recorded during November and December appeared to be due to parasitization observed in beetles that were collected in the field and taken to the laboratory.

In the field, most of the female beetles primarily laid eggs in July in soils with high organic matter content. Donaldson and Giliomee (1992) observed that *P. sinuata flaviventris* beetles seek out areas containing a high concentration of organic matter for egg laying and oviposition takes place in damp soil. Both eggs and larvae were usually found at shallow depths in the soil. In the field the depth at which *P. sinuata flaviventris* eggs are laid is determined by the soil moisture level since eggs must remain in a moist environment to hatch (Donaldson 1985).

Moist and humus-rich soil appears to be a suitable medium for development of sorghum chafer grubs. When the larva pupates, it goes deeper in the soil and makes an oval cocoon from soil particles. Seneshaw and Mulugeta (2002) made similar observations in the laboratory. In the field, it is often difficult to distinguish *P.interrupta* pupae since other cetoniinae also make similar earthen cocoons (Donaldson and Gilomee 1992). At the beginning of September a mixed population of larvae, pupae and adults are present.

Towards the end of the crop season when sorghum grains and other host plants are mature, sorghum chafer adults enter in the soil for several months, emerging as sexually mature beetles in June/July. Overseasoning or diapausing sites preferred by the beetle are usually under dense vegetation or trees that offer full canopy protection from direct sunlight. Field observations during the current and previous studies in Ethiopia (Hiwot et al. 1999) repeatedly confirmed that no oviposition by sorghum chafer occurred in crop fields. Crop fields may not be preferred sites for oviposition and overseasoning because of the low levels of organic matter in the soil and the frequent disturbance of the soil profile by plowing or shilshalo. In Mali, however, Grunshaw (1992) recovered both adults and larvae of *P. interrupta* from millet fields.

P. interrupta do not diapause and breed in compost heaps in Ethiopia although other Cetoniinae such as *Rhabdotis* are frequently found associated with compost heaps. According to observations in the current study, the high temperature (51°C) reached in compost heaps in the Afar region seemed to be too high for the insect to aestivate especially when compared to the moderate soil temperature (a mean of 23.8 °C) experienced in aestivation sites. Donaldson (1984) noted that in South Africa that several Cetoniinae larvae are found in cattle manure and compost heaps.

Sorghum chafer adults diapause in the soil for 7 to 8 months (November to June/July) and are sexually mature at the end of this period. Clarke and Crowe (1978) stated that beetles like *P. interrupta* could take up to 12 months to reach sexual maturity. Seneshaw and Mulugeta (2002) observed that under uniform laboratory conditions maintained throughout the year, the beetle took about 10 months to sexually mature. Although *P. interrupta* did not take 12 months to become sexually mature in the current study, it appears that at least 9 months is required until mating and egg laying begins in the following season. The adult beetles were largely inactive in the soil, until emergence in June/July. While rainfall has been implicated as an emergence cue; beetles did not emerge before June inspite of considerable rainfall (200–315 mm) during the belg season (March and April).

This suggests that rainfall is not the only cue to emergence.

The trigger or token stimuli prompting aestivation and emergence is not known. In fact the absence of any significant correlation between the size of beetle population in flight, and rainfall and temperature, confirmed that adult *P. interrupta* were not responsive to such factors for most of the year (aestivation maintenance period). Rather these environmental factors may have an indirect effect such as their effect on *P. interrupta* as a result of their influence on host plant phenology.

While the emergence of adult *P. interrupta* from the soil did not appear to be triggered by rainfall and atmospheric temperature, rainfall and temperature played an important role in the overall development of the insect since oviposition and larval developmental periods coincided with months of high rainfall. The prevailing temperatures during these months not only affect the developmental rate of the immature stages, but also reproductive features such as fecundity, fertility and the incubation period of eggs (Beck 1983, Fan et al. 1992). Additional investigations need to be carried out to understand how temperature and humidity specifically affect the

Figure 9. Regular monthly recovery of overseasoning *P. interrupta* beetles from the soil at Werer, 2003

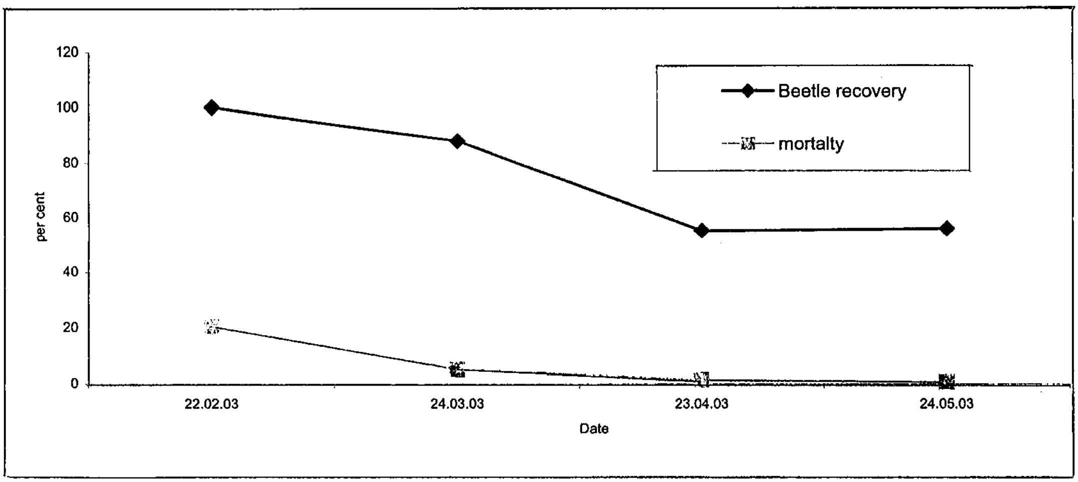
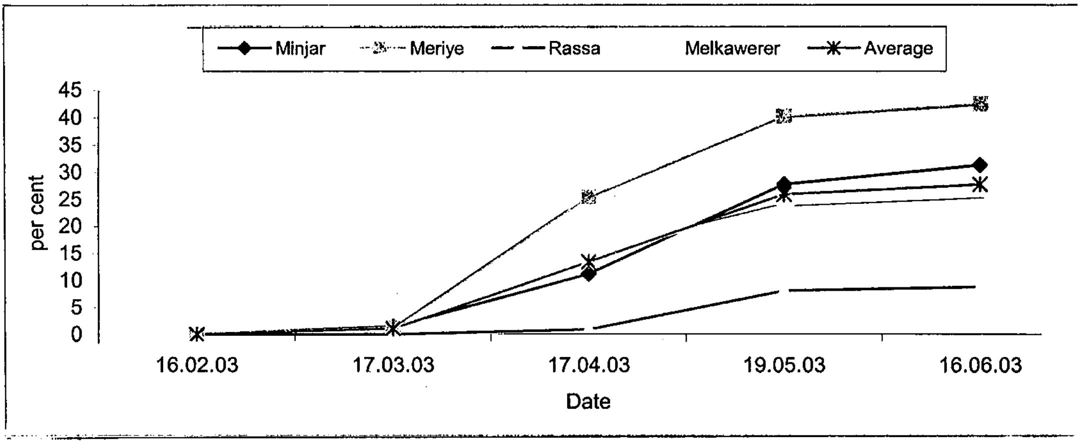


Figure 10. The percent weight loss of laboratory overseasoning *P. interrupta* beetles from February to June, 2003



development of *P. interrupta*.

The synchronization of the adult beetles' activity with the hosts' phenology reaffirmed the presence of a behavioral communication mechanism between the beetle and its hosts, which might be biochemical nature, for instance, plant metabolites. These biochemical factors might also be responsible for eliciting the onset of aestivation in the adult beetles toward the end of the season. Denlinger (1986) reviewed dormancy in tropical insects and discussed the various factors influencing diapause induction and termination in several tropical insect species.

The beetles' habit of overseasoning by entering the soil seemed to be a physiological requirement and they did not emerge from the soil until the diapause (aestivation) phase is completed. Since all beetles did not enter this dormant phase at the same time in November, they did not emerge simultaneously in June. A few remained in the soil in an inactive state in mid-July at Aroge Minjar.

The population of *P. interrupta* fluctuated between seasons. Such population fluctuations in insects can be independent of factors like food shortage and weather. Rather, the flucations may be determined by density-dependent biotic population regulators such as parasitoids, predators and pathogens, or infectious diseases (Kormondy 1996, Southwood 1978). The high percentage (96%) of mortality observed among larvae collected from Werer supported this hypothesis.

The factors responsible for breaking aestivation were not yet known, but soil moisture and temperature could play important roles. The aestivation phase of *P. interrupta* is a survival mechanism during the dry season when there is no suitable food available. Whether this dormant phase is obligatory or facultative remains to be determined. The significant decrease in adult weight towards the end of the aestivation period may be due to increased physiological activity, which might involve maturation of the reproductive system towards sexual maturity. Since beetles emerging in June and July have a lower weight than they had prior to aestivation in November, the June–July population is likely to be more susceptible to insecticides. The effect of weight on fecundity and susceptibility should be investigated further.

The reason for the re-emergence of *P. interrupta* as a serious pest in the early 1990s is unknown. Kormondy (1996) stated that under optimal conditions, a population's biotic potential, which is its intrinsic rate of increase, is inversely related to generation time. As the growth and development of any population is the result of two opposing forces, the biotic potential (capacity for reproduction) and mortality (death rate), the increase in the population of the univoltine sorghum chafer over the past decade can be viewed within the context of this basic ecological concept. It is very unlikely that the pest suddenly increased its biotic potential, although population increase through increased fecundity cannot be ruled out. The more plausible assumption would be that some of the natural mortality factors had less of an effect so that the population grew unchecked to reach outbreak status.

An in-depth ecological analysis of the mortality factors in all age groups, ranging from biotic to abiotic stresses, needs to be carried out over several years. This should include a detailed study of changes (and the reasons for these changes) in related plant and animal communities in the beetle's habitat. However, such resurgences are not unknown among insects. For instance, in 1997 the Cypress aphid (*Cinara cupressi)* occurred in a sudden outbreak affecting *Cupressus* spp. in urban and sub-urban areas of Tuscany, Italy, after a lapse of almost twenty years (Binnazi et al. 1998). Kormondy (1996) stressed the impact of predators, parasites, food quality and weather may interact in different ways at different times to cause population oscillations. Royama (1984) indicated the spruce budworm (*Choristoneura fumiferana*) populations oscillated for the last two centuries at an average interval of 35 years in USA due to a combination of biotic and abiotic factors.

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