NATURAL CONTROL OF *HELICOVERPA ARMIGERA* IN SMALLHOLDER CROPS IN EAST AFRICA

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Natural control of *Helicoverpa armigera* in smallholder crops in East Africa

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Aan mijn ouders

Stellingen

1 Alleen de evaluatie van natuurlijke vijanden in relatie tot de 'sterftetabel' (lifetable) van een plaag geeft een goede indruk van de werkelijke rol van natuurlijke vijanden.
Luck, R.F. , Shepard, B.M. & Kenmore, P.E. (1988) *Annual Review of Entomology* 33, 367-391.
Bellows, T.S., van Driesche, R.G. & Elkinton, J.S. (1992) *Annual Review of Entomology* 37, 587-614.
Dit proefschrift

2 Natuurlijke mortaliteit van Lepidoptera, bepaald middels veldbemonstering, wordt meestal sterk onderschat door te geringe aandacht voor bemonstering van het eistadium. De waarde van conclusies gebaseerd op sterftetabellen is daarom sterk afhankelijk van de wijze van bemonstering van het eistadium.
Hogg, D.B. & Nordheim, E.V. (1983) *Researches on Population Ecology* 25, 280-297.
Dit proefschrift

3 Het nut van een economische schadedrempel is beperkt omdat meestal wordt uitgegaan van een sterk vereenvoudigd, statisch ecosysteem. Wanneer biologische, fysiologische en economische variabelen in aanmerking genomen worden, wordt de bepaling van de economische schadedrempel te ingewikkeld.
Huffaker, C.B. (1980) *New Technology of Pest Control.* Wiley, New York.

4 Geïntegreerde plaagbeheersing (IPM; Integrated Pest Management) is een modeterm die vaak misbruikt wordt, bijvoorbeeld als het slechts om geleide bestrijding gaat.
Frisbie, R.E. & Adkisson, P.L. (1985), pp 41-51, In: Hoy, M.A. & Herzog, D.C. *Biological Control in Agricultural IPM Systems.* Academic, Orlando.

5 Biologen wordt vaak verweten dat hun voorkeur voor biologische bestrijding berust op een idealisme. Hoewel belangrijke gegevens over de rol van natuurlijke vijanden inderdaad veelal ontbreken, kan ervaring opgedaan in bepaalde systemen vertrouwen geven in de rol van natuurlijke vijanden in andere systemen.

6 Het gebruik van de woorden dawa en obat, ofwel medicijn, voor een insecticide in respectievelijk het Kiswahili en het Bahasa Indonesia impliceert dat de aanwezigheid van insekten gezien wordt als een ziekte die uitgeroeid moet worden, en niet als onderdeel van een gezond ecosysteem.

7 Het gebruik van insecticiden in soyaboon in Indonesië is in de meeste gevallen onwenselijk omdat daarmee natuurlijke vijanden die een grote invloed hebben op plaaginsekten worden uitgeroeid. Bovendien is de plant in staat aanzienlijke beschadiging door insekten te compenseren.
DBPT (1992) pp 12-23; In: *Pengedalian Hama Terpadu Tanaman Kedelai.* Balai Penelitian Tanaman Pangan, Malang.
H. van den Berg (1992) Report, International Institute of Biological Control, Kuala Lumpur.

8 Het streven naar duurzaamheid, in het geval van IPM, kan men realiseren door het ontwikkelen van expertise binnen de boerengemeenschap om onafhankelijk te analyseren, beslissingen te nemen, te handelen, te evalueren en te plannen in een dynamisch agroekosysteem.
Kenmore, P.E. (1983) *Returning pest control to villagers; the FAO-Intercountry IPC (rice) programme*. Conference Paper, IRRI, Los Baños, Philippines.
Lubis, M. & Dilts, R. (1991) *World Paper, October 1991*.
Slamet et al. (1993) *IPM Farmer Training: The Indonesian Case*. Indonesian National IPM Program, Jakarta.

9 Bij de beheersing van malaria gaat men te veel uit van bestrijding van de eigenlijke parasiet. Een gecoördineerde verwijdering van broedplaatsen van de vektor is de enige oplossing die voortdurende beheersing garandeert.
TIME, May 31, 1993
Takken, W., Snellen, W.B., Verhave, J.P., Knols, B.G.J. & Atmosoedjono, S. (1990) *Wageningen Agricultural University Papers* 90-7
Chan, K.L. & Counsilman, J.J. (1985) *Tropical Biomedicine* 2, 139-147.

10 De scheiding van onderzoek en de eigenlijke toepassing van onderzoek is een lang overheersende maar onterechte dichotomie die de ontwikkeling van vele projekten hindert.

11 Drie dingen zijn nodig om wetenschap te bedrijven: een raamwerk van concepten, eerlijke waarnemingen, en een sterke ontevredenheid met de discrepantie ertussen.
I. Copi & C. Cohen (1972) *Introduction to Logic, 9th Edition*.
Macmillan, New York.

12 De LUW-slagzin '75 jaar natuurlijk milieu voor wetenschap' geeft niet zozeer een lange termijn milieubewuste aanpak in de landbouw aan, maar eerder een langzaam geleerde les.

Stellingen behorende bij het proefschrift "Natural control of *Helicoverpa armigera* in smallholder crops in East Africa" door Henk van den Berg.

Wageningen, 1 oktober 1993

Contents

Preface

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Dr C.G. Ndiritu, Director, KARI, Dr A. Orodho, Regional Research Centre at Kakamega, and Mr Mambiri, National Fibre Crops Research Station at Kibos, and all their staff involved are gratefully acknowledged for KARI's co-operation and support. I would in particular like to thank the technical team who worked with me in western Kenya, Ayub Majisu, Efraim Chandi, Benson Mutulili, and Bonfas Musau, for close collaboration and friendships during the four seasons; without their assistance this work would not have been possible. Laban Akanga, Noah Aluodi and Bonfas Wabuko are thanked for preparation and management of experimental plots in western Kenya, and for acquainting me with local farming practices.

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The taxonomists of the International Institute of Entomology (IIE) and The Natural History Museum (London) are thanked for identifying insect specimens, and for providing useful information on natural enemy records during my preliminary studies in the UK in 1987. In particular, I would like to thank Andrew Polaszek and Gary Stonedahl for conducting detailed studies on our samples of Trichogrammatidae and Anthocoridae.

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Overview

The African bollworm, *Helicoverpa* (=*Heliothis*) *armigera*, is one of the worst agricultural pests in Africa, attacking a variety of food and cash crops. For development of sustainable pest management, it is essential to study the ecology and natural mortality factors of the pest, and recently, the need for the assessment of the role of natural enemies, through life table studies, has been stressed in a number of workshops that focussed on the pest.

Information available on the natural enemies of *H. armigera* in Africa is reviewed, using published, unpublished and museum sources (Chapter 3). A large variety of natural enemies is represented in almost 300 host records, including 83 parasitoids identified to species and 93 identified only to genus. The taxonomy, distribution, biology, alternative hosts or prey, host plant associations and secondary natural enemies are detailed for all recorded natural enemies, and the different aspects are summarized and evaluated for the total natural enemy complex.

During the three-year research programme reported here, *H. armigera* was studied in four crops commonly grown in smallholdings in Kenya: cotton, sunflower, maize and sorghum. The incidence of the pest varied widely between seven experimental sites in different agricultural zones of Kenya (Fig. 4.1). *H. armigera* only occasionally reached damaging levels. A number of parasitoids was recorded, but their impact on *H. armigera* was generally low; *Trichogrammatoidea* spp. egg parasitoids and *Linnaemya longirostris*, a tachinid late-larval parasitoid, were the most common species. Two groups of predators were predominant throughout Kenya: Anthocoridae (mainly *Orius* spp.) and ants (*Pheidole* spp., *Myrmicaria* spp. and *Camponotus* spp.), but their abundance fluctuated widely between sites (Fig. 4.3). Pathogens were scarce and did not play a significant role.

In-depth studies on life tables and assessment of predation were conducted at Kakamega and Kibos, both in western Kenya. Oviposition of *H. armigera* coincided with early flowering of the crops (Fig. 5.4), except for cotton, where the period of oviposition was extended (Fig. 12.6). Life tables showed that immature mortality was generally high (82-99.3 %) on sunflower, maize and sorghum, but stage-specific mortality varied greatly between seasons (Tables 5.3-5.5). Mortality of young stages was highest in maize (Fig. 12.2). Key factor analysis demonstrated that predation-and-unknown-mortality of both of young and late developmental stages was the most important mortality factor (Fig. 12.3).

Analysis of temporal and spatial association between numbers of pest stages and predators revealed that anthocorids are generally poorly associated with *H. armigera* eggs on sunflower and sorghum (Chapter 6). This partly explains the relatively high survival of young stages on sunflower. On maize, the association of anthocorids with eggs and larvae of *H. armigera* was stronger. Ants were better associated with *H. armigera* on sunflower than on maize or sorghum,

which might be responsible for the relatively high late-larval mortality on sunflower.

Parasitoids attacking this polyphagous pest are not equally common in different crops, but showed strong associations with particular crop species fed on by their host. In western Tanzania, a complex of three species attacked *H. armigera* larvae predominantly on sorghum, whereas parasitism by two other species concentrated on cotton (Fig. 7.1).

Techniques to assess the apparent and irreplaceable mortality of *H. armigera* due to predators, parasitoids and pathogens are discussed (Chapter 2). The role of predation and other, unknown mortality factors was studied in two crops where *H. armigera* causes most damage: sunflower (Chapter 8) and cotton (Chapter 9). Mortality was measured from stage-frequency data on the pest, supplemented with data on recruitment of eggs onto plants, in plots with and plots without predators. Ants were excluded by banding every plant in a sub-plot with insect trap adhesive. Anthocorids were excluded by applying low concentrations of insecticide which killed the predators but not the pest.

On sunflower, survival was higher than in previous trials. Exclusion of predators did not significantly affect survival of the pest (Table 8.2), however, anthocorids, which attack eggs but not larvae of *H. armigera*, appeared well after the oviposition peak of *H. armigera*. Moreover the density of ants was very low this particular season.

On cotton, survival was extremely low; only 6 % reached the second larval stage (Fig. 12.9), and exclusion of predators did not increase survival. Thus unknown mortality factors were very important and masked the effect of predation. This background mortality appeared to be related to the poor host-plant condition, and the low number of feeding sites (fruiting parts) for larvae due to drought.

To evaluate predators at greater pest densities, a series of predator exclusion cages and open control cages were inoculated with *H. armigera* eggs. Two weeks after inoculation, larval levels in the exclusion cages were 4 ½ times greater than those in the control (Table 10.1), indicating that predators are capable to suppress pest numbers. To evaluate mortality during the egg stage, we exposed marked egg cohorts on plants. Within 48 h, anthocorids sucked 12-65 % of the eggs, an additional 15 % was lost and 6 % parasitized (Table 11.1).

Implications of the findings for IPM, and areas for follow-up work are discussed (Chapter 12). Studies on intercropping cotton with maize or sorghum are promising and most feasible, because maize and sorghum may strongly affect natural enemy populations and pest infestation levels, while such methods stimulate sustainable agriculture in smallholdings. However, there will only be a brief period when the trap crop is attractive to ovipositing moths. A careful choice of varieties and planting dates might ensure the maximum effectiveness of trap crops in the case of sunflower. For cotton, where oviposition is extended over a period of three months (Chapter 9), planting of trap crops at regular intervals may be required, but a trap crop may be most crucial early in the season, because of its potential role to attract natural enemies into fields.

Overzicht

De Afrikaanse katoenrups, *Helicoverpa armigera* (=*Heliothis armigera*), is een van de meest schadelijke plaaginsekten in de landbouw in Afrika, en tast een groot aantal voedselgewassen aan. Voor een duurzame aanpak van plaagbeheersing is het belangrijk dat de ekologie en natuurlijke mortaliteit van de plaag bekend zijn. De noodzaak de rol van natuurlijke vijanden te evalueren is benadrukt op verschillende workshops waar deze plaag centraal stond.

Informatie beschikbaar uit gepubliceerde en ongepubliceerde bronnen en uit het Natural History Museum (Londen) over natuurlijke vijanden van *H. armigera* in Afrika is samengevat (Hoofdstuk 3). Er is een groot aantal natuurlijke vijanden van *H. armigera* bekend, afkomstig uit bijna 300 records, waarvan 83 parasieten geïdentificeerd op soort en 93 geïndentificeerd tot genus. De taxonomie, verspreiding, biologie, alternatieve gastheren of prooien, waardplant associaties en secundaire natuurlijke vijanden zijn weergegeven voor alle genoemde natuurlijke vijanden en deze verschillende aspekten zijn samengevat en geëvalueerd.

Gedurende een drie jarig onderzoeksprogramma werd *H. armigera* bestudeerd in vier gewassen die algemeen verbouwd worden in de kleinschalige landbouw in Kenia: katoen, zonnebloem, maïs en sorghum. Het voorkomen van de plaag varieerde sterk tussen de zeven experimentele velden in verschillende landbouwzones van Kenia (Fig. 4.1). Slechts enkele malen bereikte *H. armigera* dichtheden waarop ze duidelijke schade aanrichtten. Een aantal parasieten werd aangetroffen, maar hun invloed op de plaag was over het algemeen laag; *Trichogrammatoidea* spp. eiparasieten en *Linnaemya longirostris*, een tachinide parasiet die de oudere larven aanvalt, waren het meest algemeen. Twee groepen predatoren waren dominant door heel Kenia: Anthocoridae (voornamelijk *Orius* spp.) en mieren (*Pheidole* spp., *Myrmicaria* spp. en *Camponotus* spp.), maar hun aantallen varieërden sterk van lokatie tot lokatie (Fig. 4.3). Pathogenen waren zeldzaam en speelden dus geen belangrijke rol.

Gedetailleerde studies aan 'life tables' en predatie werden uitgevoerd in Kakamega en Kibos, beiden in West-Kenia. *H. armigera* ovipositeerde gedurende de vroege bloei van de gewassen (Fig. 5.4), behalve op katoen, waar ovipositie over een langere periode plaats vond (Fig. 12.6). 'Life tables' toonden aan dat de mortaliteit van vroege plaag stadia (eitjes en jonge larven) op zonnebloem, maïs en sorghum gewoonlijk hoog was (82-99.3 %), maar mortaliteit van verschillende stadia varieerde sterk van seizoen tot seizoen (Tabel 5.3-5.5). Mortaliteit van jonge stadia was het hoogst op maïs (Fig. 12.2). Sleutelfaktor analyse liet zien dat de predatie-plus-onbekende-mortaliteit van zowel jonge als late ontwikkelingsstadia de belangrijkste mortaliteits factor was (Fig. 12.3).

Een analyse van de associaties tussen plaag en predatoren in tijd en ruimte liet zien dat het voorkomen van anthocoriden weinig overeen kwam met dat van *H.*

armigera eitjes op zonnebloem en sorghum (Hoofdstuk 6). Dit verklaard ten dele de relatief hoge overleving van jonge stadia op zonnebloem. Op maïs waren anthocoriden sterker geassocieerd met eitjes en larven van *H. armigera*. Het voorkomen van mieren was sterker geassocieerd met *H. armigera* op zonnebloem dan op maïs en sorghum, en dit kan de oorzaak zijn van de relatief hoge mortaliteit van oudere larven op zonnebloem.

Parasieten van deze polyfage plaag kwamen niet in gelijke mate voor op de verschillende gewassen, maar waren veelal sterk geassocieerd met bepaalde waardplanten van hun gastheer. In het westen van Tanzania vielen drie parasieten van *H. armigera* de plaag voornamelijk aan op sorghum, terwijl twee andere soorten de plaag voornamelijk parasiteerden op katoen (Fig. 7.1).

Methodes om de rol van predatoren, parasieten en pathogenen te bepalen zijn geëvalueerd (Hoofdstuk 2). De rol van predatie en andere, onbekende, factoren werd bestudeerd op twee gewassen waar *H. armigera* de meeste schade aanricht: zonnebloem (Hoofdstuk 8) en katoen (Hoofdstuk 9). In velden met en velden zonder natuurlijke populaties van predatoren werd de mortaliteit van *H. armigera* bepaald aan de hand van dichtheden van de verschillende stadia in het veld. Bovendien werd de influx van eitjes dagelijks bepaald. Mieren werden van planten gehouden door alle planten in een veldje te voorzien van een ring van insektelijm aan de basis van de plant. Anthocoriden werden verwijderd door met een lage concentratie insekticide te spuiten, dat predatoren doodde zonder *H. armigera* te beïnvloeden.

Op zonnebloem was de mortaliteit van *H. armigera* lager dan in de voorgaande proeven. Verwijdering van predatoren gaf geen significant lagere mortaliteit te zien (Tabel 8.2). Anthocoriden verschenen echter pas nadat de eitjes van *H. armigera* zich tot larven ontwikkeld hadden, en anthocoriden vallen eitjes, maar geen of bijna geen larven van *H. armigera* aan. Bovendien was de dichtheid van mieren erg laag dit seizoen.

Op katoen was mortaliteit van *H. armigera* erg hoog. Slechts 6 % bereikte het tweede larvale stadium (Fig. 12.9) en mortaliteit werd niet verlaagd door verwijdering van predatoren. Blijkbaar overschaduwden andere, onbekende, mortaliteitsfaktoren de rol van predatie. Deze mortaliteit leek verband te houden met de slechte toestand van de waardplant en het lage aantal vruchten als gevolg van droogte.

Om hogere dichtheden van *H. armigera* te verkrijgen, werd een serie experimenten uitgevoerd met veldkooien zonder predatoren en controle kooien die ieder geïnoculeerd waren met eitjes van *H. armigera*. Twee weken na inokulatie waren er in de kooien zonder predatoren 4½ maal zoveel *H. armigera* larven als in de kontrole (Tabel 10.1), wat aangeeft dat predatoren een belangrijke invloed hebben. Verder werd de mortaliteit op het eistadium bekeken aan de hand van gemerkte eitjes van een zelfde leeftijd. Na 48 uur hadden anthocoriden 12-65 % van de eitjes leeggezogen, was 15 % verdwenen en was 6 % geparasiteerd (Tabel 11.1).

Het belang van de resultaten voor geïntegreerde bestrijding en mogelijke vervolgstudies zijn geëvalueerd (Hoofdstuk 12). Vervolgstudies aan mengteelten

van katoen met maïs of sorghum zijn veelbelovend, niet alleen omdat een dergelijke aanpak duurzame landbouw stimuleert, maar ook omdat maïs en sorghum de populaties van natuurlijke vijanden en de aantasting door de plaag sterk zouden kunnen beïnvloeden. Er is echter slechts een korte periode dat maïs en sorghum eileggende motten sterk aantrekken, en dus weghouden van het hoofdgewas. Voor zonnebloem kan een weloverwogen keuze van variëteiten en datum van aanplant een maximaal effekt van 'trap crops' worden verkregen. Voor katoen, waar ovipositie over een langere periode plaatsvindt, kan het nodig zijn de 'trap crop' regelmatig te planten, maar deze is waarschijnlijk het belangrijkst vroeg in het seizoen, vanwege zijn rol in het aantrekken van natuurlijke vijanden in het veld.

Part I

Background and Review

1

The African bollworm problem

ON A GLOBAL SCALE, few insect pests cause as much economic crop losses as does *Helicoverpa armigera* Hübner (Lepidoptera: Noctuidae), better known under its previous name *Heliothis armigera* (Reed & Pawar 1982). This species is widely distributed from the Pacific, Australia, through Southeast and South Asia, the Middle East and southern Europe to Africa (CAB 1968). As is typical of the Noctuidae, *H. armigera* is highly polyphagous (Pearson 1958, Bilapate 1984, Zalucki *et al.* 1986), attacking a great variety of agricultural crops, and is a major pest on cotton, tomato, tobacco, sunflower, legumes and cut-flowers. Damage is frequently localized on the nitrogen-rich reproductive plant parts, and thus influences yield directly.

A high fecundity and a short generation time give *H. armigera* great capacity to increase (Fitt 1989). Over a reproductive lifetime of 5-10 days, female moths produce 200-1200 near-spherical eggs (diam. 0.5 mm) (Reed 1965b), which are deposited singly on plants (Beeden 1974). Nocturnal flights and oviposition mostly occur just after dusk (Topper 1987b). Adults are strongly attracted to crops which provide honeydew or nectar, and feeding extends their lifespan. Under local temperatures in Tanzania, larvae develop in 21 days and pupae in 17 days (Reed 1965b). With a pre-oviposition period of 1-4 days (Singh & Singh 1975), and an egg development period of 4-5 days (Chapter 11), the generation time is roughly 45 days. A proportion of the pupae may enter summer diapause (Reed 1965a, Roome 1979, Hackett & Gatehouse 1982) or winter diapause (see Fitt 1989).

Generally, *H. armigera* larvae live hidden within the fruiting parts of the plant during most of their development, which makes them less vulnerable to insecticides. Moreover, *H. armigera* has a strong ability to develop resistance to insecticides (Collins & Hooper 1984), and cases of resistance of *H. armigera* to organochlorines and pyrethroids in the field have been reported in several parts of the world (Whitlock 1973, Wilson 1974, Goodyer *et al.* 1975, Gledhill 1982, Eveleens 1983, Collins 1986, McCaffery & Walker 1991). Because of low damage levels, control of *H. armigera* in some high-value crops such as cotton, tomatoes, tobacco and cut-flowers mostly depends on a heavy and regular use of insecticides.

The disadvantages of intensive pesticide usage have become widely recognized. Besides causing resistance in pests, chemical pesticides are expensive to the farmer, have adverse effects on the environment, and cause health hazards (Balk & Koeman 1984). Moreover, pesticides cause destruction of natural enemy complexes, and hence disrupt the natural balance that often exists between pests and their natural enemies (Ehler *et al.* 1973, Eveleens *et al.* 1973). In the absence of insecticides, natural enemies may maintain Heliothinae at

subeconomic levels (King & Coleman 1989). In Tanzania and the Sudan, there are indications that the impact of parasitoids on *H. armigera* in cotton declined during the last decades as the use of insecticides increased (Reed 1965b, Balla 1981). This stresses the need to develop control strategies which seek to maximize the contribution of natural enemies to depression of *H. armigera* populations (Greathead & Waage 1983). Biological control is especially important to smallholder farmers with limited capital reserves, since biological control is generally less costly than chemical methods, and does not cause degradation of resources.

There are examples from several areas in Africa, Asia and Australia where the bollworm has developed from an important but manageable agricultural pest into a major threat to agriculture, mainly in cotton, following agricultural intensification (Matthews 1989). This has led to diversion to other crops or even abandonment of certain areas. Besides the effects of pesticides, other factors that have contributed to the resurgence of *H. armigera* include the expansion of agricultural areas, improved crop husbandry and irrigation (Balla 1982, Bottrell & Adkisson 1977).

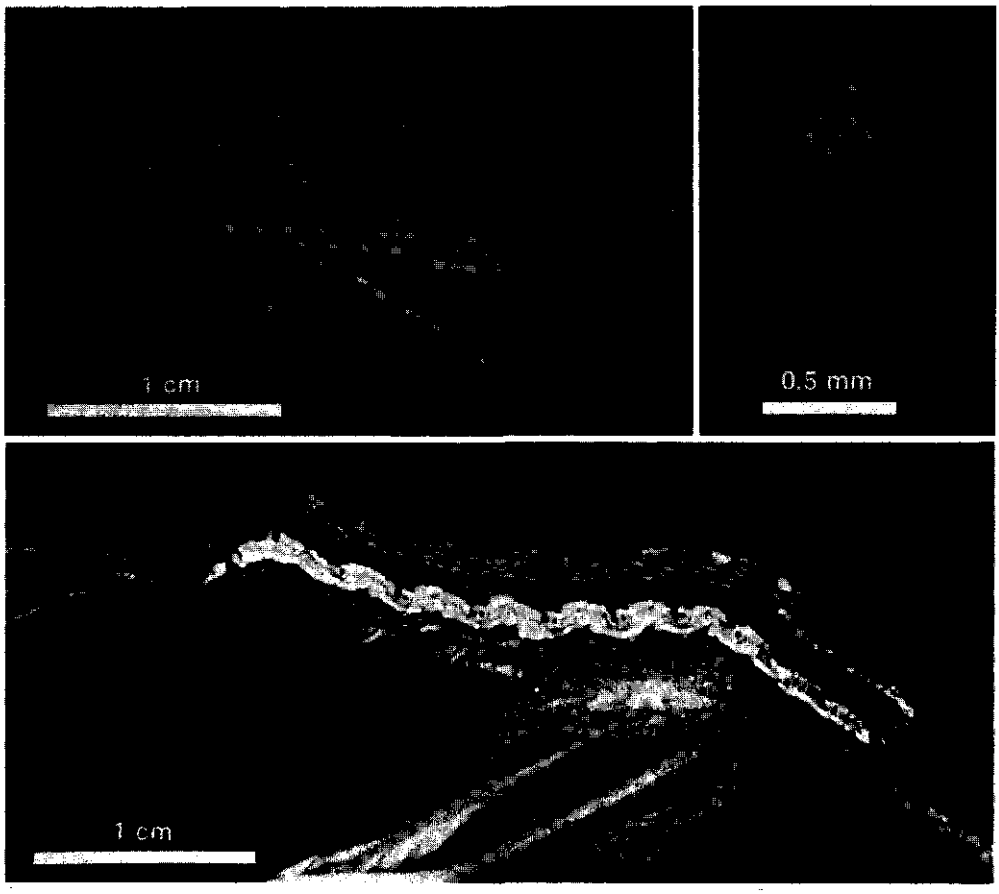

Fig. 1.1 *H. armigera* moth, egg, and larva feeding on weed-crop *Cleome* sp. (Capparidaceae).

Recently, the ecology and biological control of Heliothinae have received much attention; a number of reviews have been published (Zalucki *et al.* 1986, Fitt 1989, King & Coleman 1989), and several regional and international workshops have been held on the subject (Twine 1981, ICRISAT 1982, Johnson *et al.* 1986, Zalucki & Twine 1986, King & Jackson 1989). Despite the accumulating amount of information, it was generally concluded that there is a conspicuous lack of sound data on natural mortality and the role of predators and parasitoids for any major region, including Africa. A few exceptions are studies by Hogg & Nordheim (1983) in North America, and by Kyi *et al.* (1991) and Room *et al.* (1991) in Australia.

In Africa, a large complex of natural enemies has been recorded attacking *H. armigera* (Chapter 3, Greathead & Girling 1989), but studies mostly focused on parasitoids, particularly larval parasitoids. Data on natural mortality are restricted to percentage parasitism or pathogens in field samples. In a few cases, predators have been mentioned as potentially important control agents, but no detailed studies exist on their impact on *H. armigera*. Moreover, lifetables on *H. armigera* in Africa do not exist. Most studies on *H. armigera* were conducted in southern and eastern Africa, and commonly involved a variety of agricultural crops, with cotton as the principal crop for study.

In southern Africa, early research on *H. armigera* concentrated on the phenology of oviposition (Parsons & Ullyett 1934, Parsons 1940b), and parasitism of eggs and larvae (Parsons & Ullyett 1936, Jones 1937, Parsons 1940a). Parasitism sometimes accounted for considerable mortality of the pest, but could not explain the low level of larvae surviving from the eggs (Pearson 1958). Since the 1940s, little research has been conducted on the ecology of *H. armigera* in southern Africa (Roome 1975, van Hamburg 1981), as the emphasis was diverted to chemical methods of control.

In eastern Africa, Coaker (1959) found that *H. armigera* was not a serious pest in cotton and other crops in southern Uganda, and theorized that the year-round availability of food plants allowed a balance between the pest and its natural enemies. In western Tanzania, on the other hand, there is a distinct dry season during which pest and natural enemy populations are low. At the onset of the rains, *H. armigera* usually reached high levels, while its natural enemies arrived after damage had occurred (Reed 1965b). In this respect, a closed season during which crops are banned from certain areas (Reed 1965b, Reed & Pawar 1982), may adversely affect natural enemy populations, and could be responsible for increased *H. armigera* levels in the early crop (Pearson 1958). If natural enemies do play a crucial role in the dynamics of *H. armigera*, conservation and encouragement of their populations may have great implications for control of *H. armigera*.

Following Reed's studies in western Tanzania, Nyambo (1988) observed that increased growing of chickpea and tomato during the dry season provided food plants to *H. armigera* in the unfavourable period. Further, she found that parasitism and pathogens were important mortality factors, but could not prevent

economic damage on such crops as cotton (Nyambo 1990). In Kenya, reports on *H. armigera* are limited to the study of Rens (1977), who found that maize could distract *H. armigera* from neighbouring cotton.

In East Africa, agricultural crops are predominantly grown in smallholder systems, rather than in large schemes. These smallholdings typically consist of a mosaic of small plots of maize, cotton, sorghum, sunflower, legumes and other crops. *H. armigera* feeds on most crops, it is a serious pest in cotton, sunflower and tomato, but a minor pest in maize, legumes and sorghum. In such a system, where part of the pest population is on alternative host plants which are not sprayed, the selection pressure of resistance is limited (Matthews 1992). This may explain why resistance of *H. armigera* to pyrethroids developed rapidly in parts of Australia, where intensive control was practised (Gunning *et al.* 1984), but has not been a problem in Africa (see Wolfenbarger *et al.* 1981), with the exception of the Sudan Gezira (Abdelrahman & Munir 1989).

Because the different host plants of *H. armigera* are generally grown in adjacent plots, or interplanted, infestation of *H. armigera* on a crop is influenced by neighbouring crops. For instance, preference for one crop could divert ovipositing moths, and larvae could move between interplanted crops. It was found that ovipositional preference for maize was so strong that cotton plots would remain almost clear of *H. armigera* eggs when bordered with maize (Parsons & Ullyett 1934). In smallholdings in Swaziland, cotton had much lower oviposition than in monocultures in Transvaal, which was attributed to the attractiveness of maize and sorghum to ovipositing moths (Parsons 1940b).

Moreover, neighbouring crops could act as a source or sink of pest infestation, since *H. armigera* infestation on one crop is influenced by the population build-up or mortality level on neighbouring crops (Nyambo 1988). In this respect, associations between natural enemies and plants fed on by their host (Price *et al.* 1980) could be partly responsible for differential mortality of *H. armigera* on crops. Therefore, a combination of crops needs to be taken into account if an effective IPM strategy is to be developed in smallholder croppings.

In the following chapters, I first review methods to evaluate natural enemies, and summarize all natural enemy records from *H. armigera* in Africa. Then I attempt to provide a comprehensive research into the natural mortality of *H. armigera* in smallholder crops (Part II), and finally, I evaluate the impact of natural enemies in two of these crops, cotton and sunflower (Part III), in which *H. armigera* is a major pest (Rens 1977, Khaemba & Mutinga 1982). In Part III, I focus mainly on predation, because parasitism and pathogens are evaluated in Part II.

The study was conducted over four crop seasons from October 1988 until February 1991 in the Republic of Kenya, mainly in Western Province and Nyanza Province.

2

Evaluating natural enemies

THE IMPORTANCE OF natural enemies is often stressed in studies on insect pests, but the assessment of their impact remains poorly studied. Even in detailed life table studies of pests, the impact of natural enemies has often remained part of the unexplained mortality. Life tables describe the numbers of separate developmental stages of an organism (l_x) over one (or part of a) generation, and the numbers dying (d_x) from separate stage-specific mortality factors, including natural enemies (Southwood 1978, Room *et al.* 1991). Luck *et al.* (1988) stated that life tables cannot demonstrate the efficacy of natural enemies, but only experimental methods can. Perhaps they meant that life tables readily describe the l_x column from survival data, but generally leave the d_x values of mortality factors (e.g., natural enemies) unaccounted for, because these require additional sampling or experiments. The authors then focus on experimental methods to evaluate natural enemies, without considering natural enemies in the context of life tables.

If natural enemy assessment and life tables are combined or integrated (Ehler *et al.* 1973, Bellows *et al.* 1992), this allows for evaluating natural enemies in relation to other mortality factors that act simultaneously or at other stages of host development. This approach can best be studied by comparing life tables with and without natural enemies, but requires that natural enemies are excluded without influencing other mortality factors. Beside studying the total natural enemy complex it may be desirable to evaluate the contribution of particular groups or species of natural enemies. Although exclusion is most commonly used to evaluate predatory arthropods, it could also help to evaluate parasitoids.

In life tables, stage-specific mortality is expressed as apparent or real mortality (Southwood 1978). Apparent mortality due to a mortality factor is the number dying in a stage in relation to the number that entered the stage (d_x/l_x). Real mortality is the number dying in a stage in relation to the initial number that entered the generation (i.e., eggs) (d_x/l_0). Evaluation of apparent and real mortality is complicated by interacting mortalities. When two mortality factors occur concurrently, the action of each factor will be partly obscured by the action of the other (Morris 1965). Consequently, it is difficult to separate their apparent effects, since elimination of one factor would increase the apparent mortality caused by the other. Interactions are most complex if the actions of two factors are dependent (e.g., after parasitism the host becomes more vulnerable to predation).

The amount of apparent mortality caused if the agent acted alone on the host stage, without other interacting factors, is called the marginal attack rate (Bellows *et al.* 1992). This term expresses the potential of the agent to suppress pest

populations, even though the action of the agent may be masked by other, concurrent or subsequent mortality factors. In ecosystems where abiotic and biotic mortality factors show considerable variations between seasons, both apparent mortality and marginal attack rate should be considered to evaluate the actual and potential roles of natural enemies in pest control.

A true measure of the actual role of natural enemies is expressed by the irreplaceable mortality, which is that part of the generational mortality that would not occur if the factor in question is removed from the system, without affecting other mortality factors (Southwood 1978). If a subsequent factor is density-dependent, the effect of irreplaceable mortality can be small; for instance, the irreplaceable role of egg parasitism in stemborers is limited if surviving neonates suffer an increased mortality level due to competition in the absence of parasitism (van Hamburg & Hassell 1984).

Apparent mortality	the number dying in a stage in relation to the number that entered the stage
Real mortality	the number dying in a stages in relation to the number that entered the generation
Marginal attack rate	apparent mortality if the agent acted alone on the stage
Irreplaceable mortality	that part of the generational mortality that does not occur if the factor is removed.

In this review I will discuss techniques to assess the apparent and irreplaceable mortality of pests - but especially Heliothinae - due to three groups of natural enemies, parasitoids, pathogens and predators. Because the biology and host-associations of these three groups are generally very different, the methods to evaluate their impact will be dealt with separately.

Parasitism

The impact of parasitoids is generally measured as apparent mortality, i.e., the proportion of a host generation in a susceptible stage that is ultimately killed by parasitoids. Mortality is usually equated to percentage parasitism in a generation, but sometimes high numbers are killed through host feeding or ovipositor piercing of the adult parasitoids (Kidd & Jervis 1989). The irreplaceable role of parasitoids is difficult to assess, except in certain situations where parasitoids can be excluded without affecting other mortality factors. Three approaches to study the impact of parasitism are discussed below (van Driesche *et al.* 1991, Bellows *et al.* 1992).

1. Percentage parasitism in field samples

Traditionally, parasitism has been estimated through field samples, which are easy to obtain, and require no experimental set-up. Host stages are collected, parasitoids reared out, and the level of parasitism is calculated. Alternatively, to avoid larvae dying during the process of rearing, field-sampled hosts can be dissected, rather than reared through, to record parasitoid eggs or larvae inside the host. This improves the estimate of parasitism, since rearing may affect dying of parasitized and healthy hosts differentially, but is time-consuming and small parasitoid stages may be overlooked.

Field sampling, and subsequently rearing, of parasitoids is hampered by several errors (Marstom 1980, van Driesche 1983). It is important to recognize the sources of error, so that techniques can be adapted to avoid or limit these errors. There are four major sources of error.

Host-age specificity of parasitoids. Parasitoids attack a particular stage of the host and emerge from a different host stage; for example, some ichneumonids attack the first and emerge from the second instar of noctuid hosts. Tachinids, on the other hand, tend to attack only late host instars. If host stages beyond parasitoid attack are included in the sample, this results in underestimation of percentage parasitism. Therefore, host stages of attack and host stage of emergence should be known for each parasitoid species, and the percentage parasitism should calculated for each species separately. Fig. 2.1 shows the host stage specificity of some major parasitoids of *H. armigera.*

Exposure period of susceptible host stages. Sampling of host stages commonly interrupts the exposure period of stages susceptible to certain parasitoids, and thus results in underestimation of parasitism by that particular parasitoid species. Ideally, the host should be sampled after the stage susceptible to attack, but prior to the stage of parasitoid emergence. For example, if the parasitoid attacks the first and emerges from the third host instar, parasitism should be measured in the second instar. Fig. 2.1 demonstrates that such optimal stages do not always exist, e.g., egg parasitoids and pupal parasitoids emerge from the same stage they attack. In some parasitoid species there is an overlap between the host stages attacked and those from which they emerge. Inclusion of these host stages requires that percentage parasitism values are corrected for underestimates (Marstom 1980).

Change in host stage development. Many parasitoids slow down the rate of host development. For example, egg parasitoids continue to develop in the host egg for some time after healthy contemporary hosts have hatched into larvae, and are thus over-represented in field samples. Likewise, some larval and pupal parasitoids retard the development of their host. A partial solution for this problem (and those posed above) is to place cohorts of a particular life stage into the field for subsequent monitoring.

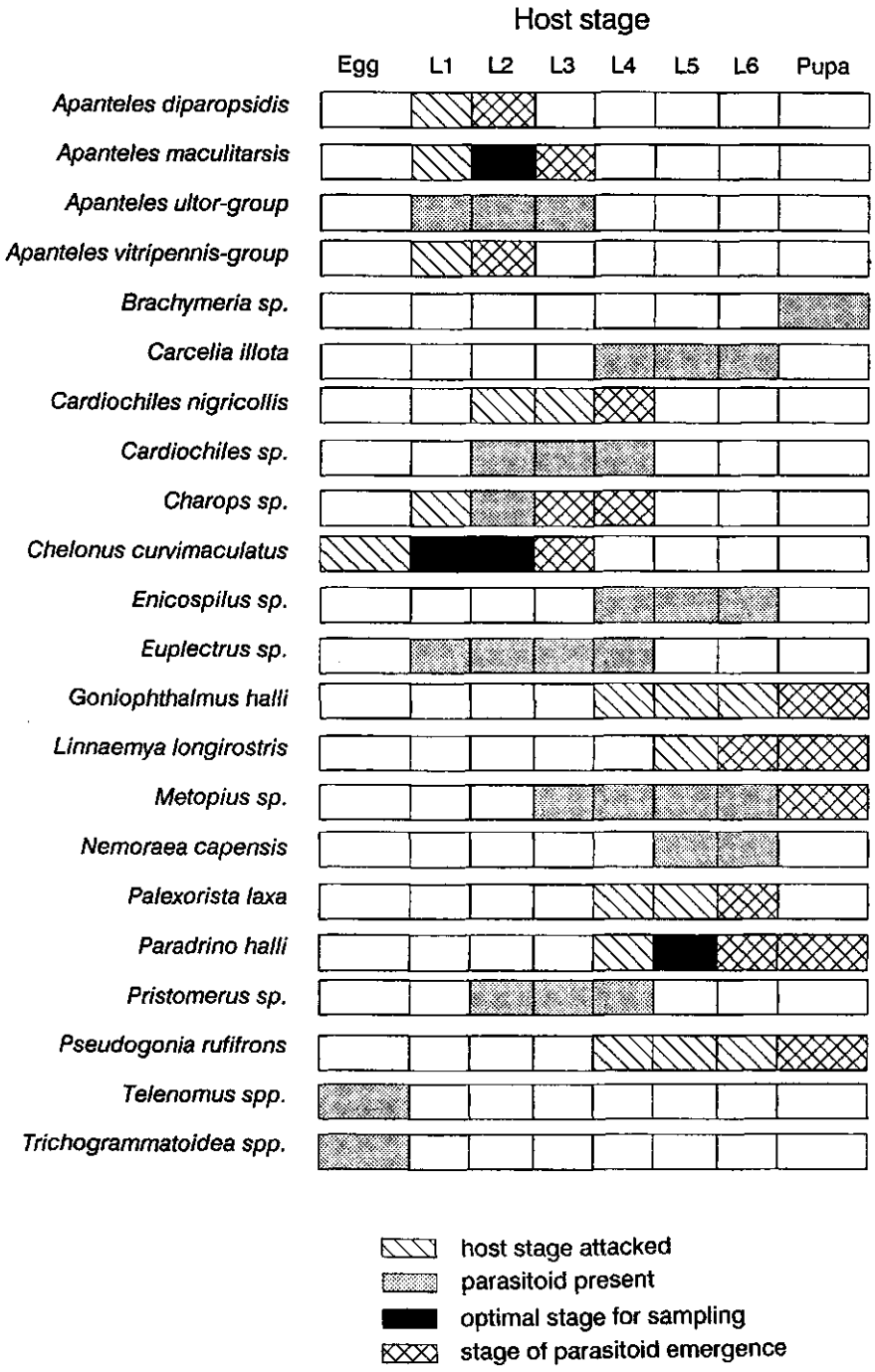

Fig. 2.1 Host stages of *H. armigera* during which its parasitoids are active. Open areas indicate that the parasitoid does not occur in the stage. Shaded areas indicate that (i) the parasitoid is present in the host stage, but no information is available on attack or emergence of parasitoid, or (ii) that the parasitoid emerges from the host stage it attacks.

Clearly, this is easier for sessile stages such as eggs and pupae, although larger larvae may be tethered to plants (Weseloh 1974, 1982). This method also measures other mortalities acting on the exposed stage, such as disappearance of hosts due to predation. Natural placement of hosts in the field is important, and if possible, it might be better to clean plants and mark newly laid cohorts of eggs (Metcalfe & Brenière 1969), or to confine pupating larvae under cages in the soil (P.J. Guest, pers. comm.) to ensure natural distribution of the stage exposed.

Mortality of parasitized hosts. When field mortality is greater for parasitized than for unparasitized hosts (and when hosts are not dissected) the contribution of parasitism to mortality of the host will be underestimated. Moreover, when parasitized hosts are sampled from the field, they are removed from possible subsequent attack by other parasitoids, hyperparasitoids, predators and diseases. This causes overestimation of the apparent mortality due to the particular parasitoid species. This problem may also arise with cohort studies depending on the time of recollection, and will be more severe when parasitism makes hosts more susceptible to other mortalities (e.g., Carroll & Risch 1983). Thus particular attention should be paid to this possible source of sampling error when parasitized hosts are rendered more sluggish than healthy hosts.

When the above sources of error are taken into account, or avoided, field samples can estimate the percentage parasitism at a particular time in the field. The role of parasitism in generational mortality of the pest can be evaluated from regular field sampling in three ways:

(1) For species with discrete generations, peak percentage parasitism (i.e., the largest measured value) can provide an estimate of generational parasitism, but this requires that all hosts are simultaneously in the susceptible stage, and that parasitoid recruitment and parasitoid emergence do not overlap (van Driesche 1983).

(2) Alternatively, numbers of the host and parasitoid in the generation can be estimated with the graphical method of Southwood & Jepson (1962), which calculates graphical estimates of parasitized hosts and total hosts each divided by their development period (which takes into account the change in residence time caused by parasitism). However, this method is often subject to large biases (see Bellows *et al.* 1989).

(3) Finally, in a simple and widely used method, all samples are pooled and the number of emerged parasitoids is divided by the total number of susceptible host stages collected (e.g., Barbosa *et al.* 1975). This measure approaches generational percentage parasitism if the sampling errors described above are taken into account, and when sample sizes reflect field densities (Chapter 5), or when populations are constant and non-dynamic.

2. Recruitment analysis

As an alternative to using density data, generational parasitism can be assessed by measuring recruitment rates, i.e., the number of hosts that enters a susceptible stage, the number that leaves the susceptible stage, and the number that enters the pool of parasitized hosts.

Host recruitment into the susceptible stage can be assessed via a double sampling scheme, by removing all larvae from selected plants and re-examining the plants a few days later (Metcalfe & Brenière 1969, van Driesche & Bellows 1988). Young larvae recovered from the plants are considered new recruits. However, this assumes that larvae do not move between plants, and that removal of larvae does not influence the recruitment or survival of younger stages. For continuous breeding, non-mobile pests where generations overlap (e.g., aphids), host recruitment can easily be estimated from the reproduction rate per adult and the adult density (Lopez & van Driesche 1989). Recruitment rates will change over time; therefore, measurements have to be made regularly over the entire generation, or for continuous breeding species, over a certain period of time.

Parasitoid recruitment over a certain period can be measured through dissection of field-collected hosts and detecting the age of the parasitoid stage, or through dissection or rearing of trap hosts (van Driesche 1988, van Driesche & Bellows 1988), but the use of trap hosts is most practical for non-mobile hosts. Recruitment analysis is a conceptually simple approach that measures the actual parameters required for life table construction, and hence avoids some major sources of bias associated with field density samples and percentage parasitism. When used in combination with stage-frequency data and percentage parasitism, the impact of parasitism may be compared to other mortality factors (van Driesche & Bellows 1988). A disadvantage is that recruitment analysis is applicable only in simple systems, where a parasitoid attacks a known stage of the host. In other cases, where the host is attacked by a complex of parasitoid species, differences in host-specificity between species or problems with the identification of their immatures at dissection complicate the measurement of recruitment rates. Another problem is that measurement of parasitism by dissection of hosts measures the attack rate of parasitoids rather than the apparent mortality. In reality, some parasitized hosts may die from other concurrent or subsequent mortality factors, as discussed above. Finally, dissection is time-consuming, and errors may arise from estimating parasitoid development stages, or from overlooking small stages.

3. Death-rate analysis

A new, simple approach measures loss due to parasitism by emergence of adult parasitoids, over time intervals, and does not take into account the stage-specificity of parasitoids (Bellows *et al.* 1992). Hosts are sampled at regular intervals during the generation, without distinguishing between stages.

Individuals are reared during each interval, and the number of hosts dying during that interval due to different parasitoids is recorded before the next sample is taken. This allows for calculation of percentage mortality and k-values for several simultaneous factors (Gould *et al.* 1990). For each mortality agent, k-values are summed over the total period (one generation) to obtain a measure of the role of the agent in generational mortality of the host. Disadvantages of this recent method are not known.

Pathogens

Assessment of the incidence of pathogens in field populations of Heliothinae has received very little attention (Yearian *et al.* 1986). Pathogen incidence in a pest population is commonly measured from stage-frequency data and percentages infected. The role of pathogens could also be evaluated by death-rate analysis (Ekbom & Pickering 1990) or measuring recruitment rates. Pathogen recruitment could be determined if early infections are detectable in collected hosts, or if trap hosts are exposed and subsequently incubated in the laboratory.

In some aspects, evaluation of pathogens differs from the evaluation of parasitism. When the pest population increases, and when the pathogen is present, a rapid epizootic might occur, followed by a decline of the pest population (Carner 1980). At this stage, pathogens should be assessed at brief intervals, in order to follow rapid population changes. The presence of pathogens can be examined immediately, by microscopic diagnosis, or after an incubation period in the laboratory. Immediate diagnosis is time-consuming, may not be accurate, and does not show the fate of infected larvae (Teakle 1989). Incubation is simpler, but is subject to biases. For instance, cross-contamination via field equipment or other larvae, and secondary infections during incubation may overestimate the percentage diseased. Therefore, collected larvae should be placed individually inside sterile diet containers and fed on sterile artificial diet or sterilized plant material (Ignoffo & Dutky 1963). Another bias arises when a pathogen infection kills the larva more easily when the latter is subjected to stress; hence numbers of larvae dying during incubation may be unrealistically high, which overestimates percentage diseased. McKinley (1971) recorded that *H. armigera* larvae in the field were less susceptible to nuclear polyhedrosis virus than those reared in the laboratory, except under conditions of physical stress.

Knowledge about the biology of pathogen-pest relations is scant; some pathogens show little stage-specificity and can infect and kill *H. armigera* or other noctuids at various larval stages (e.g., Table 2.1). This complicates the evaluation of the impact of pathogens by field sampling. In parasitism, there is usually a host stage beyond attack but before emergence of the parasitoid, that contains all parasitized individuals. For pathogens, however, there may not be such ideal host stage for collection, or at least, there is limited information on host-specificity. In *Helicoverpa zea* (Boddie), the first and second instars sustained less infection by *Nomuraea rileyi* (Farlow) than the third to fifth instar

Table 2.1 Imago and pathogen emergence from *Spodoptera litura* larval instars. Indicated are the instars at the time of sampling (van den Berg 1992). Soybean, Sumatra, 1992

Instar	Imago	*Nomuraea*	NPV
1	6	3	0
2	175	16	11
3	68	10	7
4	37	0	6
5	15	1	0
6	7	0	1

(Mohamed *et al.* 1977). Whitlock (1974) reported that most mortality of *H. armigera* due to nuclear polyhedrosis virus occurred in the young stages. If the occurrence of a pathogen in different host instars is known (Table 2.1), correction factors could aid improvement of field-sample estimates. The shorter the time infected hosts remain in the field for sampling the less the pathogen is represented in field samples; viruses for instance, kill lepidopterous hosts rapidly, and would be relatively less represented in samples than the slower *Nomuraea* fungi (Carner 1980).

Interruption of field exposure by collection influences the measured mortality due to pathogens in two ways. Firstly, healthy larvae are no longer subject to infection, which underestimates pathogen incidence. This error may be avoided by placement and monitoring of host cohorts. Secondly, if an infected larva is collected and dies during incubation, the cause of death is attributed to the pathogen, but if the larva had remained in the field, a subsequent attack of a predator or parasitoid might have been the cause of death, especially if diseased larvae are rendered more sluggish than healthy ones, and become easier prey for predators; this results in overestimation of apparent mortality of pathogens but this error is difficult to avoid. On the other hand, some parasitoids are able to recognize and avoid infected hosts (Franssen, in press).

Another bias appears if pathogen infection influences the behaviour of the host. For instance, infection with *Entomophthora* fungi or nuclear polyhedrosis viruses causes lepidopterous hosts to climb to the tops of plants (Carner 1980), so these may be over-represented in relative samples, but not if absolute units are sampled.

In conclusion, several biases may over- or underestimate the pathogen incidence in field samples; bias at incubation may be limited by sterile rearing

conditions, bias at sampling may be reduced by correction factors but requires more information about the biology and phenology of pathogens. When the recruitment analysis or death-rate analysis techniques are applied to pathogens, several sampling errors may be overcome, but cross-contamination and increased susceptibility during incubation of field samples would remain a problem.

Predation

Methods to evaluate predation have been reviewed extensively (DeBach & Huffaker 1971, Grant & Shepard 1985, Luck *et al.* 1988, Seymour & Jones 1992). Here, I will focus on quantitative methods that provide an assessment of the impact of predation. Post-mortem methods to detect consumed prey in predators are not considered, as they are difficult to interpret in terms of percentage mortality, even though some can be used quantitatively (Sunderland 1988). Three considerations are important for choosing a method:
(1) should the impact of the predator community or of separate species should be evaluated,
(2) should the impact on particular stages of the pest be evaluated or the impact on the generation, and
(3) can field levels of the pest be relied upon for assessment of predation, or do prey have to be added?

Exposure of host cohorts. Placement of prey in the field can be used to assess the impact of predation (and parasitism and pathogens, see above) on a particular non-mobile stage on the prey, such as lepidopterous eggs (Shepard & Arida 1986, van den Berg *et al.* 1988) or pupae (Watmough 1991). Care must be taken to ensure natural positions of trap prey, e.g., by overnight deposition of egg cohorts on plants by caged moths, or by allowing mature noctuid larvae to bury themselves in the soil within a confined area. Also, unrealistic densities should be avoided.

Direct observation. Visual recording of predation events in the field is the most bias-free and convincing way to evaluate predators, but studies are few because of the large amount of sampling effort needed. Direct observations are less useful in situations where predation events are relatively rare, or when the predators in question are elusive or easily disturbed. In studies involving homopterous prey (Kiritani *et al.* 1972) and lepidopterous prey (Bushman *et al.* 1977, Elvin *et al.* 1983, Brust *et al.* 1986, Godfrey *et al.* 1989), exposed prey were observed continuously or at fixed time intervals and predation events were recorded. This technique allows for identification of predators and comparison of the feeding activity of different species. In case feeding times are known, predation rates may be calculated (Kiritani *et al.* 1972).

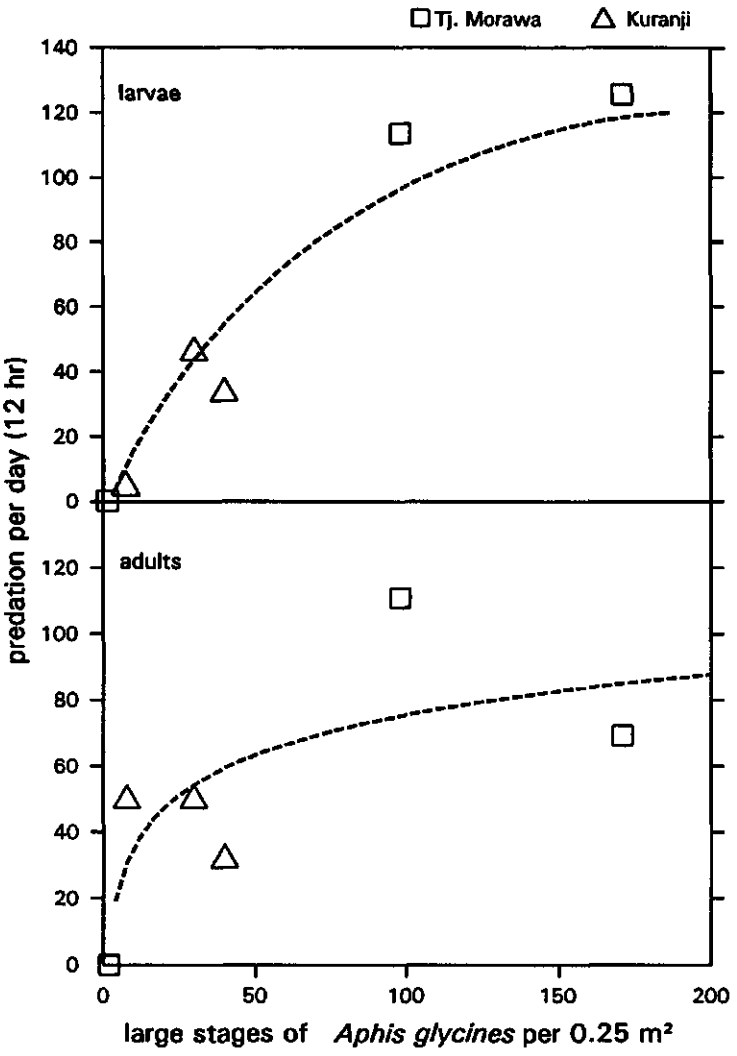

Fig. 2.2 Field predation rate of mature larvae and adults of *Harmonia* sp. on *Aphis glycines* Matsumura, in relation to concurrent densities of the prey (van den Berg 1992). Each data point represents, on average, 41 diurnal observations made on one day. Predation rates were determined by direct observations of the activity of individual predators. The diet consisted of 84 % small, and 16 % large aphid stages, while densities were based on large stages only. Triangles and squares indicate two sites. Soybean, Sumatra, 1992.

Alternatively, individual predators are followed and their predation rate is measured by recording prey eaten during a particular period. This is especially useful if prey densities reach high levels. Fig. 2.2 shows predation rates of coccinellid larvae and adults on aphids in soybean, in relation to field densities of the prey. Predation was measured in ten minute observations of individual

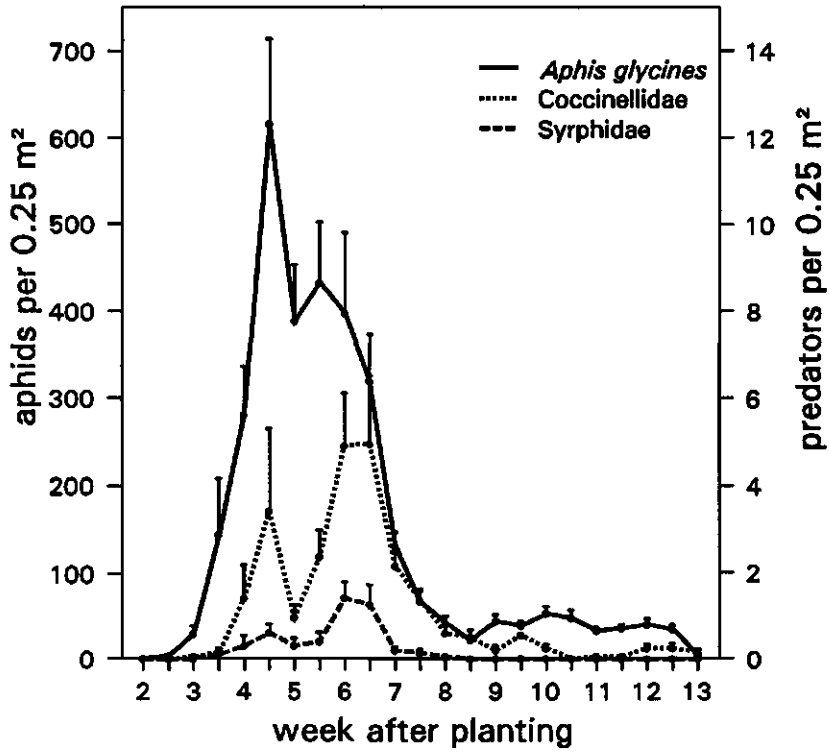

Fig. 2.3 Density of *Aphys glycines* and aphidophagous predators on soybean, Sumatra (van den Berg 1992). Coccinellidae (larvae and adults combined) were dominated by *Harmonia* sp. Bars indicate s.e.

predators in the field. In combination with known densities of aphids and predators as shown in Fig. 2.3, this allows for calculation of the percentage of the aphid population that is consumed per day (van den Berg 1992, unpublished data).

Evidence of predation. Some phytophages that develop inside plant structures leave remains after they emerge into the adult stage. In cases when they die before adult emergence, evidence of the cause of mortality may be found. This technique greatly simplifies the evaluation of mortality factors on the pest, and has been developed to determine mortality factors of the cotton boll weevil (*Anthonomus grandis*) in North America, which lives inside the cotton square during its development.

Yellowing and abscission of the square and the presence of an ovipositional puncture indicate the presence of a weevil. The weevil leaves a characteristic pupal skin inside the square upon adult emergence. In case of premature death,

several mortality factors can be identified: a parasitoid cocoon alongside the host remains indicates parasitism, the presence of a dead weevil larva implies mortality due to an unknown cause (Jones & Sterling 1979), and a characteristic hole chewed through the flower petals (Sterling 1978) provides evidence of predation by the fire ant *Solenopsis invicta* Buren, an important biocontrol agent of the boll weevil (Sterling *et al.* 1984). High predation rates in the field lead to the development of inaction levels at which fire ants caused sufficient irreplaceable mortality of the boll weevil to prevent unacceptable losses (Fillman & Sterling 1983, 1985).

Besides durable evidence of predation, several techniques are available to detect post-mortem evidence of feeding in predators (Sunderland 1988). These techniques are methodically rather complicated and are difficult to interpret in terms of generational mortality.

Cages. Predator-pest interactions can be studied under controlled, manipulated conditions by the use of exclusion, partial exclusion and inclusion cages. By comparing predator-free with open control cages, exclusion cages allow for the evaluation of the total predator (and parasitoid) community, while partial exclusion (e.g., with the mesh diameter of the netting excluding large predators only) and inclusion cages allow for evaluation of certain species or groups of predators. Potentially important predators can first be separated from unimportant ones in simple laboratory cages, and can then be tested under more realistic conditions in the field (van den Berg *et al.* 1992)

Caging of natural pest populations in the field provides a realistic density, distribution and structure of the pest. At low pest infestation, cages might have to be inoculated with known cohorts of the pest. The advantage of inoculation with cohorts is that the variance between replicates is reduced, while varying cohort sizes allow for measurement of the functional response of predators to prey density.

Various kinds of cages have been used to evaluate natural enemies, ranging from Petri dishes in the laboratory to cages covering small field plots (Luck *et al.* 1988), but the more realistic the conditions, the easier to extrapolate the results to natural populations. In the field, caging may alter certain aspects of the predator-pest interactions. For instance, because migration is limited, caging populations for an extended period of time could result in unrealistic pest densities, as natural populations would move to more suitable food sources (e.g., young plants). Also, confinement inside cages may influence the foraging behaviour of predators, which repeatedly search the same plants or areas, while free predators might recognize areas searched previously, or may leave areas with low prey densities altogether. Furthermore, cage netting may cause some degree of shading which affects the microclimate inside the cage (Sparks *et al.* 1966, van den Bosch *et al.* 1969).

Exclusion barriers. Sticky barriers on plants (Chapter 8, 9), or barriers on the ground around plots (e.g., plastic walls, or trenches with water or

insecticides) in combination with mass trapping in pitfall traps, may exclude ground predators (e.g., carabid beetles and ants) from plants or plots, without causing climatic changes or creating other unrealistic conditions for the pest population. Comparison of survival of the pest in plots with and without predators allows for the assessment of irreplaceable mortality due to predation by ground predators, but part of the mortality might be replaceable by other groups of natural enemies (Chapter 9).

Insecticidal exclusion. Insecticides can be a powerful tool to evaluate irreplaceable mortality due to predators, if the chemical has no or little effect on the pest population but effectively kills predators. This method is most effective if the pest shows some level of resistance to certain insecticides (Ehler *et al.* 1973, Eveleens *et al.* 1973, Stam & Elmosa 1990), but is also useful if predator and pest have a differential susceptibility to a particular insecticide at a certain concentration. In the latter case, a proper timing of spraying may further help to reduce an adverse effect on the pest. Depending on the type and concentration of the chemical used, this method may exclude (part of) the predator community, and is therefore less appropriate if individual species are to be evaluated.

A problem arising with the interpretation of results of the insecticidal exclusion is that the insecticides may stimulate the growth rate of the pest, as has been shown in mite, homopterous and lepidopterous pests (e.g., Barlett 1968, Reissig *et al.* 1982, Nemoto 1986, Marwoto *et al.* 1991). Moreover, Kinzer *et al.* (1977) demonstrated that oviposition by Heliothinae increased when plants were sprayed with certain insecticides. Together with other, indirect, effects of insecticides on pest-natural enemy interactions (Waage 1989), these influences may obscure the role of predators in the insecticidal removal method.

In exclusion techniques, the effect of predation on the pest can be monitored by sampling the pest at the end of the trial (e.g., in cages where interference during the experiment is not practical), or by regular sampling during the trial (in the insecticidal removal and exclusion barrier methods that exclude predators from entire plots). The latter may provide stage-frequency data for plots with and without predators. Stage-recruitment is estimated by dividing the graphical area of the stage concerned by its development period (Southwood & Jepson 1962). This provides an evaluation of the irreplaceable mortality due to predation in relation to other mortality factors, and reveals at which stages predation occurs (Chapter 5).

When considering mortality factors solely on a stage-specific, rather than time-specific basis, some important information may be lost. For decision-making in integrated pest management, it is important to know the impact of natural enemies in relation to pest infestation levels and the time that prey are attacked. This could be examined by comparing weekly pest densities taken in plots with and without predators, or by regularly conducting cage studies, exposure studies or direct observations to relate the predation level to pest density.

With the current emphasis in agricultural research on sustainability and integrated pest management, the importance of quantifying the role of natural enemies has become more clear. Reliable methods are available to assess their impact of natural enemies in various situations and for various research objectives, as I outlined in this chapter. Although methods are generally labour-intensive, evaluation of natural enemies clearly deserves more emphasis than it has received in the past.

Acknowledgement

I would like to thank J.C. van Lenteren and J.K. Waage for helpful comments on this chapter.

3

Catalogue of the natural enemies of *H. armigera* in Africa[1]

ABSTRACT - The natural enemies of *Helicoverpa armigera* Hübner in Africa are reviewed, using published, unpublished and museum sources. A large variety of natural enemies are represented in almost 300 host records, including 83 parasitoids identified to species and 93 identified only to genus. The taxonomy, distribution, biology, alternative hosts or prey, host plant associations and secondary natural enemies are detailed for all recorded natural enemies, and the different aspects are summarized and evaluated for the total natural enemy complex. Striking differences are found in the reported parasitoid complexes between eastern and southern Africa.

Introduction

In the past, information on the major parasitoids of *H. armigera* in Africa has been summarized on several occasions (e.g., Henrard 1937, Pearson 1958, Risbec 1960, Greathead 1966, Greathead & Girling 1988). In this review we attempt to give a complete picture of all natural enemy records of *H. armigera* from Africa, with comments on their taxonomy, distribution, biology, alternative hosts or prey, host-plant associations and secondary natural enemies, thereby using published, unpublished and museum sources.

Literature on natural enemies of *Helicoverpa* spp. from Africa (predominantly *Helicoverpa armigera*) is very limited as compared with that for North America (Kogan *et al.* 1978; Johnson *et al.* 1986). Most African studies are from southern Africa and East Africa (Table 3.1). Detailed studies from East Africa are limited to those from Uganda by Coaker (1959), and from Tanzania by Reed (1965) and Nyambo (1986). These studies mostly concern larval parasitoids. In East Africa, hymenopteran larval parasitoids are the most commonly recorded parasitoids, whereas in southern Africa dipterans were more frequently recorded. Egg parasitoid records are common only from southern Africa.

Taxonomy. In addition to the 83 identified species of natural enemies recorded from *H. armigera* in Africa, there are 93 records of partially identified natural enemies (Table 3.2). Some of these are important biological control agents (e.g., Nyambo 1986), and most are found in the Ichneumonidae and in the

[1] Published as: H. van den Berg, J.K. Waage & M.J.W. Cock (1988) *Natural enemies of* Helicoverpa armigera *in Africa: a review*. Ascot, UK., C.A.B. International Institute of Biological Control.

Table 3.1 Number of records of *H. armigera* parasitoids from African countries.

Country	Diptera larval/pupal parasitoids	Hymenoptera egg parasitoids	Hymenoptera (other than egg-) parasitoids	Total
East Africa	**5**	**5**	**55**	**90**
Kenya	0	0	3	9
Tanzania	2	2	29	49
Uganda	3	3	22	31
Southern Africa	**59**	**26**	**34**	**119**
Botswana	7	2	6	15
South Africa	31	17	23	71
Zimbabwe	21	7	5	33
Other	**29**	**4**	**37**	**70**
Madagascar	0	1	3	4
Nigeria	1	0	3	4
Senegal	11	1	13	25
Sudan	9	0	12	21
Miscellaneous	11	2	13	26
Total	**121**	**35**	**133**	**289**

* Predominantly Tachinidae

** Predominantly Braconidae and Ichneumonidae

smaller parasitoid families. Particularly difficult parasitoid genera are *Charops* and *Pristomerus* (Ichneumonidae), and *Apanteles* and *Cardiochiles* (Braconidae). The huge genus *Pristomerus* might have several hundreds of undescribed species in Africa (I.D. Gauld pers. comm.). Identification of the tachinid genera *Exorista*, *Carcelia*, *Pales* and *Palexorista* is difficult because species are morphologically very similar (Crosskey 1980, 1984). Furthermore, some of the currently described species in these genera may represent a complex of sibling or semi-sibling species (R.W. Crosskey pers. comm.). African parasitoids of *H. armigera* in the genera *Cardiochiles* and *Palexorista* have recently been revised (Huddleston & Walker 1988, Wyatt *in* Cock *et al.* 1990).

Alternative hosts. Data on alternative hosts of parasitoids of *H. armigera* should be treated with utmost caution, because misidentifications are frequent.

Table 3.2 Number of species of parasitoids of *H. armigera* recorded from Africa. I, identified species; II, records not identified to species level.

Family	I	II
Tachinidae	34	11
Ichneumonidae	10	24
Braconidae	21	24
Miscellaneous	18	34
Total	83	93

This is best illustrated with *Palexorista laxa* Curran, an important tachinid parasitoid of *H. armigera* which has been recorded from many alternative hosts covering several lepidopterous families. However, according to Crosskey (1967), *H. armigera* is the only proven host of *P. laxa*. *Palexorista* is a particularly difficult genus, and several closely related species have been confused under the name *P. laxa*.

Furthermore, records alone do not indicate preference of parasitoids. A parasitoid might show a preference for one particular host, and use other species as hosts only to bridge periods of absence of its preferred host. Hence, it may be necessary to identify principal and alternative hosts of parasitoids. Table 3.3 is a summary of the host range for a number of parasitoids of *H. armigera*. Note that partially identified parasitoid species, some of which are very important, cannot be included here.

Within the Tachinidae, the subfamily Tachininae seem to be parasitoids of noctuids. The important subfamily Goniinae has more generalist species, recorded from non-noctuid hosts. Exceptions are *Goniophthalmus halli* Mesnil, *Paradrino halli* Curran, and *Palexorista laxa*, common parasitoids in Africa, which are probably specific parasitoids of *H. armigera*. Again, records of alternative hosts in such taxonomically difficult groups as *Carcelia*, *Exorista* and *Pales*, must be regarded with caution.

Most braconid parasitoids of *H. armigera* are polyphagous, with the exception of *Cardiochiles* spp. Although based on few records for each species, none of the five *Cardiochiles* spp. has been recorded from a host other than *H. armigera*. *Cardiochiles nigriceps* Viereck, a well-studied species from North America, has shown a high degree of specificity to the host *Heliothis virescens* F.

In scelionid egg parasitoids of the genus *Telenomus* a combination of several physical as well as chemical cues (contact kairomones) leads to host acceptance, and allows them to select host age and host species; they generally are host

Table 3.3 Parasitoids of H. armigera and their host range in Africa. I, recorded from *H. armigera* only; II. recorded from Noctuidae only; III, recorded from several families of Lepidoptera.

	I	II	III
Tachinidae:			
(Subfamily Tachininae)			
Dejeania bombylans (1)		■	
Hystricovoria bakeri			■
Linnaemya agilis		■	
Linnaemya albifrons		■	
Linnaemya longirostris		■	
Nemoraea capensis		■	
Nemoraea rubellana		■	
(Subfamily Goniinae)			
Carcelia illota (1)		■	
Ceromya cibdela			■
Exorista sorbillans			■
Exorista xanthaspis			■
Gonia bimaculata			■
Goniophthalmus halli	■		
Pales blepharipus			■
Pales coerulea			■
Pales nigronitens			■
Pales seminitida			■
Palexorista idonea			■
Palexorista laxa	■		
Paradrino halli (2)	■		
Peribaea mitis			■
Peribaea orbata		■	
Pseudogonia rufifrons		■	
Sturmia convergens			■
Thelairosoma angustifrons			■
Winthemia dasyops (1)		■	
Zygobothria ciliata			■

	I	II	III
Ichneumonidae:			
Barylypa rufae (1)		■	
Charops ater			■
Enicospilus capensis		■	
Metopius discolor (1)	■		
Netelia opaculus		■	
Netelia testacea		■	
Braconidae:			
Apanteles diparopsidis			■
Apanteles maculitarsis			■
Apanteles ruficrus			■
Bracon brevicornis			■
Cardiochiles nigricollis (1)	■		
C. nigromaculatus (1)	■		
C. trimaculatus (1)	■		
C. variegatus (1)	■		
Chelonus curvimaculatus			■
Chelonus versatilis (1)			■
Meteorus laphygmarum		■	
Scelionidae:			
Telenomus ullyetti	■		
Eulophidae:			
Euplectrus laphygmae			■
Trichogrammatidae:			
Trichogrammatoidea lutea			■

(1) Based on few records
(2) Only once recorded from another Noctuidae (Cetola sp.)

specific. Trichogrammatid parasitoids on the other hand are generally less specific, and often attack a range of Lepidoptera host eggs available in a specific habitat.

Distribution. Information on geographical distribution of African parasitoids of *Helicoverpa armigera* is patchy. Parasitoids from the Afrotropical Region

Table 3.4 Distribution of widespread parasitoids, recorded from *H. armigera* in Africa, outside the Afrotropical Region. I, Oriental Region; II, Palearctic Region; III, Nearctic Region; IV, Neotropical Region.

	I	II	III	IV
Tachinidae:				
Carcelia illota	■			
Exorista sorbillans	■	■		
Exorista xanthaspis	■	■		
Gonia bimaculata	■	■		
Goniophthalmus halli	■			
Hystricovoria bakeri	■			
Palexorista laxa	■			
Peribaea orbata	■			
Pseudogonia rufifrons	■	■		
Sturmia convergens	■			
Voria ruralis	■	■	■	■
Zygobothria ciliata	■			
Ichneumonidae:				
Enicospilus capensis	■			
Netelia testacea		■		
Braconidae:				
Apanteles ruficrus	■			
Bracon brevicornis	■	■	■	■
Cardiochiles nigromaculatus	■			

recorded from other regions as well are presented in Table 3.4. It can be seen that the African parasitoid complex is most closely related to that of the Oriental Region. Within the African continent, striking differences exist between the parasitoid complexes reported from different areas (Table 3.5). When comparing *H. armigera* parasitoids from the two best-studied areas, southern Africa (Botswana, South Africa and Zimbabwe) and East Africa (Kenya, Tanzania and Uganda), only three species are important in both areas; these are *Palexorista laxa*, *Paradrino halli* and *Chelonus curvimaculatus* Cameron. All of the other species are important in only one of the areas, although they might be present in both.

An example of the latter is *Apanteles diparopsidis* Lyle, which is an important parasitoid of *H. armigera* in Tanzania (Nyambo 1986), while in southern Africa it is found only on *Diparopsis* spp. and *Earias* spp. (Noctuidae).

Table 3.5 Major parasitoids of *H. armigera* in East Africa and southern Africa. (a) indicates species important both in East and southern Africa.

Parasitoid	Country*	(a)	Crop	Occurrence**
EAST AFRICA				
Tachinidae:				
Carcelia illota	T	–	cotton	7%
Goniophthalmus halli	K,T	–	cotton	up to 12%
Palexorista laxa	T,U	+	mainly sorghum	up to 42%
Paradrino halli	T	+	various	common
Ichneumonidae:				
Charops sp.	T	–	various	up to 23%
Charops sp.	U	–	various	up to 10%
Enicospilus sp.	U	–	mainly cotton	11%
Braconidae:				
Apanteles diparopsidis	T	–	sorghum	up to 26%
Apanteles ultor-group	U	?	maize/groundnut	up to 20%
Apanteles vitripennis-group	T	–	various	common
Cardiochiles trimaculatus	U	–	mainly cotton	8%
Cardiochiles sp.	T	?	mainly cotton	up to 18%
Chelonus curvimaculatus	T,U	+	various	up to 12%
SOUTHERN AFRICA				
Tachinidae:				
Linnaemya longirostris	SA	–	various	important
Gonia bimaculata	SA	–	citrus	important
Palexorista laxa	B,SA,Z	+	cotton	20–30 %
Paradrino halli	Z	+	citrus	up to 25%
Braconidae:				
Apanteles maculitarsis	SA	–	various	common
Apanteles nr. aethiopicus	SA	?	peas	important
Bracon brevicornis	SA	–	antirrhinum	common
Cardiochiles nigricollis	B,SA	–	mainly cotton	common
Chelonus curvimaculatus	SA	+	maize,citrus	common
Scelionidae:				
Telenomus ullyetti	SA,Z	–	various	up to 70%
Trichogrammatidae:				
Trichogrammatoidea lutea	SA,Z	–	maize,cotton	up to 60%

* B, Botswana; K, Kenya; SA, South Africa; T, Tanzania; U, Uganda; Z, Zimbabwe
** Percentage parasitism

When comparing parasitoid guild structures of the two areas (see Table 3.4) it is apparent that egg parasitoids are important in southern Africa whereas they are rare in East Africa. This may however be attributable to the lack of attention being paid to egg parasitoids in East Africa.

Ichneumonids, on the other hand, are among the principal parasitoids of *H. armigera* only in East Africa. Similarly, Tachinidae are better represented in the parasitoid complex in southern Africa than in East Africa, while hymenopterous larval parasitoids were the major group in East Africa (Table 3.1).

Natural enemy-plant associations. Host-plant associations of natural enemies of *H. armigera* have not been studied experimentally in Africa. However, some trends appear from field collections of parasitoids. The most extensive data set in this respect is the work in western Tanzania (Nyambo 1986, Chapter 7). From these data it appears that there is a parasitoid guild, composed of *Palexorista laxa*, *Chelonus curvimaculatus* and *Apanteles diparopsidis*, attacking *H. armigera* on sorghum, but not to a significant degree on other crops. Consequently, *H. armigera* on sorghum suffers much higher parasitism levels than on other crops.

By contrast, *Cardiochiles* spp. seem to be generally associated more with cotton than with other crops. In Tanzania, *Cardiochiles* spp. were associated with cotton and the weed cleome, and were rare on sorghum and maize (Nyambo 1986). Parsons (1940) reared *C. nigricollis* Cameron mostly from larvae collected on cotton in South Africa. Moreover, Greathead (1966) found *C. trimaculatus* Cameron to be the most important parasitoid of *H. armigera* on cotton in Uganda. Nyambo (1986) commonly reared *Charops* sp. from *H. armigera* on tomato, cleome and chickpea, whereas it was rare in collections from cotton and maize. In South Africa, Taylor (1934) and Parsons (1940) reported that *H. armigera* was attacked by *Bracon brevicornis* only on antirrhinum plants, while the pest was present on various host plants.

Citrus in southern Africa seems to have its own parasitoid guild which attacks *H. armigera*, during flowering, early in the season. The tachinids *Gonia bimaculata* Wiedemann (Cuthbertson 1934), *Gonia* sp. (Hall & Ford 1933; Jones 1939) and *Paradrino halli* (Jones 1939) were important parasitoids of *H. armigera* on citrus, but were rare on cotton and food crops, usually grown later in the season (Parsons & Ullyett 1934; Parsons 1940; Jones 1939). It is unclear whether this difference is caused by seasonal occurrence of the parasitoids or host-plant associations.

In the folowing section, all parasitoids, predators and pathogens recorded from *Helicoverpa armigera* in Africa are reviewed. Depending on the information available, a number of aspects are described for each species.

a. Name in current taxonomy, with synonyms. Author's names are not parenthesized (Crosskey *et al.* 1985). Synonyms are limited to those that refer to *H. armigera* records from Africa.

b. Taxonomic comment, including misidentifications and commentary on the reliability of records. Bracketed references refer to taxonomists' comments as follows:
   (1) R.W. Crosskey, pers. comm.
   (2) A.K. Walker, pers. comm.
   (3) T. Huddleston, pers. comm.
   (4) A. Polaszek, pers. comm.
   (5) Z. Boucek, pers. comm.
c. Distribution; within the Afrotropical Region by country, other regions by region.
d. Biology; relevant notes on adults, oviposition (including host location/recognition), development, and host stages attacked.
e. Alternative hosts or prey. Host records are not exhaustive; noctuids are given by species (African records only), non-noctuid lepidopterans by family, and non-lepidopterans by order (worldwide records).
f. Host-plant associations.
g. Secondary natural enemies.
h. *H. armigera* records; including country, host plant, occurrence (or percent parasitism or predation) and source. The initials 'BMNH' are given for specimens in the British Museum (Natural History) collection.

Families and orders are arranged in accordance with recent classification. Within each family species are listed alphabetically.

Parasitoids

DIPTERA

Bombyliidae

Sp. indet
***H. armigera* records:**

South Africa	Maize	Important	Parsons & Ullyett 1934

Phoridae

***Dohrniphora paolii* Schmitz**
Diploneura paolii Schmitz (Risbec 1960).
Biology: Dudious record as a true parasitoid; might well be a general saprozoic species.
Distribution: Afrotropical Region: Somalia.
***H. armigera* records:**

Somalia	-	-	Risbec 1960

Sarcophagidae

The majority of species of Sarcophaginae are opportunist saprophages depositing their larvae in wounds, corpses and damaged tissues of animals and plants. Most *Sarcophaga* spp. *sensu lato* fall into this catogory but a few, chiefly Neotropical species, have been shown to be obligate parasitoids. Thus, records of *Sarcophaga* spp. as parasitoids of *H. armigera* should be treated with caution and careful observation made on the circumstances under which larvae and pupae are fed on by the fly larvae before they are accepted as true parasitoids (Greathead 1963).

***Amobia signata* Meigen**
Pachyophthalmus signatus Meigen (Hall & Ford 1933)
Distribution: Afrotropical Region: southern Africa, West Africa; Nearctic Region; Oriental Region; Palaearctic Region.
Biology: This is possibly a hyperparasitoid.
Alternative hosts: HYMENOPTERA; ORTHOPTERA.
***H. armigera* records:**

Zimbabwe	Citrus	Common	Hall & Ford 1933

***Sarcophaga hirtipes* Wiedemann**
Distribution: Widespread mainland Afrotropical Region; Mediterranean Subregion; Oriental Region.
***H. armigera* records:**

Tanzania	-	-	Robertson 1965

***Sarcophaga* sp.**
***H. armigera* records:**

Somalia	Maize	-	Chiaromonte 1933

***Sarcophaga* sp.**
***H. armigera* records:**

Senegal	Maize, millet	Rare	Bhatnagar 1987

Tachinidae

The biology of Tachinidae is reviewed by Clausen (1940) and Herting (1960).

Subfamily Tachininae

***Dejeania bombylans* Fabricius**
Taxonomic comment: Records are regarded as reliable (1).
Distribution: Afrotropical Region: widespread from Ethiopia to South Africa, Angola, Sierra Leone, Zaire.
Alternative hosts: LEPIDOPTERA Noctuidae: *Cucullia terrensis* Felder.
***H. armigera* records:**

Tanzania	-	-	Robertson 1965
Zimbabwe	Cotton	Abundant	Cuthbertson 1934

***Hystricovoria bakeri* Townsend**
Distribution: Afrotropical Region: Botswana, Ghana, Kenya, South Africa; Oriental Region.
Alternative hosts: LEPIDOPTERA Noctuidae: *Xanthodes graellsi* Feisthamel; Arctiidae; Lymantriidae; Tortricidae.
***H. armigera* records:** Although this species occurs in the Afrotropical Region, host records on *H. armigera* have been reported only from the Oriental Region (Crosskey 1976).

Genus *Linnaemya* Robineau-Desvoidy
Limited information exists on the biology of this genus. Strickland (1923) reported that *Bonnetia* (=*Linnaemya*) *compta* Fallen deposits its incubated eggs on the plant, in the vicinity of a host. Eggs hatch immediately and larvae attach to the passing host to bore through its integument. Many parasitoid larvae are actively killed by the host while entering the host's body, or die inside the host. The parasitoid pupates outside the host.

***Linnaemya agilis* Curran**
Taxonomic comment: Records are regarded as reliable (1).
Distribution: Afrotropical Region: Benin, Kenya, Malawi, Nigeria, South Africa, Tanzania, Uganda, Zaire, Zimbabwe.
Alternative hosts: LEPIDOPTERA Noctuidae: *Diparopsis castanea* Hampson, *Earias biplaga* Walker, *E. insulana* Boisduval.
***H. armigera* records:**

South Africa	Cotton	-	Curran 1934
Tanzania	Cotton	-	Curran 1934
Uganda	Cotton	-	Nyiira 1970a
Uganda	-	-	Coaker 1959

***Linnaemya albifrons* Smith**
Micropalpus affinis Corti (Taylor 1932)
Taxonomic comment: Records are regarded as reliable (1).

Distribution: Afrotropical Region: widespread West Africa to East Africa, north-east Africa & southern Africa, Zaire.

Alternative hosts: LEPIDOPTERA Noctuidae: *Leucania leucosticha* Hampson.

***H. armigera* records:**

South Africa	Cotton	-	Taylor 1932
Zimbabwe	-	-	Risbec 1960

***Linnaemya longirostris* Macquart**

Taxonomic comment: Records are regarded as reliable (1).

Distribution: Afrotropical Region: widespread eastern Africa from Sudan and Ethiopia to South Africa, Zaire.

Biology: The larval period of *L. longirostris* is 10-12 d, the pupal period 14-19 d. Occurs mostly during the fifth and sixth larval stages of the host *H. armigera*, and often emerges from the host pupa (Parsons 1940).

Host-plant associations: *L. longirostris* occurs on a variety of food crops and wild plant species. It appears from Parsons' (1940) data that *L. longirostris*, together with *Palexorista* sp., is more abundant on maize than on cotton.

Alternative hosts: LEPIDOPTERA Noctuidae: *Cucullia* sp., *Plusia limbirena* Guenee.

***H. armigera* records:**

Kenya	Tomato	-	BMNH (Cock Coll 1987)
Kenya	Cotton	-	Le Pelley 1959
Kenya	-	-	Rens 1977
Kenya	-	-	van Emden 1960
South Africa	Various crops	Important	Parsons 1940
South Africa	Cotton	-	Taylor 1932
South Africa	Cotton	-	Simmonds 1960
Tanzania	Cotton	Rare	Robertson 1973
Uganda	-	-	Coaker 1959

***Linnaemya* sp.**

***H. armigera* records:**

Zimbabwe	Tobacco	-	Bünzli & Büttiker 1957

***Nemoraea capensis* Robineau-Desvoidy**

Taxonomic comment: Records are regarded as reliable (1).

Distribution: Afrotropical Region: widespread north-east Africa, East Africa and southern Africa, Nigeria, Zaire.

Biology: Occurs in the fifth and sixth instars of *H. armigera* (Parsons 1940).

Alternative hosts: LEPIDOPTERA Noctuidae: *Agrotis segetum* Schiffermuller, *Diparopsis castanea*, *Spodoptera exempta* Walker.

***H. armigera* records:**

Botswana	Cotton, sorghum	Rare	Roome 1971a
South Africa	Peas, citrus	Rare	Parsons 1940
South Africa	Cotton	-	Simmonds 1960

***Nemoraea rubellana* Villeneuve**

Taxonomic comment: Records are regarded as reliable (1).

Distribution: Afrotropical Region: Cameroun, Ethiopia, Kenya, Rwanda, South Africa, Tanzania, Uganda, Zaire, Zimbabwe.

Alternative hosts: LEPIDOPTERA Noctuidae: *Spodoptera exempta*.

***H. armigera* records:**

Kenya	-	-	Rens 1977

***Paratachina obliqua* Loew**

Paratachina ingens Brauer & Bergenstamm (Taylor 1932)

Taxonomic comment: The record is regarded as reliable (1).

Distribution: Afrotropical Region: South Africa.

***H. armigera* records:**

South Africa	Cotton	-	Taylor 1932

Subfamily Goniinae

***Carcelia evolans* Wiedemann**

Taxonomic comment: There is a complex of sibling or semi-sibling species around '*evolans*'. The record below is regarded as doubtful (1).

Distribution: Afrotropical Region: Ivory Coast, Senegal, Sierra Leone.

Biology: Jacquemard (1969) described the biology of *C. evolans* parasitizing *Diparopsis watersi* Rothschild in Cameroun. The females oviposit on cotton bolls that have been infested with bollworms. The eggs hatch almost immediately. First instars attack and enter the host, and remain inside for about 12 d. The host is killed in its fifth instar, and mature parasitoid larvae leave the dead host to pupate outside. Pupal period: 10 d. *C. evolans* enters diapause simultaneously with the host.

Alternative hosts: LEPIDOPTERA Noctuidae: *Busseola fusca* Hampson, *Diparopsis* spp.; Lasiocampidae; Papilionidae.

***H. armigera* records:**

Tanzania	Cotton	Rare	Robertson 1973

***Carcelia illota* Curran**

Taxonomic comment: This is probably a complex of sibling or semi-sibling species (1). Misidentified as *C. evolans* in Reed (1965).

Distribution: Afrotropical Region: Nigeria, Tanzania, South Africa; Oriental Region.

Alternative hosts: LEPIDOPTERA Noctuidae: *Acontia* sp., *Spodoptera littoralis* Boisduval; Limacodidae.

***H. armigera* records:**

Nigeria	-	-	BMNH (Beeden Col.1974)
Tanzania	Cotton	7%	Robertson 1973
Tanzania	Cotton	Low numbers	Reed 1965, BMNH
Tanzania	Cotton, pigeon pea	-	BMNH (Ritchie Col.1923)

***Carcelia* sp.**

***H. armigera* records:**

Senegal	-	Rare	Bhatnagar 1987

***Carcelia* sp.**

***H. armigera* records:**

Tchad	Cotton	-	Silvie pers. comm. 1988

***Ceromya cibdela* Villeneuve**

Actia cibdela Villeneuve (Cut`hbertson 1934)

Taxonomic comment: Reliable record (1).
Distribution: Afrotropical Region: Mozambique, Nigeria, Tanzania, Zaire.
Alternative hosts: LEPIDOPTERA Noctuidae; Sphingidae.
***H. armigera* records:**

South Africa	Cotton	-	Cuthbertson 1934

***Chetogena* sp.**
***H. armigera* records:**

Senegal	Various crops	-	Bhatnagar 1987

***?Drino* sp.**
***H. armigera* records:**

Uganda	Cotton	-	Nyiira 1970a

***Exorista sorbillans* Wiedemann**
Tricholyga sorbillans Wiedemann (Taylor 1932)
Taxonomic comment: Records must be regarded as suspect (1). Many undescribed species have been confused under *E. sorbillans* (Crosskey 1984).
Distribution: Afrotropical Region: Cameroun, Kenya, Malawi, Sierra Leone, Uganda; Mediterranean Subregion; Oriental Region.
Biology: Datta & Mukherjee (1978) studied the biology of *Exorista ?sorbillans* (as *Tricholyga sorbillans*) on *Bombyx mori* Linnaeus (Lep.: Bombycidae). Oviposition: Macrotype eggs are laid on the host, mostly on intersegmental regions, with an average of 2 eggs per host. Development: Eggs hatch within 2-3 d, larvae enter the host and feed inside for 5-6 d. The third instar emerges from the host to pupate outside. Egg+larval period: 8-12 d; pupal period: 10 d.
Alternative hosts: LEPIDOPTERA Lasiocampidae; Limacodidae; Lymantriidae; Noctuidae; Papilionidae; Psychidae; Saturniidae; HYMENOPTERA.
***H. armigera* records:**

South Africa	Cotton	-	Taylor 1932

***Exorista xanthaspis* Wiedemann**
Exorista fallax Meigen (Lazarévic 1971)
Taxonomic comment: Records are regarded as reliable (1).
Distribution: Afrotropical Region: widespread (incl. Madagascar, Seychelles, Socotra); Oriental Region; Palaearctic Region.
Biology: Achan *et al.* (1968) described the life-history of this parasitoid, under its synonym *E. fallax*, parasitizing *H. armigera*. Adult: Mating occurs soon after emergence. The pre-oviposition period is 7-10 d. Oviposition: Females attack the late instars of the host. Eggs are attached to the host near its head region, and hatch after 3-8 d. The parasitoids emerge from the host after 7-10 d (Herting 1960).
Alternative hosts: LEPIDOPTERA Noctuidae: *Agrotis segetum*, *Earias* sp., *Plusia orichalcea* Fabricius, *Serrodes partita* Fabricius, *Spodoptera exempta*, *S. exigua* Hubner, *Xanthodes intersepta* Guenee; Arctiidae; Lasiocampidae; Lymantriidae; Pieridae; Pyralidae; Sphingidae.
***H. armigera* records:**

Senegal	Millet	Rare	Bhatnagar 1987
Sudan	Cotton	-	Lazarévic 1971

***Gonia bimaculata* Wiedemann**
Taxonomic comment: Records are regarded as reliable (1).

Distribution: Afrotropical Region: widespread (excl. West Africa); Oriental Region; Palaearctic Region.

Biology: *Gonia* spp. oviposit microtype eggs on the plant, to be ingested by late instar host larvae.

Alternative hosts: LEPIDOPTERA Noctuidae: *Agrotis segetum*, *Apopestes limbata* Staudinger; Arctiidae.

***H. armigera* records:**

Somalia	Maize	-	Chiaromonte 1933
South Africa	Cotton	Rare	Parsons 1940
South Africa	Cotton	2%	Parsons & Ullyett 1934
South Africa	Cotton	-	Simmonds 1960
South Africa	Citrus	Important	Cuthbertson 1934

***?Gonia* sp.**

***H. armigera* records:**

Zimbabwe	Citrus	V. important	Hall & Ford 1933

***?Gonia* sp.**

***H. armigera* records:**

Zimbabwe	Citrus	Important	Jones 1939

***Goniophthalmus halli* Mesnil**

Taxonomic comment: All records below are regarded as reliable (1).

Distribution: Afrotropical Region: Botswana, Kenya, Namibia, Sudan, Tanzania, West Africa, Zimbabwe; Oriental Region.

Biology: Patel & Singh (1972) described the biology of *G. halli* parasitizing *H. armigera*. Adults: Mating occurs generally on the day of emergence. Pre-oviposition period: 5-7 d. Fecundity: 5,000 eggs per female. Oviposition: Numerous microtype eggs (0.18x0.1 mm) are attached to the host plant, near the edges of feeding spots of the target host, in order to be ingested together with the plant material. Development: Eggs hatch in the host gut and the parasitoid larvae inhabit the haemolymph until they reach the third instar; they then attack other organs. Mortality of parasitoid eggs or larvae is generally high (Mück 1985). Parasitized hosts are not easily distinguishable from unparasitized and will continue feeding. Although several larvae can be found per host, no more than one parasitoid will eventually emerge, due to strong intraspecific competition. The parasitoid usually pupates within the host pupa, but sometimes the parasitoid larva leaves the host pupa to pupate outside. Egg+larval period: variable, 9-17 d; pupal period: 8-16 d (27°C). In Tanzania this species has been reported to diapause for 130 d within its host pupa during the dry season (Reed 1965). Host stages: The fourth, fifth or sixth instars of *H. armigera* are attacked. The adult parasitoid usually emerges from the host pupa.

Alternative hosts: No records from Africa. *G. halli* is regarded as a parasitoid specific on *H. armigera*. Out of 19 host records of this parasitoid worldwide only 2 are records of hosts (Lepidoptera) other than *H. armigera*.

***H. armigera* records:**

Botswana	Cotton	0.1%	Roome 1971a, BMNH
Cape Verde	-	-	Mück 1985
Kenya	Cotton	-	BMNH (Rens Coll 1970)
Kenya	-	-	Dewhurst unpubl. 1985
Senegal	Maize, millet	Up to 2%	Bhatnagar 1987
Sudan	-	-	BMNH (Wood Coll 1933)

Tanzania	Cotton	Up to 12%	Reed 1965, BMNH
Tanzania	Cotton	Rare	Robertson 1973
Tchad	Cotton	-	Silvie pers. comm. 1988
Zimbabwe	-	-	Mesnil 1956
Zimbabwe	Citrus	-	BMNH (Jones Coll 1938)
Zimbabwe	-	-	BMNH (Hall Coll 1929)

***Pales blepharipus* Brauer & Bergenstamm**

Phorocera blepharipus Brauer & Bergenstamm (Taylor 1932)

Taxonomic comment: The specific name must be regarded as doubtful (1).

Distribution: Afrotropical Region: South Africa, Zaire.

Alternative hosts: LEPIDOPTERA Noctuidae: *Anomis auragoides* Guenee, *Cucullia terrensis*, *Plusia* sp., *Spodoptera exempta*, *Xanthodes graellsi*; Lasiocampidae; Lymantriidae; Pyralidae; Saturniidae; Sphingidae.

***H. armigera* records:**

South Africa	Cotton	-	Cuthbertson & Munro 1941
South Africa	Cotton	-	Taylor 1932

***Pales coerulea* Jaennicke**

Taxonomic comment: The specific name must be regarded as doubtful (1).

Distribution: Afrotropical Region: north-east Africa to southern Africa; ?Oriental Region.

Alternative hosts: LEPIDOPTERA Noctuidae: *Spodoptera littoralis*; Hesperiidae; Lasiocampidae; Lycaenidae; Lymantriidae; Papilionidae.

***H. armigera* records:**

South Africa	Various crops	Rare	Parsons 1940
Zimbabwe	Citrus	-	BMNH (Jones Coll 1938)

***Pales nigronitens* Villeneuve**

Taxonomic comment: The specific name must be regarded as doubtful (1). Parsons (1940) recorded *P. nigronitens* as well as *P. pavida* Meigen, but according to Cuthbertson & Munro (1941) they were both *P. nigronitens*.

Distribution: Afrotropical Region: South Africa, Zaire.

Biology: Occurs in the second to the sixth instar of *H. armigera* and emerges from its pupa. Development egg-adult: 29-40 d (Parsons 1940).

Alternative hosts: LEPIDOPTERA Limacodidae.

***H. armigera* records:**

South Africa	Citrus, vegetables	Rare	Parsons 1940

***Pales seminitida* Villeneuve**

Taxonomic comment: The specific name must be regarded as doubtful (1).

Distribution: Afrotropical Region: Malawi, Nigeria, Zaire.

Alternative hosts: LEPIDOPTERA Lasiocampidae; Thaumetopoeidae.

***H. armigera* records:**

Zimbabwe	Malvaceae	- (from ?*H. armigera*)	Cuthbertson & Munro 1941

***Palexorista idonea* Brauer & Bergenstamm**

Sturmia partitor Curran (Cuthbertson 1939).

Taxonomic comment: The specific name below must be regarded as suspect (1).

Distribution: Afrotropical Region: Mozambique, South Africa.
Alternative hosts: LEPIDOPTERA Lasiocampidae.
***H. armigera* records:**

Zimbabwe	Cotton	-	Cuthbertson 1939

***Palexorista imberbis* Wiedemann**
Taxonomic comment: Records from Africa must be regarded as suspect. Despite many records in literature, there is no evidence that '*imberbis*' occurs in the Afrotropical Region (1). All BMNH specimens from Africa, that were recorded as '*imberbis*', are *Palexorista laxa*.
Distribution: Djibouti, Egypt, Israel.
Alternative hosts: LEPIDOPTERA Noctuidae: *Spodoptera exigua, S. littoralis, Xylina exoleta* Linnaeus; Lasiocampidae.
***H. armigera* records:**

Sudan	Cotton	V. important	Tunstall 1958
Sudan	Cotton	Important	Lazarévic 1971
Tchad	Cotton	-	Silvie pers. comm. 1988
Uganda	Cotton	Rare	Greathead 1966

***Palexorista laxa* Curran**
Sturmia laxa Curran (Taylor 1932; Cuthbertson & Munro 1941)
Taxonomic comment: This is probably a complex of sibling or semi-sibling species (1), and is currently being studied at the BMNH. In current taxonomy, *P. laxa* has been misidentified as *Sturmia* (=*Palexorista*) *inconspicua* Meigen (Jones 1939) and *Drino* (=*Palexorista*) *imberbis* (Reed 1965; Robertson 1973), neither occurring in the Afrotropical Region.*H. armigera* records are reliable for specimens present in the BMNH collection only; other records must be regarded as doubtful.
Distribution: Afrotropical Region: Botswana, Malawi, Senegal, South Africa, Sudan, Tanzania, Uganda, Zimbabwe; Oriental Region.
Biology: Jackson *et al.* (1976) described the biology of *P. ?laxa* parasitizing *Helicoverpa zea* Boddie. Adults: Mating occurs soon after emergence. Pre-oviposition period: 6.9 d (25°C), 4.6 d (30°C); oviposition period: 24.5 d (25°C), 17.5 d (30°C). Oviposition: Female attaches the incubated, macrotype eggs to the host body from a position standing beside the host. Development: Eggs hatch immediately after oviposition and the emerging larvae enter the host. During development of the parasitoid larvae the host feeds normally, until the larvae emerge. Depending on the size of the host, one to seven parasitoid larvae emerge per host; they pupate outside. Egg+larval period: 6.0 d (25°C), 4.6 d (30°C); pupal period: 9.4 d (25°C), 6.7 d (30°C) (Jackson *et al.* 1976), 12 d (Reed 1965). Host stages: Mostly, fourth to sixth instars are attacked. The parasitoid emerges from the sixth instar or from the prepupa.
Alternative hosts: LEPIDOPTERA Noctuidae: *Anomis auragoides, Busseola fusca, Leucania leucosticha, L. loreyi* Duponchel, *Lycophotia oliveata* Hampson, *Spodoptera exempta, S. exigua, Tarache nitidula* Fabricius, *Xanthodes graellsi*; Arctiidae; Lasiocampidae; Pyralidae; Sphingidae. According to Crosskey (1967) *H. armigera* is the only proven host of *P. laxa*. In this respect, the above alternative host records must be regarded as suspect. Gerling & Rotary (1973) demonstrated that *P. laxa* failed to develop in the noctuid *Spodoptera littoralis*. The parasitoids died at an early stage, together with their hosts. In the Sudan, Tunstall (1958) reported that *P. ?laxa*, an important parasitoid of *H. armigera*, did not parasitize *Diparopsis watersi* to any extent.

Host-plant associations: Data from Tanzania reveal a strong association of *P. laxa* with sorghum, compared with maize, cotton or cleome (Nyambo 1986). It was observed that *H. armigera* on sorghum feeds in a more exposed position than on other crops. This phenomenon might explain the differences in parasitism levels. See also *Palexorista* sp. below.

***H. armigera* records:**

Botswana	Sorghum	-	BMNH (Roome Coll 1970)
Botswana	-	14.5%	Roome 1971a
Mali	-	-	BMNH (Doumbia Coll 1978)
Senegal	-	-	Risbec 1960
Senegal	Sorghum	Rare	Bhatnagar 1987
South Africa	Cotton	-	Cuthbertson & Munro 1941
South Africa	Cotton	-	Taylor 1932
Sudan	-	-	BMNH (Wood Coll 1933)
Tanzania	Cotton	Up to 25%	Reed 1965, BMNH
Tanzania	Various crops	Up to 42%	Nyambo 1986, BMNH
Tanzania	Cotton	14%	Robertson 1973, BMNH
Tanzania	-	-	BMNH (Ritchie Coll 1923)
Tanzania	-	-	BMNH (Disney Coll 1949)
Uganda	-	-	BMNH (Mubbin Coll 1939)
Zaire	-	-	Risbec 1960
Zimbabwe	-	-	BMNH (Gatuma Coll 1969)
Zimbabwe	-	-	Jones 1939, BMNH

***Palexorista quadrizonula* Thomson**

Distribution: Afrotropical Region: widespread (incl. Sao Tome, Seychelles).

***H. armigera* records:**

Senegal	Various crops	Up to 10%	Bhatnagar 1987

***Palexorista* sp. nr. *inconspicua* Meigen**

***H. armigera* records:**

Somalia	Maize	-	Chiaromonte 1933

***Palexorista* sp. nr. *laxa* Curran**

***H. armigera* records:**

Botswana	Abutilon	- (from *Heliothis* sp.)	BMNH (Ingram Coll 1968)

***Palexorista* sp.**

Taxonomic comment: Misidentified as *Sturmia* (=*Palexorista*) *inconspicua*, which is not Afrotropical (1). This might well be *P. laxa*.

Biology: Larval period: 10-14 d; pupal period: 8-17 d. Occurs mainly in the fifth and sixth instars of *H. armigera* (Parsons 1940).

Host-plant associations: In South Africa, higher parasitism by this species was observed on maize than on cotton. This might have been a density response; densities were higher on maize (Parsons & Ullyett 1934; Parsons 1940).

***H. armigera* records:**

South Africa	Various crops	V. important	Parsons 1940
South Africa	Cotton	-	Simmonds 1960
South Africa	Cotton	20-30%	Parsons & Ullyett 1934

South Africa	Maize	Important	Parsons & Ullyett 1934
Sudan	-	-	Balla 1982

***Palexorista* sp.**

***H. armigera* records:**

Senegal	Various crops	Rare	Bhatnagar 1987

***Paradrino halli* Curran**

Drino halli Curran (Robertson 1973)

Sturmia halli Curran (1939)

Sturmia rhodesiensis Jones (1939)

Taxonomic comment: This is a distinctive species; records are therefore regarded as reliable (1).

Distribution: Afrotropical Region: Botswana, Tanzania, Uganda, Zimbabwe.

Biology: Jones (1939) studied the biology of *P. halli* as the most important parasitoid of *H. armigera* on citrus in Zimbabwe. Adult: Males can copulate directly after emergence, females only after 3 d. Pre-oviposition period is 7 d. Longevity: 12-33 d for females, 6-22 d for males; without food longevity is 5 d shorter for both sexes. Oviposition: The adult female alights on the host to oviposit; oviposition occurs very quickly to prevent defence by the host. The ovipositor is short. Fully incubated macrotype eggs (0.7x0.23 mm) are attached to the integument of the host. The number of eggs per host varies with the abundance of hosts, most commonly 1-3 eggs are laid per host. Development: Within 15 min after oviposition eggs hatch and the first instars enter the host by boring through the integument. The parasitoid larvae enter the host's fat bodies and create a hole for respiration in one of the tracheae; they place their spiracles in the opening. A funnel of wound tissue is formed around the parasitoid. Fully grown parasitoid larvae emerge from the host to pupate outside. When emerging from the host pupal stage they do so from between the segments of the pupa; this species bores no hole in the host pupa. In Tanzania, usually one parasitoid emerged per host (Robertson 1973). Egg+larval period: 16-20 d; pupal period: 7-16 d (Robertson 1973). Host stages: The mostly attacked of *H. armigera* is the fourth. Parasitoid larvae emerge from the sixth instar or pupa of the host.

Host-plant associations: Parasitism is rather low on different crops. Jones (1939) however found high levels of parasitism on citrus during spring, much higher than on maize or vegetable crops later in the season. This could be attributable to a seasonal rather than a host plant effect.

Alternative hosts: LEPIDOPTERA Noctuidae: occasionally *Busseola fusca* and *Cetola* sp.; no other record. This species is regarded as a specialist parasitoid of *H. armigera*.

***H. armigera* records:**

Botswana	Various crops	Rare	Roome 1971a
Tanzania	Cotton	Rare	Robertson 1973
Tanzania	Various crops	Common	Nyambo 1986
Zimbabwe	Citrus	Up to 25%	Jones 1939, BMNH
Zimbabwe	Various crops	Up to 5%	Jones 1939
Zimbabwe	Cotton	-	Bünzli & Büttiker 1957
Zimbabwe	-	-	Curran 1939

***Peribaea mitis* Curran**

Taxonomic comment: Records are regarded as reliable (1).

Distribution: Afrotropical Region: Kenya, South Africa, Sudan.

Alternative hosts: LEPIDOPTERA Noctuidae: *Spodoptera exigua*; Geometridae.

***H. armigera* records:**

Sudan	Clover	-	BMNH (Johnston Coll 1927)
Sudan	-	-	BMNH (Bedford Coll 1929)

***Peribaea orbata* Wiedemann**

Actia aegyptia Villeneuve (Ismael & Swailem 1975)

Taxonomic comment: Records are regarded as reliable (1).

Distribution: Afrotropical Region: East Africa & southern Africa, Congo basin, West Africa to north-east Africa; Oriental Region.

Biology: This parasitoid attacks mostly the second or third instar of the host *Spodoptera littoralis*. Pupal period: 7-10 d (Hegazi, Hammad & El-Minshawy 1977).

Alternative hosts: LEPIDOPTERA Noctuidae: *Spodoptera exempta, S. exigua, S. littoralis*.

***H. armigera* records:**

Egypt	-	-	Ismael & Swailem 1975

***Plagiomima rufolateralis* Crosskey**

Taxonomic comment: Records are regarded as reliable (1).

Distribution: Afrotropical Region: Botswana, Namibia.

***H. armigera* records:**

Botswana	Carnations, sunflower	-	Crosskey 1984 (from *Heliothis* sp.)

***Pseudogonia rufifrons* Wiedemann**

Gonia ritchiei Cuthbertson & Munro (1941)

Isomera cinerascens Rondani (Lazarévic 1971)

Pseudogonia cinerascens Rondani (Parsons 1940; Simmonds 1960)

Taxonomic comment: Records are regarded as reliable (1).

Distribution: Afrotropical Region: widespread (incl. Cape Verde Islands, Socotra); Oriental Region; Palaearctic Region.

Biology: The biology of *P. rufifrons*, under its synonym *Gonia cinerascens*, has been extensively studied on the host *Galleria mellonella* Linnaeus (Lep.: Pyralidae) by Campadelli and others in Italy. Adult: Mating occurs on the day of emergence. Pre-oviposition period: 16 d at 24°C. Longevity : 22 d for females, 15 d for males at 24°C (Campadelli & Baronio 1979). Fecundity: several thousands of eggs (Gardenghi & Mellini 1980). Oviposition: Numerous microtype eggs are attached to the leaves to be ingested by the host together with the plant material. Development: Eggs hatch in the fore- or mid-gut; hatching is mainly induced by digestive enzymes of the host (Mellini & Campadelli 1979). The first instar develops within the abdominal muscles of the host. Ecdysteroid hormones of the host act directly on parasitoid development (Barinio & Sehnal 1980). The second instar moves to the space between the old larval skin and the developing pupa. The mature third instar pupates inside the cocoon of the host. No more than one parasitoid will emerge per host, due to intraspecific competition. Pupal period: 10 d (27°C). Total development period: 30-37 d (Parsons 1940). Host stages: Most commonly, fourth to sixth instars of *H. armigera* are attacked. The adult parasitoid emerges from the host pupa (Parsons 1940).

Host-plant associations: Parsons (1940) found *P. rufifrons* more frequently on *H. armigera* on peas, than on other crops.

Alternative hosts: LEPIDOPTERA Noctuidae: *Leucania loreyi, Spodoptera exempta, S. exigua*.

***H. armigera* records:**

Senegal	Maize	Up to 14%	Bhatnagar 1987

South Africa	Various crops	Rare	Parsons 1940
South Africa	Cotton	-	Simmonds 1960
South Africa	Citrus	-	Cuthbertson & Munro 1941 (from ?*H. armigera*)
Sudan	Cotton, beans	-	Lazarévic 1971

***Sturmia convergens* Wiedemann**

Sturmia flavohalterata Bischof (Milner 1967)

Taxonomic comment: Records are regarded as reliable (1).

Distribution: Afrotropical Region: Ethiopia, Kenya, Malawi, Nigeria, Sierra Leone, South Africa, Tanzania, Zambia, Zimbabwe; Oriental Region.

Biology: The female deposits microtype eggs in the vicinity of the host, mostly on the underside of the leaves. First instar larvae find and enter the host. Mature larvae leave the host pupae and pupate in the soil (Herting 1960).

Alternative hosts: LEPIDOPTERA Danaidae; Nymphalidae.

***H. armigera* records:**

Tanzania	Striga	-	Milner 1967

?*Sturmia* sp.

Taxonomic comment: This might well be *Palexorista* sp.

***H. armigera* records:**

Zimbabwe	Citrus	V. important	Hall & Ford 1933

***Thelairosoma angustifrons* Villeneuve**

Taxonomic comment: Records must be regarded as doubtful (1).

Distribution: Afrotropical Region: Malawi, Nigeria, South Africa, Tanzania, Uganda, Zaire.

Alternative hosts: LEPIDOPTERA Bombycidae; Sphingidae.

***H. armigera* records:**

Zimbabwe	Cotton	-	Pearson 1958

***Voria capensis* Villeneuve**

Taxonomic comment: The record below is regarded as reliable (1).

Distribution: Afrotropical Region: widespread eastern Africa from Kenya to South Africa, Ghana, Nigeria.

***H. armigera* records:**

South Africa	-	-	Cuthbertson & Munro 1941

***Voria ruralis* Fallen**

Taxonomic comment: This species is very near to *V. capensis*.

Distribution: Afrotropical Region: from Kenya to South Africa; Nearctic Region; Neotropical Region; Oriental Region; Palaearctic Region.

Biology: This cosmopolitian species has been studied extensively as a parasitoid of the noctuid *Trichoplusia ni* Hubner in North America.

Adults: Mating occurs soon after emergence. Pre-oviposition period: 9 d; oviposition period: 14 d (Brubaker 1968). Fecundity: 60 eggs per female (Elsey & Rabb 1970). Longevity: 28 d for females, 20 d for males (Grant & Shepard 1983). Oviposition: Fully incubated eggs are laid on the host and hatch immediately. Development: First instar larvae bore into the host body and settle in the muscle fibre. After a few days, the parasitoid larvae create a hole for respiration in the integument of the host and place their abdominal spiracles in the opening (Elsey & Rabb 1970). The parasitoids pupate inside the host larva or pupa. This

species is gregarious, with an average of 2.2 pupae emerging per *T. ni* host. Egg+larval period: 7-9 d; pupal period: 7-8 d (27°C) (Grant & Shepard 1983); see also Jackson, Butler & Bryan (1969). Host stages: Late host instars are preferred for oviposition. Adult parasitoids emerge from the host larval or pupal stage.

Alternative hosts: LEPIDOPTERA Noctuidae: *Plusia chalcites* Esper, *P. limbirena*, *P. orichalcea*. Worldwide, *V. ruralis* is mainly a parasitoid of Noctuidae.

***H. armigera* records:** Although this species occurs in the Afrotropical Region, host records on *H. armigera* have been reported only from the Oriental Region.

***Winthemia dasyops* Wiedemann**

Taxonomic comment: Records are regarded as reliable (1).

Distribution: Afrotropical Region: Ethiopia, Ghana, Kenya, Madagascar, Malawi, Mozambique, Nigeria, South Africa, Tanzania, Uganda, Zaire; South Yemen.

Biology: It has been recorded that *Winthemia* species have a short pre-oviposition period (2-3 d). They inject their eggs in the host larva or attach the eggs to the host integument. Eggs hatch in about one week. The larval period is very short (Clausen 1940).

***H. armigera* records:**

South Africa	Cotton	-	Cuthbertson & Munro 1941

***Zygobothria ciliata* van der Wulp**

Sturmia munroi Curran (Cuthbertson 1934; Jones 1939)

Taxonomic comment: Records are regarded as reliable (1).

Distribution: Afrotropical Region: widespread mainland; Oriental Region.

Alternative hosts: LEPIDOPTERA Noctuidae: *Diparopsis castanea*, *Spodoptera exigua*; Geometridae; Lasiocampidae; Psychidae; Sphingidae.

***H. armigera* records:**

South Africa	Citrus	-	Cuthbertson 1934
Zimbabwe	Citrus	Rare	Jones 1939

HYMENOPTERA

Ichneumonidae

***Barylypa humeralis* Brauns**

Distribution: Palaearctic Region.

Alternative hosts: LEPIDOPTERA Noctuidae.

***H. armigera* records:**

Egypt	Tomato	Up to 16%	Megahed *et al.* 1977

***Barylypa rufa* Holmgren**

Distribution: Palaearctic Region.

Alternative hosts: LEPIDOPTERA Noctuidae.

***H. armigera* records:**

Egypt	-	Common	Ismael & Swailem 1975

***Campoplex xanthostoma* Gravenhorst**

Distribution: Palaearctic Region.

Alternative hosts: LEPIDOPTERA Gelechiidae; Noctuidae; Pyralidae.

***H. armigera* records:**

Egypt	-	Rare	Megahed *et al.* 1977

Genus *Charops* Holmgren

The African fauna in this genus is still largely undescribed. Likewise, very limited information exists on the biology of *Charops* spp. Duodu & Lawson (1983) studied *C. diversipes* Roman on the nymphalid host *Acraea terpsicore* Linnaeus. *Charops* spp. generally attack exceptionallly young host larvae (mostly first instars), although a *Charops* sp. has been reported to attack the third instar of *Orgyia mixta* Snellen (Lymantriidae) more than the first or second instar (Migunda 1970). The development of *C. diversipes*, from egg to adult, is 13-17 d. The mature larva emerges from the host larva and starts spinning a cocoon. The cocoon remains on the plant during pupation. Pupae of *Charops* spp. are commonly hyperparasitized by *Brachymeria* spp. (Chalcididae). The records below might include many different species.

***Charops ater* Szepligeti**

Taxonomic comment: Records are regarded as reliable (2).
Distribution: Afrotropical Region: Madagascar, Mozambique, Nigeria.
Alternative hosts: LEPIDOPTERA Noctuidae: *Spodoptera littoralis*; Nymphalidae.
***H. armigera* records:**

Mozambique	-	-	BMNH (Umbeluzi Col 1982)

***Charops* sp.**
***H. armigera* records:**

Tanzania	Legumes	Common	Reed 1965

***Charops* sp.**
Biology: This species is common year-round in Tanzania. The parasitoid larva emerges from the third or fourth instar of the host (Nyambo 1986).
Host-plant associations: Common on tomato, cleome and chickpea; rare on cotton and maize (Nyambo 1986).
***H. armigera* records:**

Tanzania	Various crops	Up to 23%	Nyambo 1986

***Charops* sp.**
***H. armigera* records:**

Tanzania	Cotton	2.1%	Robertson 1973

***Charops* sp.**
***H. armigera* records:**

Tanzania	Pigeon pea	-	BMNH (Disney Coll 1949)

***Charops* sp.**
***H. armigera* records:**

Tanzania	Striga	-	Milner 1967

***Charops* sp.**
***H. armigera* records:**

Uganda	Various crops	10%	Coaker 1959

***Charops* sp.**
***H. armigera* records:**

Uganda	Cotton	-	Nyiira 1970a

***Charops* sp.**
***H. armigera* records:**

Botswana	Cotton, cleome	-	Roome 1975a

***Charops* sp.**
***H. armigera* records:**

Tchad	Cotton	-	Silvie pers. comm. 1988

***Charops* spp.**
Alternative hosts: LEPIDOPTERA Noctuidae: *Plusia orichalcea.*
***H. armigera* records:**

South Africa	Cotton, tomato	V. rare	Parsons 1940

***Charops* sp.**
***H. armigera* records:**

Nigeria	-	-	BMNH (Beeden Coll 1974)

***Charops* sp.**
***H. armigera* records:**

Senegal	Sorghum, acanthospermum	Rare	Bhatnagar 1987

***Diadegma* sp.**
Angitia sp. (Parsons 1940)
Taxonomic comment: Probably many undescribed species in Africa (2).
Biology: Larval period: 7-11 d; pupal period: 12-15 d. Attacks mostly the third host instar (Parsons 1940).
***H. armigera* records:**

South Africa	Peas, maize	Rare	Parsons 1940

Genus *Enicospilus* Stephens

Moutia & Courtois (1952) report that *Enicospilus* sp. has a pre-ovipostition period of 8-10 d and a fecundity of 8-14 eggs per female. The female deposits one egg in the body cavity of the host, and the egg hatches after 2 d. The larva develops in the haemolymph of the host. When fully grown, it emerges from the host and spins a cocoon on the plant. Oviposition is probably most frequent in the third and fourth instars of the host. In general, *Enicospilus* spp. are parasitoids of Noctuidae; many are thought to be host specific. Some species are adapted to dry conditions, e.g. *E. capensis* Thunberg, is known as a dry season parasitoid of noctuids in India (Gauld & Mitchell 1978).

***Enicospilus capensis* Thunberg**
Distribution: Afrotropical Region: throughout (incl. Madagascar); Oriental Region.
Alternative hosts: LEPIDOPTERA Noctuidae: *Sesamia* sp., *Spodoptera exempta*, many other Noctuidae; occasionally Pyralidae.
***H. armigera* records:** Although this species occurs throughout Africa, host records on *H. armigera* have been reported only from the Oriental Region.

Enicospilus ?communis Szepligeti
***H. armigera* records:**

Uganda	Cotton	11%	Coaker 1959

Enicospilus sp.
***H. armigera* records:**

Tanzania	Cotton	Rare	Robertson 1973

Metopius discolor Tosquinet
Distribution: Afrotropical Region: South Africa, Tanzania.
Biology: Endoparasitoid. Attacks late host instars. Egg-adult period: 32-39 d (Parsons 1940). *Metopius* spp. are the only ichneumonids that emerge from the host pupal stage.
Alternative hosts: No records.
***H. armigera* records:**

South Africa	Various crops	Rare	Parsons 1940
South Africa	Cotton	-	Taylor 1932
South Africa	Cotton	-	Simmonds 1960
Tanzania	Cotton	Rare	Reed 1965

Netelia ?capensis Holmgren
Distribution: Afrotropical Region: Ethiopia, Kenya, South Africa, Uganda.
Biology: *Netelia* spp. oviposit one black egg with a hard shell on the host. Usually full-grown host larvae (fifth and sixth) are attacked. The host is killed before it pupates.
***H. armigera* records:**

Uganda	-	Rare	Coaker 1959

Netelia opacula Schrank
Taxonomic comment: Specific name must be regarded as doubtful (2).
Distribution: Afrotropical Region: Ethiopia, Kenya, South Africa, Uganda; Palaearctic Region.
Alternative hosts: LEPIDOPTERA Noctuidae: records from Palaearctic Region only.
***H. armigera* records:**

Kenya	-	-	Le Pelley 1959

Netelia testacea Gravenhorst
Taxonomic comment: Record below is regarded as reliable (2).
Distribution: Afrotropical Region: Zimbabwe; Palaearctic Region.
Alternative hosts: LEPIDOPTERA Noctuidae, records from outside the Afrotropical Region only; Arctiidae; Lasiocampidae; Notodontidae; Sphingidae.
***H. armigera* records:**

Zimbabwe	-	-	BMNH (Gatooma Coll 1969)

Netelia sp.
***H. armigera* records:**

Kenya	Tomato	-	BMNH (Cock Coll 1987)

Netelia sp.
***H. armigera* records:**

Tanzania	Cotton	Up to 3%	Reed 1965

***Netelia* sp.**
***H. armigera* records:**

Tanzania	Various crops	Rare	Nyambo 1986

***Netelia* sp.**
***H. armigera* records:**

Tanzania	Cotton	Rare	Robertson 1973

***Netelia* sp.**
***H. armigera* records:**

Uganda	Cotton	-	Nyiira 1970a

***Pristomerus* sp. nr. *fumipennis* Wilkinson**
***H. armigera* records:**

Uganda	-	Rare	Coaker 1959

***Pristomerus* sp.**
Taxonomic comment: Many undescribed *Pristomerus* spp. in Africa.
Biology: Solitary endoparasitoid. Occurs mainly in second and third host instars. Larval period: 7-9 d; pupal period: 9-11 d (Parsons 1940). The fully grown larva spins a cocoon near the host remains.
***H. armigera* records:**

South Africa	Various crops	Rare	Parsons 1940

***Pristomerus* sp.**
***H. armigera* records:**

Tanzania	Cotton	Rare	Reed 1965

***Pristomerus* sp.**
***H. armigera* records:**

Tanzania	Various crops	Rare	Nyambo 1986

***Pristomerus* sp.**
***H. armigera* records:**

Botswana	Various crops	-	Roome 1975a

***Pristomerus* sp.**
***H. armigera* records:**

South Africa	Cotton	-	Simmonds 1960

***Pristomerus* sp.**
***H. armigera* records:**

Senegal	Sorghum	-	Bhatnagar 1987

Braconidae

***Aleiodes* sp.**
Taxonomic comment: Recorded as *Rogas* sp.; the genus *Rogas* was later transferred to *Aleiodes*.

***H. armigera* records:**

Uganda	Cotton	-	Nyiira 1970a

***Aleiodes* sp.**

***H. armigera* records:**

Senegal	Various crops	Up to 7%	Bhatnagar 1987

Genus *Apanteles* Foerster

Taxonomic comment: This huge genus was classified in species-groups by Nixon (1965), and has been reclassified by Mason (1981) in a number of new genera. Because Mason's reclassification is based only on American species, excluding species from all other parts of the world, it is not generally accepted. We therefore use Nixon's classification.

Biology: Species in this genus are larval, in some cases egg-larval, endoparasitoids of Lepidoptera. Mature larvae emerge from the host and pupate in cocoons alongside the host remains. Some species emerge from very young host larvae, some from the host's final instar. Species are either solitary or gregarious (Le Masurier 1987). Although some species attack a wide variety of host species of different lepidopterous families, most are restricted to a small number of closely related hosts.

***Apanteles diparopsidis* Lyle**

Taxonomic comment: The record below is regarded as reliable (2).

Distribution: Afrotropical Region: Malawi, Rwanda, South Africa, Sudan, Tanzania, Uganda, West Africa, Zaire.

Biology: Attacks the first and emerges from the second instar of *H. armigera*. Pupal period: 5-8 d (Nyambo 1986).

Host-plant associations: Common on sorghum, rare on cotton (Nyambo 1986).

Alternative hosts: Mainly known as a parasitoid of *Diparopsis* and *Earias* spp.; LEPIDOPTERA Noctuidae: *Diparopsis castanea, D. watersi, Earias biplaga, E. insulana*; Gelechiidae; Lyonetiidae; Pyralidae.

***H. armigera* records:**

Tanzania	Various crops	Up to 26%	Nyambo 1986

***Apanteles maculitarsis* Cameron**

Taxonomic comment: The records below are regarded as doubtful (2).

Distribution: Afrotropical Region: Kenya, Malawi, Senegal, South Africa.

Biology: Larval period: 8-10 d; pupal period: 6-8 d. Mostly, it attacks the first instar and emerges from the third instar of *H. armigera* (Parsons 1940).

Alternative hosts: LEPIDOPTERA Noctuidae: *Spodoptera exempta*; Lasiocampidae; Saturniidae.

Host-plant associations: Most frequent on peas (Parsons 1940).

***H. armigera* records:**

Senegal	-	-	Risbec 1950
South Africa	Various crops	Common	Parsons 1940
South Africa	Various crops	-	de Saeger 1944

***Apanteles ruficrus* Haliday**

Taxonomic comment: Recognizable species; records are regarded as reliable (2).

Distribution: Afrotropical Region: Cameroun, Madagascar, Senegal, Somalia, South Africa, Sudan, Uganda; Oriental Region; Palaearctic Region; introduced in North America and New Zealand.

Biology: Gregarious species. Hafez (1947) described the biology of *A. ruficrus* parasitizing *Agrotis ipsilon* Rottenburg. Mating occurs directly after emergence. There is no pre-oviposition period, because eggs are fully developed upon emergence. Fecundity: 220 eggs per female. Longevity of female: 6.3 d (26°C). Sex ratio 2:1, in favour of males. Oviposition: The female deposits a large number of eggs per host, just under the host integument. During the next 5 d the eggs swell up from 0.13x0.04 mm to 0.56x0.25 mm, and hatch. The larvae feed within the host during their development. The host gradually becomes inactive and stops feeding. The fully grown third instar parasitoids leave the host almost simultaneously and start spinning their white cocoons alongside the host remains. Hafez reported that about 60 parasitoids emerge per *Agrotis* host. Egg+larval period: 11-18 d; pupal period: 3-6 d (28°C) (McCutcheon, Salley & Turnipseed 1983).

Alternative hosts: LEPIDOPTERA Noctuidae: *Agrotis ipsilon, Euxoa spinifera* Hubner, *Leucania loreyi, Plusia circumflexa* Linnaeus, *P. gamma* Linnaeus, *Sesamia cretica* Lederer, *Spodoptera exempta, S. exigua, S. littoralis*; Arctiidae; Geometridae; Hesperiidae; Lycaenidae; Lymantriidae; Nymphalidae; Pyralidae; Yponomeutidae.

Secondary natural enemies: A pteromalid has been recorded from *A. ruficrus* cocoons in Egypt (Hafez 1947).

***H. armigera* records:**

Egypt	-	Common	Ismail & Swailem 1975
Egypt	-	Rare	Megahed *et al.* 1977
Senegal	-	-	Risbec 1950
Somalia	Maize	-	de Saeger 1944
Sudan	Cotton	-	Greathead 1966

***Apanteles sesamiae* Cameron**

Taxonomic comment: Distinct species; records are regarded as reliable (2).

Distribution: Afrotropical Region: Cameroun, Kenya, Malawi, Mozambique, Senegal, South Africa, Sudan, Uganda, Zaire.

Biology: Ullyett (1935) described the biology of *A. sesamiae* parasitizing *Busseola fusca*. Adult: Mating occurs shortly after emergence. Longevity: 3-4 d. Development: Egg+larval period: 14-21 d; pupal period: 5-7 d (26°C, 80%RH). High humidity seems to be essential for development. Commonly, 60-100 larvae emerge per host larva. Host stages: Mature parasitoid larvae emerge from the fifth or sixth instar of the host.

Alternative hosts: Known mainly as a stemborer parasitoid; LEPIDOPTERA Noctuidae: *Busseola fusca, Sesamia* spp.; Pyralidae. The stout body and short appendages suggest the adaptation of this species to parasitize stemborers (see Ullyett 1935).

***H. armigera* records:**

Zaire	-	-	de Saeger 1944 (from *Heliothis* sp.)

***Apanteles* sp. nr. *aethiopicus* (*ultor*-group of Nixon (1965))**

Biology: Occurs in the first to the third host instar of *H. armigera*. Larval period: 7-10 d; pupal period: 6-8 d (Parsons 1940).

Host-plant associations: Frequent on peas (Parsons 1940).

***H. armigera* records:**

South Africa	Peas	Important	Parsons 1940

***Apanteles* sp. *ultor*-group of Nixon (1965)**
***H. armigera* records:**

Uganda	Various crops	Up to 20%	Coaker 1959

***Apanteles* sp. *vitripennis*-group of Nixon (1965)**
Biology: This species attacks the first instar of the host (Nyambo, unpublished). *A. vitripennis* is a solitary species (Le Masurier 1987).
***H. armigera* records:**

Tanzania	Various crops	Common	Nyambo 1986

***Apanteles* sp.**
***H. armigera* records:**

Uganda	Cotton	-	Nyiira 1970a

***Apanteles* sp.**
***H. armigera* records:**

Kenya	Pigeon pea	-	BMNH (KARI Coll 1985)

***Apanteles* sp.**
***H. armigera* records:**

Botswana	Sorghum, sunflower	-	Roome 1975a

***Apanteles* sp.**
***H. armigera* records:**

Somalia	Cotton	-	Russo 1940

***Apanteles* sp.**
***H. armigera* records:**

Tchad	Cotton	-	Silvie pers. comm. 1988

***Apanteles* sp.**
***H. armigera* records:**

Egypt	Various plants	Up to 27%	Megahed *et al.* 1977

***Apanteles* sp.**
***H. armigera* records:**

Madagascar	Cotton	Important	Vaissayre 1977

***Ascogaster ?cava* de Saeger**
Distribution: Afrotropical Region: Zaire.
***H. armigera* records:**

Uganda	-	Rare	Coaker 1959

***Bracon brevicornis* Wesmael**
Microbracon brevicornis Wesmael (in all references below)
Taxonomic comment: *Bracon brevicornis* is now thought to be a synonym of *B. hebetor* Say (2).
Distribution: Afrotropical Region: South Africa, Sudan, West Africa; Nearctic Region; Neotropical Region; Oriental Region; Palaearctic Region.

Biology: Gregarious larval ectoparasitoid. Taylor (1932) described the biology of *B. brevicornis* parasitizing *H. armigera* in South Africa. Adult: Pre-oviposition period less than a day. Fecundity: 200 eggs per female. Longevity: 25 d for females; 9 d for males. Arrhenotokous. Host feeding by adult females has been recorded. Oviposition: The host is paralysed and 3-8 eggs, depending on the size of the host, are deposited on the integument. Eggs hatch after 1.5-2 d. Development: Larvae develop outside the host. Mature larvae spin a cocoon and pupate alongside the host remains. Larval period: 4-5 d; pupal period: 6-8 d.

Alternative hosts: Wide host range; LEPIDOPTERA Noctuidae: *Busseola fusca, Diparopsis watersi, Earias insulana, Leucania* sp., *Spodoptera exempta, S. exigua*; Gelechiidae; Pieridae; Pyralidae; Stenomidae; Tortricidae; COLEOPTERA.

Host-plant associations: In South Africa, *B. brevicornis* was found associated almost exclusively with *H. armigera* on *Antirrhinum majus*, a garden plant, while *H. armigera* was present on various crops (Taylor 1932; Parsons 1940).

***H. armigera* records:**

Egypt	Various plants	Up to 17%	Megahed *et al.* 1977
South Africa	Exclusively on antirrhinum	-	Taylor 1932
South Africa	Cotton	-	Simmonds 1960
South Africa	Maize	10%	Ullyett 1933
South Africa	Various crops	Rare	Parsons 1940
South Africa	Antirrhinum	V. common	Parsons 1940
South Africa	Lucerne, antirrhinum	Common	Pettey 1948
Tchad	Cotton	-	Silvie pers. comm. 1988

***Bracon hebetor* Say**

Taxonomic comment: *Bracon brevicornis* is now thought to be a synonym of *B. hebetor* (2).

Distribution: Afrotropical Region; Neotropical Region; Oriental Region; Palaearctic Region.

Alternative hosts: Wide host range; LEPIDOPTERA Blastoblasidae; Gelechiidae; Hesperiidae; Lycaenidae; Noctuidae; Oecophoridae; Pyralidae; Stenomidae; Tineidae; Yponomeutidae; HYMENOPTERA.

***H. armigera* records:**

Senegal	Maize, millet	Rare	Bhatnagar 1987

***Bracon kirkpatricki* Wilkinson**

Microbracon kirkpatricki Wilkinson (Balla 1982)

Distribution: Afrotropical Region: Congo, Egypt, Ivory Coast, Malawi, Senegal, Somalia, Sudan; Oriental Region; introduced in North America in 1969.

Biology: Engroff & Watson (1975) described the biology of *B. kirkpatricki* parasitizing *Pectinophora gossypiella* Saunders (Gelechiidae).

Alternative hosts: LEPIDOPTERA. Mainly known as a parasitoid of *Pectinophora gossypiella* (Gelechiidae); Pyralidae.

***H. armigera* records:**

Sudan	-	-	Balla 1982

***Bracon* sp.**

***H. armigera* records:**

Tanzania	Cotton	-	Le Pelley 1959

***Bracon* sp.**
***H. armigera* records:**

Senegal	Millet	Rare	Bhatnagar 1987

***Braunsia* sp.**
***H. armigera* records:**

Tanzania	Cotton	-	Le Pelley 1959

Genus *Cardiochiles* Nees

Taxonomic comment: There are several undescribed species in Africa. Species from the Sahelian Subregion have recently been revised (Huddleston & Walker in press). Revision for tropical Africa is underway.

Biology: *Cardiochiles* spp. are solitary endoparasitoids of Lepidoptera. They usually attack their host during early host instars and emerge from the fourth, fifth or sixth instar, depending on the parasitoid species. The North American *Cardiochiles nigriceps* is the best studied species in this genus, and is regarded as a highly specific parasitoid of *Heliothis virescens*. It has been shown that the females locate their host by close range chemoreception. They examine areas contaminated with mandibular gland secretions of *H. virescens* (Vinson 1968; Vinson & Lewis 1965; Vinson *et al.* 1975). The active chemical compounds are specific to *H. virescens*; the parasitoid will show a weaker response to frass of the closely related *Helicoverpa zea* (Vinson *et al.* 1975). The latter is an unsuitable host for *C. nigriceps*, because it will encapsulate the parasitoid egg (Lynn & Vinson 1977). *C. nigriceps* deposits one egg per host larva. Oviposition temporarily paralyses the host. The egg hatches within 1.5-2 d, and the new larva develops and remains inside the host until the host enters the soil to pupate (Danks, Rabb & Southern 1979). When the larva emerges from the host it feeds externally on the host remains, and starts spinning a cocoon to pupate in the ground (Lewis & Vinson 1968). Compare also Singh & Parshad (1970) for the biology of *Cardiochiles hymeniae* Fisher & Parshad. Although there is no evidence that the African *Cardiochiles* spp., which parasitize *H. armigera*, are host specific, none of the species presented below has been found on a host other than *H. armigera*. It has been reported that *C. nigriceps* is associated with tobacco plants (Vinson 1975; Martin *et al.* 1981). In Tanzania, *Cardiochiles* spp. seem to be associated with cotton more than other crops (Nyambo 1986).

***Cardiochiles nigricollis* Cameron**

Taxonomic comment: Records are regarded as reliable (2).

Distribution: Afrotropical Region: Botswana, South Africa, Zaire.

Biology: Larval period: 10-13 d; pupal period: 9-12 d. Mainly, second and third instars of *H. armigera* are attacked (Parsons 1940).

Host-plant associations: In South Africa, *C. nigricollis* was mostly found in cotton-bred hosts (Parsons 1940).

***H. armigera* records:**

Botswana	Cotton, maize, cleome	-	Roome 1975a
South Africa	Predom. cotton	Common	Parsons 1940
South Africa	Cotton, maize	-	de Saeger 1948

***Cardiochiles nigromaculatus* Cameron**

Taxonomic comment: Reliable records (2).

Distribution: Afrotropical Region: Malawi, South Africa, Uganda, Zaire; Oriental Region.
***H. armigera* records:**

Tanzania	-	-	Reed 1965, BMNH
Uganda	Cotton	-	Nyiira 1970a

***Cardiochiles trimaculatus* Cameron**
Taxonomic comment: Records are regarded as reliable (2).
Distribution: Afrotropical Region: Equatorial Guinea, South Africa, Tanzania, Uganda, Zaire.
Biology: According to Greathead (1966), *C. trimaculatus* was the most important parasitoid of *H. armigera* on cotton in Uganda.
***H. armigera* records:**

Tanzania	Cotton	Rare	Robertson 1973
Uganda	Various crops	8%	Coaker 1959
Uganda	Cotton	Important	Greathead 1966

***Cardiochiles* sp. nr. *trimaculatus* Cameron**
***Cardiochiles* sp.**
Taxonomic comment: These are two separate species.
Host-plant associations: These species seem to be associated with cotton and cleome; they are rare on sorghum (Nyambo 1986).
***H. armigera* records:**

Tanzania	Various crops	Important	Nyambo 1986

***Cardiochiles* sp. nr. *trimaculatus* Cameron**
***H. armigera* records:**

Uganda	Cotton	-	Greathead 1966

***Cardiochiles variegatus* Szepligeti**
Taxonomic comment: Reliable records (2).
Distribution: Afrotropical Region: Gambia, Niger, Nigeria, Senegal, Tanzania, Zaire.
***H. armigera* records:**

Nigeria	-	-	BMNH (Beeden Coll 1975)
Senegal	Maize, millet, acanthospermum	Up to 40%	Bhatnagar 1987, BMNH

***Cardiochiles* sp.**
***H. armigera* records:**

South Africa	Cotton	-	Simmonds 1960

***Cardiochiles* sp.**
***H. armigera* records:**

Tchad	Cotton	-	Silvie pers. comm. 1988

***Chelonus bifoveolatus* Szepligeti**
Taxonomic comment: Record below is regarded as reliable (2).
Distribution: Afrotropical Region: Tanzania, Zaire.
***H. armigera* records:**

Tanzania	-	-	Robertson 1970

***Chelonus curvimaculatus* Cameron**

Chelonella curvimaculatus Cameron (Parsons 1940)

Neochelonella curvimaculatus Cameron (Coaker 1959)

Taxonomic comment: Probably a complex of species. In current taxonomy records are regarded as reliable (2).

Distribution: Afrotropical Region: Madagascar, Mauritius, Somalia, South Africa, Sudan, Tanzania, Uganda, Zaire, Zimbabwe.

Biology: Solitary egg-larval parasitoid. Broodryk (1969) described the biology of *C. curvimaculatus*. Adult: Copulation occurs soon after emergence. No pre-oviposition period. The fecundity is high (520 eggs per female at 26.5°C). Longevity: 8.2 d for females, 6.4 d for males at 26.5°C; longevity at 32°C is only 1.5 d for both sexes. Oviposition: Females attack the host in its egg stage. They deposit one egg (0.2x0.05 mm) per host, and do not distinguish between parasitized and unparasitized host eggs. Also, freshly laid eggs are attacked to about the same extent as are older eggs. In young host eggs the parasitoid deposits its egg in the yolk, in older host eggs the parasitoid oviposits directly into the haemocoel of the host embryo. Adult females of *Chelonus* sp. nr. *curvimaculatus* respond to kairomones of their host; the kairomones are emitted by the scales the moths leave at oviposition sites (Chiri & Legner 1982). Development: Eggs hatch after 1-1.5 d (26.5°C). Larvae emerging in the yolk of the host egg will soon enter the haemocoel of the embryo. Parasitized larvae of *H. armigera* are arrested in their third larval instar and start spinning their cocoon; spinning normally takes place in the host's sixth instar. The parasitoid larva consumes the host and pupates outside. According to Nyambo (1986) parasitoid larvae emerge from the second or third instar of the host. Broodryk demonstrated that *C. curvimaculatus* adjusts its development period to the host species. Consequently, this parasitoid can synchronize its life-cycle with that of different host species. On *H. armigera* the egg-to-adult period is 29 d (26.5°C) (Broodryk 1969). Larval period: 8-10 d; pupal period: 9-12 d (Parsons 1940). Also, diapause synchronization has been reported from *C. curvimaculatus* (Broodryk 1969).

Alternative hosts: LEPIDOPTERA Noctuidae: *Celama squalida* Staudinger, *Earias insulana*; Gelechiidae; Pyralidae; COLEOPTERA. Broodryk (1969) reports that *Spodoptera littoralis* encapsulated the larva of *C. curvimaculatus* in 78% of the cases, whereas *H. armigera* did not encapsulate the parasitoid.

***H. armigera* records:**

Madagascar	Cotton	Important	Vaissayre 1977
South Africa	Maize	Common	Parsons 1940
South Africa	Citrus	-	Prinsloo 1984
Tanzania	Various crops	Up to 12%	Nyambo 1986
Uganda	-	Rare	Coaker 1959

***Chelonus pilosulus* Szepligéti**

Taxonomic comment: Probably correct identification in current taxonomy (2).

Distribution: Afrotropical Region: Sudan, Tanzania.

***H. armigera* records:**

Sudan	Cotton	-	Lazarévic 1971

***Chelonus versatilis* Wilkinson**

Chelonella versatilis Wilkinson (1932)

Microchelonus versatilis Wilkinson (Robertson 1970)

Taxonomic comment: Probably correct identification in current taxonomy (2).

Distribution: Afrotropical Region: Botswana, Sudan, Tanzania; Mediterranean Subregion.

Biology: Adults emerge from the third or fourth instar of *H. armigera*.
Alternative hosts: LEPIDOPTERA Gelechiidae: *Pectinophora gossypiella*; Pyralidae.
***H. armigera* records:**

Botswana	-	0.6%	Roome 1971a
Sudan	Cotton	-	Wilkinson 1932
Tanzania	Various crops	-	Robertson 1970

***Chelonus* sp.**
***H. armigera* records:**

South Africa	Cotton	-	Simmonds 1960

***Chelonus* sp.**
***H. armigera* records:**

Zimbabwe	Citrus	V. rare	Hall & Ford 1933

***Disophrys lutea* Brullé**
Taxonomic comment: Record is regarded as reliable (2).
Distribution: Afrotropical Region: widespread; Palaearctic Region.
Alternative hosts: LEPIDOPTERA Noctuidae: *Spodoptera exempta*.
***H. armigera* records:**

Senegal	Sorghum	Rare	Bhatnagar 1987

***Disophrys nigricornis* Brullé**
Taxonomic comment: Record must be regarded as doubtful (3).
Distribution: Afrotropical Region: Senegal, Tanzania, Zaire.
***H. armigera* records:**

Senegal	-	-	Risbec 1950

***Disophrys* sp.**
Taxonomic comment: Record must be regarded as doubtful (3).
***H. armigera* records:**

Sudan	Cotton, beans	-	Lazarévic 1971

***Meteorus clytes* Nixon**
Taxonomic comment: Record is regarded as reliable (3).
Distribution: Afrotropical Region: South Africa, Tanzania.
Alternative hosts: No records.
***H. armigera* records:**

Tanzania	Groundnut	-	BMNH (Disney Coll 1952)

***Meteorus laphygmarum* Brues**
Taxonomic comment: All the records below are regarded as reliable (3).
Distribution: Afrotropical Region: Madagascar, Nigeria, South Africa, Sudan, Uganda, Zimbabwe.
Alternative hosts: LEPIDOPTERA Noctuidae: *Earias biplaga, Spodoptera exempta, S. exigua*.
***H. armigera* records:**

Madagascar	-	-	Brénière 1965
Nigeria	-	-	BMNH (Beeden Coll 1974)
Sudan	-	-	BMNH (Bedford Coll 1927)
Sudan	-	Rare	Nixon 1943

Tanzania	Cotton	Rare	Robertson 1973
Tchad	Cotton	-	Silvie pers. comm. 1988
Uganda	-	Rare	Coaker 1959

***Meteorus* sp.**
***H. armigera* records:**

Tanzania	Cotton	Rare	Reed 1965
Tanzania	Various crops	Rare	Nyambo 1986

***Meteorus* sp.**
***H. armigera* records:**

Botswana	-	-	Roome 1975a

***Meteorus* sp.**
***H. armigera* records:**

Senegal (from *Heliothis* sp.)	-	-	BMNH

***Meteorus* sp.**
***H. armigera* records:**

Tchad	Cotton	-	Silvie pers. comm. 1988

***Microplitis sufiventris* Kokujev**
***H. armigera* records:**

Egypt	Various plants	Up to 50%	Megahed *et al.* 1977

Ceraphronidae

Genus *Ceraphron* Jurine

Gregarious endoparasitoids. Most species are recorded in the literature as hyperparasitoids, especially through *Apanteles* spp. on Lepidoptera. Chaudhary & Chand (1973) described the biology of *C. fijiensis* Ferrière from India. Newly formed cocoons or mature *Apanteles* larvae which had emerged from the phytophagous host, were attacked. Larval period: 7-8 d; pupal period: 8-9 d at 30°C.

***Ceraphron* sp.**
***H. armigera* records:**

Uganda	-	Rare	Coaker 1959

***?Ceraphron* sp.**
***H. armigera* records:**

Uganda	-	-	Nyiira 1970a

Scelionidae

***Platytelenomus busseolae* Gahan**
Taxonomic comment: This is probably a misidentification (4).
Distribution: Afrotropical Region: Nigeria, Tanzania.
Alternative hosts: LEPIDOPTERA Noctuidae: *Busseola fusca*, *Sesamia* sp.; Pyralidae.
***H. armigera* records:**

Uganda	Cotton	-	Coaker 1959

***Telenomus ullyetti* Nixon**
Phanurus ullyetti Nixon (Parsons & Ullyett 1936)
Taxonomic comment: The records below are regarded as reliable (4). Parsons & Ullyett (1934) recorded *Phanurus* sp., which was later considered to be *P. ullyetti* (Parsons & Ullyett 1936), a synonym of *T. ullyetti*.
Distribution: Afrotropical Region: Cameroun, South Africa, Tanzania, Zimbabwe.
Biology: Jones (1937) described the biology of this species parasitizing *H. armigera*. Adults: Mating occurs immediately after emergence. No pre-oviposition period. Fecundity: 30-90 eggs per female. Sex ratio: 7:3, in favour of females. Arrhenotokous. Longevity: 18 d for females, 14 d for males (22°C); non-oviposition extends the female life-span. Oviposition: Eggs are deposited in the yolk of young host eggs (1 egg per host). Females can distinguish between parasitized and unparasitized hosts. Detailed studies on the related *Telenomus heliothidis* Ashmead, a parasitoid of *Helicoverpa zea* in North America, have revealed that several physical cues as well as chemical cues (contact kairomones) are involved in recognizing and accepting the host egg (Strand & Vinson 1982, 1983). Development: The parasitoid remains for a comparatively long period passively as a first instar in the yolk of the host egg. There is evidence that the female of *T. heliothidis* injects an arrestment factor in the host egg at oviposition. Consequently, the host ceases development (Strand *et al.* 1986). The second instar attacks the host embryo. If the embryo has grown beyond a certain size, the parasitoid larva will not be able to attack, and starves. Egg-adult period: 25 d at 19.4°C or 14 d at 26°C.
Alternative hosts: LEPIDOPTERA Pyralidae: *Chilo* sp., *Scirpophaga* sp. (doubtful records)
Host-plant associations: Parsons (1940) observed higher egg parasitism levels, mainly by *T. ullyetti*, on tomato, and to a lesser extent on cucumber and marrow, than on legumes. He attributed this to the distribution of host eggs which are aggregated near the flowers on the former crops.
***H. armigera* records:**

South Africa	Cotton	Up to 70%	Parsons 1940
South Africa	Maize	Up to 16%	Parsons & Ullyett 1934
South Africa	Cotton	Up to 2%	Parsons & Ullyett 1934
South Africa	Winter crops	Up to 50%	Parsons & Ullyett 1936
Tanzania	-	-	BMNH (Tapley Coll 1955)
Zimbabwe	Cotton	Up to 25%	Jones 1937
Zimbabwe	Citrus	< 1%	Jones 1936, 1937

***Telenomus* sp.**
***H. armigera* records:**

Zimbabwe	Citrus	-	Hall & Ford 1933

***Telenomus* sp.**
***H. armigera* records:**

Botswana	Various crops	-	Roome 1975a

***Telenomus* sp.**
***H. armigera* records:**

South Africa	Cotton	Up to 19%	van Hamburg 1981

***Telenomus* sp.**
Phanurus sp. (Taylor 1932).
***H. armigera* records:**

South Africa	Bean, tomato	Up to 80%	Taylor 1932

Chalcididae

Genus *Brachymeria* Westwood in Stephens
Little is known about this genus in the Afrotropical Region. *Brachymeria* spp. are pupal parasitoids, many species attack the pupae of beneficial hymenopterans.

***Brachymeria bottegi* Masi**
Taxonomic comment: Record below must be regarded as suspect (5).
***H. armigera* records:**

Zimbabwe	Tobacco	Rare	Bünzli & Büttiker 1957

***Brachymeria cowani* Kirkby**
Taxonomic comment: Record below must be regarded as suspect (5).
***H. armigera* records:**

Tanzania	Cotton	Rare	Reed 1965

***Brachymeria* sp.**
Biology: Recorded as a secondary parasitoid.
***H. armigera* records:**

Uganda	-	-	Coaker 1959

***Brachymeria* sp.**
***H. armigera* records:**

Tanzania	Cotton	Rare	Robertson 1973

***Hyperchalcidia soudanensis* Steffan**
Distribution: Afrotropical Region: Cameroun, Kenya, Nigeria, Sudan, Uganda.
Biology: Pupal ectoparasitoid.
Alternative hosts: LEPIDOPTERA Noctuidae: *Busseola fusca*; Psychidae; Pyralidae.
***H. armigera* records:**

Sudan	-	-	Balla 1982

Eurytomidae

***Eurytoma* sp.**
Biology: Hyperparasitoid of *Apanteles* sp.
***H. armigera* records:**

Uganda	-	-	Coaker 1959

***Eurytoma* spp.**
Biology: Hyperparasitoid of *Apanteles* sp.
***H. armigera* records:**

Zimbabwe	Tobacco	Rare	Bünzli & Büttiker 1957

Eulophidae

***Euplectrus laphygmae* Ferrière**
Distribution: Afrotropical Region: Ethiopia, Kenya, Malawi, Senegal, South Africa, Sudan, Tanzania, Uganda, Zimbabwe.
Biology: Neser (1973) studied *E.* sp. nr. *laphygmae* parasitizing the noctuid *Plusia acuta* Walker. Gerling & Limon (1976) described the biology of *E. laphygmae* parasitizing *Spodoptera littoralis*. Adult: Males emerge before females. Most females are arrhenotokous. Sex ratio is about 1:1 (Gerling & Limon 1976). Longevity: 45 d for females, 29 d for males (26°C). Fecundity: 165 eggs per female (Gerling & Limon 1976). Host feeding by adult females has been recorded. Oviposition: Females briefly paralyse the host during oviposition and attach their eggs (0.2x0.1 mm) to the host integument, mostly to the first three abdominal segments. Females can discriminate between host species and host instars. The number of eggs deposited per host depends on the host size. Eggs hatch after 1-2 d (Neser 1973). Development: The first instar larvae start feeding while still contained in the eggshell. The host stops feeding within 2 d after emergence of the parasitoid larvae and its body gradually collapses during the next 3 d. The entire parasitoid development takes place at the oviposition site. When mature, the larvae move underneath the dead host and spin their cocoons. Larval period: 3-5 d; total development (egg-adult): 7.5-9 d (30°C) (Neser 1973); compare also Parsons (1940). 3-5 larvae develop per *Spodoptera littoralis* host (Hegazi, Hammad & El-Minshawy 1977). Host stages: According to Neser (1973) the first and sixth instars of *Plusia* are rejected for oviposition. Gerling & Limon (1976) found that only the first four instars of *Spodoptera littoralis* were attacked. *E. laphygmae* oviposited normally on *H. armigera*, but failed to complete development on this host.
Secondary natural enemies: Multiparasitism by *E. laphygmae* and the endoparasitoids *Microplitis* sp., *Meteorus laphygmarum* and *Copidosoma* sp. was found on *Plusia acuta* (Neser 1973).
Alternative hosts: LEPIDOPTERA Noctuidae: *Achaea catella* Guenee, *Anomis leona*, *Plusia gamma*, *P. orichalcea*, *Spodoptera exempta*, *S. exigua*; Arctiidae; Geometridae; Pyralidae.
***H. armigera* records:**

Senegal	-	-	Risbec 1960
Sudan	-	-	Ferrière 1941 (from *Heliothis* sp.)
Sudan	-	-	BMNH Coll 1976
Tanzania	-	-	Robertson 1970

***Euplectrus* sp.**
***H. armigera* records:**

South Africa	Peas	-	Parsons 1940

***Euplectrus* sp.**
***H. armigera* records:**

Tchad	Cotton	-	Silvie pers. comm. 1988

***?Euplectrus* sp.**
***H. armigera* records:**

Uganda	Cotton	-	Nyiira 1970a

***Pediobius furvus* Gahan**
Distribution: Afrotropical Region: Cameroun, Ghana, Ivory Coast, Kenya, Mali, Nigeria, Senegal, Sudan, Tanzania, Uganda, Zimbabwe.
Biology: Gregarious pupal endoparasitoid. Mohyuddin (1968) described the biology of *P. furvus* parasitizing *Chilo partellus* Swinhoe (Pyralidae). 17-330 adults emerge per host pupa. Development egg-adult: 25-29 d (25°C).
Alternative hosts: Mainly known as a graminaceous stemborer parasitoid. LEPIDOPTERA Noctuidae: *Busseola* spp., *Sesamia* spp.; Pyralidae.
***H. armigera* records:**

Sudan	-	-	Balla (1982)

***Pediobius mediopunctatus* Waterston**
Distribution: Afrotropical Region: Ivory Coast, Senegal.
Biology: Often recorded as a hyperparasitoid.
Alternative hosts: LEPIDOPTERA Noctuidae: *Anomis leona* (hyper), *Eublemma gayneri* Rothschild, *Spodoptera littoralis* (hyper); Arctiidae; Hesperiidae; Lycaenidae; HYMENOPTERA.
***H. armigera* records:**

Senegal	-	-	Risbec 1960

Elasmidae

***Elasmus johnstoni* Ferrière**
Distribution: Afrotropical Region: Sudan, Uganda, Zimbabwe; Oriental Region.
Biology: Larval ectoparasitoid. Haroon Khan & Verma (1946) described the biology of *E. johnstoni* parasitizing *Earias* spp. Fecundity: 18 eggs per female. Longevity female: 7-46 d. Arrhenotokous. 1-2 eggs are deposited per host larva. Development egg-adult: 10-28 d.
Alternative hosts: Mainly recorded from *Earias* spp. (Noctuidae). and *Pectinophora gossypiella* (Gelechiidae). Facultative hyperparasitoid.
***H. armigera* records:**

Sudan	-	-	Balla 1982

Encyrtidae

***Copidosoma* sp.**

Biology: Gregarious egg-larval parasitoid. El-Heneidy & Abbas (1983) described the biology of this particular *Copidosoma* sp.

Adults: Mating occurs within a few hours of emergence. Sex ratio: 3:2, in favour of females. Longevity: 3-6 d (25°C).

Development: Eggs are deposited in the host egg. *Copidosoma* sp. has a polyembryonic mode of reproduction. The parasitoids develop inside the host larva, pupate, and emerge as adults from the sixth instar of *H. armigera*. 20-600 adults emerge per host. Diapause of the parasitoid, in its prepupal stage, occurs inside the host remains.

Host-plant associations: El-Heneidy & Abbas (1983) report that this species was found only on weeds, not on cotton or tomato, and attributed this to the seasonal occurrence of the parasitoid.

***H. armigera* records:**

Egypt	Various plants	Rare	Megahed *et al.* 1977

***Copidosoma* sp.**
***H. armigera* records:**

Senegal	Various crops	-	Bhatnagar 1987

***Copidosoma* sp.**
***H. armigera* records:**

Egypt	-	Common	Ismael & Swailem 1975 (from *Heliothis* sp.)

Mymaridae

Sp. indet
***H. armigera* records:**

Zimbabwe	-	Rare	Jones 1937

Trichogrammatidae

***Trichogramma pretiosum* Riley**

Distribution: Introduced and established in South Africa in 1975; Nearctic Region.

Alternative hosts: LEPIDOPTERA Geometridae; Pyralidae; Tortricidae; NEUROPTERA.

***H. armigera* records:**

South Africa	Cotton	Rare	van Hamburg 1981

***Trichogramma* sp. nr. *evanescens* Westwood**
***H. armigera* records:**

Madagascar	Cotton	Important	Vaissayre 1977

?*Trichogramma* sp.
***H. armigera* records:**

Tanzania	Cotton	Up to 5%	Reed 1965

?*Trichogramma* sp.
***H. armigera* records:**

Uganda	Cotton	-	Coaker 1959

?*Trichogramma* sp.
***H. armigera* records:**

Uganda	Cotton	-	Nyiira 1970a

?*Trichogramma* spp.
***H. armigera* records:**

Botswana	Various crops	-	Roome 1975a

?*Trichogramma* sp.
***H. armigera* records:**

South Africa	-	-	Taylor 1932

?*Trichogramma* sp.
***H. armigera* records:**

South Africa	-	Rare	Jones 1937

***Trichogrammatoidea lutea* Girault**

Trichogramma lutea Girault

Taxonomic comment: The records below are regarded as reliable (4).

Distribution: Afrotropical Region: Cape Verde, South Africa, Zaire, Zambia, Zimbabwe.

Biology: Jones (1937) studied the biology of *T. lutea* parasitizing *H. armigera*. Adults: Mating occurs soon after emergence. Mated females are fertilized for life, males can mate many times. No pre-oviposition period. Fecundity: 32 eggs per female; 0-15 eggs are laid per day. Longevity: 2-9 d (26°C). Arrhenotokous. Oviposition: Females oviposit 1-5 eggs into the host egg. Eggs are often superparasitized, in which case they yield no offspring (Mück 1985). Eggs are deposited in the central yolk of the host egg and are often enclosed by the embryo during its development. Development: Parasitoid eggs swell up, and hatch after one day. The first instar feeds on the yolk, the second instar starts feeding on the organs of the host embryo. Development of the host is arrested. *T. lutea* is less restricted to young host eggs than is *Telenomus ullyetti*. One to four adults (mostly 2) emerge per host. If more than one progeny of mated females develop per host, usually only one is male (Kfir 1982). Egg-adult period: 19 d at 19.4°C or 9 d at 26°C.

Alternative hosts: LEPIDOPTERA Noctuidae: *Anomis leona* Schaus, *Diparopsis castanea*, *Earias biplaga*; Pyralidae; Tortricidae.

***H. armigera* records:**

Cape Verde	-	-	Mück 1985
South Africa	Cotton	Up to 60%	Parsons 1940
South Africa	Citrus	-	Prinsloo 1984
South Africa	Cotton	-	Taylor 1932
South Africa	Cotton	Up to 19%	van Hamburg 1981
South Africa	Maize	Up to 44%	Parsons & Ullyett 1934
South Africa	Cotton	Up to 17%	Parsons & Ullyett 1934
South Africa	Maize	41%	Parsons & Ullyett 1936
South Africa	Cotton	Up to 50%	Parsons & Ullyett 1936
Zambia	Maize, cotton	Important	Bebbington & Allen 1935
Zimbabwe	Cotton	Up to 50%	Peat 1935

Zimbabwe	Cotton	Up to 48%	Jones 1937
Zimbabwe	Maize	Up to 75%	Jones 1937
Zimbabwe	Citrus	<1%	Jones 1936, 1937

***Trichogrammatoidea* sp.**
***H. armigera* records:**

Senegal	Acanthospermum	Up to 17%	Bhatnagar 1987
	Maize	Up to 27%	
	Sorghum	Up to 32%	
	Tomato	Up to 80%	

Bethylidae

***Goniozus* sp.**
Biology: Gregarious ectoparasitoid. The biology of *Goniozus* spp. is described by Gordh & Hawkins (1981).
***H. armigera* records:**

Senegal	Maize, millet	-	Bhatnagar 1987

Ceraphronidae

Genus *Ceraphron* Jurine

Gregarious endoparasitoids. Most species are recorded in the literature as hyperparasitoids, especially through *Apanteles* spp. on Lepidoptera. Chaudhary & Chand (1973) described the biology of *C. fijiensis* Ferrière from India. Newly formed cocoons or mature *Apanteles* larvae which had emerged from the phytophagous host, were attacked. Larval period: 7-8 d; pupal period: 8-9 d at 30°C.

***Ceraphron* sp.**
***H. armigera* records:**

Uganda	-	Rare	Coaker 1959

?*Ceraphron* sp.
***H. armigera* records:**

Uganda	-	-	Nyiira 1970a

Scelionidae

***Platytelenomus busseolae* Gahan**
Taxonomic comment: This is probably a misidentification (4).
Distribution: Afrotropical Region: Nigeria, Tanzania.
Alternative hosts: LEPIDOPTERA Noctuidae: *Busseola fusca*, *Sesamia* sp.; Pyralidae.
***H. armigera* records:**

Uganda	Cotton	-	Coaker 1959

***Telenomus ullyetti* Nixon**

Phanurus ullyetti Nixon (Parsons & Ullyett 1936)

Taxonomic comment: The records below are regarded as reliable (4). Parsons & Ullyett (1934) recorded *Phanurus* sp., which was later considered to be *P. ullyetti* (Parsons & Ullyett 1936), a synonym of *T. ullyetti*.

Distribution: Afrotropical Region: Cameroun, South Africa, Tanzania, Zimbabwe.

Biology: Jones (1937) described the biology of this species parasitizing *H. armigera*. Adults: Mating occurs immediately after emergence. No pre-oviposition period. Fecundity: 30-90 eggs per female. Sex ratio: 7:3, in favour of females. Arrhenotokous. Longevity: 18 d for females, 14 d for males (22°C); non-oviposition extends the female life-span. Oviposition: Eggs are deposited in the yolk of young host eggs (1 egg per host). Females can distinguish between parasitized and unparasitized hosts. Detailed studies on the related *Telenomus heliothidis* Ashmead, a parasitoid of *Helicoverpa zea* in North America, have revealed that several physical cues as well as chemical cues (contact kairomones) are involved in recognizing and accepting the host egg (Strand & Vinson 1982, 1983). Development: The parasitoid remains for a comparatively long period passively as a first instar in the yolk of the host egg. There is evidence that the female of *T. heliothidis* injects an arrestment factor in the host egg at oviposition. Consequently, the host ceases development (Strand *et al.* 1986). The second instar attacks the host embryo. If the embryo has grown beyond a certain size, the parasitoid larva will not be able to attack, and starves. Egg-adult period: 25 d at 19.4°C or 14 d at 26°C.

Alternative hosts: LEPIDOPTERA Pyralidae: *Chilo* sp., *Scirpophaga* sp.

Host-plant associations: Parsons (1940) observed higher egg parasitism levels, mainly by *T. ullyetti*, on tomato, and to a lesser extent on cucumber and marrow, than on legumes. He attributed this to the distribution of host eggs which are aggregated near the flowers on the former crops.

***H. armigera* records:**

South Africa	Cotton	Up to 70%	Parsons 1940
South Africa	Maize	Up to 16%	Parsons & Ullyett 1934
South Africa	Cotton	Up to 2%	Parsons & Ullyett 1934
South Africa	Winter crops	Up to 50%	Parsons & Ullyett 1936
Tanzania	-	-	BMNH (Tapley Coll 1955)
Zimbabwe	Cotton	Up to 25%	Jones 1937
Zimbabwe	Citrus	< 1%	Jones 1936, 1937

***Telenomus* sp.**

***H. armigera* records:**

Zimbabwe	Citrus	-	Hall & Ford 1933

***Telenomus* sp.**

***H. armigera* records:**

Botswana	Various crops	-	Roome 1975a

***Telenomus* sp.**

***H. armigera* records:**

South Africa	Cotton	Up to 19%	van Hamburg 1981

***Telenomus* sp.**

Phanurus sp. (Taylor 1932).

***H. armigera* records:**

South Africa	Bean, tomato	Up to 80%	Taylor 1932

Chalcididae

Genus *Brachymeria* Westwood in Stephens

Little is known about this genus in the Afrotropical Region. *Brachymeria* spp. are pupal parasitoids, many species attack the pupae of beneficial hymenopterans.

***Brachymeria bottegi* Masi**

Taxonomic comment: Record below must be regarded as suspect (5).

***H. armigera* records:**

Zimbabwe	Tobacco	Rare	Bünzli & Büttiker 1957

***Brachymeria cowani* Kirkby**

Taxonomic comment: Record below must be regarded as suspect (5).

***H. armigera* records:**

Tanzania	Cotton	Rare	Reed 1965

***Brachymeria* sp.**

Biology: Recorded as a secondary parasitoid.

***H. armigera* records:**

Uganda	-	-	Coaker 1959

***Brachymeria* sp.**

***H. armigera* records:**

Tanzania	Cotton	Rare	Robertson 1973

***Hyperchalcidia soudanensis* Steffan**

Distribution: Afrotropical Region: Cameroun, Kenya, Nigeria, Sudan, Uganda.

Biology: Pupal ectoparasitoid.

Alternative hosts: LEPIDOPTERA Noctuidae: *Busseola fusca*; Psychidae; Pyralidae.

***H. armigera* records:**

Sudan	-	-	Balla 1982

Eurytomidae

***Eurytoma* sp.**

Biology: Hyperparasitoid of *Apanteles* sp.

***H. armigera* records:**

Uganda	-	-	Coaker 1959

***Eurytoma* spp.**

Biology: Hyperparasitoid of *Apanteles* sp.

***H. armigera* records:**

Zimbabwe	Tobacco	Rare	Bünzli & Büttiker 1957

Eulophidae

***Euplectrus laphygmae* Ferrière**

Distribution: Afrotropical Region: Ethiopia, Kenya, Malawi, Senegal, South Africa, Sudan, Tanzania, Uganda, Zimbabwe.

Biology: Neser (1973) studied *E.* sp. nr. *laphygmae* parasitizing the noctuid *Plusia acuta* Walker. Gerling & Limon (1976) described the biology of *E. laphygmae* parasitizing *Spodoptera littoralis*. Adult: Males emerge before females. Most females are arrhenotokous. Sex ratio is about 1:1 (Gerling & Limon 1976). Longevity: 45 d for females, 29 d for males (26°C). Fecundity: 165 eggs per female (Gerling & Limon 1976). Host feeding by adult females has been recorded. Oviposition: Females briefly paralyse the host during oviposition and attach their eggs (0.2x0.1 mm) to the host integument, mostly to the first three abdominal segments. Females can discriminate between host species and host instars. The number of eggs deposited per host depends on the host size. Eggs hatch after 1-2 d (Neser 1973). Development: The first instar larvae start feeding while still contained in the eggshell. The host stops feeding within 2 d after emergence of the parasitoid larvae and its body gradually collapses during the next 3 d. The entire parasitoid development takes place at the oviposition site. When mature, the larvae move underneath the dead host and spin their cocoons. Larval period: 3-5 d; total development (egg-adult): 7.5-9 d (30°C) (Neser 1973); compare also Parsons (1940). 3-5 larvae develop per *Spodoptera littoralis* host (Hegazi, Hammad & El-Minshawy 1977). Host stages: According to Neser (1973) the first and sixth instars of *Plusia* are rejected for oviposition. Gerling & Limon (1976) found that only the first four instars of *Spodoptera littoralis* were attacked. *E. laphygmae* oviposited normally on *H. armigera*, but failed to complete development on this host.

Secondary natural enemies: Multiparasitism by *E. laphygmae* and the endoparasitoids *Microplitis* sp., *Meteorus laphygmarum* and *Copidosoma* sp. was found on *Plusia acuta* (Neser 1973).

Alternative hosts: LEPIDOPTERA Noctuidae: *Achaea catella* Guenee, *Anomis leona*, *Plusia gamma*, *P. orichalcea*, *Spodoptera exempta*, *S. exigua*; Arctiidae; Geometridae; Pyralidae.

***H. armigera* records:**

Senegal	-	-	Risbec 1960
Sudan	-	-	Ferrière 1941 (from *Heliothis* sp.)
Sudan	-	-	BMNH Coll 1976
Tanzania	-	-	Robertson 1970

***Euplectrus* sp.**

***H. armigera* records:**

South Africa	Peas	-	Parsons 1940

***Euplectrus* sp.**

***H. armigera* records:**

Tchad	Cotton	-	Silvie pers. comm. 1988

***?Euplectrus* sp.**

***H. armigera* records:**

Uganda	Cotton	-	Nyiira 1970a

***Pediobius furvus* Gahan**

Distribution: Afrotropical Region: Cameroun, Ghana, Ivory Coast, Kenya, Mali, Nigeria, Senegal, Sudan, Tanzania, Uganda, Zimbabwe.

Biology: Gregarious pupal endoparasitoid. Mohyuddin (1968) described the biology of *P. furvus* parasitizing *Chilo partellus* Swinhoe (Pyralidae). 17-330 adults emerge per host pupa. Development egg-adult: 25-29 d (25°C).

Alternative hosts: Mainly known as a graminaceous stemborer parasitoid. LEPIDOPTERA Noctuidae: *Busseola* spp., *Sesamia* spp.; Pyralidae.

***H. armigera* records:**

Sudan	-	-	Balla (1982)

***Pediobius mediopunctatus* Waterston**

Distribution: Afrotropical Region: Ivory Coast, Senegal.

Biology: Often recorded as a hyperparasitoid.

Alternative hosts: LEPIDOPTERA Noctuidae: *Anomis leona* (hyper), *Eublemma gayneri* Rothschild, *Spodoptera littoralis* (hyper); Arctiidae; Hesperiidae; Lycaenidae; HYMENOPTERA.

***H. armigera* records:**

Senegal	-	-	Risbec 1960

Elasmidae

***Elasmus johnstoni* Ferrière**

Distribution: Afrotropical Region: Sudan, Uganda, Zimbabwe; Oriental Region.

Biology: Larval ectoparasitoid. Haroon Khan & Verma (1946) described the biology of *E. johnstoni* parasitizing *Earias* spp. Fecundity: 18 eggs per female. Longevity female: 7-46 d. Arrhenotokous. 1-2 eggs are deposited per host larva. Development egg-adult: 10-28 d.

Alternative hosts: Mainly recorded from *Earias* spp. (Noctuidae). and *Pectinophora gossypiella* (Gelechiidae). Facultative hyperparasitoid.

***H. armigera* records:**

Sudan	-	-	Balla 1982

Encyrtidae

***Copidosoma* sp.**

Biology: Gregarious egg-larval parasitoid. El-Heneidy & Abbas (1983) described the biology of this particular *Copidosoma* sp. Adults: Mating occurs within a few hours of emergence. Sex ratio: 3:2, in favour of females. Longevity: 3-6 d (25°C). Development: Eggs are deposited in the host egg. *Copidosoma* sp. has a polyembryonic mode of reproduction. The parasitoids develop inside the host larva, pupate, and emerge as adults from the sixth instar of *H. armigera*. 20-600 adults emerge per host. Diapause of the parasitoid, in its prepupal stage, occurs inside the host remains.

Host-plant associations: El-Heneidy & Abbas (1983) report that this species was found only on weeds, not on cotton or tomato, and attributed this to the seasonal occurrence of the parasitoid.

***H. armigera* records:**

Egypt	Various plants	Rare	Megahed *et al.* 1977

***Copidosoma* sp.**
***H. armigera* records:**

Senegal	Various crops	-	Bhatnagar 1987

***Copidosoma* sp.**
***H. armigera* records:**

Egypt (from *Heliothis* sp.)	-	Common	Ismael & Swailem 1975

Mymaridae

Sp. indet
***H. armigera* records:**

Zimbabwe	-	Rare	Jones 1937

Trichogrammatidae

***Trichogramma pretiosum* Riley**
Distribution: Introduced and established in South Africa in 1975; Nearctic Region.
Alternative hosts: LEPIDOPTERA Geometridae; Pyralidae; Tortricidae; NEUROPTERA.
***H. armigera* records:**

South Africa	Cotton	Rare	van Hamburg 1981

***Trichogramma* sp. nr. *evanescens* Westwood**
***H. armigera* records:**

Madagascar	Cotton	Important	Vaissayre 1977

?*Trichogramma* sp.
***H. armigera* records:**

Tanzania	Cotton	Up to 5%	Reed 1965

?*Trichogramma* sp.
***H. armigera* records:**

Uganda	Cotton	-	Coaker 1959

?*Trichogramma* sp.
***H. armigera* records:**

Uganda	Cotton	-	Nyiira 1970a

?*Trichogramma* spp.
***H. armigera* records:**

Botswana	Various crops	-	Roome 1975a

?*Trichogramma* sp.
***H. armigera* records:**

South Africa	-	-	Taylor 1932

?*Trichogramma* sp.
***H. armigera* records:**

South Africa	-	Rare	Jones 1937

***Trichogrammatoidea lutea* Girault**
Trichogramma lutea Girault
Taxonomic comment: The records below are regarded as reliable (4).
Distribution: Afrotropical Region: Cape Verde, South Africa, Zaire, Zambia, Zimbabwe.
Biology: Jones (1937) studied the biology of *T. lutea* parasitizing *H. armigera*. Adults: Mating occurs soon after emergence. Mated females are fertilized for life, males can mate many times. No pre-oviposition period. Fecundity: 32 eggs per female; 0-15 eggs are laid per day. Longevity: 2-9 d (26°C). Arrhenotokous. Oviposition: Females oviposit 1-5 eggs into the host egg. Eggs are often superparasitized, in which case they yield no offspring (Mück 1985). Eggs are deposited in the central yolk of the host egg and are often enclosed by the embryo during its development. Development: Parasitoid eggs swell up, and hatch after one day. The first instar feeds on the yolk, the second instar starts feeding on the organs of the host embryo. Development of the host is arrested. *T. lutea* is less restricted to young host eggs than is *Telenomus ullyetti*. One to four adults (mostly 2) emerge per host. If more than one progeny of mated females develop per host, usually only one is male (Kfir 1982). Egg-adult period: 19 d at 19.4°C or 9 d at 26°C.
Alternative hosts: LEPIDOPTERA Noctuidae: *Anomis leona* Schaus, *Diparopsis castanea*, *Earias biplaga*; Pyralidae; Tortricidae.
***H. armigera* records:**

Cape Verde	-	-	Mück 1985
South Africa	Cotton	Up to 60%	Parsons 1940
South Africa	Citrus	-	Prinsloo 1984
South Africa	Cotton	-	Taylor 1932
South Africa	Cotton	Up to 19%	van Hamburg 1981
South Africa	Maize	Up to 44%	Parsons & Ullyett 1934
South Africa	Cotton	Up to 17%	Parsons & Ullyett 1934
South Africa	Maize	41%	Parsons & Ullyett 1936
South Africa	Cotton	Up to 50%	Parsons & Ullyett 1936
Zambia	Maize, cotton	Important	Bebbington & Allen 1935
Zimbabwe	Cotton	Up to 50%	Peat 1935
Zimbabwe	Cotton	Up to 48%	Jones 1937
Zimbabwe	Maize	Up to 75%	Jones 1937
Zimbabwe	Citrus	<1%	Jones 1936, 1937

***Trichogrammatoidea* sp.**
***H. armigera* records:**

Senegal	Acanthospermum	Up to 17%	Bhatnagar 1987
	Maize	Up to 27%	
	Sorghum	Up to 32%	
	Tomato	Up to 80%	

Bethylidae

***Goniozus* sp.**

Biology: Gregarious ectoparasitoid. The biology of *Goniozus* spp. is described by Gordh & Hawkins (1981).

***H. armigera* records:**

Senegal	Maize, millet	-	Bhatnagar 1987

Predators and Pathogens

HEMIPTERA

Anthocoridae

Genus *Orius* Wolff, J.F.

Taxonomic comment: Little is known about Afrotropical *Orius* species (Gauri 1980). It is doubtful whether the African species recorded as *O. insidiosus* Say is the same as the Nearctic species.

Biology: *Orius* spp. have been extensively studied in North America (Ryerson & Stone 1979). Mating can occur directy after moulting from the last nymphal stage. In *O. tristicolor* White, the pre-oviposition period is 2-3 d, the oviposition period 22 d, the fecundity 130 eggs per female (25°C) (Askari & Stern 1972) and the longevity 15 d (Iglinsky & Rainwater 1950). Eggs (0.42x0.4 mm) are deposited in the plant tissue, sometimes in clusters, and hatch after 3-5 d (25.5°C). The five nymphal stages of *O. tristicolor* will develop in 14.4 d at 25.5°C or 8.4 d at 33°C (Askari & Stern 1972). In small laboratory containers at 27°C, *O. insidiosus* consumed 0.7 eggs, or 4.4 first instar larvae, of *Heliothis* spp. per day per predator (Lingren, Ridgway & Jones 1968).

Alternative food: *Orius* spp. feed on a wide variety of arthropod prey (Marshall 1930); they are in particular important predators of spider mites, thrips and noctuid pests. Besides arthropods they also feed on plant tissues, such as pollen (Salas-Aguilar & Ehler 1977), and a coincidence in population build-up of *O. insidiosus* and the period of pollen-shed has been reported from maize (Dicke & Jarvis 1962) and soybean (Isenhour & Yeargan 1981). Alternative food may also be provided as floral or extrafloral nectaries. Trelease (1879) suggested that extrafloral nectaries of cotton can provide an alternative food source during the absence of insect prey. Although *O. tristicolor* has been observed feeding on extrafloral nectaries (van den Bosch & Hagen 1966) populations did not increase until their insect prey became abundant (Yokoyama 1978).

Host-plant associations: *Orius insidiosus* occurs on many wild plant species (Barber 1936). In North America it has been shown that *O. insidiosus* was more abundant in soybean fields with grass and mixed weeds, than in weed-free or broadleaf-weed soybean habitats (Shelton & Edwards 1983); it was suggested that predators are likely to be attracted to weedy habitats as a result of alternative food sources and favourable microclimatic conditions.

***Orius albidipennis* Reuter**
***H. armigera* records:**

Egypt	-	-	Megahed *et al.* 1977

***Orius ?insidiosus* Say**
***H. armigera* records:**

South Africa	Cotton	Important	Pearson 1958
Uganda	Cotton	-	Nyiira 1970a

***Orius laevigatus* Fieb.**
***H. armigera* records:**

Egypt	-	-	Megahed *et al.* 1977

***Orius* sp. nr. *insidiosus* Say**
***H. armigera* records:**

South Africa	Cotton, maize	40%	Parsons & Ullyett 1934

***Orius* sp.**
***H. armigera* records:**

Zimbabwe	Cotton	V. important	Peat 1935

***Orius* sp.**
***H. armigera* records:**

South Africa	Cotton	-	Parsons 1940

***Orius* sp.**
***H. armigera* records:**

Senegal	Maize, millet	-	Bhatnagar 1987

***Orius* spp.**
***H. armigera* records:**

Egypt	-	-	Ismael & Swailem 1975

Reduviidae

***Coranus papillosus* Thunberg**
***H. armigera* records:**

South Africa	Cotton	-	Taylor 1932

***Ectomocoris fenestratus* Klug**
***H. armigera* records:**

Senegal	Various crops	Rare	Bhatnagar 1987

***Rhinocoris albopunctatus* Stål**

Distribution: Afrotropical Region: Cameroun, South Africa, Uganda.

Biology: Nyiira (1970b) studied the biology of this species in Uganda. Oviposition: Brown eggs (1.5x0.5 mm) are deposited in a cluster (5-250 eggs per cluster) on the foliage or stems, mostly on the underside of leaves. Eggs are brooded by the male parent. Nymphs hatch after 5-15 d (21-28°C). Nymphal development (5 stages) takes 54-92 d (21-28°C). Nyiira reports that adults consumed 1-3 *H. armigera* larvae per day in the laboratory.

Alternative prey: *Rhinocoris* spp. are polyphagous. Nyiira reported their feeding on *Earias* spp. (Noctuidae) and several Coleoptera, Hemiptera and Hymenoptera species, among which beneficial insects including *Orius* sp. (Anthocoridae), nymphs of *Rhinocoris* sp. (Reduviidae) and ants.

Secondary natural enemies: In Uganda, Odhiambo (1959) found that the related *Rhinocoris albopilosus* Signoret, despite parental care, suffered 10-20% egg parasitism by two *Hadronotus* species (Hym.: Scelionidae).

***H. armigera* records:**

South Africa	Cotton	-	Taylor 1932
Uganda	Cotton	-	Nyiira 1970b

***Rhinocoris segmentarius* Stål**
***H. armigera* records:**

South Africa	Cotton	-	Taylor 1932
Uganda	Cotton	-	Nyiira 1970a

***Cosmolestes pictus* Klug**
***H. armigera* records:**

Uganda	Cotton	-	Nyiira 1970a

Pentatomidae

***Glypsus conspicuus* Westwood**
Distribution: Afrotropical Region: Central Africa, Kenya, South Africa, Uganda.
Biology: Reed (1965) reported that *G. conspicuus* attacked the eggs and all larval stages of *H. armigera*.
***H. armigera* records:**

South Africa	Cotton	-	Taylor 1932
Tanzania	Cotton	Regular	Reed 1965

***Macrorhaphis acuta* Dallas**
Macrorhaphis spurcata Walker (Nyiira 1970b)
Microrhaphis spurcata Walker (Taylor 1932)
Biology: Reed (1965) reported that *M. acuta* attacked the eggs and all larval stages of *H. armigera*.
Distribution: Afrotropical Region: Malawi, South Africa, Uganda.
***H. armigera* records:**

South Africa	Cotton	-	Taylor 1932
Tanzania	Cotton	Common	Reed 1965
Uganda	Cotton	-	Nyiira 1970a

THYSANOPTERA

***Scolothrips sexmaculatus* Pergande**
Distribution: Afrotropical Region: Nearctic Region; Neotropical Region; Oriental Region; Palearctic Region.
Biology: Adults are bisexual. Low capacity of increase; fecundity: 4-5 eggs per female; longevity: 7-14 d (Bailey 1939). The eggs are inserted in the plant tissue and hatch after 6-10 d. Egg+nymphal period: 17-37 d (Lewis 1973).
Alternative prey: *S. sexmaculatus* is known as a mite predator; it can become cannibalistic when crowded (Bailey 1939).
***H. armigera* records:**

Egypt	-	-	Ismael & Swailem 1975

NEUROPTERA

Chrysopidae

Chrysopidae are known for their predacious habits during the larval stages and have been recorded feeding on a wide variety of arthropods, including many agricultural pests. It has been demonstrated that larvae of *Chrysoperla carnea* Stephens respond to kairomones in the scales of *Helicoverpa zea* moths (Lewis *et al.* 1977; Nordlund *et al.* 1977); moths leave scales at their oviposition sites. Adult chrysopids are nocturnal and feed on soft plant parts. In cotton, extrafloral nectaries encourage population build-up of *C. carnea* (Schuster, Lukefahr & Maxwell 1976). Chrysopids, especially *C. carnea*, are commonly mass-reared and released against various insect pests, including *Helicoverpa* spp. (Hassan 1974).

***Chrysopa congrua* Walker**

Distribution: Afrotropical Region: Tanzania, Zimbabwe.

Biology: Brettell (1982) described the biology of *C. congrua*.

Oviposition period: 35 d. Fecundity: 177 eggs per female. Longevity of adults: 50 d (25°C). In the laboratory, the number of *H. armigera* eggs consumed during larval development was 20 during the first instar, 55 during the second instar and 219 during the third instar. Development period egg: 4 d; larva 11.9 d; pupa: 8.9 d (25°C), when fed on *H. armigera* eggs.

Alternative prey: In the laboratory, a wide variety of prey is consumed (Brettell 1982).

***H. armigera* records:**

Zimbabwe	Cotton	Common	Brettell 1982

***Chrysopa pudica* Navas**

Biology: Brettell (1982) described the biology of *C. pudica*. Adult: Oviposition period: 39 d. Fecundity: 139 eggs per female. Longevity: 55 d (25°C). Development period egg: 4 d; larva 10.5 d; pupa: 9.9 d (25°C) when fed on *H. armigera* eggs.

Alternative prey: In the laboratory, a wide variety of prey is consumed (Brettell 1982).

***H. armigera* records:**

Zimbabwe	Cotton	Common	Brettell 1982

***Chrysopa* sp.**

Biology: Feeds on eggs and larvae of *H. armigera*. In the laboratory, predator larvae consumed up to 14 eggs per day and were able successfully to attack third instars (Reed 1965).

***H. armigera* records:**

Tanzania	Cotton	Common	Reed 1965

***Chrysopa* sp.**

***H. armigera* records:**

South Africa	Cotton	-	Pearson 1958

***Chrysopa* sp.**

***H. armigera* records:**

South Africa	Cotton	-	Parsons 1940

***Chrysopa* sp.**

***H. armigera* records:**

Uganda	Cotton	-	Nyiira 1970a

***Chrysoperla carnea* Stephens**

Chrysopa carnea Stephens (Ismael & Swailem 1975; Balla 1982)

Distribution: Mediterranean Subregion; Nearctic Region; Neotropical Region; Oriental Region; Palaearctic Region.

Biology: Adult: Pre-oviposition period 9 d. Longevity 36 d. Fecundity 39 eggs per female at 27.4°C, when fed on *H. armigera* (Awadallah, Abou-Zeid & Tawfik 1975). Incubation period egg: 3 d; larval period: 10 d; pupal period 6.7 d (27-30°C), when fed on *H. armigera*. Predation: daily consumption of the third instar of the predator is 26 eggs or 90 first instars of *H. armigera* (El-Dakroury *et al.* 1977). *C. carnea* responds to kairomones emitted by *Helicoverpa zea* (Nordlund *et al.* 1977).

Alternative prey: A wide variety of prey is consumed.

***H. armigera* records:**

Egypt	-	-	Ismael & Swailem 1975
Egypt	-	-	Megahed *et al.* 1977
Sudan	-	-	Balla 1982

***Mallada boninensis* Okamoto**

Chrysopa boninensis Okamoto (Brettell 1979)

Distribution: Afrotropical Region: Cape Verde, Guinea, Kenya, Mozambique, South Africa, Tanzania, Zaire, Zimbabwe; Oriental Region.

Biology: Brettell (1979) described the biology of *M. boninensis*. Longevity of adults: 25 d (25°C). In the laboratory, the number of *H. armigera* eggs consumed during development was 20 during the first instar, 40 during the second instar and 240 during the third instar. Larvae of this species carry debris of dead prey on their back. Development period, egg: 3.7 d; larva 10.6 d; pupa: 9.5 d (25°C), when fed on *H. armigera* eggs. Lee & Shih (1983) describe the biology and predation of this predator from China.

Alternative prey: In the laboratory, a wide variety of prey is consumed (Brettell 1979).

***H. armigera* records:**

Zimbabwe	Cotton	Common	Brettell 1979

COLEOPTERA

Carabidae

Genus *Chlaenius* Bonelli

African *Chlaenius* spp. feed on a variety of arthropods (Larochelle 1974). Adults of this carabid genus are ground-dwelling and nocturnal. Eggs are laid singly in the soil (David, Banerji & Kalra 1973). Larvae move up and down the plants in search of prey and feed on first to third instars of noctuids (Katiyar *et al.* 1976). According to Chen & Chen (1982), larvae of *C. bioculatus* Chaudoir consume about 30 young lepidopterous larvae during their development.

***Chlaenius boisduvali* Dejean**

***H. armigera* records:**

Senegal	Various crops	-	Bhatnagar 1987

***Chlaenius dusaultii* Dufour**

***H. armigera* records:**

Senegal	Various crops	-	Bhatnagar 1987

***Graphipterus obsoletus* Olivier**
***H. armigera* records:**

Senegal	Various crops	-	Bhatnagar 1987

***Pheropsophus* sp. nr. *lafertei* Arrow**
***H. armigera* records:**

Senegal	Various crops	-	Bhatnagar 1987

Staphilinidae

***Paederus alfierii* Koch**
***H. armigera* records:**

Egypt	-	-	Megahed *et al.* 1977

Coccinellidae

***Coccinella undecimpunctata* Linnaeus**
Biology: Ibrahim (1955) described the biology of *C. undecimpunctata*.
***H. armigera* records:**

Egypt	-	-	Megahed *et al.* 1977

***Scymnus* spp.**
***H. armigera* records:**

Egypt	-	-	Megahed *et al.* 1977

DIPTERA

Asilidae

Asilid larvae are well known as predators of egg-pods of locusts in the soil (Greathead 1963).

***Promachus* sp.**
***H. armigera* records:**

Senegal	Various crops	-	Bhatnagar 1987

HYMENOPTERA

Vespidae

***Polistes* sp.**
Biology: Adults collect prey larvae and fly them to their nest, and feed them to their offspring.
***H. armigera* records:**

Senegal	Maize, millet	-	Bhatnagar 1987

Eumenidae

***Delta* sp.**

Biology: Adults collect *H. armigera* larvae and fly them to their nest, and feed them to their offspring.

***H. armigera* records:**

Senegal	-	-	Bhatnagar 1987

***Eumenes maxillosus* De Geer**

***H. armigera* records:**

Madagascar	-	-	Brenière 1965
South Africa	Cotton	-	Taylor 1932
Sudan	-	-	Balla 1982

Sphecidae

The majority of sphecids are predators. Their biology and behaviour is reviewed by Bohart & Menke (1976).

***Ammophila* sp.**

Biology: Adults collect *H. armigera* larvae and fly them to their nest, and feed them to their offspring.

***H. armigera* records:**

Tanzania	-	Common	Reed 1965

***Chlorion* sp.**

***H. armigera* records:**

Zimbabwe	Citrus	-	Jones 1936

Formicidae

The ant fauna in tropical agroecosystems is usually well developed, and ants have been shown to play a significant role in the control of insect pests (e.g. Leston 1973). Although research has mainly been concentrated on tree crops (Leston 1973; Room 1975), it is believed that ants are also important control agents of insect pests in annual cropping systems, because ant faunas can develop very rapidly (Carroll & Risch 1983). The ant fauna and its impact in African annual cropping systems is still poorly understood. Some observations in South Africa indicate that *Dorylus* sp., a ground-dwelling species, has a great impact on populations of *H. armigera* pupae in the soil (P.J. Guest pers. comm.). On the other hand, ants have been reported to carry away parasitized *H. armigera* larvae (Taylor 1932). The ecology of foraging by ants is reviewed by Carroll & Janzen (1973).

***Myrmicaria* sp.**

***H. armigera* records:**

Tanzania	Cotton	Common	Reed 1965

***Pheidole megacephala* Fabricius**

***H. armigera* records:**

South Africa	-	-	Steyn 1955

***Pheidole* sp.**

***H. armigera* records:**

South Africa	Maize, cotton	V. important	Parsons & Ullyett 1934
Tanzania	Cotton	Common	Reed 1965
Uganda	Cotton	-	Nyiira 1970a

Sp. indet.

***H. armigera* records:**

Botswana	-	Common	Roome 1975a

NEMATODA

Mermithidae

***Hexamermis* sp.**

Biology: In India, Achan *et al.* (1968) found that *Hexamermis*-infested larvae of *Helicoverpa armigera* turned green and subsequently yellow in colour before they stopped feeding. After 4-5 d the nematodes emerged from the host.

***H. armigera* records:**

Senegal	Groundnut, acanthospermum	Up to 2%	Bhatnagar 1987

PATHOGENS

Nuclear Polyhedrosis Virus (NPV)

Biology: Diseased larvae are yellow and eventually turn brown-black. First and second instars of *H. armigera* are most susceptible to NPV (Ripper & George 1965; Daoust 1974); mortality occurs shortly after infestation, while larvae are still in a young stage (Whitlock 1974). North American strains of this biocontrol agent have been introduced and applied as a biological insecticide against *H. armigera* in Africa (Angelini & Labonne 1970; McKinley 1971; Roome 1971b, 1975b).

***H. armigera* records:**

Botswana	Sorghum	Up to 61%	Roome 1971a,b
Senegal	Various crops	-	Bhatnagar 1987
Sudan	-	-	Bergold & Ripper 1957
Tanzania	Various crops	V. important	Nyambo 1986
Tanzania	-	-	Reed 1965
Uganda	Cotton	-	Coaker 1958
Zimbabwe	-	-	McKinley 1971

Bacteria

Biology: Probably only young larvae are susceptible to bacterial disease. Mortality occurs at later instars, often when larvae are fully grown (Nyambo 1986).

***H. armigera* records:**

Tanzania	Various crops	V. important	Nyambo 1986

Fungi

***Nomuraea rileyi* (Farlow) Samson**

Biology: In the laboratory, Mohamed, Sikorowski & Bell (1977) found that first and second instars and of *H. zea* were less susceptible to infection by the fungus than were third to fifth instars. This fungus has been reviewed by Ignoffo (1981). In general, the occurrence of fungi in the field is irregular and unpredictable, mainly determined by weather conditions (rainfall).

Alternative hosts: LEPIDOPTERA: species from various families; some Coleoptera.

***H. armigera* records:**

Tanzania	-	-	Nyambo, unpublished

Sp. indet.

Tanzania	-	Rare	Reed 1965

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Part II

Ecology of *H. armigera* and Natural Enemies

4

Incidence of *Helicoverpa armigera* and its natural enemies in Kenya[1]

ABSTRACT - Smallholder crops (sunflower, maize, sorghum and cotton) were grown in experimental plots at seven sites, representing different agricultural zones of Kenya, over four seasons. *Helicoverpa armigera* (Hübner) (formerly known as *Heliothis armigera*) only occasionally achieved population densities sufficient to cause obvious damage to the crops, and was virtually absent from the coastal sites. At the inland sites, infestation and mortality levels varied greatly. Information is presented on the incidence of *Helicoverpa armigera*, and the identity, distribution and frequency of its common parasitoids and (potential) predators, sampled in the experimental plots. *Trichogrammatoidea* spp., egg parasitoids, and *Linnaemya longirostris* (Macquart), a tachinid late-larval parasitoid, were the most common parasitoid species, but total percentage parasitism was rather low. Of the large complex of predators, only anthocorids and ants (predominantly *Pheidole* spp., *Myrmicaria* spp. and *Camponotus* spp.) were sufficiently common and widespread to be of importance in suppressing *H. armigera*. The abundance of predators fluctuated widely between sites, but anthocorids were most abundant at the western sites.

Introduction

The African bollworm, *Helicoverpa armigera* (Hübner) (formerly known as *Heliothis armigera*), is a major constraint to food and cash-crop production in East Africa, and throughout the Old World tropics, attacking various crops including cotton, legumes, maize, sorghum, sunflower, tobacco and tomato. Damage is frequently localized on the reproductive parts of crops, i.e., those parts which are harvested.

Larvae of *Helicoverpa armigera* usually live hidden within the fruiting parts of the plant during most of their development. Thus, either large amounts of insecticide, or small amounts carefully targeted and timed, are needed if larvae are to ingest a lethal dose during their short period of contact with the foliage between hatching and entering the host plant. Moreover, *H. armigera* has a

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review). For sustainable crop production, ecologically sound pest control practices are required that utilize and conserve the natural enemies of insect pests. The natural enemies of *H. armigera* have been studied in several countries in Africa (Chapter 3, for review), but these studies have concentrated mostly on parasitoids (Parsons 1940a, Coaker 1959, Reed 1965, Nyambo 1990).

In Kenya, agriculture is practised under diverse ecoclimatic conditions, ranging from the cool highland areas with regular bimodal rainfall with short dry spells, to the hot, dry lowland areas with unreliable rainfall of short duration. *H. armigera* occurs throughout the country, and is generally recognized as an important pest (Cock *et al.* 1991). Smallholder subsistence farming is the predominant form of agriculture, and *H. armigera* typically infests a mosaic of different crops and wild host plants. *H. armigera* has been reported as a major pest on cotton (*Gossypium hirsutum*) and sunflower (*Helianthus anuus*) (Rens 1977, Khaemba & Mutinga 1982), but only a minor pest on other crops, such as maize (*Zea mays*) and sorghum (*Sorghum bicolor*).

In general, there are two rainy seasons in Kenya, the long rains extending from March to July, and the short rains from October to December, but their period and intensity depends very much on the area - rains start earlier in the west of the country, and increase with altitude. In dryer areas, the short or long rains may fail altogether. The Great Rift Valley runs from north to south and acts to some extent as an ecological barrier dividing Kenya in two parts.

In order to start evaluation of the incidence of *H. armigera* and its natural enemies in different parts of the country, a sampling programme was set up at seven sites at research centres of the Kenya Agricultural Research Institute, which represented different agricultural zones. They were located at the wet and high altitudes of Kakamega and Kisii, at Kibos (near Kisumu) in the Lake Victoria Basin, at the dry central sites of Mwea Tebere and Makueni, and at the coastal sites of Msabaha and Mtwapa. We present here the incidence of *H. armigera* and information gathered as to which predator species were found in the experimental plots at these seven sites. Subsequent studies as to the degree of spatial and temporal overlap between predator species and *H. armigera*, life tables of *H. armigera*, and evaluation of the role of natural enemies, will be presented in the following chapters.

Materials and methods

Field sites

Kakamega, Western Province, is an upland site (altitude 1550 m) with a high annual rainfall of 1950 mm. Crops are grown two seasons per year, but land often remains uncultivated during the short rains. Major crops grown are maize, bean, sorghum, oil crops, cowpea, and horticultural crops. Kibos (altitude 1200 m), Nyanza Province, located in the Lake Victoria Basin near Kisumu, an area with black cotton soil, is considerably warmer and dryer than Kakamega. Major

crops are maize, bean, cotton, cassava, and sweet potato, which are only grown during the long rains; the short rains are unreliable. Kisii (altitude 1800 m), Nyanza Province, is similar to Kakamega, a wet upland site with two seasons per year. Major crops at Kisii are maize, bean, coffee, and oil crops.

Mwea Tebere (altitude 1200 m), Central Province, is located in a rather dry area. Crops are usually grown two seasons per year. Major crops are maize, bean, sorghum, sweet potato, oil crops, and cotton. The site of Makueni (altitude 1100 m), Eastern Province, is situated in a dryland area, where crops are usually grown during one or two somewhat inconsistent and unreliable rainy seasons per year. Common crops are maize, sorghum, pigeonpea, cowpea, cotton, sweet potato, and cassava.

At Msabaha (sea level), Coast Province, maize, cowpea, cassava and cotton, are the usual crops, and are grown two seasons per year. Mtwapa (sea level), Coast Province, receives more rainfall than Msabaha. Common crops are maize, cassava, simsim and cowpea.

The trials started at the beginning of the short rains of 1988/89, and continued for four seasons: two short and two long rains seasons. Trials consisted of replicated plots of three crops, all of which are known food plants of *H. armigera*. Three crops from cotton, sorghum, maize and sunflower, were selected for each site, to reflect what was grown locally. Crops were grown according to locally recommended practices.

The sampling sites were divided into major and minor sites. At the major sites, which were sampled more intensively and frequently, the three crops were grown in four replicates; these trials were 0.4-0.5 ha, with an individual plot size of approximately 14x20 m. The minor sites were smaller (0.12-0.2 ha), and crops were grown in only three replicates.

Kakamega was run as a major site for all four seasons; Kibos was a major site for both long rains (no crops are grown at Kibos in the short rains, due to unreliable rainfall). After the second season (long rains 1989), three of the initial minor sites - Mwea Tebere, Makueni and Msabaha -- were upgraded to major sites (the latter two only during the third season, the short rains of 1989/90, after which trials were stopped). Kisii and Mtwapa were run as minor sites for only the first two seasons.

Sampling

A standard sampling protocol was set up for comparable sampling between the seven field sites. Plants for sampling were selected randomly. First, without touching the plant, all plant parts were briefly checked for any fast-moving predators.

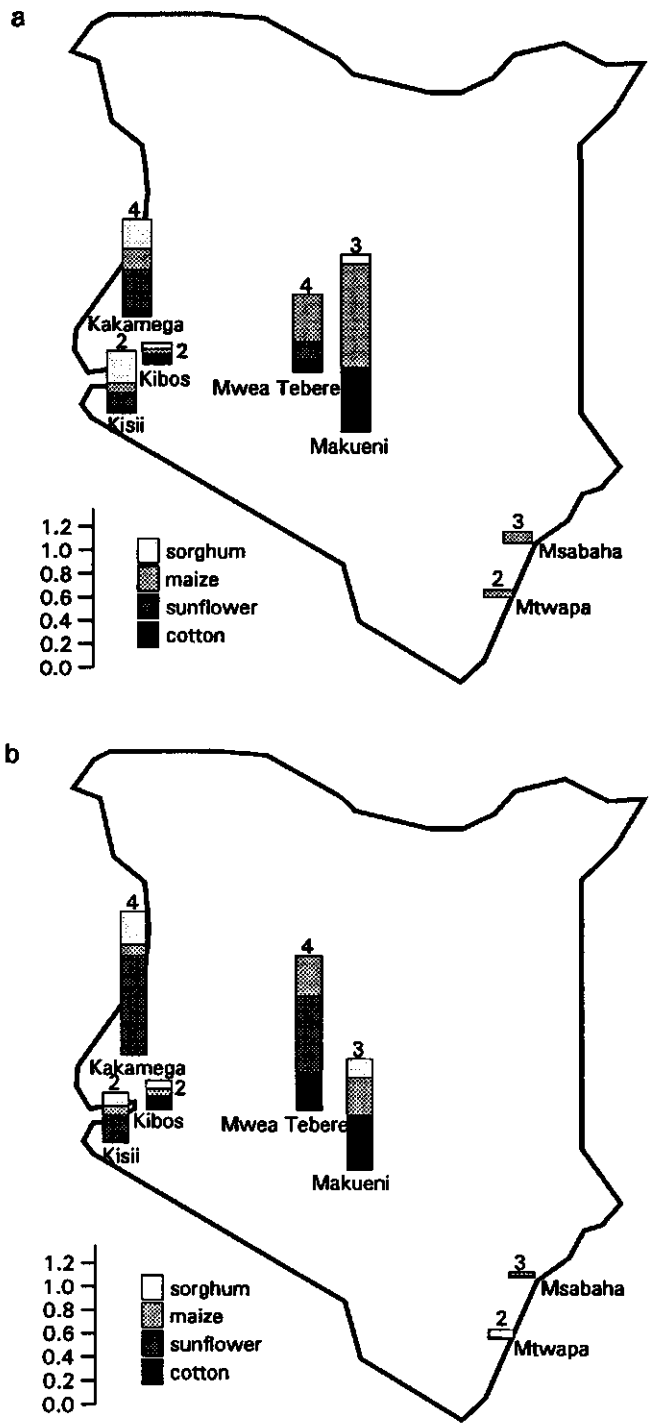

Fig. 4.1 Incidence of *H. armigera* (average number per plant during the growing season) in smallholder crops in Kenya, 1988-90. (a) eggs (b) larvae; number of sample seasons is indicated.

Thereafter all plant parts were thoroughly checked for any arthropod stages, taking apart leaves, leaf axils (of maize and sorghum) and flowering/fruiting parts of the plant, such as the panicle of sorghum, the flower head of sunflower, the tassel and cob of maize, and the flowering and fruiting bodies of cotton, in order to sample small stages, such as *H. armigera* eggs and anthocorids, more accurately.

A sample consisted of 30 plants for major sites, and 20 for minor sites. Samples were taken of each crop at regular intervals from pre-flowering until harvest. At major sites, samples were taken weekly, at minor sites, samples were taken every two or more weeks. Consequently, the number of sampling occasions during a season was 9-16 for major sites and 3-6 for minor sites. In the results presented here, data were pooled over the season, and seasons' averages were combined to provide an overall average density per crop per site.

H. armigera eggs could be recognized in the field using a 10x hand-lens. The instar of larvae was estimated in the field from head-capsule widths (Chapter 5), and was regularly verified under a binocular microscope. All eggs and larvae were taken to the laboratory for rearing of parasitoids. Eggs were reared through singly in labelled tubes, with a minimum of attached plant material to avoid condensation inside the tube. Larval instars were reared through singly in diet containers (Cock *et al.* 1991).

In order to minimize sampling errors, percentage parasitism was calculated with respect to the actual stages attacked by the parasitoids (Chapter 3), in order to minimize sampling errors. Inclusion of stages beyond those susceptible to parasitoid attack would give an underestimate of percentage parasitism. Average percentage parasitism during the season was calculated with respect to concurrent host densities. The percentage parasitism of eggs was corrected for the retarded development of parasitized hosts (Chapter 5).

Results and Discussion

Incidence of H. armigera

Fig. 4.1 depicts the incidence of eggs and larvae at the seven field sites. At the coast, eggs and larvae of *H. armigera* were rare throughout all three seasons. Oviposition was highest in Makueni, and was concentrated on maize and cotton (Fig. 4.1a). Overall levels found at Kakamega, Mwea Tebere and Kisii were similar, but there were considerable differences between crops.

Maize was the most preferred crop for oviposition at the sites east of the Rift Valley; while west of the Rift Valley, it was generally the least preferred crop for oviposition (compare Parsons, 1940b). This may be due to the varieties of maize used; vars. Katumani and Coast Composite were grown in the east, and H-511 and H-614 were grown in the west. At the highland sites of Kakamega and Kisii, sorghum was relatively more favoured by ovipositing moths than at the other sites where sorghum was grown.

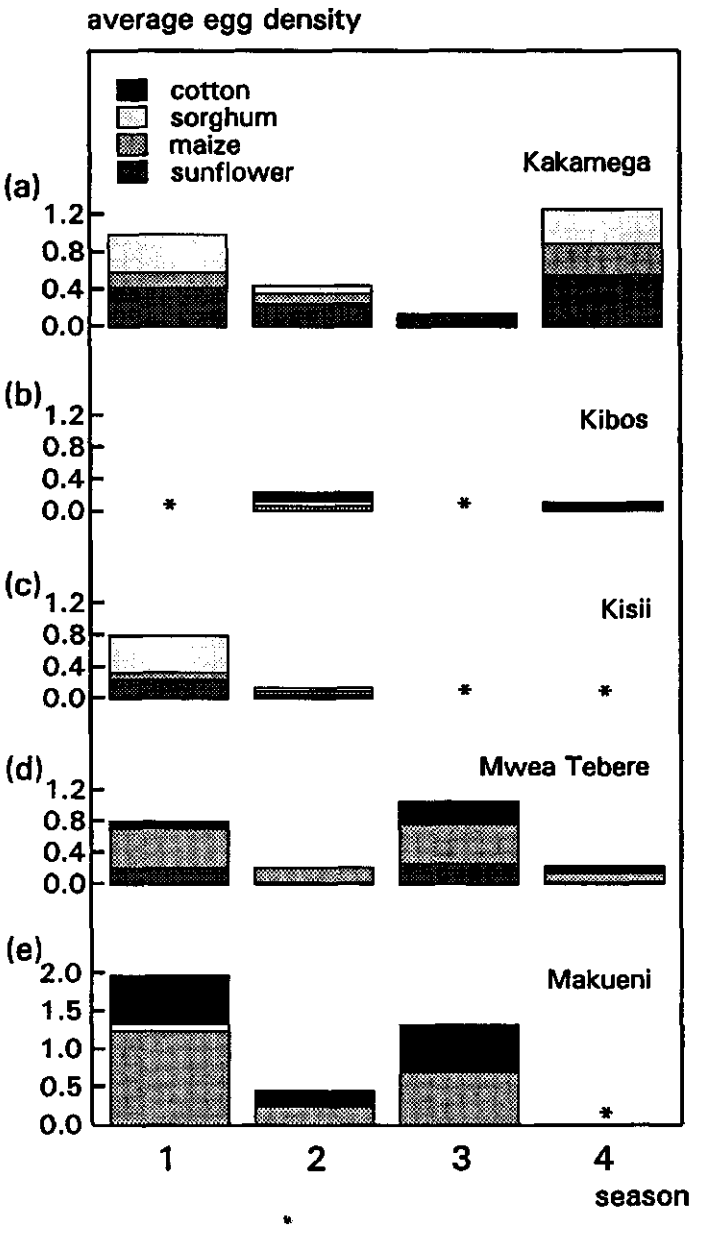

Fig. 4.2 Average seasonal egg density at the experimental field sites, during the sample seasons. Data are averages of three crops. An asterisk indicates that no data are available for the season concerned.

Oviposition at Kibos was exceptionally low, considering the local pest status of *H. armigera* on cotton, and egg densities were even lower on maize and sorghum.

Fig. 4.2 depicts the average oviposition per season. The two coastal sites were ignored because of low oviposition levels. In the first two seasons, *H. armigera* infestation was more or less consistent throughout the five sites; oviposition levels were greater during the first than during the second season (no short rain crop was grown at Kibos). However, during the last two seasons, infestation showed strong differences between locations. Oviposition at Kakamega was very low during the third season, while at Mwea Tebere and Makueni, on the other side of the Rift Valley, oviposition was moderate to high. Finally, during the fourth season, the oviposition level at Kakamega was high, while oviposition at the nearby site of Kibos, and at Mwea Tebere, was low. Low and constant light- and pheromone-trap catches at Kakamega suggest that the infestation was caused by a local population of *H. armigera*, rather than by immigrating moths (Chapter 5).

Larval densities (Fig. 4.1b) were highest at Kakamega, Mwea Tebere and Makueni, and infestation was surprisingly low at Kibos, where *H. armigera* is considered the key pest on cotton. In general, infestation was highest on sunflower and cotton. On cotton, levels occasionally reached two larvae per plant at Mwea Tebere and five larvae per plant at Makueni. At these levels, damage may be considerable. Levels on sunflower occasionally reached four larvae per plant at Kakamega and eight larvae per plant at Mwea Tebere. Damage relations for *H. armigera* on sunflower have not been studied.

There is little correspondence between the egg densities and larval densities either by sites or by crops. Eggs on maize generally gave rise to remarkably low larval densities, indicating a high mortality level of *H. armigera* on maize throughout the country. Survival of eggs was highest on sunflower, especially at Mwea Tebere and Kakamega, where moderate egg levels gave rise to considerable larval levels. Mortality on cotton appeared to be greater at Makueni than at Mwea Tebere or Kibos.

Natural enemies

Table 4.1 lists the natural enemies found at our sites, which are actual or potential natural enemies of *H. armigera*. Specimens were identified by taxonomists of the International Institute of Entomology (an Institute of CAB International) and The Natural History Museum (London), as indicated in Table 4.1. Of the large complex of predators recorded from the field sites, only two groups stood out as common at most sites: ants (Hymenoptera: Formicidae) and Anthocoridae (Hemiptera), each represented by a rich variety of species. Several members of each family were observed feeding on *H. armigera* eggs or larvae in the field (van den Berg & Cock 1993).

Table 4.1 Natural enemies identified from the field sites, 1988-90.

Species*	Site**	Comments***
PREDATORS (KNOWN AND PROBABLE)		
Hemiptera:		
Anthocoridae		
Blaptostethus sp. [2]	Kb	
Cardiastethus exiguus (Poppius) [2]	Kb	common,egg
Cardiastethus sp. [2]	Kb	
Orius albidipennis (Reuter) [2]	Kb, Ka	common,egg
Orius tantillus (Motschulsky) [2]	Kb, Ka	common
Orius thripoborus (Hesse) [2]	Kb, Ka	common,egg
Orius sp. A nr. *thripoborus* (Hesse) [2]	Mw, Kb	
Orius sp. B [2]	Mu	
Orius sp. C [2]	Lu	
Lygaeidae		
Geocoris amabilis Stål [2]	Kb	lab
Nabidae		
Tropiconabis capsiformis (Germar) [2]	Ka	lab
Neuroptera:		
Chrysopidae		
Brinckochrysa sp. [4]	Mw	homopt
Chrysoperla spp. [4]	Ka, Ki	common,homopt,lab
Mallada sp. [4]	Mw	homopt
Hemerobiidae		
Micromus sjostedti Weele [4]	Ka, Ma, Mw	homopt
Micromus timidus Hagen [4]	Mw	homopt
Coleoptera:		
Carabidae		
Calleida fasciata Dejean [8]	Kb	
Hexagonia sp. nr *punctatostriata* (Laferté Sénectère) [8]	Ka	
Stenidia sp. [8]	Ka	
Coccinellidae		
Cheilomenes aurora (Gerstaecker) [7]	Na	homopt,lab
Cheilomenes lunata (Fabricius) [7]	Ka, Ki, Ma, Mw	comm,homopt
Cheilomenes propinqua (Mulsant) [7]	Ka, Ki, Ma, Ms	comm,homopt
Cheilomenes sulpurea (Olivier)	Ka, Ma, Mw	common,homopt
Declivitata ?olivieri (Gerstaecker) [7]	Ma	homopt
Exochomus ventralis Gerstaecker [7]	Ms, Mt	homopt,lab
Platynaspis capicola Crotch [7]	Ma	homopt
Staphylinidae		
Paederus eximius Reiche [8]	Mw, Na	common
Paederus riftensis Fauvel [8]	Ka	common

Table 4.1 (cont.)

Hymenoptera:		
Formicidae		
Acantholepis sp. [5]	Mw	
Camponotus flavomarginatus Mayr [5]	Kb, Na	
Camponotus sp. nr *flavomarginatus* Mayr [5]	Kb	
Camponotus sp. 2 *acvapimensis*-group [5]	Ka	
Camponotus sp. 1 *maculatus*-group [5]	Ka	
Camponotus sp. 3 *rufoglaucus*-group [5]	Ms	
Monomorium opacum Forel	Mw	pitfall
Myrmicaria opaciventris Emery [5]	Kb	larva
Myrmicaria sp. or spp. [5]	Ka, Ki	larva
Odontomachus troglodytes Santschi [5]	Ka	pitfall
Oligomyrmex sp. [5]	Kb	pitfall
Pachycondyla sennaarensis (Mayr) [5]	Ms	pitfall
Pheidole sp. 1 [5]	Kb, Mw	egg,larva
Pheidole sp. 2 [5]	Ka, Ms	egg
Serrastruma ?maynei (Forel) [5]	Kb	pitfall
Tetramorium sericeiventre Emery	Mw	pitfall
Tetramorium zonacaciae (Weber) [5]	Ka	pitfall
Vespidae		
Belonogaster sp. [1]	Mu	lab
Polistes sp. [1]	Ka	
PARASITOIDS		
Diptera:		
Tachinidae		
Linnaemya longirostris (Macquart) [3]	Ka, Mw	L5-6
Palexorista laxa (Curran) [3]	Ka	L4-6
Palexorista quadrizonula (Thomson) [3]	Mw	L4-6?
Hymenoptera:		
Braconidae		
Dolichogenidea sp. (=*Apanteles* sp. *ultor*-group of Nixon) [6]	Ka	L1-3
?Dolichogenidea sp. [6]	Ka, Ma	L1-3
Meteorus laphygmarum Brues [6]	Ka	L3-4
Eulophidae		
Euplectrus laphygmae Ferrière [10]	Mw	L1-5
Ichneumonidae		
Charops ater Szepligeti [6]	Ka, Mw	L1-3
Netelia sp. or spp. [9]	Ka	L5-6
Scelionidae		
Telenomus ullyetti Nixon [1]	Ka, Ma	E

Table 4.1 (cont.)

Trichogrammatidae		
Trichogramma sp. nr *bournieri* Pintureau & Babault [1]	Ma	E
Trichogramma sp. [1]	Ka, Ma	E
Trichogrammatoidea armigera Nagaraja [1]	Ma,Ka	E
Trichogrammatoidea eldanae Viggiani [1]	Kb, Ki	E
Trichogrammatoidea lutea Girault [1]	Kb, Ka	E
Trichogrammatoidea simmondsi Nagaraja [1]	Kb,Ka	E
PATHOGENS		
Nuclear polyhedrosis virus	Ka	L1-3

* Specimens identified by the following taxonomists: [1] A. Polaszek (IIE), [2] G.M. Stonedahl (IIE), [3] N.P. Wyatt (NHM), [4] S.J. Brooks (NHM), [5] B. Bolton (NHM), [6] A.K. Walker (IIE), [7] R.G. Booth (IIE), [8] R. Madge (IIE), [9] I.D. Gauld (NHM), [10] J. LaSalle (IIE).

** *Ka*, Kakamega; *Ki*, Kisii; *Ma*, Makueni; *Ms*, Msabaha; *Mt*, Mtwapa; *Mu*, Muguga; *Mw*, Mwea Tebere; *Na*, Nairobi.

*** *homopt.*, often associated with homopterous prey; *egg*, known predator of *H. armigera* eggs; *larva*, known predator of *H. armigera* larvae; *lab*, observed feeding on *H. armigera* larvae in the laboratory; *pitfall*, caught only in pitfall traps; *E*, parasitizes *H. armigera* eggs; *L1-6*, parasitizes *H. armigera* larvae of instars indicated.

Of the complex of ant species, three genera dominated on plants in smallholder fields: *Pheidole*, *Myrmicaria*, and *Camponotus*. The composition and abundance of these genera fluctuated widely from site to site and is discussed below under "Incidence of predators".

Anthocorid samples studied by Dr G.M. Stonedahl of the International Institute of Entomology, showed a total of nine species were present at our field sites, six of which were *Orius* spp. (Cock *et al.* 1991). In our population density sampling, however, we did not distinguish between individual species.

Predators belonging to the families Chrysopidae (Neuroptera), Hemerobiidae (Neuroptera), Syrphidae (Diptera), and Coccinellidae (Coleoptera) were generally less common, and were predominantly found in association with aphid prey. Some members (*Chrysoperla* sp., *Cheilomenes aurora, Exochomus ventralis*) readily fed on *H. armigera* stages presented to them in the laboratory. They and related groups were included in Table 4.1 as possible predators of *H. armigera*. Various widespread species of *Cheilomenes* (Coccinellidae) were occasionally common, particularly at Makueni. Syrphid larvae, *Allograpta nasuta* (Macquart) and *Melanostoma annulipes* (Macquart) (Diptera: Syrphidae) (Det. N.P. Wyatt, NHM), were not included in Table 4.1, because they did not feed on *H. armigera* stages in the laboratory.

Paederus riftensis and *P. eximius* (Coleoptera: Staphylinidae) were common in the crop canopy at several sites. This genus includes known predators in rice in Southeast Asia (van den Berg *et al.* 1992), but their role as predators in Kenya requires further study. Spiders were never abundant at the field sites.

Other predators, such as *Pirates (Cleptocorus) ?nitidicollis* (Reuter) (Hemiptera: Reduviidae) (Det. G.M. Stonedahl, IIE), *Apristus latipennis* Chaudoir and *Elaphropus optimus* (Péringuey) (Coleoptera: Carabidae), and *Astenus tricolor* Cameron and *Paederus sabaeus* Erichson (Coleoptera: Staphylinidae) (Det. R. Madge, IIE), all from Kakamega, were not included in Table 4.1 because they were sporadically recorded from pitfall traps only.

Table 4.1 indicates a rich ant fauna is present in Kenyan agro-ecosystems, but ant communities showed large local differences. *Myrmicaria opaciventris, Myrmicaria* sp., *Pheidole* sp. 1 and *Pheidole* sp. 2 were the most abundant ant species. Some species from Table 4.1 were recorded from pitfall traps only. Possibly, these include nocturnal species foraging in the vegetation at night.

Pathogens were rarely encountered in the field. Larvae reared through in the laboratory were sometimes diseased, but this was probably because of secondary infection or reduced resistance in the laboratory (McKinley 1971).

Incidence of parasitism

Average parasitism was generally low (< 5%) or absent at our sites, and highest levels of parasitism were found at Kakamega and Kibos. Here, *Trichogrammatoidea* spp. (Hymenoptera: Trichogrammatidae), *Telenomus ullyetti* Nixon (Hymenoptera: Scelionidae) and *Linnaemya longirostris* (Macquart) (Diptera: Tachinidae) were the dominant parasitoids. Taxonomic studies by Dr A. Polaszek revealed a complex of at least six trichogrammatids, of which *Trichogrammatoidea armigera* Nagaraja, *T. eldana* Viggiani and *T. simmondsi* Nagaraja were newly recorded parasitoids of *H. armigera* in Africa (Cock *et al.* 1991). Samples sometimes yielded three species occurring concurrently at the same site.

The occurrence of parasitoids can vary greatly between seasons and between sites. However, the levels of parasitism were much lower and the species diversity was poorer at our Kenya sites than was found in a recent study in western Tanzania (Nyambo 1990).

At Kakamega, generational egg parasitism by *Trichogrammatoidea* spp. and *Telenomus ullyetti* combined was about 10%. Parasitism of young larvae, mainly due to *Dolichogenidea* (*Apanteles*) sp. (Hymenoptera: Braconidae), was very low (< 5%). Older larvae were commonly attacked by *Linnaemya longirostris*, especially on sunflower, where occasionally, late in the season, parsitism levels as high as 20% were recorded. The incidence of pathogens was negligible. The same parasitoid species were found at Kisii, but parasitism levels were slightly lower. At Kibos, the level of egg parasitism by *Trichogrammatoidea* spp.

Here, *Cardiastethus* spp. were abundant during the 1989 long rains, but were not encountered during the 1990 long rains when *Orius* spp. dominated, which reflects the large fluctuations in species composition. Anthocorids are common predators of a variety of pests worldwide, and their role in reducing pest populations is receiving increased attention. Reports from southern Africa indicated that *Orius* sp. or spp. may be an important predator of *H. armigera* eggs (Parsons & Ullyett 1934, Peat 1935), and recent quantitative data from Kenya support this (Chapter 11).

Conclusions

In most seasons, *H. armigera* levels were low in our field trials, but on some occasions *H. armigera* reached damaging population levels on sunflower at Kakamega and Mwea Tebere, and on cotton at Mwea Tebere and Makueni. *H. armigera* was almost absent at the coast during the study period; but since then it has been reported to be common (Okweyo-Owuor, pers. comm. 1992).

H. armigera egg and larval levels varied largely between the study sites. Moreover, comparison of egg and larval levels reveals that survival of *H. armigera* varied between sites: at Makueni larval levels were low in comparison to egg levels, while at Mwea Tebere egg levels gave rise to relatively more larvae.

Parasitoids were seldom common, except egg parasitoids which were occasionally common, and late-larval parasitoids (particularly *Linnaemya longirostris*), which could be common on sunflower towards the end of the season (Chapter 5). Thus, parasitism had little impact on *H. armigera* on the four crops studied.

Predator communities were rich, and predation is a potentially important mortality factor of *H. armigera*. The occurrences of ants and anthocorids varied largely between sites; anthocorids were generally more common in western Kenya. Differential mortality levels of *H. armigera* may be partly attributable to predators, and are dealt with in separate studies on life tables and predator evaluation (Chapter 5, 8 and 9).

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5

Stage-specific mortality of *H. armigera* in three crops[1]

ABSTRACT - (1) Partial life tables of *Helicoverpa armigera* were constructed for three crops, sunflower, maize and sorghum, commonly grown on smallholdings in Kenya.
(2) Oviposition coincided with early flowering of the crops; this was due to the preference of ovipositing moths for flowering plants rather than to narrow periods of oviposition activity. Consequently, single cohorts of *H. armigera* developed on each crop.
(3) The partial life tables show that mortality during development was generally high (82-99.3 %) on sunflower, maize and sorghum, but stage-specific mortality varied greatly from season to season. Mortality was highest on maize, particularly during the young stages. Mortality was generally higher in the short rainy seasons than in the long rainy seasons.
(4) The contribution of parasitism and pathogens was rather small; only a tachinid attacking old larvae was common. Most mortality was due to unknown causes which includes predation.
(5) The potential role of predators was partially evaluated by relating their temporal association with the prey to stage-specific mortality, but was obscured by the variety of predators that feed on *H. armigera*, and thus requires further study. Mortality of young stages of *H. armigera* was most strongly associated with the incidence of anthocorid bugs. *Myrmicaria* sp. ants are likely to be more important on sunflower than on maize and sorghum.
(6) Implications of the findings for improving biological control through habitat manipulation and importation of exotic natural enemies are discussed.

Introduction

Helicoverpa armigera (Hübner) (Lepidoptera: Noctuidae), a major pest on a variety of food and cash crops, is attacked by a large complex of natural enemies (King & Jackson 1989; Chapter 3). Although parasitoids and predators cannot be relied upon for total control of *H. armigera* in unsprayed fields, to understand their role is an essential component in the development of integrated pest management in cropping systems where *H. armigera* is an important pest. As the degree of natural control can be substantial, the destruction of natural enemies is one of the factors responsible for the increase of *H. armigera* after intensive

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insecticide spraying (Eveleens 1983, Zalucki *et al.* 1986, Abdelrahman & Munir 1989). However, quantitative data on the impact of natural enemies on pest numbers are generally lacking, particularly regarding predation (Fitt 1989), and a recent workshop on biological control of Heliothinae stressed the need to assess the impact of natural enemies in the context of life table studies (King & Jackson 1989).

The few life table data on *H. armigera* that have been published refer to single-crop situations (Room 1979, Bilapate 1981, Bilapate *et al.* 1988, Nanthagopal & Uthamasamy 1989, Kyi, Zalucki & Titmarsh 1991), and the only data available from Africa are unpublished survival rates of *H. armigera* on cotton in southern Africa (Pearson 1958, p. 156). Females lay their eggs singly, dispersed over various plant structures of different crops and weeds (probably because the larvae are cannibalistic), thus making it a difficult and labour-intensive species to sample accurately for population studies.

In western Kenya three of the host plants of *H. armigera*, sunflower, maize and sorghum, are commonly grown on smallholder farms either in small adjacent plots or in mixed plantings. *H. armigera* is a problem on sunflower (Khaemba & Mutinga 1982), sometimes on sorghum, but rarely on maize, although moths readily oviposit on this crop. A prerequisite for improving biological control of *H. armigera* in crops is to understand the ecology of the pest in local cropping systems.

When different host plants of *H. armigera* are planted in adjacent plots, or interplanted, *H. armigera* (and natural enemy) numbers on a crop are influenced by neighbouring crops, both directly and indirectly. Direct influences include preference for one crop over the other by ovipositing moths and the movement of larvae and natural enemies between interplanted crops; indirect influences arise when *H. armigera* infestation on one crop is influenced by the population build-up or mortality level on neighbouring crops (Nyambo 1988). Hence, the effect of neighbouring crops could be to act as a source or sink of pest infestation. The use of diversionary, attractant or trap hosts has been suggested as a control tactic several times (e.g., Fitt 1989). The parasitoids of *H. armigera* in East Africa are associated with particular food plants (Chapter 7), and the same may be true for predators, resulting in differential mortality of *H. armigera* in different crops or cropping systems.

The present study describes partial life tables of *H. armigera* based on smallholder farm systems in Kenya consisting of replicated plots of three crops, sunflower, maize and sorghum, over four seasons in two years. We explicitly evaluate the possible role of predators by relating their temporal association with prey to the stage-specific mortality of the prey. Quantification of the impact of different groups of predators will be presented separately (Chapter 8-11).

Materials and Methods

Experimental field site

The study site was at the KARI (Kenya Agricultural Research Institute) Regional Research Centre at Kakamega, Western Province, located in an area which receives among the highest and most reliable rainfall (1950 mm per year) in Kenya, where annual crops can be grown in two seasons each year. The study started from the short rains (October to February) of 1988/89 and continued for four seasons until the long rains (April to August) of 1990.

Mono-crop plots of sunflower, maize and sorghum were grown in four replicates within a 0.4 ha field plot. The individual plot size was chosen such that not more than 10% of the plants would have been destructively sampled by the end of the season; this was 19x20 m for sunflower, 17x20 m for maize, and 12x20 m for sorghum. Such plot sizes are normal at local farms. Locally recommended varieties and plant spacings were used. For sunflower, maize and sorghum, plant spacings were 30x75 cm, 30x75 cm, and 10x50 cm, respectively, and varieties were Comet, Hybrid-511 (short rains) / Hybrid-614 (long rains), and E525-HR, respectively. After the first season of the 1988/89 short rains, the experimental site had to be moved to a similar site 300 m away, where the experiments were continued for the subsequent three seasons. Consequently, some conditions, such as the local ant communities, changed after the first season.

Mean daily temperature values were calculated from hourly records obtained at the research centre (for meteorological data, see Cock *et al.* 1991).

Sampling methods

Sampling was conducted weekly from Monday to Friday, during the morning hours (7.30-11.00 h) (in the first season also late afternoon, 16.30-19.00 h) to avoid the hottest time of the day. During each week, 30 plants of each crop were destructively sampled; plants were selected based on random row numbers and random plant numbers within the rows. Data were pooled over the week and were treated as one sampling occasion.

It took about 20 minutes to sample each plant. First, without touching the plant, fast-moving insects were recorded; then, the whole plant was checked and any relevant arthropod was recorded. Special attention was given to dissection of complex plant structures, such as the flower head of sunflower, the cob and tassel of maize, and the panicle of sorghum, because they are preferred microhabitats of *H. armigera* stages and/or common anthocorid predators (Chapter 6). *H. armigera* eggs could be distinguished from other noctuid eggs, mainly *Plusia* spp. (van den Berg & Cock 1993) using a hand-lens.

To enable identification of the six larval instars of *H. armigera*, we established the head-capsule width of each stage. *H. armigera* larvae were reared

individually on semi-synthetic diet (Cock *et al.* 1991), and the head-capsule width of each instar was measured using a 40x binocular microscope with eye-piece graticule. The production of cast head-capsules was monitored to confirm each moult to the next instar. During field sampling, larval instars were estimated, and samples regularly measured in the laboratory to check field estimates.

Measurement of percentage parasitism

The percentage parasitism and the percentage infection by pathogens was measured from field samples. Eggs and larvae encountered during field sampling were collected and reared individually in the laboratory. Eggs were kept in ventilated tubes and failure to hatch, and emergence of first instar larvae or parasitoids were recorded. Larvae were reared individually on a sterile semi-synthetic diet (Cock *et al.* 1991), in 1 fluid oz. (28.35 ml) clear plastic cups, 4.5 cm high, 2.5 and 4.0 cm diameter at the base and top, respectively, with a ventilated lid. Larvae were reared to adult, disease expression or parasitoid emergence.

Percentage parasitism was calculated with respect to the actual stages of the host attacked by the parasitoids (Table 5.1), since inclusion of stages too young or too old for parasitoid attack would underestimate percentage parasitism (van Driesche 1983). P_i, the mortality in each seasonal cohort due to parasitoid or pathogen *i*, was calculated as the total number parasitized (or diseased) from all samples divided by the total number of susceptible *H. armigera* from all samples:

$$P_i = \sum_{t=0}^{T} (d_{it}\, p_{it}) \Big/ \sum_{t=0}^{T} d_{it}$$

where d_{it} is the density of the relevant host stages (i.e., those susceptible to parasitoid or pathogen *i*) at week *t*, p_{it} is the proportion of these parasitized by parasitoid *i* (or diseased by pathogen i) in the sample of week *t*, and T is the total number of weeks.

The mortality due to parasitism of eggs was derived from the field parasitism rate corrected with respect to the retarded development of parasitized hosts. Parasitized eggs remain in the field for a considerable period after unparasitized eggs have emerged, and will thus be over-represented in field samples, resulting in an overestimation of mortality due to parasitism. Therefore, the development periods of parasitized and unparasitized eggs were measured, and a correction factor calculated. In a test tube in the laboratory, half-day old *H. armigera* eggs laid on tissue paper were exposed for three hours to *Trichogrammatoidea* spp. adults, and were kept at 18-23°C.

Trichogrammatoidea spp. were more common than the scelionid egg parasitoid *Telenomus ullyetti* Nixon. Adult parasitoids, newly emerged from field-collected *H. armigera* eggs, were allowed to mate and feed on honey

Table 5.1 Percentage parasitism and pathogens of *H. armigera* eggs and larvae; data are averages of three (for maize and sorghum) or four (for sunflower) seasons.

Parasitoid/pathogen	host stages*	SUNFLOWER	MAIZE	SORGHUM
Linnaemya longirostris	L5-6	23.5	0.0	5.8
Charops ater	L1-3	3.1	0.0	0.0
Dolichogenidea sp.	L1-3	0.0	6.8	4.0
Meteorus laphygmarum	L3-4	1.3	0.0	2.8
Trichogrammatoidea spp.	E	3.5	11.5	7.3
Telenomus ullyetti	E	2.1	0.0	1.1
Nematoda	L2-5	0.2	1.9	1.0
Nuclear polyhedrosis virus	L1-3	0.7	0.0	0.0

* Host stages selected for calculations of the level of percentage parasitism and pathogens; E, egg; L1-6, larval instars.

solution prior to exposure to the host eggs. Half of the eggs were kept in a separate test tube without parasitoids under identical conditions. The eggs were checked regularly, depending on the rate of emergence (up to 15 minute-intervals during peak emergence), first for eclosion of unparasitized eggs, then for emergence of parasitoids.

Table 5.2 Graphical calculation of stage recruitment, where Rt is the average residence time (=dev. period) in weeks, GA the Graphical Area (week/plant), and Lx the graphical estimate of recruitment per plant (GA/Rt). Lx' is the corrected recruitment of eggs, calculated as GA/(Rs/5.17), because only young eggs (< 1 d old) were encountered during sampling (see text).

		SUNFLOWER			MAIZE			SORGHUM		
X	Rt*	GA	Lx	Lx'	GA	Lx	Lx'	GA	Lx	Lx'
Season 1 (av. temp. 20.6°C)										
Egg	0.75	4.37	5.85	30.26	1.67	2.24	11.56	3.71	4.98	25.73
L2-3	0.76	1.90	2.52		0.30	0.38		0.33	0.42	
L4-6	2.10	0.57	0.28		0.35	0.16		0.38	0.19	
Season 2 (av. temp. 19.5°C)										
Egg	0.75	2.68	3.59	18.55	1.50	2.01	10.41	0.70	0.94	4.86
L2-3	0.88	6.10	6.86		1.39	1.55		4.36	4.85	
L4-6	2.38	0.42	1.74		0.89	0.37		2.10	0.88	
Season 3 (av. temp. 20.4°C)										
Egg	0.75	1.13	1.51	7.80						
L2-3	0.78	1.23	1.58							
L4-6	2.14	0.73	0.34							
Season 4 (av. temp. 19.4°C)										
Egg	0.75	6.01	8.06	41.68	3.53	4.73	24.46	3.42	4.58	23.68
L2-3	0.89	8.21	9.61		0.38	0.46		2.26	2.69	
L4-6	2.40	13.57	5.67		1.26	0.53		2.06	0.87	

* For eggs, the development period was measured at 20.1°C; for L2-3 and L4-6, temperature-dependent development rates were calculated over weekly intervals, using the equations of Fig. 5.1. Differences in Rt among crops (due to different development periods of crops) are negligible.

Estimation of recruitment

For *H. armigera* larvae, recruitment was estimated by dividing the graphical area of the stage concerned by its development period (Southwood & Jepson 1962). This method was chosen because it is computationally simple, and is not restricted by conditions set by other methods, yet is applicable to realistic situations in which survival rates vary from stage to stage (Southwood 1978).

Instead of considering individual larval instars of *H. armigera* for the construction of the life table, it was necessary to combine the second and third instars, and the instars four to six, in order to provide sufficient data when *H. armigera* densities were low. The first instar was ignored, because this small stage was under-represented in field samples and would thus underestimate recruitment of young larvae.

The development period of *H. armigera* stages, required for calculation of recruitment, is dependent on local temperatures. Fig. 5.1 shows the development rate of eggs, second to third instars (L2-3) and fourth to sixth instars (L4-6) in relation to temperature. The development period of egg cohorts deposited by moths on plants was measured under two temperature conditions (average temperature of 20.1°C [n=79 eggs], and 23.0°C [n=43 eggs]) in the field; eggs were checked daily for emergence (Chapter 11). Because average seasonal temperatures in our trials were around 20°C (see Table 5.2), we used the development period at 20.1°C (5.2 days) for all seasons.

The development periods of larval instars of *H. armigera* were studied by Twine (1978) under six constant temperatures in the laboratory. It is assumed

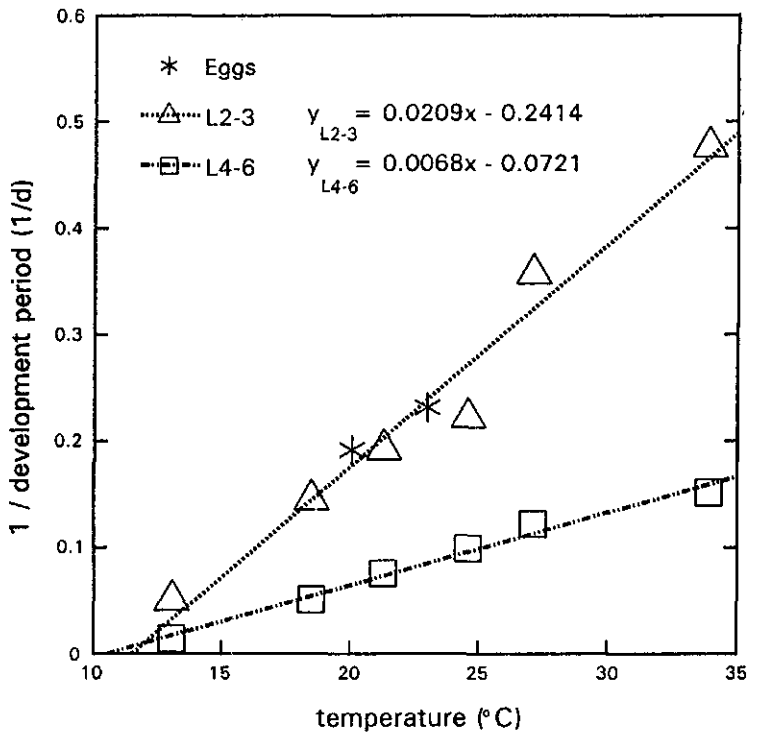

Fig. 5.1 Relationship between the rate of development of *H. armigera* stages and temperature. Data for eggs were collected in western Kenya, 1990; data for larvae were derived from Twine (1978).

that these development periods apply equally to larvae on sunflower, maize and sorghum. Firempong & Zalucki (1990) showed that the development period of an Australian *H. armigera* population on sunflower or maize was not significantly different from that on a diet similar to that used by Twine (1978), although *H. armigera* developed slightly faster on sunflower than on maize. However, development may also be affected by the growth stage and condition of the host plant, so that generalizing from Twine's data is reasonable.

The regression equations of Fig. 5.1 were used to calculate development rates for L2-3 and L4-6 at local temperatures. Calculations were made for each week, based on the average weekly temperature values at the field site, which varied between 19 and 23°C over the four seasons studied. Accordingly, weekly recruitment was estimated by the graphical area during week t, divided by the development period during that week. Summation of the weekly recruitment estimates over the season provides recruitment L_χ.

The egg-recruitment estimates obtained with the graphical method sometimes resulted in negative mortality levels, indicating an underestimation of egg densities. In a separate study on sunflower (Chapter 8), we monitored every morning, from the third week after planting until harvest, eggs laid during the previous night on six trap plants (i.e., plants daily cleared of eggs) in unsprayed fields. Trap plants were checked daily for one week, after which new plants were selected randomly. Simultaneously, we sampled the density of eggs on other plants in the same fields, just as in the present study (thirty plants sampled weekly during the season). Care was taken that the same sampling effort was put into both types of data collection. Thus, we were able to compare the graphical estimate of recruitment with the measured influx of new eggs. The influx of eggs in unsprayed plots was 8.33 per plant, while the estimated recruitment from density data was 1.61 per plant. Thus, the measured influx was 5.17 times greater than the graphical estimate of recruitment.

This may have two causes. Firstly, eggs older than one day may have disappeared. It is a shortcoming of the graphical method that it assumes that there is no mortality during a stage, but that mortality only occurs at the end of the stage (Southwood 1978). However, it is unlikely that all eggs disappeared after one day. Secondly, after a certain age, eggs become more difficult to find on plants. Young *H. armigera* eggs are conspicuously yellow/white in colour, but after one day they have darkened and are difficult to distinguish against host plant structures. In separate experiments, where eggs were marked and their fate was followed, most eggs were still present after two days (Chapter 8), but they would have been difficult to detect without marking. Thus, because eggs recorded in density samples are predominantly newly laid eggs, the graphical estimate should not be divided by the development period d_t of eggs, but by $d_t/5.17$, which equals 1 day. With an egg development period of 5.2 days, this implies that eggs older than 1 day were not included in samples. This correction factor was found to be similar on cotton (Chapter 9) so the same factor was also applied to all crops here.

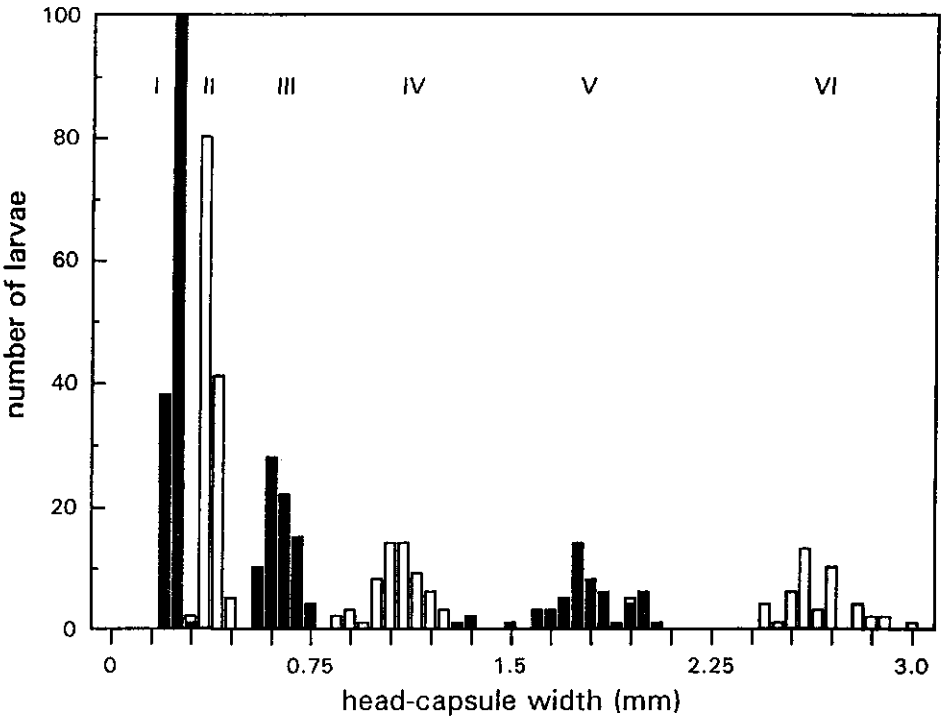

Fig. 5.2 Head-capsule width distribution of larval instars of *H. armigera* in a laboratory population, followed during development; black and white bars differentiate consecutive instars.

If ovipositing moths avoid plants that carry conspecific eggs (Gilbert 1977), for instance visually or by recognition of a pheromone on the eggs, hand-removal of eggs may induce an increased oviposition rate on trap plants, and cause overestimation of egg recruitment. However, subsequent egg laying would only be influenced in this respect if the pheromone were removed together with the egg, which is not the case if ovipositing moths use moth scales around the eggs for recognition. Moreover, because measured densities of eggs were low (maximally 0.6 per plant), influences of conspecific eggs are not likely to be important.

Temporal overlap

In order to compare the role of predators during different seasons and in different crops, we examined how their temporal occurrence corresponded with that of their prey. The degree of overlap y_t between the temporal occurrences of predator and prey was determined as follows.

$$y_t = 1 - \tfrac{1}{2} \sum_{t=0}^{T} \sqrt{(p_t - q_t)^2}$$

whereby p_t and q_t, the relative occurrences of the predator and *H. armigera* stage, respectively, are the proportions of the total graphical area found during week t, and T is the total number of weeks. If $y_t = 0$, there is no overlap, and therefore the predator would have no effect on the prey. The higher y_t ($0 \leq y_t \leq 1$) the higher the predation level to be expected. The shape of the phenology curves was not considered; however, a low but constant occurrence of a predator may have a different effect on the pest than a single predator peak during one week, even though they give the same degree of overlap y_t.

y_t, the degree of overlap of relative occurrences, is independent of the density of predators. Therefore, we multiplied y_t with the average predator density during the sample season, P, to obtain a measure of predator pressure, Z.

$$Z = y_t . P$$

This measure provides an indication only of the potential impact of predators, and gives no indication of mortality caused, as is required for a life table, yet it does help us to understand the potential role of predators when life tables of different seasons and crops are compared.

Results

The head-capsule width distribution of *H. armigera* instars in the laboratory is presented in Fig. 5.2, and shows little overlap between the head-capsule widths of the different instars. The data are similar to those of N.J. Armes (unpublished, 1989). Head-capsule width is, therefore, the only reliable characteristic for identifying the instar of a larva, although the difference between instars might be obscured in a field population, where exposure of the larvae to more diverse nutritional and climatic conditions could give rise to more varied head-capsule widths.

Oviposition levels during the four seasons were low to moderate with peak levels up to 3.2, 1.7 and 1.7 eggs per plant on sunflower, maize and sorghum, respectively. In most crop seasons, there was one distinct oviposition period of one to three weeks.

Fig. 5.3 shows the occurrence of *H. armigera* eggs in relation to the plant stage. The results were obtained by combining data for the first, second, and fourth seasons; data for the third season were ignored because *H. armigera* laid no eggs on maize or sorghum. The occurrence of anthocorids, the major predators of eggs, is also given; three species were found, *Orius thripoborus* (Hesse), *O. tantillus* (Motschulsky) and *O. albidipennis* (Reuter).

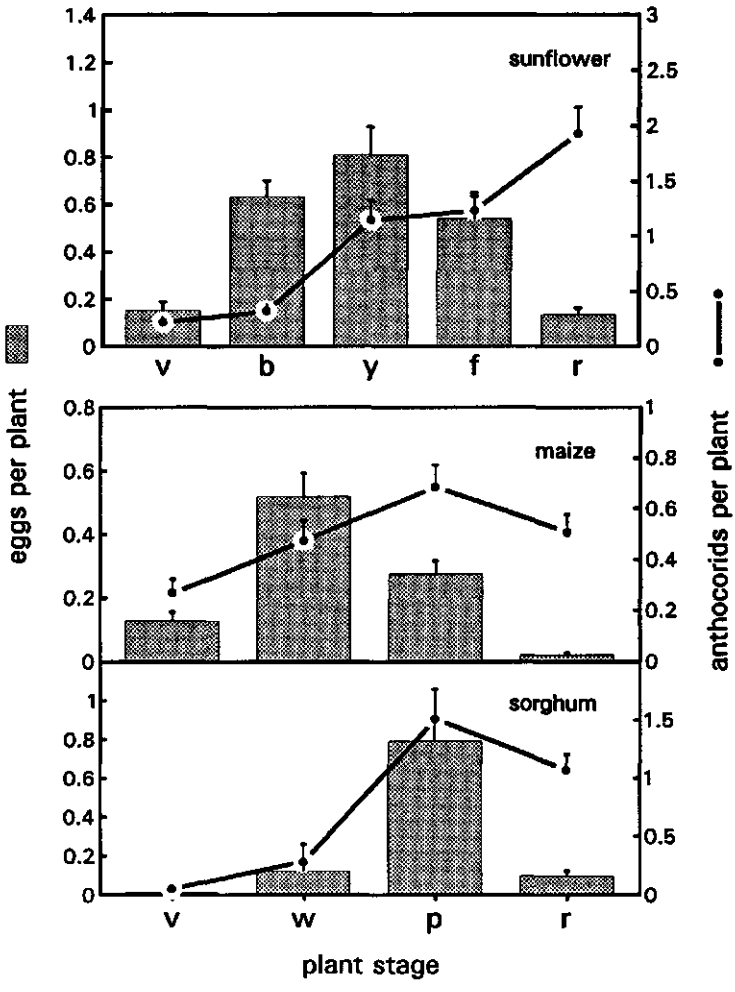

Fig. 5.3 Average levels of *H. armigera* eggs and anthocorid adults on plants of different crop stages of sunflower, maize and sorghum. Data are pooled over entire seasons (see text). Plant stages indicated are v, vegetative; b, budding; y, young inflorescence; f, flowering, r, ripening, w, whorl, p, pollen shedding. Vertical bars indicate s.e.

Besides insect prey, anthocorids consume plant products such as pollen (Dicke & Jarvis 1962). On sunflower, oviposition was highest on budding and early flowering plants.

Anthocorids were attracted to plants after the budding stage, densities increased in young inflorescences and were greatest during ripening, when densities of *H. armigera* eggs were low. On maize, egg densities were greatest on plants in the whorl stage, while anthocorid densities were highest at the pollen-shedding stage. On sorghum, the frequency of both eggs and anthocorids was strikingly associated with plants that were shedding pollen. *H. armigera* eggs were rarely found on maturing crops.

The data as presented in Fig. 5.3 were pooled for all seasons, and therefore it remains unclear whether the observed patterns are due to preference for particular crop stages, or to narrow periods of activity of ovipositing moths and anthocorids alike. Fig. 5.4 shows the oviposition of *H. armigera* during seasons 1, 2 and 4. In general, oviposition was highest on sunflower, but this depended on the condition of the crop. For example, during the first season the crops received

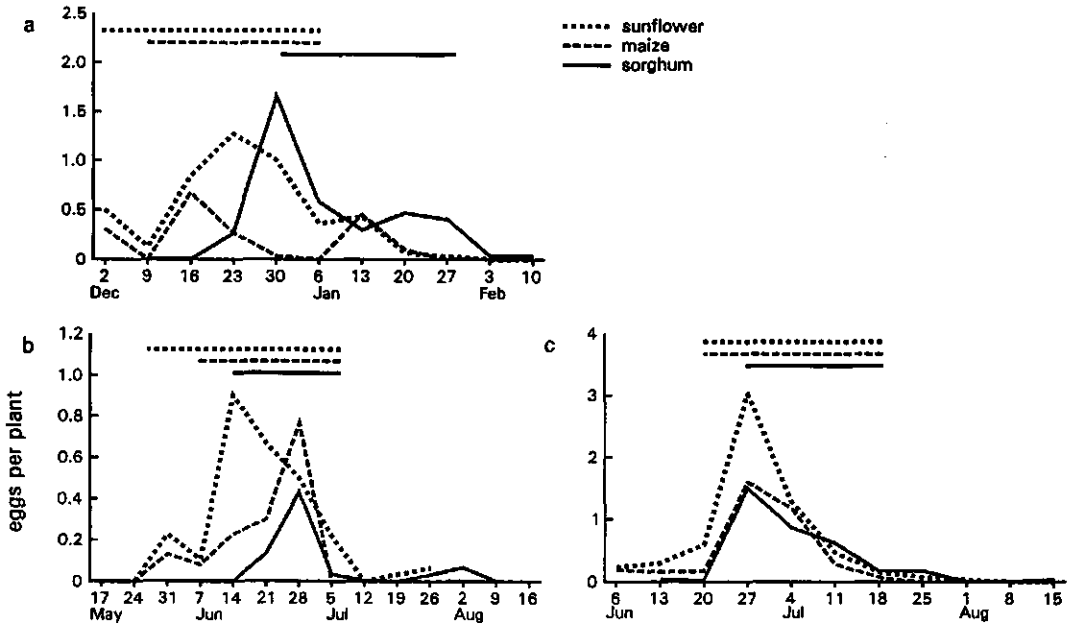

Fig. 5.4 *H. armigera* egg densities on sunflower, maize and sorghum; horizontal lines indicate periods when the three crops are most attractive to *H. armigera*: early flowering for sunflower, whorl stage for maize, and pollen-shedding for sorghum. Seasons were a, short rains 1988/89; b, long rains 1990; c, long rains 1991.

little rain and relatively more eggs were deposited on sorghum, which suffered least from water stress. In the fourth season, the three crops reached their attractive stage simultaneously, but in the first and second seasons, the attractive stages of the crops occurred at different times. Thus, during the first season oviposition started on sunflower and maize which flowered first, but shifted to sorghum only when pollen shedding started. This indicates that the coincidence of oviposition with certain crop stages is due to ovipositional preference of moths, rather than to narrow periods of moth oviposition. This is supported by data from a light trap about 200 m away which caught small numbers of *H. armigera* throughout the seasons (H. van den Berg, unpublished data).

As a consequence of the short periods of oviposition, only single distinct cohorts of *H. armigera* developed on each crop; these cohorts are treated as generations in the life tables presented here. The density of larvae differed markedly from season to season. Sometimes larvae were almost absent, while during other seasons densities would build up to as many as five larvae per plant. Fig. 5.5 shows that on sunflower an egg peak of 1.3 per plant during the first season (short rains 1988-89) gave rise to virtually no larvae, whereas an egg peak of 3.0 per plant during the fourth season gave rise to a proportionately much greater density of larvae (2.9 per plant). Thus, the level of stage-specific mortality varies greatly from season to season, and could determine whether the pest develops to a damaging level or not.

Larvae generally developed from pollen-shedding or flowering onwards. On maize, larvae were able to complete their development, but on sunflower and sorghum, which mature about two to three weeks earlier than maize, many larvae did not complete their development before harvest. Comprehensive data are presented by Cock *et al.* (1991), but note, for example, that in Fig. 5.5b the mid-August harvest occurs while a significant proportion of L4-6 have yet to complete their development.

The development period of unparasitized eggs under laboratory conditions was 4.86 d (s.d. 0.19 d; n=95), and the development period of eggs parasitized by *Trichogrammatoidea* spp. (including the half day prior to parasitization) was 12.52 d (s.d. 0.41 d; n=89). Egg development in the field was slightly slower (5.0-5.4 d), but we assume that the relative times will be similar. This means that parasitized eggs remain in the field 2.6 times longer than unparasitized eggs, and would thus be over-represented in samples by that factor. However by remaining longer in the field, parasitized eggs are more prone to predation or disappearance than unparasitized eggs. Moreover, parasitized eggs may be more difficult to find than unparasitized eggs, because they are darker in colour. These factors would lead to underestimation of percentage parasitism. Hence, instead of a correction factor of 2.6, we divided the observed egg parasitism rates in our samples by the arbitrarily lower value of 2.0.

Table 5.2 outlines how stage recruitment is computed from graphical areas and residence times, and how recruitment of eggs was corrected for sampling errors.

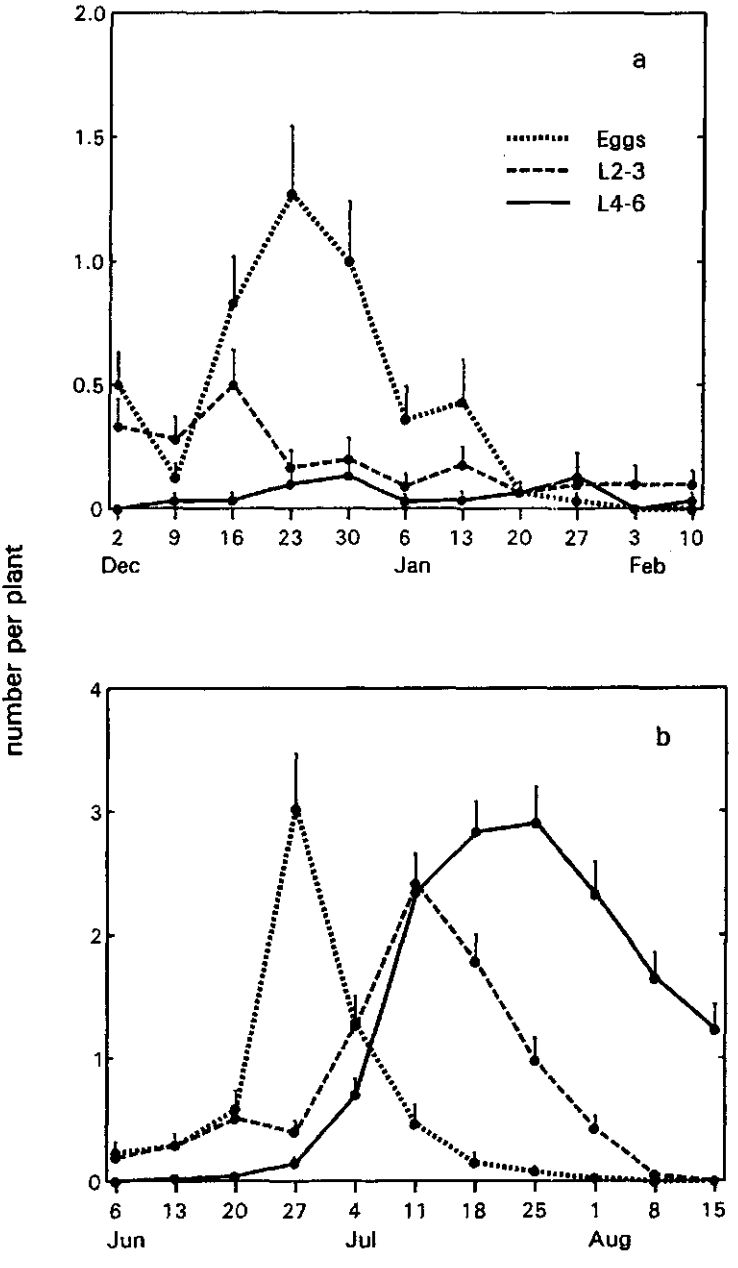

Fig. 5.5 Population densities of *H. armigera* eggs and larvae on sunflower during (a) season 1 (short rains 1988/89), and (b) season 4 (long rains 1990).

Table 5.3 Partial life tables for *H. armigera* on sunflower, Kakamega.

X	dxF	Lx	dx	100 Qx	Lx	dx	100 Qx*
		season 1 (short rains 1988/89)			*season 2 (long rains 1989)*		
Eggs		30.26			18.55		
	failed to hatch		0.00	0.0		1.22	6.6
	parasitism		3.69	12.2		0.00	0.0
	unknown		24.05	79.5		10.47	56.4
L2–3		2.52			6.86		
	parasitism		0.00	0.0		0.36	5.2
	unknown		2.24	89.0		4.76	69.5
L4–6		0.28			1.74		
	parasitism		0.07	27.0		0.00	0.0
	total mortality			99.3			90.6
		season 3 (short rains 1989/90)			*season 4 (long rains 1990)*		
Eggs		7.80			41.68		
	failed to hatch		0.91	11.7		2.79	6.7
	parasitism		0.23	2.9		3.08	7.4
	unknown		5.08	65.1		26.20	62.9
L2–3		1.58			9.61		
	parasitism		0.09	6.0		0.89	9.3
	unknown		1.15	72.5		3.05	31.7
L4–6		0.34			5.67		
	parasitism		0.18	54.1		0.73	12.9
	total mortality			98.0			88.2

* X, stage; dxF, mortality factor; Lx, graphical estimate of recruitment (per plant) into the stage (recruitment of eggs is corrected for sampling errors [see text]); dx, number dying during the stage; 100 Qx, percentage mortality during the stage.

Table 5.3 shows the partial life table on sunflower during four seasons. In the first season, the recruitment of eggs was 30 eggs per plant, but only 0.28 of these entered the L4-6 stage. Mortality was 91.7 % during the young stages (from egg to L2-3), and almost as high during the older developmental stages (from L2-3 to L4-6). Parasitism contributed little to mortality; only the parasitism level of older instars was moderate. By far the greater part of the mortality was due to unknown factors, which included predation. During the second season, egg recruitment was lower, but these eggs gave rise to a considerable number of larvae. Total survival was 13 times higher than in the preceding season.

Table 5.4 Partial life tables for *H. armigera* on maize, Kakamega.

X	dxF	Lx	dx	100 Qx	Lx	dx	100 Qx*
		season 1 (short rains 1988/89)			*season 2 (long rains 1989)*		
Eggs		11.56			10.41		
	failed to hatch		0.00	0.0		0.78	7.5
	parasitism		0.00	0.0		1.32	12.7
	unknown		11.18	96.7		6.76	65.0
L2–3		0.38			1.55		
	parasitism		0.00	0.0		0.17	11.0
	unknown		0.21	56.4		1.00	64.9
L4–6		0.16			0.37		
	parasitism		0.00	0.0		0.00	0.0
	total mortality			98.6			96.4
		season 3 (short rains 1989/90)			*season 4 (long rains 1990)*		
Eggs		0.00			24.46		
	failed to hatch					0.22	0.9
	parasitism					5.31	21.7
	unknown					18.48	75.5
L2–3		0.00			0.46		
	parasitism					0.07	15.1
	unknown					−0.14	−30.4
L4–6		0.00			0.53		
	parasitism					0.00	0.0
	total mortality						97.9

* X, stage; dxF, mortality factor; Lx, graphical estimate of recruitment (per plant) into the stage (recruitment of eggs is corrected for sampling errors [see text]); dx, number dying during the stage; 100 Qx, percentage mortality during the stage.

Oviposition was low during the third season, but mortality was considerable, although not as high as during the first season. During the fourth season, a combination of a relatively high oviposition rate and a relatively low mortality resulted in large numbers of larvae which caused considerable damage to the crop. An average of 41.7 eggs was laid per plant, and of these, 9.6 and 5.7 reached the L2-3 and L4-6 stages, respectively. Mortality occurred predominantly during the young stages.

Table 5.5 Partial life tables for *H. armigera* on sorghum, Kakamega.

X	dxF	Lx	dx	100 Qx	Lx	dx	100 Qx*
		season 1 (short rains 1988/89)			*season 2 (long rains 1989)*		
Eggs		25.73			4.86		
	failed to hatch		0.00	0.0		0.00	0.0
	parasitism		2.42	9.4		0.00	0.0
	unknown		22.89	89.0		0.01	0.2
L2–3		0.42			4.85		
	parasitism		0.00	0.0		0.99	20.4
	unknown		0.24	55.4		2.98	61.5
L4–6		0.19			0.88		
	parasitism		0.00	0.0		0.01	1.2
	total mortality			99.3			82.1
		season 3 (short rains 1989/90)			*season 4 (long rains 1990)*		
Eggs		0.00			23.68		
	failed to hatch					1.18	5.0
	parasitism					3.72	15.7
	unknown					16.08	67.9
L2-3		0.00			2.69		
	parasitism					0.08	2.9
	unknown					1.74	64.7
L4–6		0.00			0.87		
	parasitism					0.14	16.1
	total mortality						96.9

* X, stage; dxF, mortality factor; Lx, graphical estimate of recruitment (per plant) into the stage (recruitment of eggs is corrected for sampling errors [see text]); dx, number dying during the stage; 100 Qx, percentage mortality during the stage.

In general, mortality in sunflower was mainly attributable to "unknown" factors. Parasitism, pathogens and failure to hatch accounted for little of the egg mortality.

Egg parasitism over the generation, due to *Telenomus ullyetti* and a complex of trichogrammatids, was at most 12%. Parasitism and pathogens of young larvae were both rare, although Nyambo (1990) found both common in western Tanzania. Parasitism of older larvae due to a tachinid, *Linnaemya longirostris*, was higher (Table 5.1), but this impact would not have important implications for control during that season because parasitized larvae are killed in the sixth instar

or pupa stage, after damage has occurred. Parasitism by *L. longirostris* was highest during the third season, when *H. armigera* levels were very low and this suggests that the parasitoid moved from another host to *H. armigera*. Total mortality was considerably higher during both short rainy seasons (98.0-99.3%) than during the long rainy seasons (88.2-90.6%).

Table 5.4 shows the partial life table for maize. Every season, the egg recruitment was lower on maize than on sunflower, and during the third season no eggs were found at all. Mortality on maize was very high, and occurred mainly during the young developmental stages (from egg to L2-3). In the last season, a negative mortality was recorded for the older developmental stages, because the recruitment estimate of L4-6 was slightly higher than that of L2-3. Recruitment of young larvae is likely to be underestimated relative to that of older larvae; since both were very low, the difference is not significant. Egg parasitism, due to *Trichogrammatoidea* spp., was 22% during the fourth season. Generational parasitism of young larvae was up to 15%, mainly due to *Dolichogenidea* (*Apanteles*) sp. (Hymenoptera: Braconidae). Older larvae were not parasitized at all.

On sorghum, mortality was very high during the first season (Table 5.5), especially for the young stages; egg recruitment was 25.7 per plant, but less than 1% of these reached the L4-6 stage. The second season showed a totally different picture; few eggs were laid and mortality of young stages was nil (even slightly negative in our sample), but mortality of older stages was over 80%.

It should be noted that *H. armigera* eggs laid on sorghum are hidden within the complex structure of the panicle, and are thus more difficult to find than on sunflower and maize, where the majority of eggs are laid on simpler structures (Chapter 6). Therefore, egg recruitment and mortality on sorghum may be underestimated in this study. As on maize, no eggs were deposited during the third season. During the fourth season, egg recruitment was similar to that in the first season, and total mortality was almost 97%. Percentage parasitism of *H. armigera* generations on sorghum was low to moderate. Egg parasitism was 0-16%. Parasitism of young larvae, due to *Dolichogenidea* sp., *Meteorus laphygmarum* Brues (Hymenoptera: Braconidae), and *Charops ater* Szepligeti (Hymenoptera: Ichneumonidae) was highest during the second season (20%). Mortality of older larvae, due to *L. longirostris*, was up to 16%.

For comparison with the graphical method, alternative calculations were made of larval recruitment, to allow for mortality during an age group. Assuming that the mortality rate during the age group is constant, recruitment N_S' is estimated as

$$N_S' = N_S \ln(S)/(S-1),$$

where N_S is the graphical estimate of recruitment and S is survival (van Driesche *et al.* 1989).

Table 5.6 Recruitment estimates averaged over four sampled seasons, and percentage mortality. Kakamega, 1988-90.

X	SUNFLOWER Lx	SUNFLOWER 100 Qx	MAIZE Lx	MAIZE 100 Qx	SORGHUM Lx	SORGHUM 100 Qx
Egg	24.57	79.1	15.48	94.9	18.09	85.3
L2-3	5.14	61.0	0.79	55.3	2.66	75.6
L4-6	2.00		0.35		0.65	
total mortality		91.8		97.7		96.4

Table 5.7 Average density (P) of predators during the sample seasons, and the degree of predator pressure (Z), on *H. armigera* eggs and larvae, as a measure of temporal overlap between predator and prey.

Season	predator	SUNFLOWER P	SUNFLOWER Zegg	SUNFLOWER Zl2-3	MAIZE P	MAIZE Zegg	MAIZE Zl2-3	SORGHUM P	SORGHUM Zegg	SORGHUM Zl2-3
1	Anthocorid nymphs	2.45	1.20		1.82	0.77		2.19	0.72	
	Anthocorid adults	4.83	0.93		2.02	0.72		2.39	1.22	
	Myrmicaria sp. *	0.77	0.55	0.63	0.67	0.30	0.35	0.11	0.04	0.03
2	Anthocorid nymphs	0.60	0.10		0.07	0.00		0.30	0.05	
	Anthocorid adults	0.76	0.15		0.04	0.03		0.38	0.03	
	Pheidole sp.	1.92	0.47	0.40	1.39	0.40	0.50	0.76	0.15	0.42
3	Anthocorid nymphs	0.54	0.78							
	Anthocorid adults	2.01	0.31							
	Pheidole sp.	0.94	0.59	0.58						
4	Anthocorid nymphs	0.42	0.13		0.10	0.01		0.56	0.03	
	Anthocorid adults	0.85	0.11		0.08	0.02		0.14	0.09	
	Pheidole sp.	0.96	0.28	0.52	1.97	0.53	0.48	0.57	0.18	0.23

* Myrmicaria sp. (present in season 1 only) also attacks older H. armigera larvae; Zl4-6 for Myrmicaria sp. was 0.47, 0.35, and 0.05, on sunflower, maize, and sorghum, respectively.

Using our data, this method gives a lower estimate of the mortality between eggs and L2-3 instars, and usually a higher estimate of the mortality between L2-3 and L4-6 instars than the original graphical method. However, this alternative method only improves recruitment estimates if mortality rates are similar between the age groups - which does not apply to our data.

On sunflower, mortality was higher during the short rainy seasons than during the long rainy seasons, both for young and older stages of *H. armigera*. For maize and sorghum, data are available for only one short rainy season; but again, mortality during the short rains was higher than during the long rainy seasons, especially of the younger stages.

Table 5.6 summarizes the life tables of sunflower, maize and sorghum, and shows that mortality is considerably higher on maize, where only 2.3% of the eggs reached the L4-6 stage, than on sunflower, where 8.2% of the eggs reach the L4-6 stage. In general, mortality is higher during the young stages than during the older stages. This is most extreme in maize, where only 5.1% of the young stages survive whereas more than 45% of the older stages survive. Mortality of older stages is highest in sorghum.

Table 5.7 presents the predator pressure of two dominant predator groups, anthocorids and ants, on *H. armigera* eggs and larvae on sunflower, maize and sorghum. The temporal overlap of anthocorids with eggs was generally low, because anthocorid levels usually reached their peak after the main oviposition peak of *H. armigera*. The predator pressure on the eggs was highest during the first season, when anthocorid densities were high, but was much lower during the second and fourth seasons. Anthocorids were frequently observed feeding on *H. armigera* eggs, but were not seen feeding on young larvae. In the laboratory, anthocorid adults were able to feed on young larvae, but we assume that they consume more eggs than larvae.

During the first season, *Myrmicaria* sp. was the most common ant, but after moving the experiment to another plot, *Pheidole* sp. was dominant. The predator pressure of *Myrmicaria* sp. on *H. armigera* larvae was considerable on sunflower and, to a lesser extend on maize, but was very low on sorghum. The predator pressure of *Pheidole* sp. was more or less similar on sunflower and maize, but was lower on sorghum, both because the densities were lower on sorghum, and because *Pheidole* sp. appeared later in the season than eggs.

Discussion

Mortality due to natural enemies

In previous studies on the natural mortality of *H. armigera* in Africa, parasitoids have received much attention (Parsons 1940a, Coaker 1959, Reed 1965, Nyambo 1990). The present study shows that the role of parasitism in Kenya is small, and that mortality of *H. armigera* is mainly attributable to other, unknown, factors. The mortality due to unknown factors (or 'unknown mortality') can be very

different from season to season. Mortality of *H. armigera* was greater during the short rains than during the long rains. This could be attributed to the effect of drought on host plant quality (rainfall was considerably lower during the short rains), due to the direct effect of climate on *H. armigera*, or due to the level of predation, as anthocorids were more abundant during the short rains.

The level of 'unknown mortality' of young stages (see Tables 5.3-5.5) appeared to be linked to the predator pressure of anthocorids (Table 5.7), even though other mortality, irrespective of the presence of anthocorids, was generally high. On sunflower, 'unknown mortality' of young stages was highest during the first season (79%), when the predator pressure of anthocorids was relatively high, but was less during the second season (55%) when anthocorid levels were low. In the third season when the predator pressure of anthocorids was moderately high, the 'unknown mortality' of young stages was 64%, but in the fourth season, it was 62%, while predator pressure was rather low.

Also on maize, highest mortality of young stages occurred during the first season, when anthocorids were most abundant. However, mortality of young stages due to unknown factors was considerably higher on maize than on sunflower, indicating that mortality factors other than predation by anthocorids had more impact on young stages on maize than on sunflower. On sorghum, the mortality of young stages was highest during the first season, when predator pressure of anthocorids was highest; and mortality was lowest during the second season, when anthocorids were almost absent. As discussed earlier, the high level of egg survival in the second season suggests that eggs on sorghum may still be undersampled, despite the correction made.

In the first season, *Myrmicaria* sp. was frequently seen attacking older larvae on sunflower, and this ant could be responsible for the high mortality level of older larvae during that time. The predator pressure of *Myrmicaria* sp. was higher on sunflower than on maize or sorghum, which might explain the lower mortality level of older larvae on the last two crops. The mortality of older stages was never as high in the following seasons, when *Myrmicaria* sp. was absent.

Because the levels of *Pheidole* sp. on sunflower and maize were similar from one season to the next (excluding the first season, when *Myrmicaria* sp. was the dominant ant species), it is difficult to evaluate its role. An exclusion study demonstrated that *Pheidole* sp., occurring at a level of 25 ants per plant (see Chapter 9), was responsible for a reduction in *H. armigera* levels on sunflower of 85%, but in the present study with levels of 1-2 ants per plant, *Pheidole* sp. probably contributed little to the "unknown mortality" in the life tables.

Although the data suggest a relationship between the levels of certain predators and mortality of *H. armigera* stages, it remains difficult to determine their role from density samples, because their impact may be obscured by other mortality factors acting on *H. armigera* populations. Evaluation of the impact of these predator groups was studied separately (Chapter 8-11).

Population dynamics of H. armigera

Diversification of agroecosystems often reduces pest infestation (Andow 1991), but studies suggest that highly polyphagous Heliothinae are more abundant in diverse habitats, where attractive hosts occur in a sequence and provide a continued food supply for pest generations (Fitt 1989). In our study, *H. armigera* moths were present in the field for a prolonged period, as shown in Fig. 5.4, but would oviposit during the brief flowering period of a crop. Light- and pheromone-trap catches were low throughout the four seasons, without peak catches. This suggests that infestation is caused by a local population, although low level immigration from other sources cannot be ruled out. After the favoured crop stage for oviposition, moths shift to weeds and other food plants (Nyambo 1988, Greathead & Girling 1989).

Further studies could examine whether *H. armigera* infestation on a combination of crops is lower when those crops flower simultaneously than when they flower sequentially. In the first case, *H. armigera* is attracted during a short time, whereas in the second case, moths can oviposit during an extended period and total recruitment of eggs into a field may be higher. However, prior adult experience of host plant availability (Zalucki *et al.* 1986, Firempong & Zalucki 1990) and the ability of ovipositing moths to switch to other hosts (Papaj & Prokopy 1989) may have implications for utilization of host plants by the herbivore, although the significance of switching is limited by the short oviposition period (< 8 d) of *H. armigera* (Topper 1987).

Two factors may be responsible for the high mortality of young stages on maize. Firstly, eggs were laid predominantly on the smooth upper surface of the leaf blade, whence they are easily dislodged by rain and wind; only few eggs were laid on other plant parts (Chapter 6). Nuessly *et al.* (1991) showed that dislodgement of eggs of *Helicoverpa zea* on cotton due to rain or wind was highest on the leaf upperside. Secondly, newly eclosed larvae have to move over a considerable distance in order to reach their feeding sites, the soft plant structures of the silks and tassels; very few young larvae feed on the leaves (Chapter 6). In comparison to sunflower and sorghum, where eggs are deposited on or near the larval feeding, *H. armigera* neonates on maize can be expected to suffer higher mortality while searching for feeding sites.

Implications for integrated pest management

H. armigera was more common on sunflower than on maize and sorghum, because the recruitment was highest and mortality was lowest on this crop. *H. armigera* often could not complete its development on sunflower; many larvae were found at harvest. Here, 'host evasion' by early crop maturity (Painter 1951) could further reduce damage caused by *H. armigera*. Fast-maturing sunflower varieties can be harvested about two weeks earlier than variety Comet used in the

present study, which is probably before the peak level of L4-6 instars, the most damaging stage, is reached.

Earlier studies in eastern and southern Africa have suggested the use of maize as a trap crop. Ovipositional preference of *H. armigera* for maize resulted in reduced infestation on cotton plots if bordered or interplanted with maize, as reported by Parsons (1940b) and Rens (1977), but Coaker (1959) found maize and cotton equally attractive to *H. armigera* moths. Of several crops tested in Ethiopia, maize was the most suitable trap crop for haricot beans (*Phaseolus vulgaris*), even though other potential trap crops contained higher *H. armigera* populations (Abate 1988). In our study, oviposition was greater on sunflower and sorghum than on maize, and in a parallel study in Central Kenya, oviposition was greater on cotton than on maize and sorghum (Cock *et al.* 1991). This implies that the use of maize as a trap crop would have limited potential in western Kenya. Nevertheless, the mortality of *H. armigera* on maize was extremely high, and maize could therefore act as a sink for *H. armigera*. Besides, oviposition on maize may strongly depend on local conditions or on the variety used. For instance, at sites east of Kenya's Rift Valley, where different maize varieties were used, ovipositing moths preferred maize to cotton, sunflower and sorghum (Chapter 4). Further studies may be desirable, particularly on intercropping maize varieties with cotton, the crop subject to most economic damage by *H. armigera*.

In this study parasitoids seemed to be associated with some crops more than others. Parasitism by *Linnaemya longirostris* was considerably higher on sunflower than on maize or sorghum. *Dolichogenidea* sp. was common on maize, and to a lesser extent on sorghum, but was not found on sunflower. Similar associations between parasitoids and crops have been reported for *H. armigera* parasitoids from western Tanzania (Chapter 7), and may have important implications for the control of *H. armigera* where parasitism levels are high. In general however, parasitism was low, especially of eggs and young larvae. In other regions, parasitoids of young larvae, such as *Campoletis chlorideae* Uchida, *Glabromicroplitis croceipes* (Cresson), *Hyposoter didymator* (Thunberg) and *Cotesia kazak* Telenga, often have a considerable impact on *H. armigera* or related Heliothinae (King *et al.* 1985, Carl 1989, Mohyuddin 1989). Their introduction into East Africa might improve the overall level (and the reliability) of biological control, although, at low infestation and high mortality levels of *H. armigera* as shown in the present study, this may not be worthwhile.

On sunflower, anthocorid numbers built up to levels as high as four adults and 14 nymphs per plant, but these peak levels usually occurred just after the main oviposition peak of *H. armigera*; on young plants, *H. armigera* eggs would escape predation by anthocorids, because anthocorids built up only after plants started to flower. On the other hand, the functional response of anthocorids to eggs could be greater on buds than on flower heads, because of greater searching area and more alternative food (thrips, nectar and pollen) on the latter.

The impact of anthocorids on *H. armigera* eggs (or, their 'predator pressure' on eggs) would increase if they occurred earlier in the season. Measures that

encourage colonization and population build-up of natural enemies in smallholder crops early in the season could involve mixed planting with particular weeds or fast-maturing crops that provide alternative food and attract natural enemies during the critical period, but that do not attract *H. armigera*. Clearly, application of chemical insecticides early in the season would disrupt natural enemy build-up, and may have important consequences for natural control thereafter.

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6

Spatial association between *H. armigera* and its predators[1]

ABSTRACT - (1) The between-plant and within-plant distributions of *H. armigera* eggs and larvae are presented on four crops commonly grown in small-scale agriculture in Kenya: sunflower, maize, sorghum and cotton. The association of *H. armigera* with its predominant predators, anthocorids and ants, was analysed both within plants and between plants.
(2) The distribution of *H. armigera* eggs between plants was slightly aggregated, but the degree of aggregation tended to decline as *H. armigera* larvae matured.
(3) The distribution of predators was more aggregated than for *H. armigera*. Generally, the number of predators per plant was not associated with the number of *H. armigera* per plant, but associations may have been obscured by the foraging strategy of ants. Only on sunflower were predatory ants associated with *H. armigera* larvae.
(4) Oviposition and larval feeding of *H. armigera* were concentrated on the flower head of sunflower and the panicle of sorghum. On maize and cotton, however, the majority of eggs were deposited away from the soft plant parts suitable for larval feeding. Implications for survival of hatchlings is discussed.
(5) Anthocorids were concentrated in the same types of microhabitat as *H. armigera* eggs on sorghum, but regression analysis showed that their association within plants was low, mainly because anthocorid populations increased after the *H. armigera* oviposition had peaked.
(6) Ants (*Pheidole* sp. and *Myrmicaria* sp. combined) were generally more closely associated with *H. armigera* stages within plants than were anthocorids.

Introduction

The African bollworm, *Helicoverpa armigera* (Hübner) (=*Heliothis armigera*) (Noctuidae) is a polyphagous pest, attacking several crops grown in East Africa (Nyambo 1988; Chapter 5). In smallholder farming, which is the prevalent form of agriculture in East Africa, various crops are grown adjacent to, or intercropped with, each other. In some of these crops, such as cotton and sunflower, *H. armigera* is a major pest, whereas in other crops, such as maize and sorghum, it is only of occasional importance.

Studies were carried out at two field sites, Kakamega and Kibos, in western Kenya. Life tables of *H. armigera* in Kenya on three different crops showed that

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the developmental stages of *H. armigera* suffered a high level of mortality, mostly due to unknown factors but including predation (Chapter 5). Both stage-specific mortality and the generational mortality differed between sunflower, maize and sorghum, and a relationship between stage-specific mortality and the density of certain predatory insects was indicated. Predators found on the crop were all generalist species, or specialized on prey other than *H. armigera*. Anthocoridae and ants (mainly *Pheidole* spp. and *Myrmicaria* sp.) were the two predominant predator groups in every crop. We have already reported (Chapter 4) on the overall levels of incidence of *H. armigera* and the dominant predator groups on smallholder crops in Kenya.

Because levels of *H. armigera* were consistently low during our studies (average numbers of eggs and larvae per plant varied from 0.05 to 0.9 over the season), and the levels of predators were higher (average seasonal levels of ants and anthocorids were 0.3 to 8 and 0 to 5 per plant, respectively) it is considered unlikely that eggs and larvae of *H. armigera* were the principal food of the polyphagous predators. However, these predators are likely to prey on *H. armigera* as and when they encounter them, and so their searching behaviour is important. Do they search the plant parts where and when *H. armigera* occur? If they don't, they are likely to have little impact on these low density populations of *H. armigera*. To understand the potential role of individual predator species, we studied the distribution of predators and *H. armigera* between and within plants, and their association with each other. As a next step, the impact of predation is measured (Chapter 8-11).

Two predator groups, anthocorids and ants, are considered in the present analysis. Anthocorid adults and nymphs have been observed as important predators of *H. armigera* eggs, and adults may also attack neonate noctuid larvae (Isenhour *et al.* 1990). Anthocorid species occurring at Kakamega were *Orius thripoborus*, *O. tantillus* (Motschulsky) and *O. albidipennis*, while at Kibos, *Cardiastethus exiguus*, *Cardiastethus* sp. and *Blaptostethus* sp. were found, in addition to the three *Orius* species mentioned above. Common ants at Kakamega were *Pheidole* sp. "2" and *Myrmicaria* sp.. At Kibos, *Myrmicaria opaciventris* Emery, *Camponotus flavomarginatus* Mayr, and *Pheidole* sp. "1" were the most common species (Chapter 4). Of these ants, the *Pheidole* spp. were observed dislodging and carrying off the eggs of *H. armigera* and *Myrmicaria* spp. were observed carrying *H. armigera* larvae.

Materials and Methods

The study was conducted at two KARI (Kenya Agricultural Research Institute) research centres, 50 km apart in western Kenya: the Regional Research Centre at Kakamega, Western Province, and at the Cotton Research Sub-Centre, at Kibos, Nyanza Province. Data were collected concurrently with the four seasons' life table studies reported earlier (Chapter 5), starting from the short rains of 1988/89

(October-February) and continuing until after the long rains (April-August) of 1990.

At Kakamega, plots of sunflower, maize and sorghum were grown in four replicates. Individual plot sizes were 19x20 m, 17x20 m, and 12x20 m, for sunflower, maize and sorghum, at plant spacings of 30x75 cm, 30x75 cm, and 10x50 cm, and varieties Comet, Hybrid 511 (short rains) / Hybrid 614 (long rains) and E525-HR, respectively. For analysis of associations, data of the third season (short rains 1989/90) were omitted because of low *H. armigera* densities.

A similar trial was set up at Kibos, but because of unreliable short rains, crops were grown only during the long rains. Cotton, maize and sorghum were grown in four replicates; plot sizes were 19x20 m, 17x20 m, and 12x20 m, at plant spacings of 30x90 cm, 30x75 cm, and 15x60 cm, of varieties BPA-75, Hybrid 511, and Serena, respectively. The present analysis only reports on the 1989 data from cotton, because *H. armigera* densities were very low on maize and sorghum in that season, and on all three crops in the 1990 long rains.

Sampling methods

Thirty randomly selected plants were sampled weekly from each crop and site. Plant were divided into a top, middle and bottom sections, based on leaf numbers, and all parts were thoroughly checked and dissected when necessary. Numbers of all relevant arthropods were recorded per plant part. *H. armigera* eggs were distinguished from other noctuid eggs, mainly *Plusia* spp. (van den Berg & Cock 1993), using a hand-lens. The average time spent sampling per plant was approximately 20 minutes. Sampling started from the vegetative stage of the crops, and continued until harvest; i.e., a period of 11 weeks for sunflower, 11-14 weeks for maize, 10-11 weeks for sorghum, and 13-15 weeks for cotton. Sampling was conducted during the morning hours, from Monday to Friday. This assumes that the densities and positions of the arthropods on plants do not change during the day (or night), which may be realistic for *H. armigera* and anthocorids, although ants are very likely to show diel foraging. Samples, however, would give a relative indication of ant distribution and abundance. Pitfall trapping data, set up inside the plots throughout the study, indicated that species other than the ones sampled in the day-time (i.e., possible nocturnal species) were not common (van den Berg & Cock, unpublished data).

Distribution between plants

To describe the degree of spatial aggregation of organisms, a number of indices are available that relate the sample variance (s^2) to the sample mean (m) (Southwood 1978). Of these, we chose Taylor's (1961) power law, $s^2 = am^b$, which provides a robust relationship between variance and mean for a wide range of organisms (e.g., Taylor *et al.* 1980). Taylor's power law is computationally

convenient because its parameters a and b are readily estimated by linear regression of $\log(s^2)$ on $\log(m)$. A combination of the parameters a and b (the intercept and slope, respectively) provides a measure of the degree of aggregation (if $b=1$ and $a=0$, random; if $b>1$ and $a>0$, aggregation; if $b<1$ and $a<0$, regular). Parameter b is claimed to be a species-specific characteristic which is not affected by the environment (Taylor 1984), while parameter a is affected by sampling procedures and environmental conditions (Taylor *et al.* 1980).

This relationship appears to be consistent over changing density conditions (Taylor 1984), and has been applied to data combined from several sampling occasions during a season combined (Hudon & LeRoux 1986, Fitt *et al.* 1989, Coll & Bottrell 1991, Boavida *et al.* 1992). Mean-variance pairs of sampling occasions are thus combined into one regression, with the assumption that parameters a and b remain constant during the season. We used the mean-variance pair of 30 sampled plants of one occasion (1 week) as one data point for the regression, and combined data points of all occasions and seasons into one regression.

To test whether parameters a and b are constant, or whether they depend on the time of the season, data were divided into two groups: early season and late season (for sunflower, three groups: early, middle and late season). Analysis of covariance was used to examine whether fitting different intercepts a or slopes b for different times of the season significantly improved the regression (Sokal & Rohlf 1981).

For measurement of association between predator and prey on plants, density data (numbers per plant) were combined over three seasons. With 30 plants sampled per week, and 10-15 weeks per season, the total number of plants was 1182 for sunflower, 1187 for maize, and 1115 for sorghum. Cotton was left out of the analysis, because limited data were available.

Multiple regression was used to determine whether a significant amount of deviance in *H. armigera* numbers was explained by the occurrence of predators, using the GLIM package (McCullagh & Nelder 1989, Aitkin *et al.* 1990). GLIM uses maximum likelihood techniques to fit models to data. A measure of goodness of fit is provided by the deviance - the equivalent of variance in traditional least square regression and ANOVA models. We divided the sampling season into periods in order to reduce category levels: early, middle and late season. Hence, the saturated regression model consisted of the category variables season, period, their interaction, and replicate, and the non-category variables anthocorids and ants. For computational reasons, we assumed a normal, instead of Poisson, error distribution, and used the square-root transformation in those cases where the mean was less than one.

Distribution within plants

In order to evaluate to what degree predator and prey occupy the same microhabitat types, we divided sunflower, maize and sorghum into 12, 15 and 14

microhabitats or plant parts respectively (details on plant parts are presented below), and developed the following descriptive statistic which shows how the within-plant distribution of predators overlaps with that of its prey:

$$y = 1 - \tfrac{1}{2} \sum_{i=0}^{I} \sqrt{(p_i - q_i)^2}$$

where y ($0 \leq y \leq 1$) is coefficient of coincidence, p_i is the relative occurrence of *H. armigera* on plant part i, and q_i the relative occurrence of the predator on plant part i. If $y=0$, none of the *H. armigera* and predators occupy the same type of microhabitat, i.e., their relative distributions over the microhabitats of a plant do not overlap each other; if $y=1$, *H. armigera* and its predators have the same relative distribution pattern within the plant. Data were pooled over weeks and seasons.

Apart from the question of whether predator and prey occupy the same types of microhabitat, we were interested in whether they are found together in microhabitats at the same time; i.e., do predator numbers explain a significant amount of the variance in pest numbers? Factors in the data-set were plant parts (12-15 levels, see above), 10-15 weeks (10-15 levels), and seasons (3 levels). For computational reasons, we pooled the data per week (i.e., 30 plants at a particular occasion was considered one sample). Hence, the number of data units for sunflower, maize and sorghum was 396, 495 and 462, respectively.

We used multiple regression with Poisson error distribution (log-link) to explain sources of variance (McCullagh & Nelder 1989, Aitkin *et al.* 1990). In the saturated regression model we fitted the category variables season, period, their interaction, plant part, and the plant part x period interaction, and the non-category variables anthocorids and ants. Again, we used periods (three levels: early, middle and late season), instead of weeks, to minimize the number of categorial levels. The explanatory power of a variable is roughly estimated by the percentage of the total deviance that is attributable to that variable in the saturated model. Variables were dropped from the model if they did not explain a significant amount of deviance ($P < 0.05$, X^2-test).

Results

Distribution between plants

The parameter estimates of the $\log(s^2)$ x $\log(m)$ regressions, presented in Tables 6.1 and 6.2, describe the spatial distribution pattern of prey stages and predators between plants on four crops. The r^2 of the regressions were always high (82-98 %). Even though *H. armigera* moths deposit their eggs singly on plants, the distribution of eggs is significantly different from random on most crops ($P < 0.05$, t-test), although the degree of aggregation is low (slope b is only

Table 6.1 Parameter estimates of log(variance) x log(mean) regressions (Taylor's power law, 1961), to determine the spatial distribution of *H. armigera* stages and its predators on sunflower and maize. Significant differences within each crop are indicated by different letters ($P<0.05$, t-test).

		INTERCEPT			SLOPE			
Crop	Stage/species	mean	s.e.		mean	s.e.	*	n**
SUNFLOWER	Eggs	0.31	0.03	b	1.23	0.04	c	49
	L1-3	0.13	0.02	a	1.11	0.03	bc	61
	L4-6	0.14	0.02	a	1.09	0.03	b	51
	Pheidole sp.	0.85	0.05	d	1.63	0.10	d	44
	Anthocorid nymphs	0.53	0.04	c	1.39	0.05	cd	57
	Anthocorid adults	0.50	0.04	c	1.43	0.05	d	61
MAIZE	Eggs	0.33	0.05	abc	1.21	0.06	b	18
	L1-3	0.17	0.04	ab	1.12	0.03	b	21
	L4-6	0.09	0.07	a	1.06	0.07	ab	20
	Pheidole sp.	0.87	0.04	d	1.58	0.09	c	26
	Anthocorid nymphs	0.39	0.04	c	1.26	0.05	b	23
	Anthocorid adults	0.36	0.05	bc	1.22	0.06	b	30

* "a" indicates that the slope is not significantly different from 1
** Number of mean-variance pairs in the linear regression, with each pair representing 30 plants sampled

slightly greater than 1; $a \geq 0$). The degree of aggregation appears to decline from L1-3 to L4-6 instars, but was significant only on sunflower. On cotton, *H. armigera* larvae were slightly aggregated, while the distribution of eggs was not significantly different from random.

Aggregation of anthocorids is also slightly different from random on all crops studied, and on sunflower anthocorid adults were significantly more aggregated than the eggs of *H. armigera*. Moreover, ants are significantly more aggregated than *H. armigera* stages on sunflower, maize and sorghum. *Myrmicaria* sp. and *Pheidole* sp. ants were often seen tending *Rhopalosiphum maidis* (Fitch), a common aphid on maize and sorghum, which showed a high degree of aggregation similar to that of *Pheidole* ants.

To test whether parameters *a* and *b* are influenced by the time of the season, we conducted analysis of covariance on *H. armigera* stages and predators for all crops. By fitting a single slope, total deviance was reduced by more than 90 %,

Table 6.2 Parameter estimates of log(variance) x log(mean) regressions (Taylor's power law, 1961), to determine the spatial distribution of *H. armigera* stages and its predators on sorghum and cotton. Significant differences within each crop are indicated by different letters ($P<0.05$, t-test).

		INTERCEPT			SLOPE			
Crop	Stage/species	mean	s.e.		mean	s.e.	*	n**
SORGHUM	Eggs	0.48	0.08	bc	1.32	0.08	bc	21
	L1-3	0.31	0.06	ab	1.20	0.05	bc	21
	L4-6	0.10	0.06	a	1.10	0.06	ab	19
	Pheidole sp.	1.08	0.07	d	1.75	0.12	d	20
	Anthocorid nymphs	0.69	0.06	c	1.40	0.07	cd	23
	Anthocorid adults	0.58	0.07	c	1.45	0.09	cd	24
COTTON	Eggs	0.18	0.08	a	1.06	0.10	ab	20
	L1-3	0.18	0.07	a	1.13	0.06	b	19
	L4-6	0.39	0.16	abc	1.31	0.13	b	13
	Myrmicaria sp.	0.49	0.08	abc	1.34	0.07	b	16
	Camponotus sp.	0.40	0.05	ab	1.17	0.13	ab	30
	Pheidole sp.	0.51	0.09	abc	1.24	0.16	ab	25
	Anthocorid nymphs	0.58	0.04	c	1.31	0.08	b	28
	Anthocorid adults	0.50	0.03	bc	1.37	0.07	b	29

* "a" indicates that the slope is not significantly different from 1
** Number of mean-variance pairs in the linear regression, with each pair representing 30 plants sampled

which indicates a strong linear relationship. Fitting different slopes for different times of the season did not significantly improve the fit in any instance. Furthermore, fitting different intercepts did not significantly reduce the deviance on sunflower, maize and cotton. However on sorghum, deviance of both larvae and ants declined significantly if different intercepts were fitted ($P<0.05$, F-test). In both cases the intercept was smaller in the second than in the first part of the season; with a constant slope, this implies that aggregation declined with time.

In addition to *H. armigera* stages and predators, a similar analysis was conducted for *R. maidis* aphids on maize and sorghum, which is an alternative food source for generalist predators. After fitting a single slope, about 20 % of the deviance in aphid numbers remained unexplained.

On sorghum, the remaining deviance significantly reduced when different slopes were fitted for different times of the season, whereas both on maize and sorghum, fitting different intercepts reduced deviance ($P<0.05$, F-test). On maize, the intercept was lower in the second part than in the first part of the season, but on sorghum the intercept was lower and the slope greater in the second part of the season.

Further, we analysed whether predators (ants and anthocorids) are associated with *H. armigera* prey on a per-plant basis on sunflower, maize and sorghum. Multiple linear regression, with eggs or larvae (all instars combined) as response variables for ants, and eggs as response variable for anthocorids, showed that the saturated model left much (56-94 %) of the deviance unaccounted for. No predator group explained a significant amount of deviance in egg numbers in the saturated model.

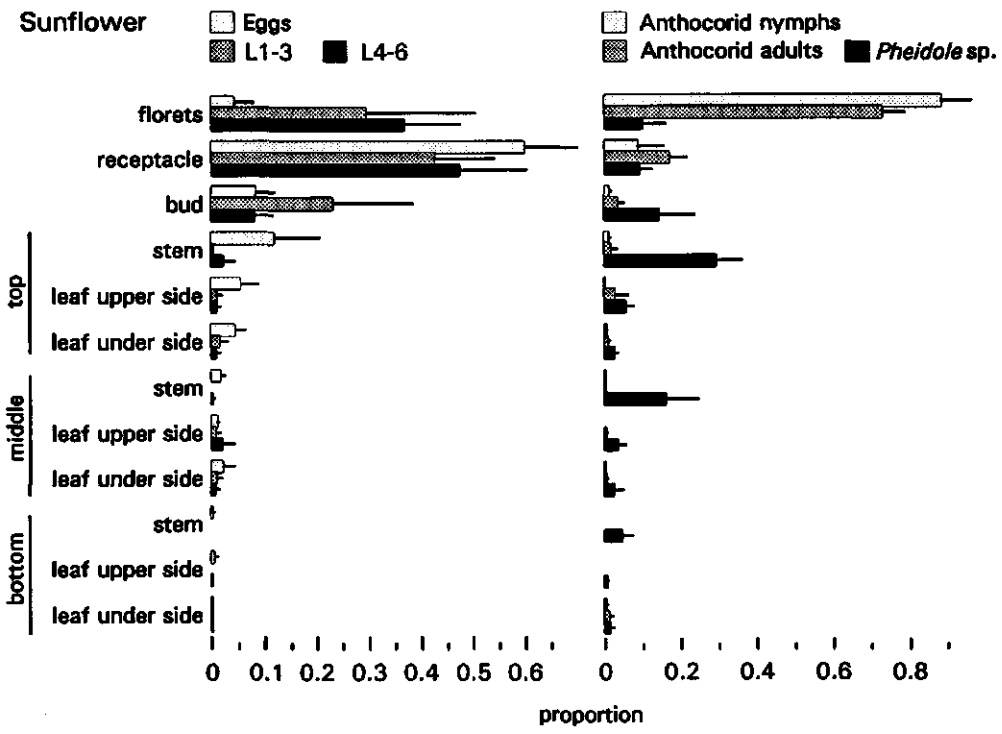

Fig. 6.1 Relative distribution of *H. armigera* stages and predators within plants of sunflower, expressed as the proportion of prey or predator group on each plant part. Data are four season's averages with standard deviations. Kakamega 1988-90.

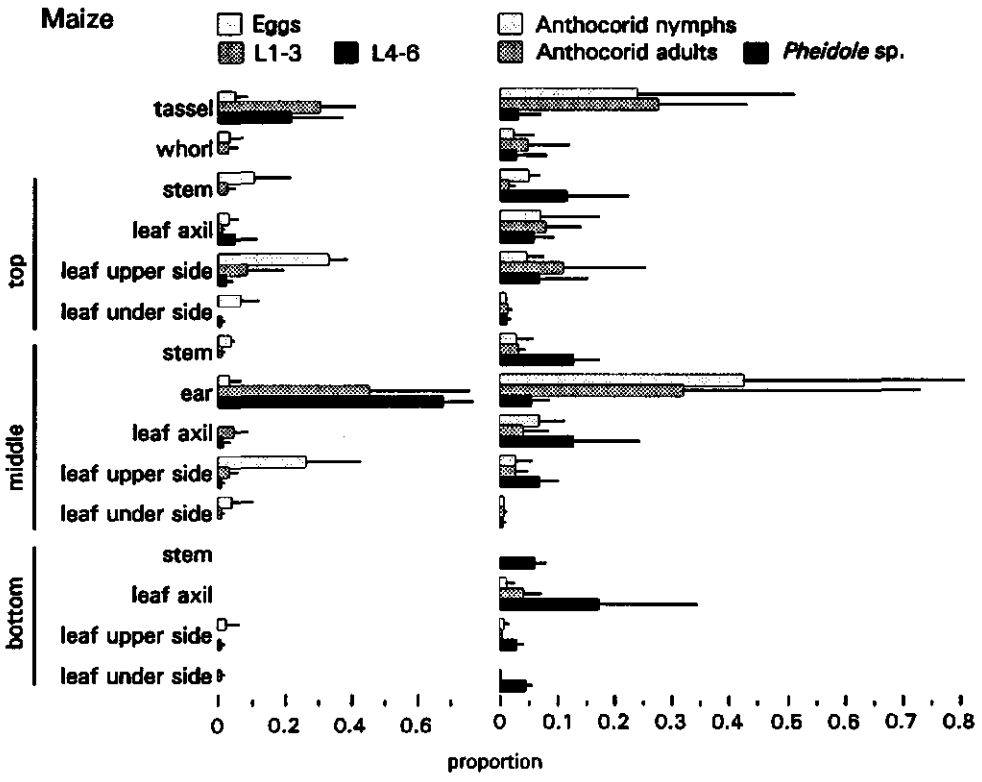

Fig. 6.2 Relative distribution of *H. armigera* stages and predators within plants of maize, expressed as the proportion of prey or predator group on each plant part. Data are three season's averages with standard deviations. Kakamega 1988-90

Moreover, ants did not explain any deviance in larval numbers, with the exception of sunflower, where ants accounted for a small (0.2 % of the total deviance), but significant ($P < 0.01$, F-test) amount of deviance.
On maize, ants explained a small (0.4% of the total deviance) but significant ($P < 0.05$, F-test) amount of deviance in *R. maidis* numbers per plant. Ants showed no significance in this respect on sorghum. As mentioned above, ants often tended the aphids on these two crops.

Distribution within plants

Figs. 6.1-6.4 show how the prey stages and predators are distributed over plant parts of sunflower, maize, sorghum and cotton.

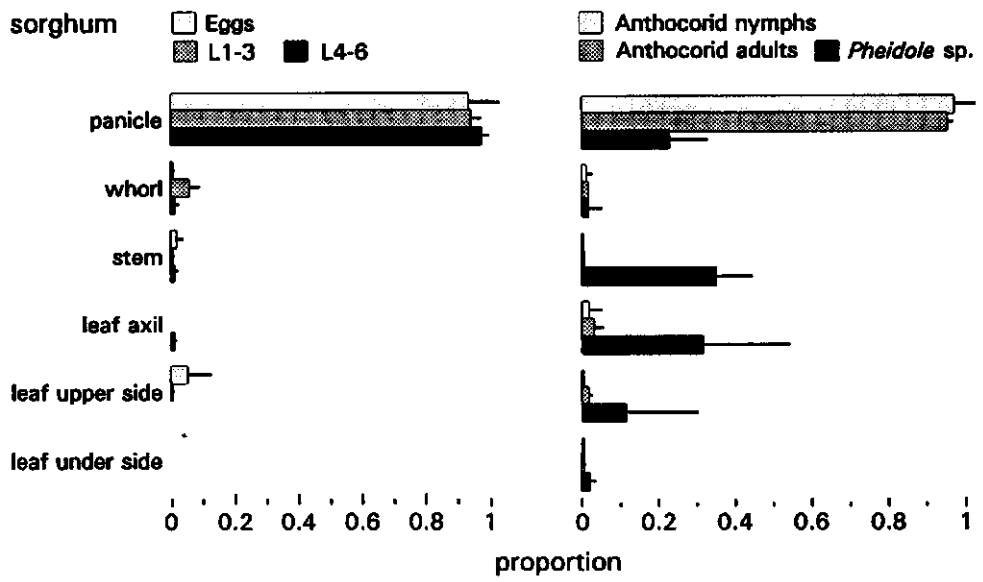

Fig. 6.3 Relative distribution of *H. armigera* stages and predators within plants of sorghum, expressed as the proportion of prey or predator group on each plant part. Data are three season's averages with standard deviations. Kakamega 1988-90

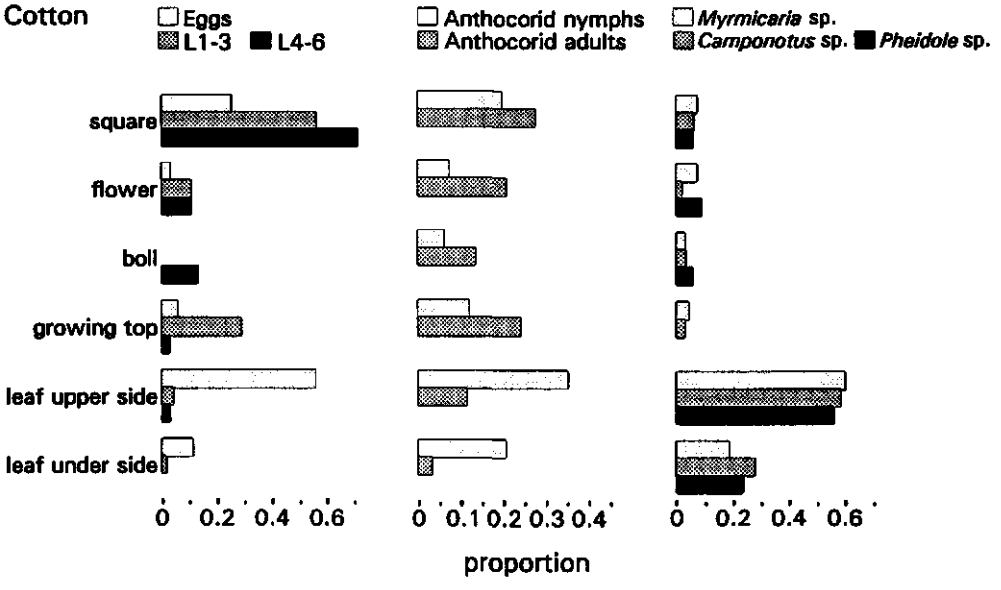

Fig. 6.4 Relative distribution of *H. armigera* stages and predators within plants of cotton, expressed as the proportion of prey or predator group on each plant part. Kibos 1989.

The data are averages of four seasons, with standard deviations between seasons, except for the data for cotton (at Kibos) which were based on one season.

On sunflower (Fig. 6.1), eggs are mainly found on the receptacle (the base of the flower head, including the bracts), some were found on the stem, bud, and the upper-side of leaves, but few in the florets. Larvae occupied the flower head, or, prior to flowering, the bud. Within the flower head, slightly more larvae were found on the receptacle, feeding inside the soft plant tissue, than in the florets. Anthocorids predominantly occupied the florets; only a small portion, and these were mostly adults, were found on the receptacle. Ants were rather evenly distributed over the different plant parts, but were more common in the upper section of the plant.

On maize (Fig. 6.2), eggs were deposited on all plant structures in the top and the middle sections of the plant, but mostly on the upper-side of leaves. Surprisingly few eggs were found on the tassel and on the ear (including the silks). Larvae, on the other hand, fed mostly in the ear (especially the silks) and the tassel. Anthocorids occupied tassels, silks and leaf axils. As on sunflower, ants were more evenly distributed over the plant. The distribution of anthocorids and ants varied considerably, as shown by the standard deviations between seasons. On sorghum (Fig. 6.3), *H. armigera* stages and anthocorids were strongly concentrated in the panicle. Ants were more evenly distributed over the other plant parts.

On cotton (Fig. 6.4), eggs were mostly deposited on the upper-side of leaves and on squares. Larvae were concentrated on the growing tip and on the squares. *H. armigera* larvae were found more on squares than on flowers or bolls, because *H. armigera* densities on cotton had decreased by the time bolls started to develop. Anthocorids occupied all plant parts, but the distribution pattern of nymphs and adults was slightly different. The three species of ants, which were common on cotton (*Pheidole* sp., *Myrmicaria* sp. and *Camponotus* sp.) were mostly found foraging on the leaves (including the stems).

Table 6.3 shows how the within-plant distributions of predators overlap with those of their prey. In general, the within-plant distribution of *Myrmicaria* sp. and *Pheidole* sp. ants overlapped reasonably with those of eggs and larvae of *H. armigera*, with some exceptions. On cotton, ants overlapped better with eggs than with larvae of *H. armigera*. On sorghum, *Myrmicaria* sp. overlapped little with *H. armigera* because the predator rarely visited the panicle. Anthocorids showed strong differences between crops; the overlap with eggs was small on sunflower and maize, but much larger on cotton and sorghum. On the last two, the overlap was more than 90 %, because both the prey and anthocorid predators occurred almost exclusively in the panicle.

The data were pooled over weeks and seasons, assuming that the distribution of prey and predators within plants do not change during the season or between seasons. However, changes e.g., due to changing crop phenology may be considerable. This is best illustrated in maize, where anthocorids occupied the leaves and whorl during the vegetative stage, but moved to tassels and leaf axils at pollen-shed, while during ripening most are found on the ear. Therefore, we

Table 6.3 Percentage overlap between the within-plants distributions of *H. armigera* stages and predators.

	SUNFLOWER		MAIZE		SORGHUM		COTTON	
Predator	Egg	L1-3	Egg	L1-3	Egg	L1-3	Egg	L1-3
Myrmicaria sp.	41	58	46	16	1	6	81	24
Pheidole sp.	34	32	30	27	25	24	75	20
Anthocorid nymphs	15	35	17	56	91	95	74	44
Anthocorid adults	25	46	27	59	93	94	48	67

used a regression model which included season and period as variables (see 'materials and methods'). In general, the model fitted the data well, leaving only 7 to 28 % of the total deviance unexplained. On sunflower, ants explained less than 3 % of the total deviance of *H. armigera* eggs, but this was highly significant (X^2-test). Ants explained 14 times as much deviance as anthocorid nymphs, the latter still being significant. With *H. armigera* larvae as response variable, ants explained 9 and 3 times as much deviance as anthocorid nymphs and adults, respectively.

On maize, 2 % of the total deviance in egg numbers was attributable to ants, four times more than for anthocorid nymphs (adults did not explain significant deviance). Anthocorids explained 1.5 % of the deviance in larval numbers, which is two times higher than for ants. Again on sorghum, ants explained 3 % of the total deviance of *H. armigera* eggs, and this was 5 and 19 times more deviance than for anthocorid nymphs and adults, respectively. Neither predator explained significant deviances of *H. armigera* larvae on sorghum.

The within-plant distribution of *H. armigera* and predators varied largely with the time of sampling, because of different stages of plant development. The occurrence of anthocorids in tassels and leaf axils, for instance, is clearly related to the provision of pollen in the tassel, that shed and accumulate in the leaf axils during tasselling of maize (Chapter 5). The period x plant part interaction unambiguously explained 7.3 and 3.2 % of the total deviance in numbers of eggs and larvae, respectively, on sunflower. On maize the interaction explained almost 5 % of the deviance in egg and larval numbers. On sorghum, the interaction was not significant (X^2).

Discussion

Distribution between plants

Although Taylor's power law has proved a useful tool with a strong descriptive ability, there has been much recent criticism on the interpretation of parameters *a* and *b*, which together determine the degree of aggregation. The parameters appear to have no clear biological meaning and may be influenced by various non-behavioural variables (Anderson *et al.* 1982, Downing 1986, Soberon & Loevinsohn 1987, Sawyer 1989, Yamamura 1990).

In our data, *a* and *b* were generally constant at different times of the season, but in a few cases *a*, and in one case *b*, was influenced by the time of the season. This implies on the one hand that the relationship is robust in most instances, and justifies its use for seasonal sampling data. On the other hand, our data support recent criticism that parameters *a* and *b* are not species-specific constants. Our data on sorghum suggest that the degree of aggregation of *H. armigera* larvae and ants declined as the season progressed. Density-dependent mortality factors could explain the declining aggregation of *H. armigera* larvae, as larval densities increased towards the end of the season, but the observed pattern for ants may have other causes.

Adult females often oviposit on flowering or pollen-shedding plants (Chapter 5). The distribution of eggs is likely to be slightly aggregated, because several plant stages are concurrent, and because the egg stage is short-lived (4-5 d). Larval stages, which are longer-lived, become more evenly distributed on plants. The declining degree of aggregation during the development from eggs to L4-6 may also be caused by dispersal of older larvae to neighbouring plants or density-dependent mortality of larvae (e.g., due to natural enemies or cannibalism).

The lack of association between predators and *H. armigera* prey on a per plant basis, would imply that numbers of predators per plant are not affected by the presence of *H. armigera* prey. Other food sources, such as plant pollen, nectar and aphids, may be more important in this respect. The only exception is sunflower, which had the highest larval numbers; here, ants were positively associated with larvae. Ants have been shown to be important predators on sunflower, capable of reducing natural *H. armigera* infestation by 85 % (Chapter 8).

The observed associations may be obscured if predators quickly consume their prey. Hence, an effective predator well associated with its prey may not appear associated because its prey has already been consumed. This may have obscured associations for ants, because of their foraging strategy is based on chemical communication and recruitment of workers to food sources. In our data, such biases only partly apply to eggs, because eggs are deposited at night and were sampled early in the morning, and only those newly laid were effectively recorded (see Chapter 5).

Distribution within plants

The selection of oviposition sites of *H. armigera* may be in response to various factors. Pubescent plant surfaces, for instance, are preferred over smooth surfaces for oviposition (Zalucki *et al.* 1986), and feeding on floral or extra-floral nectaries, required for egg production, may stimulate oviposition nearby. Moreover, oviposition near the favoured feeding sites of larvae may increase survival of neonates. On sunflower and sorghum, for instance, eggs are deposited at or near the fruiting parts. However on cotton, eggs are laid mainly on the leaves, whereas larvae feed on the fruiting parts and the terminal leaves. Likewise on maize, eggs are predominantly laid on the leaves, whereas larvae feed on the silks and tassel; this is supported by Parsons (1940) in South Africa who recorded only 4.1 % of the eggs of *H. armigera* from the cob and silks, and 78 % on the stem and leaves. Thus, hatchlings have to move over a considerable distance in order to reach soft plant parts for feeding, which may partly explain the extremely low establishment of young larvae on maize in comparison to sunflower (Chapter 5).

In this respect, the New World *Helicoverpa zea* (Boddie) may suffer lower mortality of hatchlings in search of feeding sites than *H. armigera*, because the former oviposits mainly on the reproductive parts of maize (e.g., Nishida & Napompeth 1974). *H. zea* has been reported to build up on early maize before it moves in increased numbers to other crops (Stinner *et al.* 1982). Even though it has been argued that a similar build-up of *H. armigera* on early-sown maize in Tanzania may be responsible for more frequent severe attacks on cotton (Reed 1965), there are no data to support this view, which may have been partly extrapolated from *H. zea*. Maize is highly attractive to ovipositing *H. armigera* moths (Parsons & Ullyett 1934, Reed 1965), but due to low survival rates of the pest, maize could act as a sink rather than a source of *H. armigera* populations (Chapter 5, Parsons & Ullyett 1934). This suggests the mechanism by which maize can be an effective trap crop for *H. armigera*.

If polyphagous pests, such as *H. armigera*, coexist with the same predator species in different crop ecosystems, the relationships between pest and predators are often different from one crop to the other, as indicated in this study. The measure of microhabitat-overlap, developed from pooled data, showed to what extent predator and prey occupy the same type of microhabitat. The pooled data suggested that ants greatly overlapped with *H. armigera* stages on most crops, but not on sorghum. Anthocorids showed greatest overlap with *H. armigera* eggs on sorghum and cotton. The multiple regression, which determined whether predator and prey are found together in microhabitats at the same time, revealed that generally ants were more closely associated with *H. armigera* stages than were anthocorids. Even on sorghum, where anthocorids showed a much larger overlap with eggs in the pooled data, ants were more closely associated with eggs than anthocorids. This is largely because most anthocorids were recorded just after the egg peaks, and were most common in seasons with low egg numbers.

Choice of microhabitat by predators may be affected by the presence of alternative food. For instance, anthocorids were predominantly found in plant parts where pollen was available. Ants were often seen feeding on plant exudates on the stem, leaf veins and flower head of sunflower, on leaves and fruiting parts on cotton, and on the stem of maize. Exudates may thus influence the within-plant distribution and plant visitation by ants (Bentley 1977). Likewise, the presence of aphids could influence the within-plant distribution of ants on maize and sorghum. Thus, additional regressions with the plant pollen, nectar or aphids as response variables might reveal the role of these alternative food sources (which were generally more abundant than *H. armigera* prey) in determining the within-plant distribution of predators, but this was beyond the scope of this study.

Besides the analysis of microhabitat-associations between predator and prey presented in this study, it is important to realize that chances of prey encounter and hence predation rates may vary between different microhabitats. On a large, complex plant part (e.g., panicle of sorghum) the chances of encounter are likely to be lower than on more simple plant parts (e.g., stem), and information on this aspect would help to interpret associations in terms of predation rates.

Implications for integrated pest management

The inter-plant and intra-plant distribution of pest and predators are fundamental to the design of sampling methods. As *H. armigera* tends to be more abundant on particular plant parts, which depend on the crop (e.g., 93, 80, 94 and 80 % of the larvae are commonly found on only the fruiting parts of sunflower, maize, sorghum and cotton) appropriate sampling units may be chosen to simplify monitoring of pest numbers. However, the standard deviations of Figs. 1-4 suggest that microhabitat-distribution patterns may vary substantially.

The distribution of small *H. armigera* larvae suggests that were insecticides to be applied for their control, they would be most effective if applied to the flowering parts of the crops where most larvae are found. However, this is also where most anthocorids are found so they would be adversely affected. Our observation that *H. armigera* is present on the flowering parts before anthocorid populations have built up may suggest that there is a 'window' when *H. armigera* could be sprayed with minimal effect on anthocorids, i.e., during flower formation before nectar and pollen are available to attract the anthocorids. However, spraying would discourage early build-up of anthocorids, and the exact way in which the spatial and temporal distribution of *H. armigera* and its predators affect the optimum insecticide application strategy can vary enormously, as indicated by standard deviations of Figs. 1-4 and the phenology patterns reported earlier (Chapter 5).

In several crops studied, anthocorids were probably more effective egg predators during the vegetative crop stage than during flowering. Firstly because microhabitats of anthocorids and *H. armigera* eggs overlap more during the vegetative stage of maize and sunflower (when both occur on leaves or buds) than

during tasselling or flowering (when eggs are found on leaves or receptacles, and anthocorids mostly inhabit tassels and florets). Secondly, as discussed above, the searching efficiency of predators is likely to be higher on vegetative plant structures than on complex flowering parts. For example in North America, Dicke & Jarvis (1962) observed *Orius insidiosus* (Say) (Hemiptera: Anthocoridae) feeding on eggs of *Ostrinia nubilalis* (Hübner) (Lepidoptera: Noctuidae) more often in vegetative maize than during pollen-shedding.

The densities of anthocorids, however, are usually low during the vegetative stages of crops, when most *H. armigera* eggs are deposited, and they colonize the field only during or after the main oviposition peak (Chapter 5), when plants start shedding pollen (Dicke & Jarvis 1962). If anthocorids could be attracted to the field earlier they would be more closely associated with *H. armigera* eggs and cause greater mortality. Inter-planting with weeds or fast-maturing crops may improve the attraction of anthocorids through the provision of alternative food, but requires further study. In this respect, Letourneau & Altieri (1983) demonstrated that anthocorids in North America colonized squash plants more rapidly and nymphal levels built up earlier, while the densities of thrips prey were lower, if squash was interplanted with maize and cowpea, than when grown in monoculture.

In conclusion, the important groups of generalist predators are associated in time and space with *H. armigera* stages, to a degree varying between crops and between seasons, and any control strategy should take this into account. We will evaluate the impact of these predator groups in subsequent publications.

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7

Analysis of parasitoid-crop associations[1]

ABSTRACT - Parasitism rates were analysed for *Helicoverpa armigera* feeding on four different crops in western Tanzania (1982-85), during a period in which all crops were inhabited by the herbivore. The major parasitoid species differed markedly in their crop associations, with *Palexorista laxa*, *Apanteles diparopsidis* and *Chelonus curvimaculatus* strongly associated with sorghum, *Cardiochiles* spp. mostly associated with cotton, and *Charops* sp. mostly associated with the weed-crop *Cleome* sp. For *P. laxa*, *Cardiochiles* spp. and *Charops* sp., the crop effect explained about 50 % of the variance in parasitism between crop, month and year. This was less for *A. diparopsidis* and *Chelonus curvimaculatus*, which were erratic in their occurrence from year to year. Implications of parasitoid-crop associations for biological control of *H. armigera* are discussed.

Introduction

The importance of host plants in the interaction between herbivorous insects and their insect parasitoids has received much recent attention (Price *et al.* 1980, Boethel & Eikenbary 1986). Preference for foraging on particular food plants of a polyphagous insect host is frequently found in parasitoids, and can be mediated by responses to stimuli produced by the host plant as well as response to plant-derived stimuli produced by the insect host, such as visual damage or kairomones (Vinson 1981). This has important implications for the use of parasitoids in the biological control of polyphagous insect pests attacking several agricultural crops.

In Africa, *Helicoverpa* (=*Heliothis*) *armigera* (Hübner) feeds on a range of crops, including cotton, tomato, pigeonpea, cowpea, sunflower, sorghum and maize. Parasitism has been reported as important in regulation of populations of *H. armigera* (Coaker 1959, Reed 1965), but data on generational mortality are lacking. A large parasitoid complex is known from this herbivore in Africa (Chapter 3), but surveys were focused mainly on cotton. Where other crops and wild plants have been included in surveys, parasitism seemed to be associated more with certain crops than with others (Taylor 1932, Parsons 1940, Coaker 1959, Roome 1975). Taylor (1932), for example, mentions that *Bracon brevicornis* Wesmael (Hymenoptera: Braconidae) parasitized *H. armigera* only on

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Antirrhinum sp. (Scrophulariaceae), and Parsons (1940) found the braconid *Cardiochiles nigricollis* more prevalent on cotton than other crops. However, because the crops attacked by *H. armigera* often occur in a sequence during the season, it is not clear whether these patterns of parasitism reflect crop preference of parasitoids or narrow periods of activity of parasitoids, during which only certain crops are present.

A recent study on larval parasitism of *H. armigera* on different crops has been made at Ukiriguru in the Mwanza region of western Tanzania (Nyambo 1990), where cotton, maize, sorghum, tomatoes, chickpeas and the native weed-crop *Cleome* sp. (Capparidaceae) are the main hosts of the pest. This paper reports an analysis of the use of *H. armigera* by parasitoids on cotton (*Gossypium* spp.), maize (*Zea mays* L.), sorghum (*Sorghum vulgare* Persoon) and *Cleome* sp., in the period 1982-1985. Only larval parasitoids were studied. Insect predators and egg parasitoids were not collected during the surveys. Although 11 parasitoid species were found on these crops, this analysis concentrates on six major species that accounted for 90 % of total parasitism: *Palexorista laxa* (Curran) (Diptera: Tachinidae), *Charops* sp. (Hymenoptera: Ichneumonidae), *Cardiochiles* spp. (Hymenoptera: Braconidae) (two species present), *Apanteles diparopsidis* Lyle *sensu lato* (Braconidae) and *Chelonus curvimaculatus* Cameron (Braconidae).

Material and Methods

The study area comprised farmers' fields at six villages within the Ukiriguru ward. On maize and sorghum, sampling began when 50 % of the plants had reached the flowering stage and continued until grains passed the dough stage. Maize tassels, silk and ears were examined; only the head was examined on sorghum. Cotton was examined from the first square stage until the crop was harvested, whereas *Cleome* sp. was sampled from the first leaf stage onwards. Whole plants of cotton and *Cleome* sp. were examined. In every site, the four crops were generally sampled in monoculture, but occasionally sorghum and maize were intercropped.

Larval densities of *H. armigera* were determined weekly by visual inspection of 10 randomly selected plants per crop per site. These and additional larvae, were taken to the laboratory where the larval stage was estimated from the general appearance, and where they were put individually into sterile Petri dishes which were observed daily for emergence of moths or parasitoids. For practical reasons, larvae were reared on plant material instead of artificial diet. Eggs were not recorded.

A period (January - June) was selected for analysis in which developmental stages of the herbivore occurred on all crops in all years (1982-1985). Thus, the data reflect crop-associations of parasitism when parasitoids are given the choice of hosts on different crops. Data of weekly samples were pooled per month.

To minimize errors with calculations of percentage parasitism from field populations (van Driesche 1983), percentage parasitism values for particular

species were calculated as far as possible with respect to the actual stages of *H. armigera* attacked by the parasitoid. Ideally, host stages beyond the stage of parasitoid oviposition, but before the stage of parasitoid emergence should be selected. However, where such optimal stages were not present, we included the stages of oviposition and stages of emergence, and hence slighty underestimated percentage parasitism. This information, assembled largely from the literature, is shown in Table 7.1.

Analysis of parasitism levels was based on logit analysis of data with a binomial error distribution, using the GLIM package (Payne 1986). GLIM uses maximum likelihood techniques to fit models to data. A measure of goodness of fit is provided by the deviance - the equivalent of variance in traditional least squares regression and ANOVA models. Explanatory category variables included crop, parasitoid, year and month, with four, five, four and six categories per variable, respectively. Here, parasitoid refers to parasitism levels of individual parasitoid species, rather than to densities of adults of the parasitoid species.

Consequently, a parasitoid-crop association refers to parasitism of *H. armigera* in a particular crop by a particular parasitoid, and is not to be interpreted as the physical presence of adult parasitoids in that crop. The explanatory power of a variable is roughly estimated by the percentage of the total deviance that is unambiguously attributable to that variable.

From the perspective of the crop and herbivore, the categories of month (Jan., Feb., etc.) are not always representative of the same period each year. Rather, they depend on the growing season within a particular year (e.g., if delayed rains cause the growing season to begin late, the month February in one year may be, in effect, similar to the month January of the preceding year). Therefore, in our regression models, we chose to nest month as a sub-factor within year (Sokal & Rohlf 1981). Total temporal variation (between-season and within-season

Table 7.1 Host-stage specificity of parasitoids of *H. armigera*

Parasitoid	Host stage attacked for oviposition	Host stages of parasitoid emergence	Host stages selected for calculations of % parasitism
Palexorista laxa	(IV), V	VI	V, VI
Charops sp.	I	III, (IV)	I–III
Apanteles diparopsidis	I	II	I, II
Cardiochiles sp..	II, III	IV	II–IV
Chelonus curvimaculatus	E	III, IV	I–IV

E, egg; I–VI, instars; brackets signify host stages of occasional oviposition or emergence.

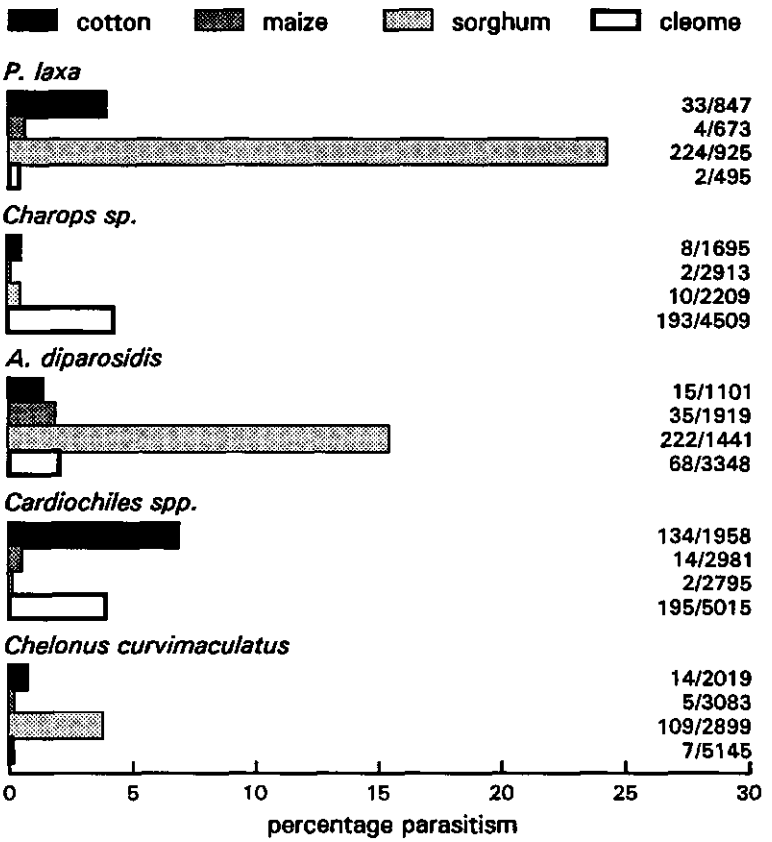

Fig. 7.1 Average percentage parasitism of *H. armigera* on four crops by *Palexorista laxa*, *Charops* sp., *Apanteles diparopsidis*, *Cardiochiles* spp., and *Chelonus curvimaculatus* during January-July. Numbers of parasitoids (numerator) and numbers of host larvae of the appropriate stage (denominator) are given. Ukiriguru, Tanzania, 1982-1985.

variation), is obtained in the analysis by adding the factor year and the interaction year x month. To compare the effect of crop and year, and their interactions between parasitoid species, separate regressions were made for individual species.

Results

Larval densities (seasonal averages) of *H. armigera* (all stages) on the different crops ranged between 0.08 and 0.66 larvae per plant during the sample period.

Table 7.2 Explanatory power (EP) of the main effects and their interaction for the total parasitoid complex expressed as a precentage of the total deviance.

Variable	% EP	Deviance*	df
Main effects			
Parasitoid	12.8	551	4
Crop	12.6	542	3
Year	1.7	73	3
Interaction			
Crop x parasitoid	22.7	976	12
Year x parasitoid	11.2	479	12
Crop x year	2.4	104	9

* $P < 0.001$ (X^2-test)

In general, densities were highest early in the season and declined later on. Fig. 7.1 shows the percentage parasitism values per crop per parasitoid. Parasitism values are averaged over months and years, dividing numbers of parasitoids by numbers of host larvae of the appropriate stage.

Parasitism levels indicate clear parasitoid associations with particular crops, and the patterns are strikingly different between individual parasitoid species. Larvae parasitized by *Palexorista laxa* were often found on sorghum, but rarely on maize and *Cleome* sp. On the other hand, *Charops* sp. was common on *Cleome* sp. but rare on sorghum, cotton and maize. *Cardiochiles* spp. were associated with cotton and *Cleome* sp. but were rare on maize and sorghum. *A. diparopsidis* and *Chelonus curvimaculatus* were mostly found on sorghum, but these species were erratic in their appearance from year to year. Fig. 7.1 also indicates that *H. armigera* sustains much higher parasitism levels on sorghum than on the other crops.

Statistical analysis of the data set for the total parasitoid complex is given in Table 7.2. There are significant effects ($P<0.001$; X^2-test) of parasitoid, crop and year, indicating that parasitism levels differ among parasitoid species, among crops and between years, but the explanatory powers of parasitoid and crop are much larger than that of year (i.e., differences among parasitoids, and among crops are larger than differences between years).

The second-order interaction, crop x parasitoid is highly significant and explains 23 % of the deviance, indicating that parasitism has distinct crop associations. Also, a considerable amount of deviance (11 %) is attributable to the year x parasitoid interaction, which represents the variation in the occurrence

Table 7.3 Explanatory power (EP) of the main effects and their interaction for individual parasitoid species expressed as a percentage of the total deviance.

	Crop (df=3)		Year (df=3)		Crop x year (df=3)	
Parasitoid	% EP	Deviance	% EP	Deviance	% EP	Deviance
Palexorista laxa	48.9	394*	10.4	84*	3.0	24**
Charops sp.	50.0	274*	5.6	28*	8.2	40*
Apanteles diparopsidis	28.9	356*	21.0	259*	4.9	60*
Cardiochiles sp.	51.0	322*	4.5	28*	10.1	64*
Chelonus curvimaculatus	32.1	182*	29.2	166*	3.1	17***

*, significant at P<0.001; **, significant at P<0.005; ***, significant at P<0.05 (X^2-test)

of parasitoid species from year to year. This reflects in part the erratic appearance of *A. diparopsidis* and *Chelonus curvimaculatus*.

Regressions made for the individual parasitoid species are presented in Table 7.3. Comparison of parasitism levels of the individual species is hampered by the fact that they are not independent; a host parasitized by one species cannot be parasitized by another. However, this error is most severe when parasitism levels are high, which was generally not the case (Fig. 7.1).

The crop effect is significant for each parasitoid species. It explains as much as 50% of the total deviance of *P. laxa*, *Cardiochiles* spp., and *Charops* sp., but less in case of *A. diparopsidis* and *Chelonus curvimaculatus*. This means that the first three species have stronger crop associations than the last two species.

The explanatory power of the year x crop interaction is small. Hence, crop associations of parasitism by particular parasitoids are relatively consistent from year to year. *Cardiochiles* spp. are least consistent in this respect.

The nested variable year x month accounted for much of the remaining deviance of individual species (16-35%), almost twice the amount that is attributable to the year effect. This implies that the effect of month is different from year to year, and justifies nesting of month within year for the analysis.

Discussion

This study has shown that parasitism by major parasitoids of *H. armigera* in Tanzania is strongly associated with particular crops fed on by their host, and that these associations are not a result of narrow periods of activity of parasitoids imposed on a seasonal shifting crop spectrum.

What causes these associations remains unknown. Host-finding behaviour may be one factor which affects host plant selection. In North America, host-plant odours are known to be important in the attraction of several species of *Heliothis* parasitoids to particular host plants (Lewis & Nordlund 1985) and may be responsible for the preference for tobacco and cotton by *Cardiochiles nigriceps* (Vinson 1981) and for the somewhat wider range of *Heliothis* spp. host plants by *Campoletis sonorensis* (Elzen *et al.* 1983). Plant chemicals also may be involved in the attraction and arrestment of *Heliothis* spp. parasitoids to larval frass (Nordlund & Sauls 1981) or faeces, a response which may be innate or learned (Lewis & Tumlinson 1988).

Besides host-finding responses, differences in parasitism levels among plant species may be attributed to the accessibility of the host. Some *Heliothis* species gain protection by feeding within the fruiting bodies of their host plants. In North America, this may limit attack rates by *Cardiochiles nigriceps* on *Heliothis subflexa* in ground cherry (Lewis *et al.* 1967) and on *H. virescens* F. in cotton bolls (Lewis *et al.* 1972). Also, the degree of pubescence on leaves or fruits may influence the accessibility of hosts. In our study, *Helicoverpa armigera* fed in a more exposed position on the heads on sorghum than in the squares and bolls of cotton or in the ears of maize (although late instars on cotton bolls often feed with the terminal part of their bodies exposed and thus are less able to defend themselves against attack). This may explain the higher level of overall parasitism on sorghum, and perhaps the preference of *P. laxa* for this plant, insofar as tachinids are generally not effective at reaching unexposed hosts with their short ovipositors.

Still other factors that may explain the differences in host plant associations involve initial attraction of parasitoids to plants because of refuge or food (e.g., floral and extrafloral nectaries), or differences between plant species in the quality of host insects on them. In *H. armigera*, larval weights and developmental rates are higher on certain crops (Jayaraj 1982). This factor may influence parasitoids which prefer certain host stages or sizes, or both.

Besides responses of foraging parasitoids, mortality factors such as predation could have affected the percentage parasitism on each crop (i.e., if mortality would act differently on parasitized and unparasitized hosts [Fritz 1982]). Thus, if different predator guilds existed on each crop, this could have biased the crop associations of parasitism, but it would not explain the large differences in associations found between parasitoids. Data from Kenya indicate that some potentially important predators are associated with particular crops (Chapter 5).

Egg parasitism was not included in this study. In South Africa, Parsons (1940) found a higher incidence of egg parasitism on tomato, marrow and cucumber than on maize, cotton, bean or pea.

The parasitoid-crop associations revealed in this study have two important implications for biological control of *H. armigera* in Africa. First, important natural enemies on one crop should not be assumed to be important on all. Because most work to date has focused on cotton (Chapter 3), more attention should be paid to natural enemies of *H. armigera* on food crops.

Secondly, insofar as all parasitoids studied attacked *H. armigera* on all crops, there is scope to enhance parasitoid activity on one crop by growing it adjacent and contemporary to another. Thus, the presence of *Cleome* sp. within plots or in plot margins may encourage parasitism by *Charops* sp. onto crops. Also, the effect of *Palexorista laxa* on crops other than sorghum may be enhanced by close planting to that crop. Thus, various selective measures involving encouragement of key plants within plots, overlapping of different crops on adjacent plots, and intercropping may all enhance parasitoid effects in one or another crop, but these measures require further study of the parasitoid - host - crop interaction.

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Part III

Experimental Evaluation of Natural Enemy Impact

8

Experimental analysis of stage-specific predation in sunflower[1]

ABSTRACT - In three field trials in Kenya, the seasonal population trend of *Helicoverpa armigera* (Hübner) (=*Heliothis armigera*) was followed in predator-exclusion and control plots of sunflower. In trial 1, complete exclusion of crawling predators (predominantly *Pheidole* spp. of ants occurring at levels of 25 per plant) resulted in *H. armigera* levels of six to eight larvae per plant during the time of flowering and ripening of the crop, which was 6.7 times higher than when ants were not excluded. *Pheidole* sp. had more impact on young larvae (instars two and three) than on older instars (instars four to six) of *H. armigera*. Results of trial 2 were less dramatic, because *H. armigera* infestation was low, and ant densities were moderate. Here, *Myrmicaria* spp. and *Camponotus* spp. were the predominant ants. Exclusion of ants resulted in a 1.8 fold increase in *H. armigera* levels of ca. 1.3 larvae per plant during crop maturation. These species of ants had most impact on the late larval instars of *H. armigera*.

In trial 3 the impact of predators on *H. armigera* was studied under three conditions: exclusion of crawling predators; exclusion of both crawling and flying predators; a control. To evaluate the role of predation against total natural mortality, the recruitment of *H. armigera* larvae was determined with Southwood & Jepson's graphical method and recruitment of eggs was measured on trap plants. Ants and Anthocoridae were the principal predators. The eggs of a single cohort of *H. armigera* which developed on the crop were laid during budding and early flowering and the larvae matured just before harvest. Mortality from egg to older larvae (instars four to six) was 73-78 %. The exclusion treatments did not significantly affect recruitment of larvae. Anthocorids increased only after the main oviposition peak of *H. armigera* and, therefore, their exclusion had little impact on the pest.

Introduction

Sunflower (*Helianthus annuus*) is of recent, but increasing importance as a cash crop in Kenya. It is primarily grown by smallholder farmers for oil, although the plant residues also provide nutritious meal for livestock and serve as well as hay and green manure. Of the numerous phytophagous arthropods associated with sunflower in Kenya, the African bollworm, *Helicoverpa armigera* (Hübner)

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(=*Heliothis armigera*) (Lepidoptera: Noctuidae) is the only pest of economic importance (Khaemba & Mutinga 1982). Eggs are laid singly on young sunflower heads and the larvae feed on the floral parts and developing seeds (Chapter 6). At times, larvae cause conspicuous feeding marks, but damage relations have not been assessed nor has a control strategy been developed. Application of insecticides may adversely affect natural enemies of *H. armigera* and spraying at flowering is harmful to pollinators. Sustainable pest management should be based as far as possible on utilization and conservation of natural enemies, thus avoiding problems caused by the overuse of insecticides. A thorough understanding, therefore, is required of the role natural enemies play in suppressing *H. armigera* populations (Greathead & Waage 1983, King & Jackson 1989).

A four-season study on the ecology of the pest in smallholder crops (sunflower, maize and sorghum) in western Kenya showed that natural mortality is sometimes very high, but fluctuates widely from season to season (Chapter 5). Since the level of parasitism and pathogens was generally low, predation was considered as a possible important mortality factor. Ants (Hymenoptera: Formicidae) and anthocorids (Hemiptera: Anthocoridae) are two groups of predators predominant in sunflower crops throughout Kenya (Chapter 4).

The beneficial role of ants in pest control has long been recognized, and their impact on insect pests has been studied and utilized in several crops, such as cocoa and coconut in the tropics (see Leston 1973), and in pine forests in temperate regions (Adlung 1966). Studies on ants have focused mainly on tree crops, and until recently, ants in annual or biannual crops have received little attention. Leston (1973) proposed that annual or more frequent cultivation of agricultural lands would adversely affect ant populations, so that they could never increase sufficiently to suppress pest populations, unless the crop is grown near a more permanent habitat. In several instances, however, ants have been shown to be effective biological control agents in annual cropping systems in several instances (McDaniel & Sterling 1979, Risch 1981, Sterling *et al.* 1984, Jones 1987). Many opportunist ant species are adapted to colonize open habitats (newly planted fields) and frequently have great potential as predators (Risch & Carroll 1982, Way & Khoo 1992). In Kenya, *Pheidole* spp., *Myrmicaria* spp. and *Camponotus* spp. are common in agricultural lands (Chapter 4) and the former two species were regularly observed carrying off *H. armigera* larvae from plants.

The second group of predators, anthocorid bugs, are also common on various crops. This group has been shown to have important potential as predators of small pest stages in several crops (Isenhour *et al.* 1989, 1990, Reid 1990, Coll & Bottrel 1992). Little is known, however, about their role in Africa, apart from some early work (Parsons & Ullyett 1934, Peat 1935). Anthocorids attack eggs and neonate larvae of noctuids (Isenhour *et al.* 1990), but because of their size, they are unlikely to be effective predators of the larger instars.

In this paper, we present the results of three exclusion trials and thus evaluate the role of predator communities in suppressing *H. armigera* populations on sunflower. The first trial excluded crawling predators and so studies the impact

of predation on larvae alone. The second trial studies the impact of crawling predators on both eggs and larvae of *H. armigera*. The third trial is designed to combine exclusion techniques and life tables, in order to evaluate the role of both crawling and flying predators in relation to other natural mortality factors.

Materials and methods

Locally recommended sunflower varieties and cropping practices were used in all three trials. Towards ripening of seeds, passerine birds, a common pest of seed crops, were kept out of the trials as much as possible by employing 'bird scarers'.

Trial 1: Mwea Tebere, Central Province

The first experiment was set up during the short rains of 1989/90, at a farmer's field near Mwea Tebere (longitude 37.3° E, latitude 1.2° S, altitude 1200 m), Central Province, located in a dry area. Sunflower (var. Hungarian White, spacing 30x75 cm) was planted in six small plots of 7x4 m. Plots were randomly assigned as three control and three exclusion plots.

The exclusion or 'barrier' treatment, was intended to exclude ants and other crawling predators from plants by placing a ring of insect-trap coating (Tanglefoot®) around the base of every plant in the barrier plots at ca. 15 cm above the ground surface. In order to prevent ants regaining access to plants via weeds and withered leaves, both the exclusion plots and the control plots were weeded regularly, and drooping lower leaves removed. Unfortunately, the glue barriers for this trial were not placed into position until the main oviposition peak of *H. armigera* had already passed. Therefore, we evaluated the impact of predation on the larval stages of the pest only.

Sampling was conducted on five weekly occasions, starting 6 January 1990 and continuing until 1 February 1990, just before harvest. On every sampling occasion, 10-15 plants per treatment were sampled between 8.00 and 13.00 h. *H. armigera* larvae and ants were recorded by visual inspection of whole plants. Flower heads were dissected to detect larvae hidden between the seeds or burrowing in the plant tissue of the receptacle. The larval instar was estimated in the field by head-capsule width (Chapter 5), and samples were regularly checked under the microscope. The first instar was not considered because it was under-represented in samples.

Trial 2: Lugari, Western Province

In the long rains of 1990, plots of sunflower (Hybrid 7000, spacing 75x30 cm) were planted at two on-farm sites near Lugari in Western Province (longitude 34.9° E, latitude 0.7° N, altitude 1700 m). Both sites, separated from each other

by 5 km and referred to as Lugari-1 and Lugari-2, were planted on 18 April 1990 in wet soil. Each 0.26 ha plot was divided into eight sub-plots of 14x20 m (with a space between plots of 1.5 m), randomly assigned as four exclusion and four control sub-plots. Barriers to exclude ants and other crawling predators were put in place as for trial 1 before sunflower started budding, i.e., before oviposition by *H. armigera*. All plots were maintained as described for trial 1.

Each week, starting from pre-budding of the crop and continuing until harvest, 24 plants selected at random were sampled per treatment. Sampling was conducted from Monday to Friday during the morning hours (7.30-11.00 h), when arthropods are relatively active in comparison to the hottest time of the day. Data for each week were pooled. *H. armigera* stages and possible predators were recorded as in trial 1. *H. armigera* eggs could be distinguished from eggs of two *Plusia* spp. (Lepidoptera: Noctuidae) using a hand lens (van den Berg & Cock 1993). Larvae were recorded as described above.

Trial 3: Kakamega, Western Province

Also in Western Province, a 1.4 ha field was selected at the Regional Agricultural Research Centre, Kakamega, of the Kenya Agricultural Research Institute (KARI) (longitude 34.8° E, latitude 0.3° N, altitude 1600 m), that had been used to grow maize during the previous year. The experimental plot was separated from sprayed plots by at least 100 m in either direction. Sunflower (var. Comet, spacing 75x30 cm) was planted on 16 March 1990 at the onset of the long rainy season.

Three treatments, barrier, sprayed+barrier, and control, were set up in order to evaluate the role of two groups, crawling predators (predominantly ants) and flying predators (predominantly anthocorids). Nine plots (three treatments, three replicates) of 20x20 m were assigned in a 3x3 latin square. The individual plots were separated from each other by a distance of 20 m and the distance between plots and the guardrow surrounding the whole field was 10 m. This design was to reduce the movements of predators between plots. The area between plots was initially planted with beans (var. GLP-2, spacing 45x15 cm), which were harvested just before sampling of sunflower began; thereafter, this area was kept clear of weeds. Barrier plots were treated as described for trial 1.

The sprayed+barrier treatment was for the exclusion of both crawling predators and flying predators. All flower heads in this treatment were sprayed with a low dosage of triazophos (0.071 kg a.i. per ha), using a knapsack sprayer. Because anthocorid densities were very low early in the season, spraying started 22 June and was repeated weekly until harvest. In preliminary trials, triazophos was the most effective of three selected chemicals in killing anthocorids at low dosages and had little effect on *H. armigera*. In addition to spraying, plants in this treatment were banded in the same way as in the barrier treatment. Plants in the control treatment were neither banded nor sprayed.

Sampling started on 7 May 1990 and continued until 25 July 1990, just before harvest. Each week, from Monday to Friday, thirty plants were sampled per treatment, and data for that week were pooled. Sampling was conducted during the morning hours (7.30-11.00 h). Plants were selected with row and plant numbers from a random-number table. *H. armigera* and possible predators were sampled by visual inspection of plant parts, as described above.

Eggs and larvae of *H. armigera* encountered in the unsprayed treatments were collected and reared in the laboratory to determine the incidence of parasitism and pathogens. Percentage parasitism was calculated with respect to the actual stages attacked by the parasitoids (Chapter 2), in order to minimize sampling errors; inclusion of stages beyond parasitoid attack would underestimate percentage parasitism. Average percentage parasitism during the season was calculated with respect to concurrent host densities. Percentage parasitism of eggs was corrected to allow for retarded development of parasitized eggs (Chapters 2 and 5).

Estimation of recruitment

Only in trial 3 at Kakamega, did we measure recruitment of development stages to assess stage-specific mortality. Recruitment of *H. armigera* larvae was estimated using Southwood & Jepson's (1962) graphical method, where the area under the density curve of the stage concerned is divided by the residence time in that stage (the development period). The development period for individual instars of *H. armigera* has a linear relationship with temperature (Twine 1978). Thus, we calculated temperature-driven development per week with respect to weekly average temperatures and cumulative recruitment was derived accordingly. Mean daily temperatures were determined from hourly records obtained at the research centre.

The graphical method assumes that mortality only occurs at the end of the stage, and neglects mortality during the stage (Southwood 1978). Recruitment estimated from a graphical area, however, is the resultant of the actual recruitment minus the mortality that has already acted on the stage before sampling. Thus, measured mortality between two stages is not the mortality from the beginning of one stage to the beginning of the next, but rather from some median point of one stage to the median of the next stage (Sawyer & Haynes 1989). Despite this limitation, the graphical method is still useful for assessing mortality levels between stages.

Because of low *H. armigera* densities, the larvae were divided into two groups, instars two and three (L2-3), and instars fout to six (L4-6). The first instar was not included, because this small and hidden stage was undersampled and therefore would confuse absolute density estimates.

Estimation of egg recruitment remained a problem. Since the median of the stage is measured, the actual number of eggs that enters the crop remains unknown. Consequently, total generational mortality is underestimated. To avoid this bias, we measured the actual influx of eggs into the field. At

Kakamega, twelve tagged plants were examined every morning for eggs laid during the previous night. Eggs present were recorded and removed, to avoid double-counting. Care was taken that trap-plants were examined with the same accuracy as plants in the regular sampling scheme. The plants, selected with a random-number table, were used for seven consecutive days, after which new plants were selected. In order to evaluate the effect of spraying on oviposition by *H. armigera*, six of the plants were chosen in unsprayed plots and six plants in sprayed plots.

Results

Trial 1: Mwea Tebere, Central Province

At Mwea Tebere, exclusion of crawling predators had a striking effect on *H. armigera* levels (Fig. 8.1), and a visible effect on seed damage. The average level of L2-3 was 3.4 times greater in the exclusion than in the control, and at the second sampling occasion, levels were above 6 per plant in the barrier plot. Average levels of L4-6 instars were 6.7 times greater than in the control, and the contrast with the control treatment was most obvious towards the end of the season; at the fourth sampling occasion, L4-6 reached more than 4.5 per plant, in comparison to 0.9 in the control.

One species of *Pheidole* (designated species A here) was the only crawling predator occurring in significant numbers on sunflower. It was extremely abundant in control plots, with an average of 25 ants per plant (Fig. 8.1). Because sampling was conducted in the daytime, nocturnal ground predators which may forage in the vegetation at night were ignored. However, a parallel pitfall trapping exercise suggests nocturnal predators were never present in more than small numbers (van den Berg & Cock, unpublished data). Exclusion was effective: no ants were recorded on barrier plants. Where ants were not excluded, larval levels peaked at two L2-3 instars and one L4-6 instar per plant on the third sampling occasion. At these low levels, *H. armigera* seems to cause no major damage, although as pointed out above, damage relations for *H. armigera* on sunflower are not known.

As would be expected from its small size, *Pheidole* sp. A had most impact on young larval instars of *H. armigera*. *Pheidole* sp. A removed 71% of the L2-3, and when *H. armigera* had reached the L4-6 stage, the ants were responsible for 85% suppression of larvae. These data suggest that *Pheidole* sp. A was also capable of successfully attacking older larvae (L4-6). Unfortunately, the egg stage of *H. armigera* could not be considered in this trial. This probably led to the underestimation of the role of ants, since we observed *Pheidole* sp. A carrying off *H. armigera* eggs. Apart from insect prey, the ants were observed feeding on plant exudates on the stem and flower head of sunflower.

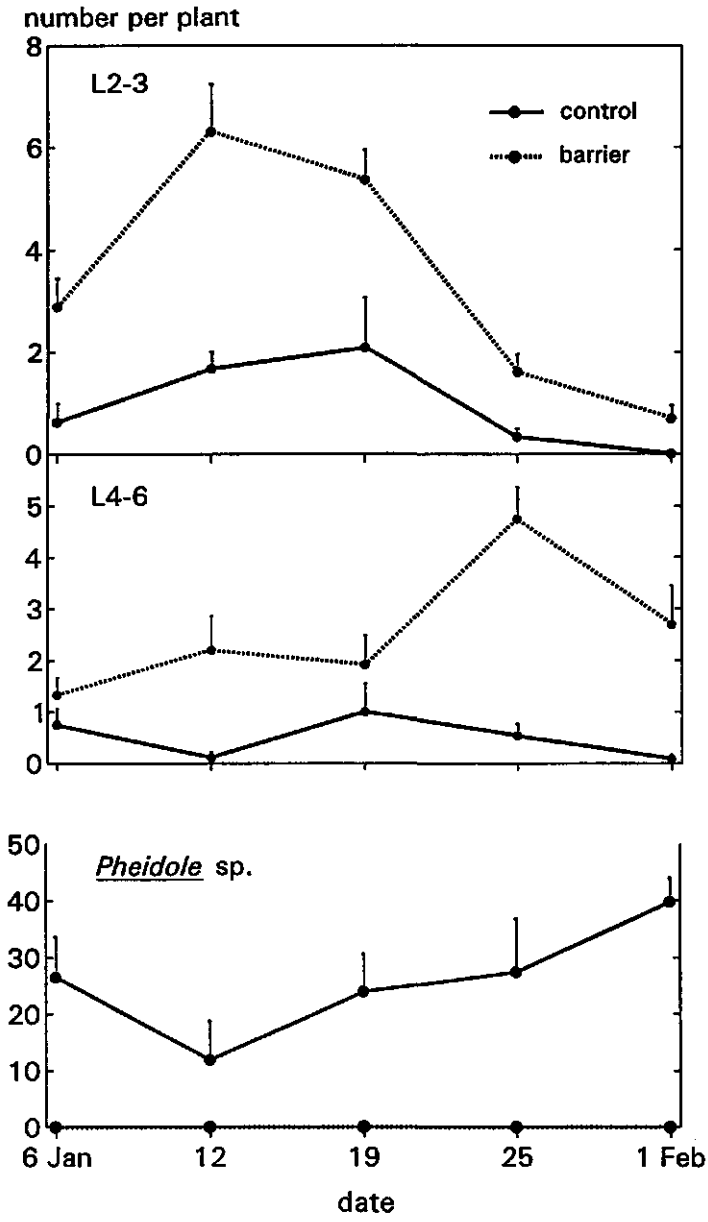

Fig. 8.1 Densities of L2-3 and L4-6 instars of *H. armigera*, and *Pheidole* sp. ants, on five sampling dates in barrier plots (ants excluded) and control plots (ants not excluded). Bars indicate s.e. Trial 1, Mwea Tebere, 1990.

Trial 2: Lugari, Western Province

At Lugari, results were less striking than at Mwea Tebere. Fig. 8.2 shows the levels of *H. armigera* stages during the season at Lugari-1. Infestation was low to moderate.

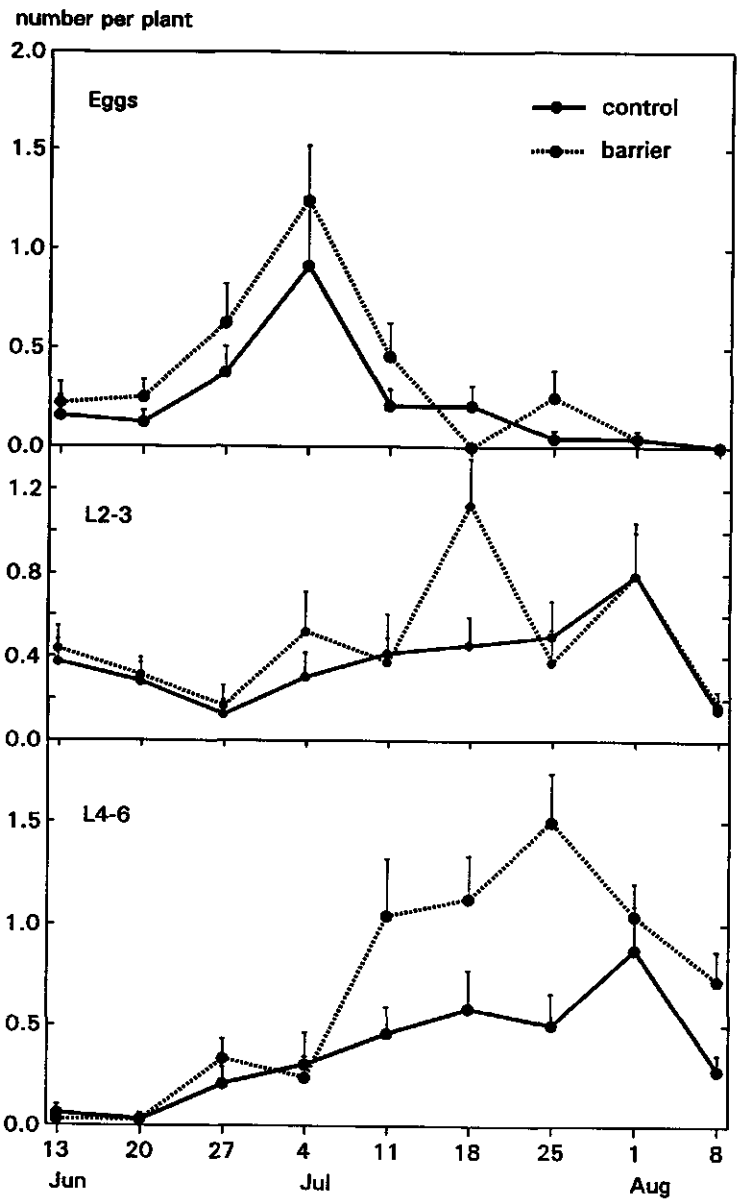

Fig. 8.2 Densities of *H. armigera* stages in barrier plots (ants excluded) and control plots (ants not excluded). Bars indicate s.e. Trial 2, Lugari-1, 1990.

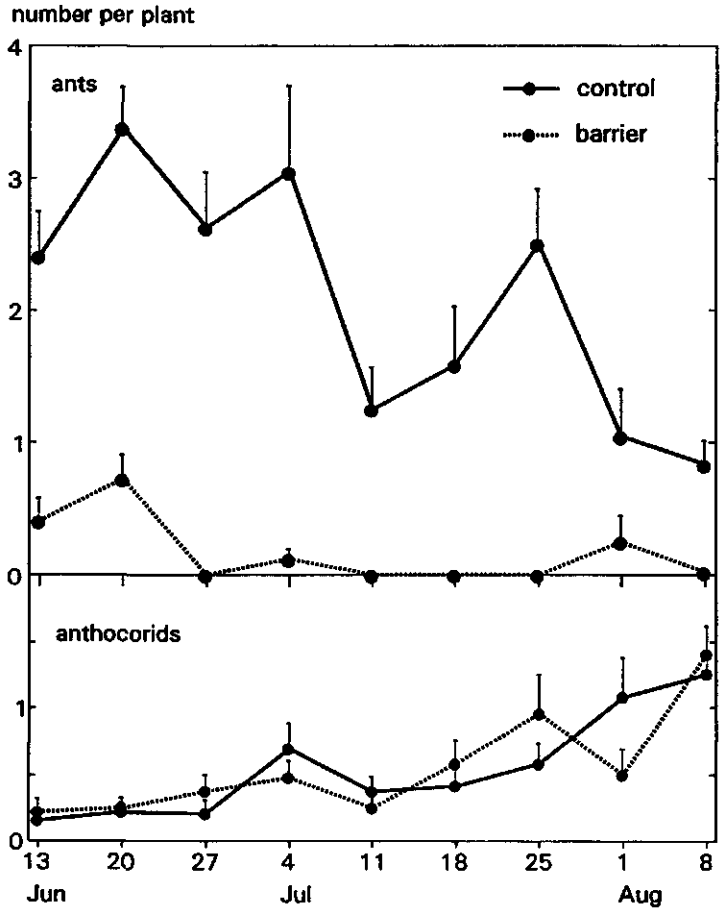

Fig. 8.3 Densities of ants and anthocorids (nymphs and adults) in barrier plots (ants excluded) and control plots (ants not excluded). Bars indicate s.e. Trial 2, Lugari-1, 1990.

Eggs were deposited mostly during budding and early inflorescence of the crop. Exclusion of ants did not have much effect on levels of eggs or L2-3. However, the average level of L4-6, the most damaging stages, was 1.8 times higher in barrier plots than in the control.

Hence, crawling predators were responsible for a 45% suppression of larvae. Ants, the only crawling predators on the vegetation, occurred at densities of two to three per plant in plots where ants were not excluded, much lower than at Mwea Tebere (Fig. 8.3).

In contrast to Mwea Tebere, where *Pheidole* sp. A was the only species present on sunflower, a complex of species was found. Most common were *Myrmicaria* sp. and *Camponotus* sp. (Table 8.1), which are considerably larger than *Pheidole* sp. A. The other

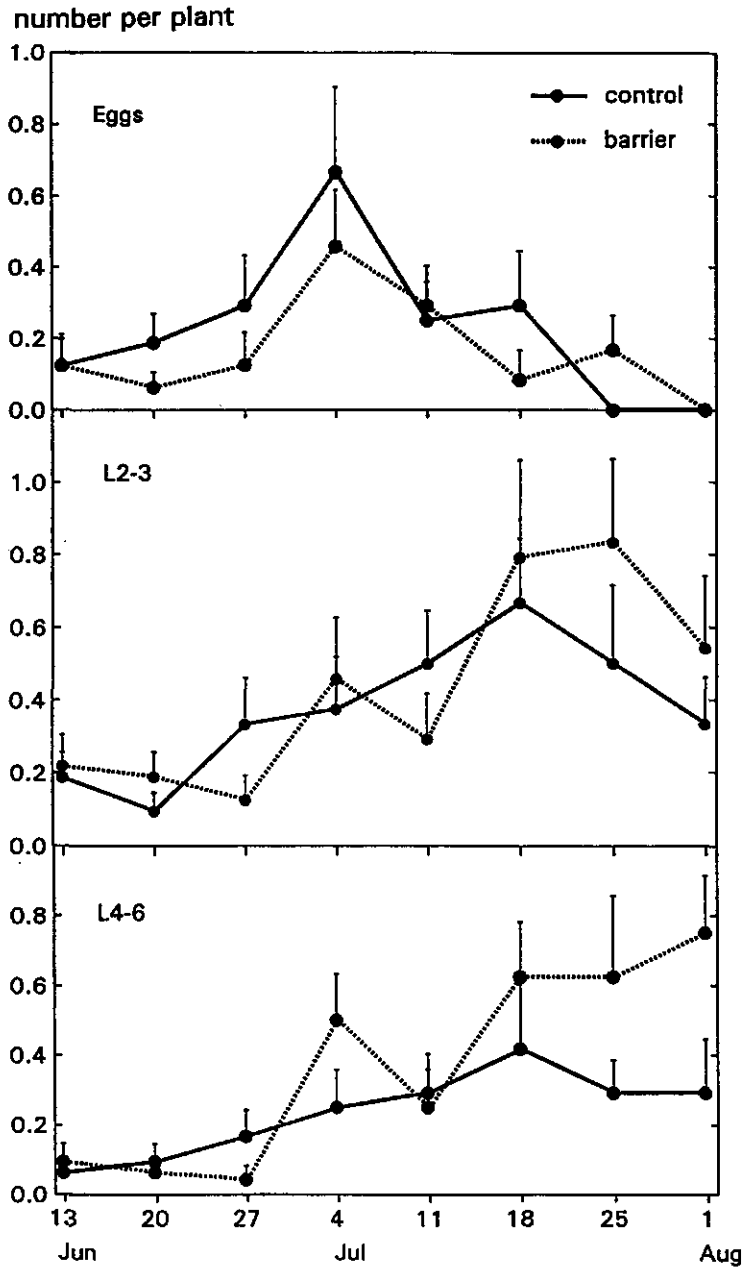

Fig. 8.4 Densities of *H. armigera* stages in barrier plots (ants excluded) and control plots (ants not excluded). Bars indicate s.e. Trial 2, Lugari-2, 1990.

Table 8.1 Relative frequency of different ant species as a percentage of the total ant community. Lugari, 1990.

Species	Lugari-1	Lugari-2
Myrmicaria sp.	52	46
Camponotus sp.	32	33
Pheidole sp.	9	6
Other	8	14

main group of predators of *H. armigera* are anthocorids, which feed on the egg stage of *H. armigera*. Two species were found at Lugari, *Orius thripoborus* (Hesse), the most common, and *O. albidipennis* (Reuter). Anthocorids (adults plus nymphs) were present during the oviposition peak of *H. armigera*; levels were moderate, and there was a slight increase during the season (Fig. 8.3). As expected, there is no difference in anthocorid levels between the treatments.

At Lugari-2, *H. armigera* levels were slightly lower than at Lugari-1, but the population followed a similar trend (Fig. 8.4). Again, there was no effect of ant exclusion on the levels of eggs and L2-3.

The level of L4-6 was slightly, but not significantly, higher in barrier than in control plots, just before harvest. Ants were effectively excluded from barrier plots from 27 June onwards (Fig. 8.5). In control plots, ant densities were moderate and decreased towards the end of the season. The ant community was similar to that of Lugari-1, with *Myrmicaria* sp. and *Camponotus* sp. the dominant species (Table 8.1). Anthocorid predators were present throughout the season, but were not common (Fig. 8.5).

Fig. 8.6 shows the density of L2-3 and L4-6 per replicate, plotted against the density of ants. Densities of larvae and ants are similar at the two nearby sites. It can be seen that plots with more ants have fewer larvae, confirming the role of ants in suppressing *H. armigera*. Low ant densities seem to have greater consequences for L4-6 levels than for L2-3 levels. This difference may be due to a cumulative effect of ant predation on *H. armigera* larvae during larval development, but a preference of ants for older larvae might also have contributed to the difference.

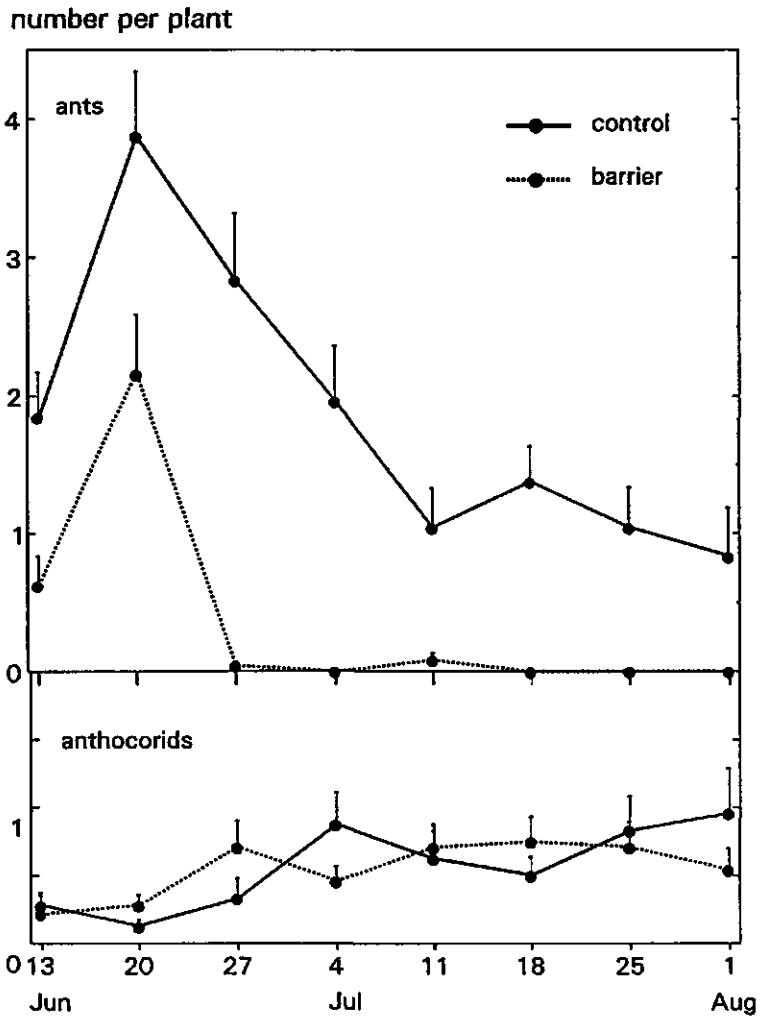

Fig. 8.5 Densities of ants and anthocorids (nymphs and adults) in barrier plots (ants excluded) and control plots (ants not excluded). Bars indicate s.e. Trial 2, Lugari-2, 1990.

When data for the two sites at Lugari are combined, non-parametric rank correlation shows a significant negative trend for L2-3 and L4-6 against number of ants ($P<0.02$, Spearman; $n=16$), which again confirms the role of ants. When data for the two sites are taken separately, there is a significant trend ($P<0.03$) at Lugari-1 when all instars are combined (L2-6), but not for L2-3 or L4-6 separately, while at Lugari-2, there is a significant trend ($P<0.04$) for L4-6, but not for L2-3. Fig. 8.6 also displays a large variation in ant and *H. armigera* numbers between the replicates. At Lugari-2, the occurrence of ants in the control treatment appears to be very patchy, and may be due to the distribution of nests.

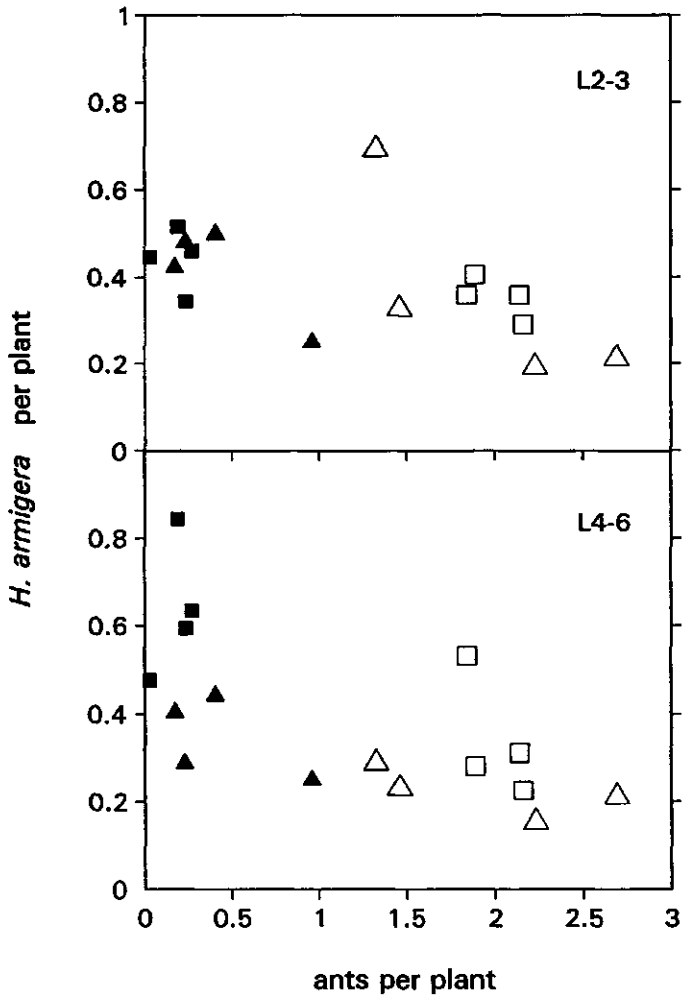

Fig. 8.6 Relationship between the densities (averages during the sampling season) of ants and *H. armigera* larvae (instars 2-3 above, instars 4-6 below) on sunflower at Lugari. Each data point represents the plants sampled from a plot replicate, pooled during the season. Open data points indicate control plots (ants not excluded), black data points indicate barrier plots (ants excluded); squares indicate Lugari-1, triangles indicate Lugari-2.

At Lugari-1, ants are more evenly distributed over the four replicates. The overall difference in ant densities between sites is small.

Parasitism levels were not assessed in this trial, but regular samples indicated a low incidence of the egg parasitoids *Trichogrammatoidea* sp. (Hymenoptera: Trichogrammatidae) and *Telenomus ullyetti* Nixon (Hym.: Scelionidae) as well as larval parasitoids *Charops ater* Szepligeti (Hym.: Ichneumonidae) and *Linnaemya longirostris* (Macquart) (Diptera: Tachinidae). Pathogens were not encountered.

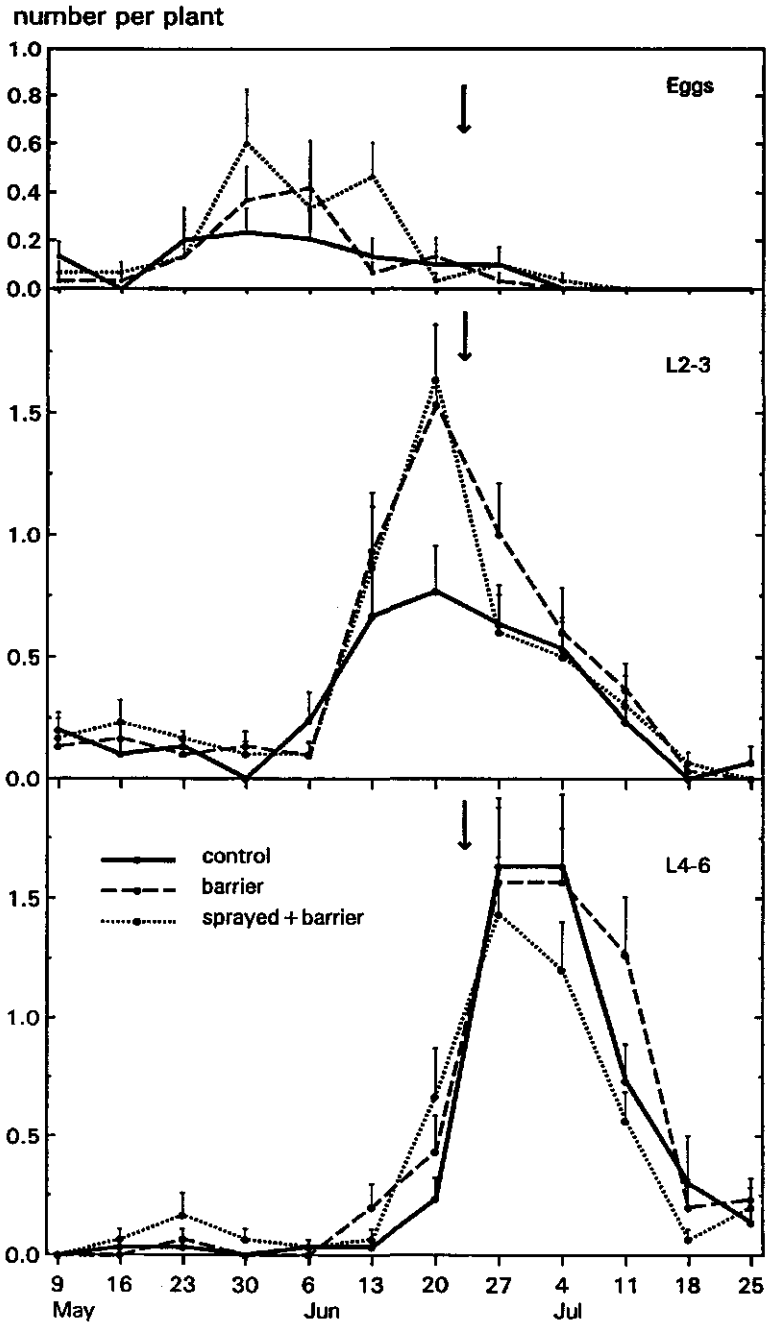

Fig. 8.7 Densities of *H. armigera* stages in control plots (no exclusion), barrier plots (ants excluded), and sprayed+barrier plots (ants and anthocorids excluded) of sunflower. Trial 3, Kakamega, 1990. Arrow indicates when weekly application of triazophos by spraying was started.

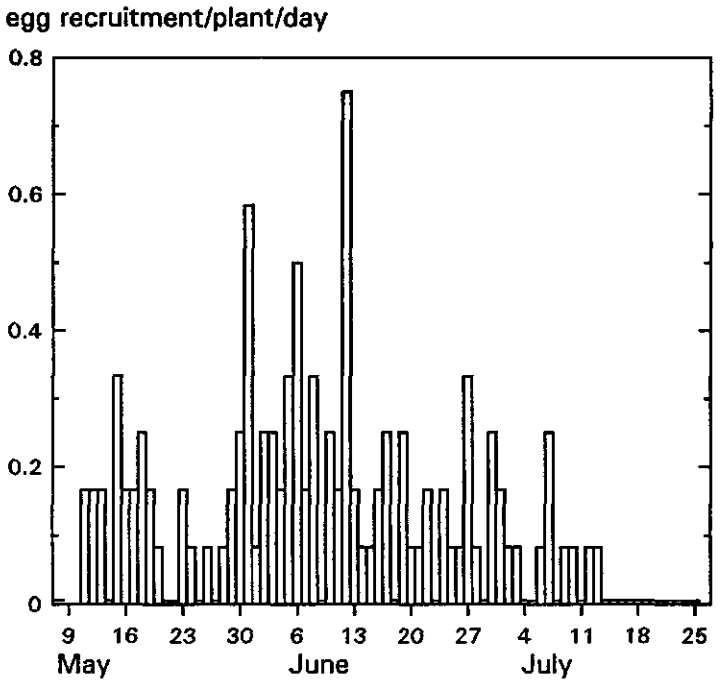

Fig. 8.8 Daily egg recruitment of *H. armigera* on sunflower. Trial 3, Kakamega, 1990.

Trial 3: Kakamega, Western Province

One distinct generation of *H. armigera* developed on the crop at Kakamega (Fig. 8.7). Oviposition mostly occurred at pollen-shedding, from late May until early June. The generation passed through the early instars (L2-3) in the period after pollen shedding but before ripening of the crop, and reached maturity (L4-6) towards ripening of the crop. In general, the egg peaks were lower than peaks of L2-3 or L4-6, indicating that eggs were undersampled or that mortality was not very high (compare Chapter 5). Egg levels in the exclusion treatments were slightly higher than those in the control. Likewise, the level of L2-3 was higher in the exclusion treatments than in the control, suggesting some effect of ant predation. In the exclusion treatments, the incidence of L2-3 reached 1.5 per plant, compared to 0.75 per plant in the control. When the *H. armigera* cohort reached the L4-6 stage, the difference between the control and exclusion treatments had diminished. L4-6 levels peaked at 1.5 per plant.

Fig. 8.8 shows the daily recruitment of eggs on the crop. The seasonal trend is similar to that of egg densities (Fig. 8.7). Total egg recruitment during the season was 9.7 eggs per plant. Recruitment in unsprayed and sprayed plots was

Table 8.2 Recruitment (Lx, in number per plant, with s.e. between plots) and percentage mortality (100 Qx) of *H. armigera* in three predator exclusion treatments in sunflower (n= 3 plots). Recruitment of eggs was measured directly, while recruitment of larval instars (L2-6) was estimated from stage-frequency data.

	CONTROL			BARRIER			SPRAYED+BARRIER			
X	Lx	s.e.	100 Qx	Lx	s.e.	100 Qx	Lx	s.e.	100 Qx	
Eggs	9.67	1.10		9.67	1.10		9.67	1.10		
L2-3	4.38	0.17	54.7	6.34	0.49	34.4	5.84	0.86	39.6	*
L4-6	2.33	0.38	46.8	2.66	0.48	58.0	2.14	0.32	63.3	*
Total mortality			75.9			72.5			77.8	

* Treatment did not affect recruitment of L2-3 or L4-6 ($P > 0.05$, ANOVA).

8.3 and 11.0 respectively, which was not a significantly difference ($P>0.05$, ANOVA; n=3), indicating that spraying had no effect on ovipositing moths. This justifies pooling egg recruitment estimates into one value for all treatments.

Table 8.2 presents the recruitment estimates of *H. armigera* stages in the three treatments. Egg recruitment (± s.e.) and L2-3 densities were slightly lower in the control than in barrier and sprayed+barrier plots. Analysis of variance showed that treatment had no significant effect on recruitment of young and mature larvae ($P>0.05$, F-test). Mortality during the young stages was 34-55 % and mortality during the older stages was 47-63 %. Total mortality was 72-78%.

In general, ants were effectively excluded from the barrier and sprayed+barrier treatments at Kakamega (Fig. 8.9). The barriers were put in place on May 15 to 17, which explains the ant peak in the exclusion treatments at the beginning of the season. The small peak in the sprayed+barrier treatment on May 30 was due to delayed removal of hanging leaves from the base of the plants in one replicate. Most ants were *Pheidole* sp. B (rather larger than species A from Mwea Tebere), but occasionally, *Myrmicaria* sp. and *Camponotus* sp. were encountered.

Fig. 8.10 shows that the incidence of anthocorids was very low during much of the growing season (compare Chapter 4) and they only increased at flowering when the outer seeds of the flower head started to mature. Therefore, we postponed spraying to kill anthocorids until rather late in the season. Clearly, spraying effectively eliminated both nymphs and adults of anthocorids. In the unsprayed treatments, nymphs increased to a density of 2-2.5 per plant, which is still low in comparison to previous seasons when levels reached 13 per plant. Three species were found: *Orius thripoborus* (Hesse), *O. tantillus* (Motschulsky) and *O. albidipennis* (Reuter), but *O. thripoborus* was most common.

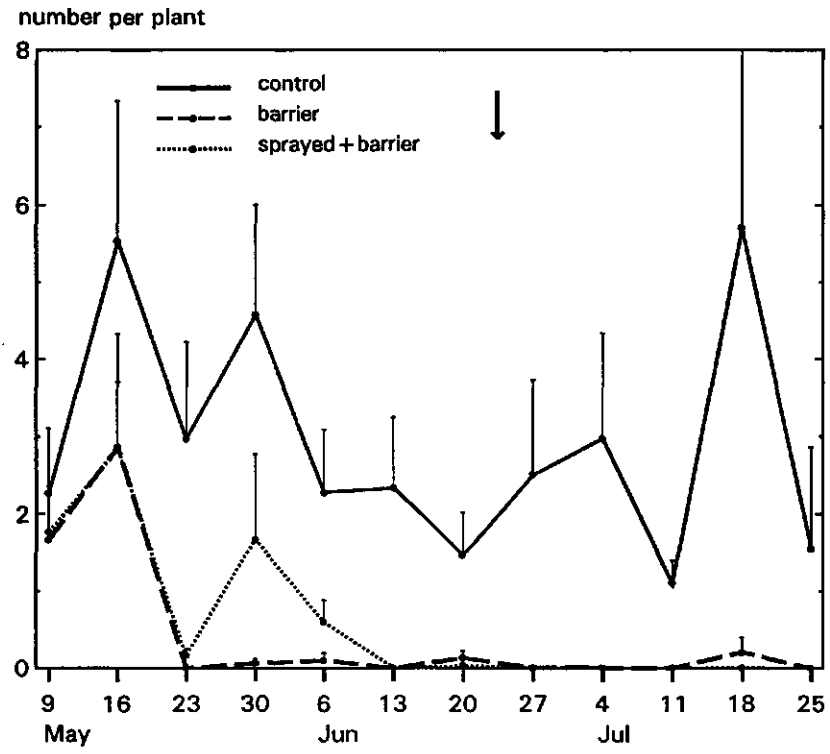

Fig. 8.9 Densities of ants in control plots (no exclusion), barrier plots (ants excluded), and sprayed+barrier plots (ants and anthocorids excluded) of sunflower. Trial 3, Kakamega, 1990.

Ants and anthocorids were the only two groups of predatory arthropods sufficiently common to be of importance to *H. armigera* population dynamics. Nocturnal ground predators which may forage in the vegetation at night were ignored and pitfall trapping data suggested they were not common. Other predators, such as Coccinellidae (Coleoptera), Chrysopidae (Neuroptera) and Syrphidae (Diptera), were regularly found in association with aphid prey on maize and sorghum (Chapter 4), but were rare on sunflower where aphids were virtually absent. Hence, the barrier treatment is roughly equivalent to exclusion of ants (the insect trap coating on the basis of the plants does not affect anthocorids) and the sprayed+barrier treatment is roughly equivalent to exclusion of both ants and anthocorids, although spraying would also affect parasitoids.

The generational mortality level due to egg parasitoids (*Trichogrammatoidea* spp. and *Telenomus ullyetti*) was 3.4 %. Young-larval mortality due to *Dolichogenidea* (*Apanteles*) sp. (Hym.: Braconidae) and *Charops ater* (Hym.: Ichneumonidae) was 1.9 and 2.7 % mortality, respectively. Adding these, total generational mortality due to parasitism was 8 %. Nematodes and nuclear polyhedrosis virus infected 0.3 and 4.9 %, respectively. With such low levels of

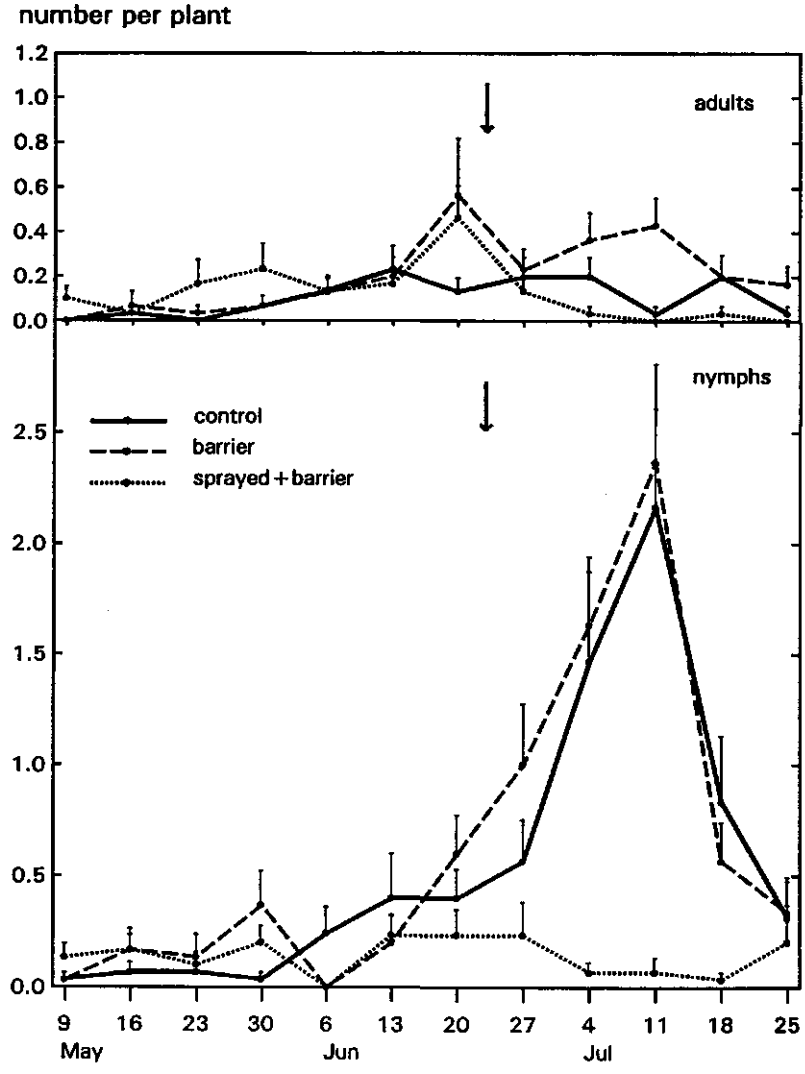

Fig. 8.10 Densities of anthocorid nymphs and adults in control plots (no exclusion), barrier plots (ants excluded), and sprayed+barrier plots (ants and anthocorids excluded) of sunflower. Trial 3, Kakamega, 1990.

parasitism and pathogens, the exclusion treatments could not have a major effect on mortality due to these factors.

In addition to the measured influx of eggs, N_r (Fig. 8.8), which was 8.3 eggs per plant in unsprayed and 11.0 eggs per plant in the sprayed treatment, a second estimate of egg recruitment, $\tilde{N}_r$, could be obtained from stage-frequency data of eggs (Fig. 8.7) by using the graphical method (Southwood & Jepson 1962). The

graphical estimate of egg recruitment $\tilde{N}_r$ for sprayed plots was 1.61 and for unsprayed plots was 2.42. Thus, the measured influx N_r was 5.17 and 4.54 times greater than $\tilde{N}_r$ in the unsprayed and sprayed treatment, respectively.

Discussion

Mortality due to predation

By combining ant-exclusion and stage-frequency sampling of *H. armigera*, this study demonstrated the role of ants in the dynamics of *H. armigera* populations. Ants can be very important in suppressing *H. armigera* populations on sunflower. At Mwea Tebere, where both densities of ants and *H. armigera* larvae were high, ant exclusion had a strong effect on the incidence of *H. armigera* larvae and on the amount of feeding damage. *Pheidole* sp. A mainly attacked young larvae (and eggs), while the larger ant species in trial 2 (Lugari) took relatively older larvae of *H. armigera*. The results from Lugari show that the local ant complex was capable of reducing *H. armigera* at low infestation levels of the pest, while average ant densities were only one-thirteenth of those at Mwea Tebere.

It is possible that when ants are excluded, other natural enemies that normally compete with, or are killed by, ants could respond with an increased predation rate and thus partly replace the predation by ants. For example, at Lugari, there was no effect of ant exclusion on the egg stage of *H. armigera*. It remains unclear, however, whether ants do not remove the eggs, or whether their actual impact is obscured by an increased egg predation of, say, anthocorids following reduced competition or interference by ants. At Mwea Tebere, we evaluated ant predation on the larval stage only, which is beyond anthocorid attack.

Predation of ants on eggs may be limited by their ability to dislodge eggs, which are tightly adhered to the plant substrate. Sucking predators (e.g., anthocorids), may be more efficient in this respect, as they consume the eggs *in situ*. Nevertheless, ants have been reported as predators of noctuid eggs in a few instances (McDaniel & Sterling 1979, Gravena & Pazetto 1987). Data from Brazil indicate that predominantly *Pheidole* sp. ants, which carried off 14% of *Alabama argillacea* (Hübner) (Lepidoptera: Noctuidae) eggs on cotton, were much less efficient predators of eggs than heteropterous sucking predators, as the ants were almost nine times more common on plants than the Heteroptera, while causing less egg mortality (Gravena & Pazetto 1987).

Trial 3 at Kakamega was designed to elucidate the irreplaceable role of crawling predators and the irreplaceable role of all (crawling and flying) predators. The results showed that the role of predation in relation to total natural mortality was negligible in this particular season. Even though anthocorids have been shown to feed readily on exposed *H. armigera* eggs in the field (Chapter 11), in this trial, anthocorids increased on the crop almost entirely after the main oviposition period, so that anthocorids could have caused little egg mortality. Hence, spraying after 22 June suppressed anthocorids but did not

affect predation on eggs. This and a previous study (Chapter 5) indicate that anthocorids generally increase too late in the season to have much influence on *H. armigera*. Ant populations were rather low, and did not significantly suppress *H. armigera* in this trial.

The glue barrier had negligible influence on other mortality factors of *H. armigera* as flying predators rarely visit the bottom part of the plant (Chapter 6) and the glue had no visible side-effects on the plant. Therefore, what was measured as the role of ants was that part of ant predation that was not replaceable by other natural mortality factors.

Since there are no common flying predators of larvae at our sites and there is negligible larval parasitism, spraying in trial 3 did not influence predation or parasitism of *H. armigera* larvae. Hence, any difference in larval numbers between the sprayed and unsprayed barrier treatments could be ascribed to the direct influence of triazophos on *H. armigera*. The results show no significant effect of the chemical on *H. armigera*.

The discrepancy between the graphical estimate ($\tilde{N}_r$) and the actual influx (N_r) of *H. armigera* eggs may have two causes. Firstly, mortality or disappearance occurring within the stage is not considered in the graphical method. Assuming a constant survival rate S within the stage, the following relationship exists between N_r and $\tilde{N}_r$ (Sawyer & Haynes 1984, van Driesche *et al.* 1989).

$$N_r/\tilde{N}_r = (S\text{-}1)/lnS$$

S is determined by iteration and our data suggest that mortality within the egg stage has to be over 99 %, even in the absence of predators. This is unrealistic, and contradicts independent observations on moth-deposited egg cohorts of *H. armigera* at Kakamega (Chapter 11)), suggesting that underestimation of $\tilde{N}_r$ is largely due to another factor.

Secondly, density sampling of eggs was less accurate than measurement the influx of newly-laid eggs. Young *H. armigera* eggs are conspicuously yellow/white in colour, but after one day they have darkened and are difficult to find on plants. Darkened eggs were rarely encountered in the field. In observations on egg cohorts discussed above, most eggs were still present after two days, but would have been difficult to detect without marking. This shows the limitations of the graphical method in this situation and stresses the importance of direct measurement of egg recruitment. Clearly, larvae are less prone to such sampling inconsistencies than eggs.

Implications for utilization of predators

By their strategy of recruiting and storing food, ant colonies are capable of remaining active and populous through periods of food scarcity, which in annual cropping is the non-growing season. Ants are about the only arthropod predators that are active and numerous in the field from the time of planting and that forage

on the early crop (Cock *et al.* 1990). Other predators, such as anthocorids, colonize the crop at the time of flowering, which is frequently after *H. armigera* infests the crop. Foraging activity of ants is affected directly by the density of food, because of the ants strategies of chemical communication and food recruitment, as discussed by Risch & Carroll (1982). Jones (1987) showed a density-dependent predation rate by *Iridomyrmex* ants: as the density of larvae of *Pieris rapae* L. (Lepidoptera: Pieridae) increased, the percentage predation by ants also increased.

Ant communities may be affected by various cultural measures. Ploughing of land may affect soil-nesting ants, but at our sites *Myrmicaria* sp. and *Pheidole* sp. nests were frequently situated in the fallow stretches with occasional trees or shrubs, that commonly border farmers plots and thus remained unaffected by cultivation. We also noted that ant nests situated inside the plots remained viable after ploughing. Ant foraging may be enhanced by changing crop composition, weed management and provision of alternative food sources (Way 1953, Leston 1973, Saks & Carroll 1980), or, by transplanting ant nests (e.g., Pavan 1979, Jones & Sterling 1979). At a site in Western Province, we tried transplanting several nests of *Myrmicaria* sp. from one field into the next, providing crushed sugar-cane to encourage establishment of the colony, but without success. Further systematic trials are required to confirm these findings.

In western Kenya, we observed that ant densities in the vegetation were not proportional to the rate ants were caught in pitfall traps on the ground surface, but ant visitation of plants appeared to differ between crops and between seasons. In replicated plots of sunflower, maize and sorghum, similar levels of *Myrmicaria* sp. and *Pheidole* sp. B were caught in pitfall traps on the ground surface of all three crops. However, ants visited sunflower plants more than maize or sorghum plants. On one variety of sunflower, *Myrmicaria* sp. was more common on the vegetation during the first than during the second short-rains season, while pitfall trap catches were greater during the second season (H. van den Berg & M.J.W. Cock, unpublished data). The proportion of ants' foraging in the vegetation would thus strongly affect their impact on *H. armigera*.

Although ants may be attracted to plants with high levels of insect prey, visits by ants to plants are often related to the presence of honeydew-producing Homoptera (Way 1963), or to the availability of extrafloral nectaries on plants (Bentley 1976, 1977, Tilman 1978). In our study, aphids and other Homoptera were rare on sunflower, and may therefore not have influenced ant activity on this crop. However, we frequently found *Pheidole* and *Myrmicaria* feeding on extrafloral nectaries and other plant exudates on cotton, sunflower and maize. By attracting ants, extrafloral nectaries on plants may be responsible for a reduced pest infestation (Tilman 1978). Selection of crop varieties with increased extrafloral nectary or other plant exudate production could thus enhance predation by ants. On the other hand, extrafloral nectaries may attract certain insect pests. On cotton for instance, bollworms oviposit more on varieties with nectaries than on those without (Schneider *et al.* 1986, for review).

Anthocorids did not cause irreplaceable mortality in this study. In Australia, Forrester (1981) observed that very high densities of eggs of *Helicoverpa* spp. on flowering sunflower produced very few larvae and suggested that predation by mirids and anthocorids was a possible cause. Separate data from a combination of crops in western Kenya demonstrated that anthocorids are poorly associated with *H. armigera* eggs on sunflower, on a per plant and per plant part basis (Chapter 6) if they increase late in the season. We suggest that interplanting with certain crops would encourage anthocorids to colonize the crop earlier, before the main oviposition peak by *H. armigera*.

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9

Experimental analysis of stage-specific predation in cotton[1]

ABSTRACT - Irreplaceable mortality of *Helicoverpa armigera* due to natural enemies was studied in cotton in western Kenya. Field populations of *H. armigera* eggs and larvae were followed in plots where crawling predators were excluded, and in plots where both crawling and flying predators were excluded and in control plots. Ants were the predominant crawling predators, whereas anthocorids were the predominant flying predators. *H. armigera* mortality from egg to late larval stage was very high (96.4-99.7%) and was greater in the second than in the first generation. Partial exclusion of the different groups of predators did not significantly increase survival of the pest. It is argued that the high level of background mortality obscured the role of predators. Background mortality appears to be related to host plant condition, which in turn depends on moisture stress.

Introduction

Helicoverpa armigera (Hübner) (=*Heliothis armigera*) is a continuing problem in cotton production throughout the Old World, both in low- and high-input farming. Overuse and misuse of insecticides have increased the problem and contributed to well-known disasters in cotton production (Matthews 1989), as the pest became resistant against a wide range of chemical compounds (Wolfenbarger *et al.* 1981), while its natural control agents were killed and secondary pests induced (Eveleens 1983, Abdelrahman & Munir 1989). To date, cotton production still depends heavily on pesticides, but different kinds of strategies have been introduced in several areas that limit the use of insecticides and reduce the risk of resistance development in *H. armigera* (Ives *et al.* 1984, Brettell 1986).

Natural enemies have long been considered important in suppressing *H. armigera* populations, but surprisingly little data exist on their role, in particular regarding predation. A recent workshop on biological control of *H. armigera* recognized this lack of substantial data, and identified the need to evaluate natural enemies through life table studies (King & Jackson 1989). Evidently in cotton, natural enemies alone cannot always be relied upon to control *H. armigera* below the economic threshold level. However, utilization of natural enemies by conserving and enhancing their populations is essential for sustainable pest

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management, which is less dependent on chemical insecticides (King & Jackson 1989, Greathead & Waage 1983).

Natural control is particularly relevant for small-scale cotton production in East Africa, where pesticides are usually a major cause of expenditure. With *H. armigera* as their key pest (Rens 1977, Nyambo 1988), many farmers spray cotton, but the number of insecticide applications during the season is generally limited. With the current agricultural intensification, caused by increasing population pressure in the region (Odingo 1988), the use of pesticides is likely to increase.

In a separate study, we showed that natural mortality of *H. armigera* stages in smallholder crops in western Kenya can be very high (Chapter 5). The role of parasitoids and pathogens was small, but predation was thought likely to be an important mortality factor. Ants and anthocorid bugs were the predominant predator groups.

Here, we present an experimental set-up in which we evaluate the irreplaceable mortality due to predation in the life table of the pest. Irreplaceable mortality due to natural enemies is that part of the impact that can not be compensated for, by other (concurrent or subsequent) mortality factors in the absence of natural enemies (Thompson 1955, Morris 1965).

Materials and Methods

Experimental treatments

At the National Fibre Crops Research Station, Kibos, South Nyanza Province, a 1.4 ha field was selected that had not received pesticide applications for at least the previous two years. The field was surrounded by a strip of weeds 1 to 5 m wide, and was separated from sprayed fields by at least 150 m. Cotton (var. BPA-75, spacing 90x30 cm) was planted on 16 March 1990.

In the experimental field, nine 20x20 m plots of cotton were planted. Three treatments which aimed at excluding different groups of predators, and which are described below, were replicated three times and assigned in a 3x3 latin square (Fig. 9.1). The plots were separated from each other by a distance of 20 m. The area between plots was initially planted with beans (var. GLP-2, spacing 45x15 cm), but these were harvested after seven weeks, before sampling of cotton began; after harvest the area between the plots was kept clear of weeds. The area between plots was to reduce the movement of arthropods between the treatments. Depending on the action radius of natural enemies, sprayed plots could influence natural enemy activity in the unsprayed plots by acting as a sink.

Three treatments were used to exclude or diminish different groups of predators: the barrier treatment for exclusion of crawling predators, the sprayed+barrier treatment for exclusion of crawling as well as flying predators, and the control where no predators were excluded.

In barrier plots, a ring of insect trap adhesive (Tanglefoot^{R}), placed from 15-18 May at about 10 cm above the ground around the stem of every plant in the plot, was used to exclude crawling predators. Crawling predators were further prevented from visiting the crop by pruning cotton branches that touched the ground, and by keeping plots clear of weeds. For consistency, branches were pruned and weeds were removed in all treatments. Ants (*Myrmicaria* spp., *Camponotus* spp. and *Pheidole* spp.) were by far the most common group of crawling predators (Chapter 4).

The sprayed+barrier treatment was set up to exclude both crawling and flying predators from the crop. Plants were banded with insect trap adhesive as in barrier plots. In addition, plots were sprayed weekly, starting 21 May, with a very low dosage of triazophos (0.053 kg a.i. per ha.), using a knapsack sprayer. Spraying was carried out early morning when the weather was calm, to avoid drift between plots. In preliminary trials of three chemical insecticides, triazophos killed anthocorids effectively at low dosage while having little effect on *H. armigera* larvae.

Plants in the control treatment were not banded or sprayed.

Meteorological data were obtained from the nearby Kisumu airport. Average daily temperature was calculated from daily minimum-maximum values.

Sampling methods

Sampling was conducted weekly from Monday to Friday during the morning

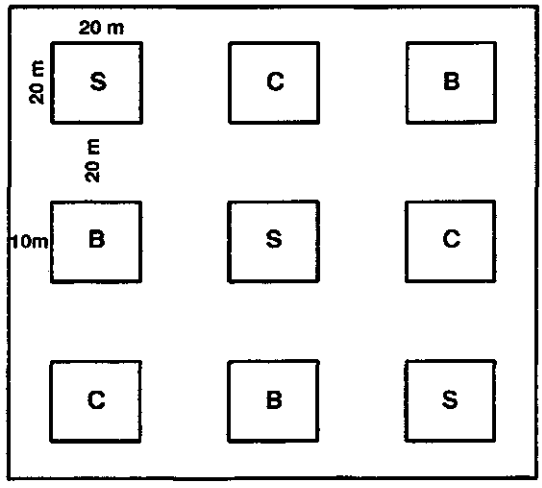

Fig. 9.1 Layout of field trial; c, control; b, barrier; s, sprayed+barrier.

hours (7.30-11.00 h), to avoid the hottest time of the day. Plants for sampling were selected with the aid of a random number table. Thirty plants per treatment (i.e., 10 per plot) were sampled during a week. Sampling started 7 May 1990, 52 days after planting (d.a.p.) and continued for 15 weeks until 17 Aug 1990 , 154 d.a.p..

Whole plants were carefully examined for *H. armigera* eggs, larvae and possible predators. Special attention was given to dissecting the squares, flowers and bolls, which are preferred sites of *H. armigera* larvae and anthocorids (Chapter 6). It took about 20 minutes to sample a plant. Eggs of *H. armigera* could be distinguished from other lepidopterous eggs using a hand-lens. The six larval instars of *H. armigera* were estimated based on head-capsule width (Chapter 5), and samples were regularly measured in the laboratory to check the field estimates.

Recruitment

For *H. armigera* larvae, recruitment was estimated by dividing the graphical area of the stage concerned by its development period (Southwood & Jepson 1962). This graphical method is applicable to situations in which survival rates vary from stage to stage (Southwood 1978). Because of low *H. armigera* densities we combined the instars two and three, and the instars four to six. The first instar was ignored, because at this stage, the small size of larvae precludes accurate sampling.

The development periods of larval instars of *H. armigera* was studied by Twine (1978). Derived from his data the following linear equations describe the development period of L2-3 and L4-6 in relation to temperature.

$$y_{L2\text{-}3} = 0.0209\ x - 0.2414$$
$$y_{L4\text{-}6} = 0.0068\ x - 0.0721$$

y is the rate of development (per day) and x is the temperature (°C). These regression equations were employed to calculate development rates of L2-3 and L4-6 at local temperatures for weekly intervals. Weekly average temperatures ranged from 22 to 24.5°C. Accordingly, recruitment was estimated per week and summed over a generation to provide L_x, with the individual plot as experimental unit (n=3). The effect of treatment on recruitment per plot was examined with analysis of variance.

A shortcoming of the graphical method is that it does not estimate the number that enters a stage, but the number somewhere near the median of a stage. This number is the resultant of the actual recruitment minus the mortality that has already acted on the stage prior to sampling. Consequently, the graphical method does not measure the mortality from one stage to the next, but rather it measures mortality from some median point of one stage to the median of the next, unless all mortality occurs at the end of the stage (Sawyer & Haynes 1984). Hence, the

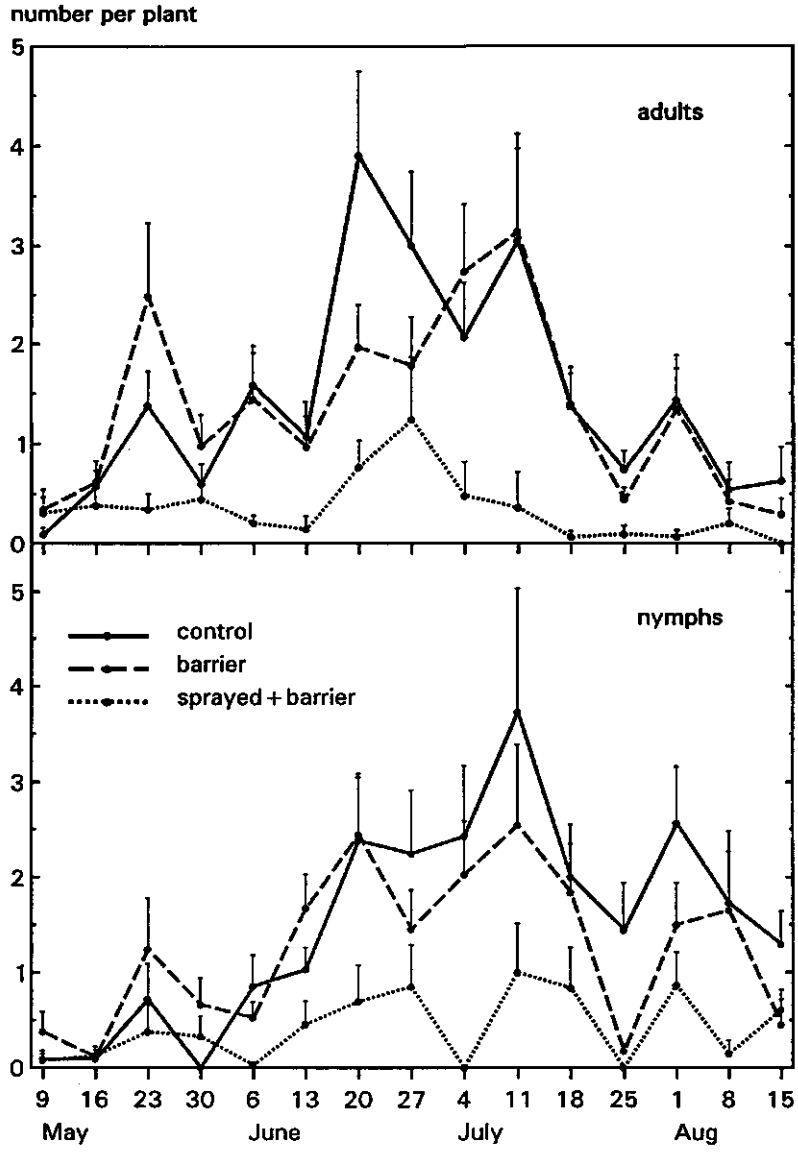

Fig. 9.2 Mean number of anthocorid nymphs and adults per plant in control, barrier, and sprayed+barrier treatments of cotton. Vertical bars indicate s.e.

graphical method underestimates recruitment, because part of the stage has disappeared before sampling.

The graphical method, although still useful in evaluating mortality levels between stages, remains a problem for the stage that enters the system (i.e., the

crop). For calculations of generational mortality, it is important to measure the absolute recruitment of the first stage (the eggs) into the system, as greatest mortality occurs between the egg and young larval stage (Chapter 5).
Therefore, recruitment of eggs was assessed by measuring the actual influx of eggs into the crop. Twelve tagged plants were checked every morning, seven days per week, for eggs laid during the previous night, which were recorded and removed. Eggs are laid primarily during the evening hours, from 18.30 to 23.00 h (Topper 1987). Care was taken to examine these plants for the presence of eggs with the same accuracy as plants in the regular sampling scheme. The trap plants which were selected randomly, were used for seven consecutive days after which new plants were selected. Kinzer *et al.* (1977) demonstrated that row crops sprayed with certain insecticides become more attractive to ovipositing Heliothinae. In order to evaluate the effect of spraying on oviposition by *H. armigera*, six of the plants were chosen in sprayed+barrier plots, and six in (unsprayed) barrier plots. Egg recruitment in control plots was not measured but was assumed to be the same as in barrier plots.

Results

Fig. 9.2 shows the densities of anthocorids in the three treatments. Data are pooled per week. In the control and barrier treatments, levels of adult anthocorids were initially low, but reached levels of 2 to 4 per plant in the middle of the sampling season. In the third treatment, weekly spraying suppressed the adults considerably, although not totally; the average seasonal density in the sprayed+barrier treatment was significantly lower than in the unsprayed treatments ($P<0.05$, Scheffé's multiple range test). It was examined graphically for each predator whether different treatments had equal variances.

The average seasonal density in the sprayed+barrier treatment was 0.34 per

Table 9.1 Average number of predators per plant during the sampling period. Multiple range test ($P<0.05$, Scheffé) of plot averages ($n=3$) is indicated.

	Anthocoridae		
Treatment	adults	nymphs	Ants
Control	1.38 b	1.35 b	2.05 b
Barrier	1.29 b	1.14 b	0.86 a
Sprayed+barrier	0.34 a	0.40 a	0.48 a

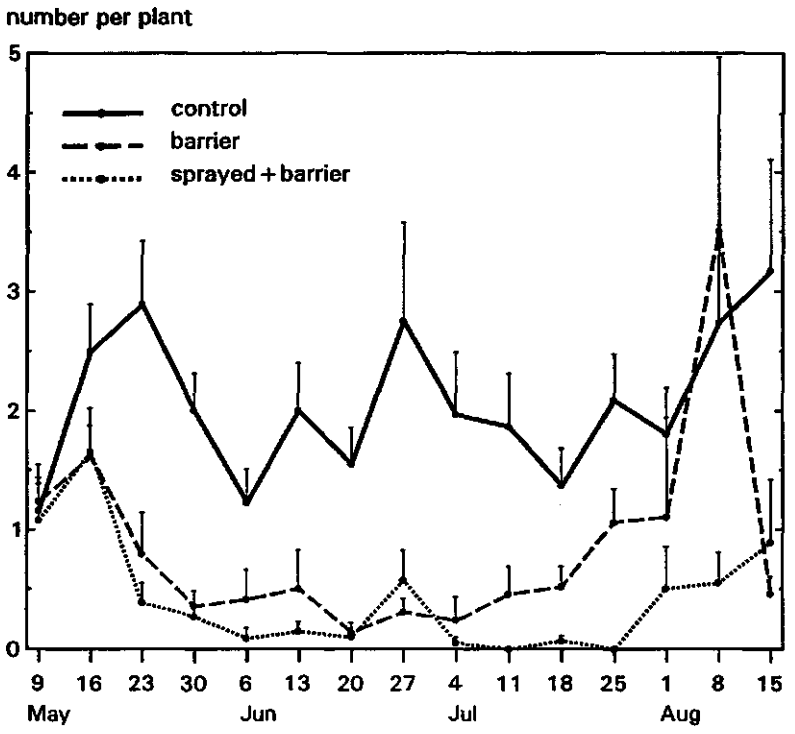

Fig. 9.3 Mean number of ants per plant in control, barrier, and sprayed+barrier treatments of cotton. Vertical bars indicate s.e.

plant as compared to 1.38 in the control and 1.29 in the barrier treatments (Table 9.1). Anthocorid nymphs built up to levels of about 3 per plant in the unsprayed treatments; this was considerably lower than in a study during the preceding year in the same plot, when nymphal densities reached more than 15 per plant (Cock *et al.* 1991). Again, nymphal density was significantly lower in the sprayed treatment (0.40 per plant) than in the unsprayed treatments (1.35 in the control and 1.14 in the barrier) (Table 9.1). Spraying, therefore, suppressed the levels of anthocorids by a factor of about 75% for adults and 68% for nymphs.

Ant barriers, which were placed during the second week of sampling, effectively excluded ants from plants in the barrier and sprayed+barrier treatments (Fig. 9.3); although ants visited the banded plants towards the end of the season via boll-bearing cotton branches that touched the ground. The average ant levels were 2, 0.86 and 0.48 per plant in the control, barrier and sprayed+barrier treatments respectively (Table 9.1).

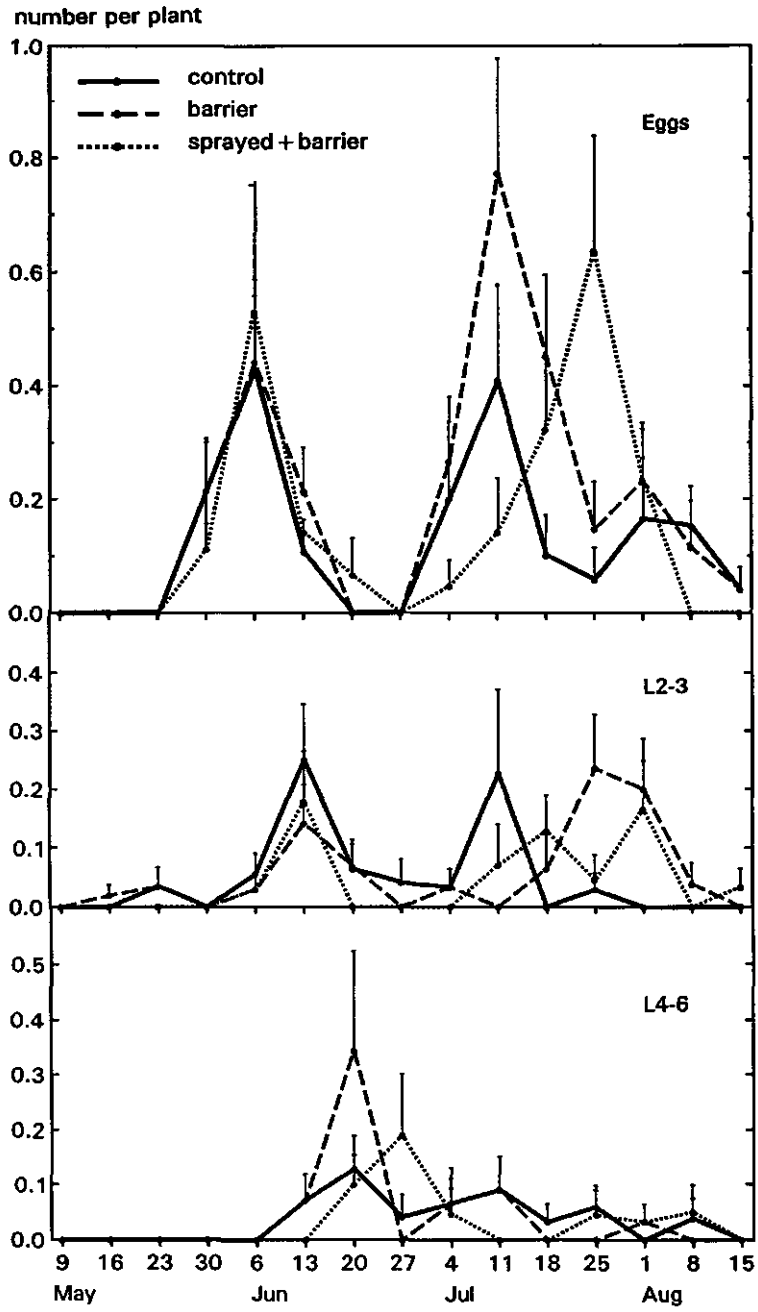

Fig. 9.4 Mean number of *H. armigera* stages per plant in control, barrier, and sprayed+barrier treatments of cotton. Vertical bars indicate s.e.

Fig. 9.4 shows the levels of *H. armigera* stages in the three treatments. In the control, egg densities were low (with a maximum of 0.4 eggs per plant), and showed two distinct peaks during the season, separated by five weeks, suggesting that two generations developed on the crop. A faint third peak was observed towards the end of the season.

The L2-3 peaks were lower than the egg peaks, which indicates a high mortality, especially because the development time of L2-3 stages is longer than that of eggs. Again, densities of L4-6 were lower than those of the preceding stages, while the development time of L4-6 is longer than that of L2-3. This is an indication that natural mortality was high. The barrier and sprayed+barrier

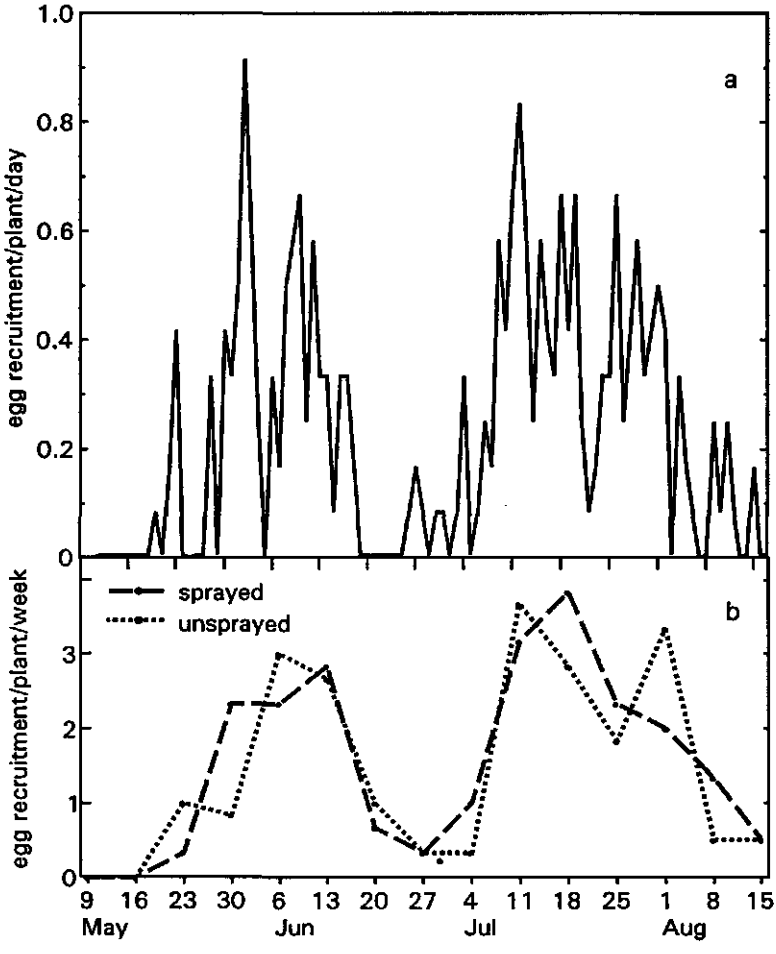

Fig. 9.5 Egg recruitment of *H. armigera* on cotton. (a) Daily recruitment pooled over unsprayed and sprayed plots. (b) Weekly recruitment in unsprayed and sprayed plots.

Table 9.2 Recruitment (Lx, in number per plant, with s.e. between plots) and percentage mortality (100 Qx) of *H. armigera* in three predator exclusion treatments in cotton (n=3 plots). Recruitment of eggs was measured directly, while recruitment of larval instars (L2-6) was estimated from stage-frequency data.

	Control			Barrier			Sprayed+barrier			
X	Lx	s.e.	100 Qx	Lx	s.e.	100 Qx	Lx	s.e.	100 Qx	
Generation 1										
Eggs	8.67	0.61		8.67	0.61		8.67	0.61		
L2-3	0.75	0.05	91.3	0.52	0.13	94.0	0.34	0.11	96.1	*
L4-6	0.21	0.16	71.6	0.30	0.15	41.9	0.20	0.06	39.8	*
Total mortality			97.5			96.5			97.7	
Generation 2										
Eggs	14.00	1.38		14.00	1.38		14.00	1.38		
L2-3	0.46	0.37	96.7	0.85	0.27	94.0	0.70	0.37	95.0	*
L4-6	0.11	0.06	75.6	0.04	0.02	95.1	0.07	0.05	89.3	*
Total mortality			99.2			99.7			99.5	

* Treatment did not affect recruitment of L2-3or L4-6 ($P > 0.05$, ANOVA).

treatments showed a similar oviposition pattern, but for both treatments the second egg peak was slightly higher than in the control. Larval levels were similar in the three treatments, indicating that mortality was about equally high in all treatments.

The daily recruitment of eggs, measured separately on trap plants, is shown in Fig. 9.5a. There are two distinct peaks of which the second is greater than the first. Fig. 9.5b shows the egg recruitment in the sprayed and unsprayed barrier plots. No significant effect of spraying was found ($P>0.05$, ANOVA, n=3), which indicates that spraying did not deter or attract ovipositing moths. We have therefore pooled egg recruitment estimates into one value for all treatments. During the total growing season, an average of 22.7 eggs was deposited per plant.

Table 9.2 shows the stage recruitment and the mortality between stages. The two generations of the *H. armigera* were taken separately, in order to evaluate mortality per generation; the boundary between the generations was set at 24 June for eggs, 1 July for L2-3 and 8 July for L4-6. In the first generation, 8.7 eggs were recruited per plant. Mortality from eggs to L2-3 was higher (91-96%) than from L2-3 to L4-6 (40-72%). In the second generation, mortality was significantly higher than in the first generation ($P<0.05$, Sign Test of paired data, n = 9). Even though recruitment of eggs in the second generation was

greater than in the first generation, the level of L4-6 was lower than in the first generation. There was no effect of treatment on the recruitment L_x of L2-3 or L4-6.

Parasitism of eggs by three *Trichogrammatoidea* spp. (*T. lutea* Girault, *T. simmondsi* Nagaraja and an unidentified species; Hymenoptera: Trichogrammatidae) was about 10%, while parasitism of larvae by *Dolichogenidea* (*Apanteles*) sp. (Hymenoptera: Braconidae) was less than 5 %, and thus contributed little to mortality.

Discussion

This study demonstrates the value of integrating exclusion methods and life table studies. In regular life tables, predation is included in the unknown mortality. Experiments on assessment of predation, on the other hand, rarely reveal the impact of predators in relation to total natural mortality of the pest, or what part of the impact is irreplaceable mortality. Moreover, exclusion experiments are frequently conducted under unrealistic density or environmental conditions, or they study the impact at one point of time without considering seasonal changes in, for instance, arthropod densities or crop architecture. By combining life tables and exclusion techniques (i.e., that do not affect the pest), the irreplaceable role of predators can be demonstrated in the context of total natural mortality of the pest.

The presented experimental set-up measures the irreplaceable mortality of two groups of predators, crawling predators (i.e., the difference in *H. armigera* levels between the barrier and the control), and crawling plus flying predators (i.e., the difference in *H. armigera* level between the sprayed+barrier and control). Comparison of barrier and sprayed+barrier treatments would not necessarily reflect the irreplaceable role of flying predators, because some of the observed difference may be replaceable by ants. Measurement of irreplaceable mortality due to individual predator groups would be relevant for accurate evaluation of pesticide effects on natural control. For instance, if a pesticide kills one predator but is tolerated by another, the latter may respond by consuming more prey because of reduced competition.

Measured mortality of eggs and larvae of *H. armigera* was very high in the control treatment (only 1.3% of the eggs deposited per plant reached the L4-6 stage in the exclusion treatments), and removal of predators did not affect survival of the pest. This indicates that background mortality due to factors other than natural enemies, for instance abiotic or host plant factors, was high, and obscured the impact of predation. In other words, the level of predation may have been considerable, but relative to other mortality factors its role was negligible.

A field cage study on cotton, which was conducted alongside the present study at Kibos, showed that local natural enemies had a strong impact on *H. armigera* cohorts; larval levels were 4½ to 6½ times higher in cages without natural

enemies than in control cages (Chapter 10). Moreover, exposures of *H. armigera* egg cohorts on trap plants in the same trial showed that anthocorids killed up to 65% of the eggs within a two-day period (Chapter 11). Although both trials were conducted with *H. armigera* densities above the local infestation level, this confirms that predators cause considerable mortality of *H. armigera* populations, although in the present study this impact was overshadowed by high background mortality.

The high mortality in the exclusion treatments may not be attributable entirely to background mortality factors, for the role of predation may have been underestimated in two ways. Firstly, the predator exclusion was not complete, and predators were still found at low densities in plots with adhesive barriers and/or triazophos spraying. The role of these predators was not taken into account, while individual predators perhaps consumed more prey in this situation with reduced competition than those in the control. Secondly, the low concentration of triazophos applied to the crop in the sprayed+barrier plots could have adversely affected the survival and development of *H. armigera* larvae, and would thus underestimate the role of anthocorids and other flying natural enemies.

Greatest mortality occurred during the early developmental stages of *H. armigera*. Kyi *et al.* (1991) showed that the survivorship of young *H. armigera* stages on cotton decreased most rapidly at the time of hatching of neonates and this decline was mainly attributable to host plant effects. Fitt (1989) argued that susceptibility of neonates to allelochemicals in the cotton plant may explain much hatchling mortality.

In the present study, mortality was greater in the second generation than in the first. Because there was no effect of predation, a change in host plant condition or microclimate could have resulted in a lower survival. In a parallel study, where egg cohorts were introduced on plants in the field, fewer larvae established as the crop matured (Chapter 10). This is supported by unpublished data from southern Africa, referred to by Pearson (1958; p.156), where survival of the first generation of *H. armigera* was 10%, while survival of the second generation was only 1-2%. Pearson argued that a shortage of fruiting bodies and a diminished nutritive value of squares later in the season were responsible for the low establishment of larvae. Hogg & Nordheim (1983) found a greater density of squares in the second than in the first generation of Heliothinae in North America, and this coincided with a greater survival of the second generation. Slosser *et al.* (1978) reported that *Helicoverpa zea* (Boddie) would develop to damaging levels only if the density of squares was above a critical level.

As cotton is extensively grown in semi-arid areas, the crop frequently suffers from water stress. From 13 June to 15 August, our crop received on average only 1.3 mm of rain per day, and consequently the number of squares per plant (i.e., preferred feeding sites of young *H. armigera* larvae) declined. Hence, moisture stress of cotton appears to be an important factor regulating *H. armigera* populations through the availability of suitable feeding sites. Furthermore, decreased humidity may contribute to the low survival of eggs (Fye & Surber

1971, Qayyum & Zalucki 1987). During moisture stress, leaf transpiration declines and consequently the humidity in the microclimate around the egg drops while the temperature increases (Willmer 1982). In seasons with higher rainfall, or where cotton is irrigated, background mortality of *H. armigera* would be lower and the impact of natural enemies more crucial.

Moisture stress also affects survival both directly and indirectly via the efficacy of natural enemies (Hogg 1986). For instance, on a crop with few squares, larvae are more accessible to predators and suffer more predation. Likewise, host plant condition influences the larval development rate and hence the time of exposure to predators. Yet, like *H. armigera*, predator populations may also increase with the density of squares in cotton (Stone *et al.*, 1984).

When natural control cannot be relied upon, microbial agents (Bell 1982, Jayaraj *et al.* 1989) or selective chemical insecticides that have limited effect on natural enemies (Plapp & Bull 1989), would be suitable to suppress *H. armigera* and other cotton pests, but are expensive for smallholder farmers. Even though natural enemies did not cause important irreplaceable mortality in this particular situation, they clearly do have a potential to suppress the pest, as we will show separately, and therefore their populations should be conserved and encouraged, in particular early in the season when populations start building up.

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10

Exclusion cage studies in cotton on the impact of predators[1]

ABSTRACT - The impact of predation on *H. armigera* was studied in four field cage exclusion trials on cotton in Kenya. *H. armigera* egg cohorts were introduced inside predator-free and open control cages, and the impact of local predator populations on the cohort was examined. Fourteen days after inoculation, exclusion cages had 4½ times more larvae than controls, indicating a strong impact of predation. Ants and Anthocoridae were the predominant predator species. Exclusion cages had more damaged fruiting plant parts (squares, flowers and bolls) than the control. In the absence of predators, natural mortality of *H. armigera* was greater as cotton matured, and is likely to be linked to the host plant condition.

Introduction

The African bollworm, *Helicoverpa armigera* (Hübner) (= *Heliothis armigera*) (Lepidoptera: Noctuidae), is a major pest of cotton throughout the Old World tropics and sub-tropics (Matthews 1989). In a previous contribution we showed that natural mortality of *H. armigera* stages in smallholder crops in western Kenya can be very high (Chapter 5). The role of parasitoids and pathogens was small, but predation was thought to be a likely important mortality factor. Ants and anthocorid bugs were the predominant predator groups. Observations of egg cohorts on cotton indicated that anthocorid populations consumed up to 65 % of the eggs within 48 hours (Chapter 11).

To evaluate the role of these predators, we excluded ants by sticky barriers around the stem of plants, whereas anthocorids were excluded with a low dosage of insecticide that killed the predator but not the pest (Chapter 9). By regular sampling of stage-frequency data of *H. armigera* we assessed mortality in plots with and in plots without predators, and thus measured the irreplaceable mortality due to predation in relation to other mortality factors. Infestation levels of *H. armigera* were unexpectedly low, and in addition, background mortality of *H. armigera* due to factors other than predation was very high (96.4-99.7%). Consequently, the levels of remaining *H. armigera* larvae were too low (0.1-0.2 larvae per plant) to measure a significant impact of predation.

The pest status of *H. armigera*, both in the area and in the region, clearly indicates that *H. armigera* larval infestation is normally more severe. For

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development of an IPM strategy of the pest it is essential to assess the potential role natural enemies play in suppressing the pest, and so in this study we measure the impact of predation on inoculated cohorts of *H. armigera* to overcome the problem of low pest densities. To exclude predators we use cages, which enable the assessment of predation under controlled, manipulated conditions at various stages of development (Luck *et al.* 1988).

Materials and Methods

At the National Fibre Crops Research Station, Kibos, South Nyanza Province, unsprayed cotton (var. BPA-75, spacing 90x30 cm) was grown in a field surrounded by a strip of weeds 1 to 5 m wide, and separated from fields where pesticides were used by at least 150 m.

Trial 1 was conducted during the 1989/90 short rains. In a 400 m^2 plot of cotton, planted on 18 October 1989, we set up four field cages - two predator exclusion and two controls. In this first trial, exclusion cages were made predator-free by hand-removal of nymphs and adults of all potential predators, including predatory bugs, coccinellids, ants and spiders, and also pests such as cotton stainer, *Dysdercus* spp. (Hemiptera: Pyrrhocoridae), and cotton seed bug, *Lygus* sp. (Hemiptera: Lygaeidae). Because predators may emerge from eggs laid before the experiment, and because small predator stages may be overlooked on plants on the first occasion, predators were removed every two days, starting four days prior to the experiment and continuing until eight days after inoculation. Aphids were not removed.

Trials 2, 3 and 4 were conducted during the 1990 long rains, in a 600 m^2 plot of cotton (planted 14 February 1990) which bordered a 1 ha experimental plot of cotton. General crop development and rainfall pattern was similar to that of the 1989 trial. Eight cages, comprising four exclusions and four controls, were set up. Four days prior to inoculation, the plants in the exclusion cages were carefully sprayed with cypermethrin (0.31 kg a.i. per ha.), a rapid-action insecticide, to remove arthropod fauna. Careful examination of plants one day after spraying confirmed that all predators had died. For each trial, cages were transferred to cover new plants, and spraying was carried out four days prior to inoculation with eggs, except that in trial 4, the plants of the preceding trial were used without transferring cages, because very few *H. armigera* larvae established during trial 3, and thus caused negligible damage to the crop.

Cages (LxWxH, 4x2x1.8 m), constructed with bamboo poles connected with a frame of metal wire on top, were covered with 0.5 mm nylon mesh. A cage enclosed on average 24 plants of cotton. Exclusion cages had the bottom margin of the net buried 10 cm deep into the soil to keep predators out. As ants occassionally managed to enter the cage through the soil, all plants in exclusions cages were banded with a ring of insect trap adhesive (Tanglefoot^R) placed at about 10 cm above the ground. Ants were further prevented from visiting the crop by pruning cotton branches that touched the ground or nylon netting, and by

keeping plots clear of weeds. For consistency, pruning of branches and weeding was done in both treatments. Control cages had the lower margin of the net lifted 30 cm above the ground to allow entry of local natural enemies. Outside control cages, plants closer than 0.8 m to the cage were removed to discourage *H. armigera* larvae from leaving the cage. Cages were positioned in a regular pattern, and were randomly assigned as exclusion or control treatments.

For provision of eggs, *H. armigera* moths were reared in the laboratory and the culture was supplemented with light trap catches. Inside 4000 ml plastic jars, with a nylon cover for ventilation, moths oviposited overnight on blue tissue paper. For inoculation, the tissue was cut into 0.3-1 cm^2 pieces, each containing 3-8 viable (two days old) eggs. Pieces of tissue paper were randomly allocated between the cages, and in each cage, fifty pieces (i.e., 150-400 viable eggs) were placed inside squares or - in the absence of squares - behind flower bracts distributed over the cotton plants. Prior to inoculation, cotton plants were carefully examined and field populations of *H. armigera*, occurring at rather low levels during the trials, were hand-removed.

Larvae of *H. armigera* and possible predators were sampled 14 days after the inoculation, before the cohorts of *H. armigera* had reached their most active larval stages that might move from plant to plant and perhaps leave the cages. All plants inside the cages were sampled, checking every individual plant part. Fruiting plant parts were counted, and those showing *H. armigera* feeding were recorded separately.

We used multiple regression with Poisson error distribution (log-link) to determine the amount of deviance in numbers of arthropods and fruiting plant parts (per cage) unambiguously attributable to treatment, trial and their interaction, using the GLIM package (McCullagh & Nelder 1989, Aitkin *et al.* 1990). The explanatory power of a variable is roughly estimated by the percentage of the total deviance (the equivalent of variance) that is attributable to that variable in the saturated model.

Results and Discussion

Results of the four trials were combined and Table 10.1 shows the average numbers of arthropods and fruiting plant parts per cage. A large difference was found in *H. armigera* levels between the treatments: fourteen days after inoculation, the exclusion treatment had 24.5 larvae per cage, which is 4.5 times more larvae than the control, indicating a strong effect of predation. The effect was strongest in trial 1 and 2, where densities in the exclusion treatment were considerably higher (2.6 larvae per plant) than in trial 3 and 4 (0.4 and 0.6 larvae per plant, respectively).

Ants and anthocorids were the commonest predators, but predators included coccinellids, *Chrysoperla* sp. (Neuroptera: Chrysopidae), and *Geocoris amabilis* Stål (Hemiptera: Lygaeidae). *Myrmicaria* sp. *Camponotus* sp. and *Pheidole* sp., were the most common ants, and *Orius albidipennis* (Reuter) and *O. thripoborus*

Table 10.1 Numbers of *H. armigera* and predators, and numbers of undamaged and damaged fruiting plant parts per cage, in predator-exclusion cages and open cages. Results are averages of four trials. Cotton, Kibos, 1989-90.

	EXCLUSION	CONTROL
H. ARMIGERA		
Total larvae	24.5	5.4
PREDATORS		
Ants	1.6	40.1
Anthocorid adults	2.6	26.7
Anthocorid nymphs	6.9	37.4
Others	5.7	8.6
UNDAMAGED PLANT-PARTS		
Undamaged squares	66.6	102.7
flowers	12.8	20.9
bolls	76.3	96.3
Total	155.7	219.9
DAMAGED PLANT-PARTS		
squares	50.7	38.4
flowers	19.4	11.0
bolls	60.5	53.0
Total	130.6	102.4

(Hesse) the predominant anthocorids. Table 10.1 of predator numbers per cage, shows that in the experimental condition predators were substantially reduced, although exclusion was not absolute. Predator densities were measured at the end of the experiment, eight days after the last hand-removal of predators (trial 1), or 16 days after spraying (trials 2-4) in the exclusion treatment.

Because predators may emerge from eggs or enter the exclusion cages during the experiment, predator densities in the exclusion were lowest at the beginning of the experiment, when the cohort of *H. armigera* stages were most vulnerable to attack by for example, anthocorids. The effect of exclusion on parasitoids was not evaluated in this study, but parasitism of *H. armigera* was assessed concurrently in a bordering plot. Total generational parasitism, by three *Trichogrammatoidea* spp. (Hymenoptera: Trichogrammatidae) and by *Dolichogenidea* sp. (Hymenoptera: Braconidae), was 15 %, and thus contributed relatively little to mortality of *H. armigera*.

Table 10.1 also presents the number of undamaged and damaged fruiting parts of cotton. Results of trials 1, 2 and 4 were combined; plant parts of trial 3 were recorded in trial 4 as described above. Undamaged squares, flowers and bolls

Table 10.2 Explanatory power (EP) and deviance of the main effects and their interactions for *H. armigera* larvae and predators, expressed as a percentage of total deviance (df=27).

		H. armigera larvae		Anthocorid adults		Anthocorid nymphs		Ants	
Factor	df	%EP	Dev.	%EP	Dev.	%EP	Dev.	%EP	Dev.
Trial	3	47.9	271.2*	6.7	32.8*	28.0	244.5*	8.6	79.6*
Treatment	1	32.9	186.1*	65.9	321.0*	37.2	325.0*	66.7	615.7*
Trial x treatment	3	3.2	17.8*	8.0	38.9*	17.3	151.3*	1.2	11.1**

* $P < 0.001$; ** $P < 0.025$ (X^2-test).

were most common in the control, and damaged squares, flowers and bolls were most common in the exclusion cages. This indicates that a two-week exclusion of predators affects damage. Despite low levels of *H. armigera* in the control, damage was only slightly lower in the control than in the exclusion cages; in the control 32 % of the fruiting plant parts were damaged, versus 46 % in the exclusion cages. This is because feeding damage by natural populations of *H. armigera* was present prior to the two-week experimental trials. In trial 1 and 2, which were conducted 17 weeks after planting (w.a.p.), there were more squares than bolls, but in the fourth trial, conducted 25 w.a.p., bolls outnumbered squares.

Table 10.2 shows the deviance unambiguously attributed to each of the factors in the regression model, trial and treatment, and their interaction. The deviance of the saturated model is overdispersed, leaving 16-23 % of the total deviance unexplained (against 20 df), therefore significance was tested not with X^2, but with the F-ratio. As expected, trial explains a large amount of deviance in *H. armigera* numbers, because numbers were much greater in the first two than in the last two trials. Treatment explained 33 % of the total deviance, a highly significant amount. Although the interaction explained only 3 % of the deviance, this was still significant ($P < 0.001$, X^2-test), indicating that the effect of treatment was different between trials; as mentioned above, exclusion affected *H. armigera* most strongly in the first two trials.

Table 10.3 Explanatory power (EP) and deviance of the main effects and their interactions for undamaged fruiting parts of cotton, expressed as a percentage of total deviance (df=18).

		Squares		Flowers		Bolls		Total	
Factor	df	%EP	Dev.	%EP	Dev.	%EP	Dev.	%EP	Dev.
Trial	2	47.2	381.9*	38.2	68.4*	62.9	438.6*	42.5	409.3*
Treatment	1	12.3	99.2*	11.5	20.5	2.4	16.8	12.2	116.9*
Trial x treatment	2	14.7	118.8*	5.2	9.3	13.5	93.9*	16.7	160.8*

* $P < 0.05$ (F-test)

The occurrence of anthocorid adults was rather constant from trial to trial, and most deviance is attributable to treatment. Numbers of anthocorid nymphs were more variable between trials. The interaction for anthocorid nymphs explained a large amount of deviance, suggesting that nymphs were not excluded equally well from every trial: in trial 1, anthocorid nymphs were more numerous in exclusion cages than in other trials, because hand-removal of these small predator stages was less satisfactory than spraying.

The bulk of deviance in ant numbers was attributable to treatment.

In a similar analysis for numbers of fruiting parts of cotton, the deviance of the saturated model was overdispersed, leaving 21-53 % of the total deviance unexplained. Therefore significance was tested not with X^2, but with the F-ratio. The degrees of freedom had dropped to 18, because plant parts were not recorded in trial 3, as discussed above. For undamaged plant parts (Table 10.3), trial explained much more deviance than treatment, but the effect of treatment was significant for squares.

For all parts combined, treatment explained a significant amount of deviance in the number of undamaged parts per cage, indicating that exclusion of predators affected the number of undamaged fruiting parts.

For numbers of damaged plant parts (Table 10.4), a major part of the deviance was explained by trial. When combining squares, flowers and bolls, treatment explained less deviance for damaged than for undamaged fruiting parts (31.3 vs 116.9). This indicates that exclusion of predators had more effect on the number of undamaged than on the number of damaged fruiting parts. Larval feeding causes squares, flower, and young bolls to shed (Hearn & Room 1979). Although this leads to undersampling of damaged plant parts, shedding of plant parts does not explain why proportionally less deviance is attributable to treatment than to trial in comparison to undamaged plant parts. However, at high

densities larvae may cause more severe feeding damage before moving to the next fruiting part, than at low densities. If plants shed fruiting parts more rapidly when damage is more severe, this may obscure the effect of treatment and may explain the low deviance attributable to treatment.

Table 10.5 shows the mortality of *H. armigera* during the experiment in the predator exclusion cages, based on the number of viable eggs per plant at inoculation and the number of larvae per plant 14 days after inoculation. The wide range of mortality estimates is due to the variable number of eggs (3-8) per piece of tissue paper; in reality however, the number of eggs per tissue fragment - and thus the mortality level - was somewhere between the two estimates. Despite these ranges, it is obvious that mortality is greatest in the last two trials. Here, only 3-9 % of *H. armigera* had established, under almost complete exclusion of predators. This suggests that major mortality factors other than natural enemies fluctuate greatly.

In a separate paper we have shown that the second generation of *H. armigera* on cotton suffered greater mortality than the first generation, and this difference was not attributable to natural enemies (Chapter 9). We suggested that change in host plant condition is a likely cause. Detailed life table studies by Kyi *et al.* (1991) showed that the survivorship of young *H. armigera* stages on cotton decreased most rapidly at the time of hatching of neonates, and this decline was not attributable to natural enemies but mainly to host plant effects. *H. armigera* oviposit most commonly on leaves of cotton, while young larvae feed almost exclusively on the soft plant parts of the squares and flowers (Chapter 6). This means that neonates have to search for and move to rather distant feeding sites. This may cause major mortality, and the proportion surviving would depend strongly on the physiological condition of the plant and the availability of squares. In our studies, the crop suffered from drought-stress more during trials 3 and 4

Table 10.4 Explanatory power (EP) and deviance of the main effects and their interactions for damaged fruiting parts of cotton, expressed as a percentage of total deviance (df=18).

		Squares		Flowers		Bolls		Total	
Factor	df	%EP	Dev.	%EP	Dev.	%EP	Dev.	%EP	Dev.
Trial	2	65.6	352.6*	35.4	106.9*	55.6	242.4*	47.0	382.9*
Treatment	1	1.9	10.1	6.8	20.4	1.9	8.2	3.8	31.3
Trial x treatment	2	3.1	16.5	4.6	14.0	2.6	11.1	2.7	21.6

* $P < 0.05$ (F-test)

Table 10.5 Natural mortality of *H. armigera* in predator exclusion cages at different ages of the crop.

Trial	w.a.p.*	plants/cage	eggs (d.0)**	larvae (d.14)***	% mortality
1	17	22.3	6.6–17.5	2.67	61–85
2	17	21.1	7.1–18.9	2.7	62–86
3	23	26.8	5.6–14.9	0.38	93–97
4	25	25.6	5.9–15.6	0.55	91–97

* week after planting
** viable eggs per plant at inoculation
*** larvae per plant 14 days after inoculation

than during trials 1 and 2, and the number of squares per plant was lowest in the last two trials. Thus host plant factors may have contributed strongly to the establishment of larvae in trials 3 and 4. This shows that high levels of oviposition of *H. armigera* on cotton do not necessarily result in damaging levels of mature larvae, but larval levels strongly depends on the level of natural mortality, e.g., according to a changing host plant condition or the local abundance of natural enemies. This highlights a limitation of the use of fixed threshold levels of young *H. armigera* stages for IPM strategies.

By introducing cohorts of *H. armigera* into the cages, densities of eggs and, subsequently, larvae were many times greater than those found locally. At inoculation, egg density was on average 12 per plant, whereas local egg densities in a bordering plot never exceeded a weekly average of 1 egg per plant, although densities are probably higher in other seasons. Likewise, larval levels were 2.7 per plant in the first two trials, while local levels were below 1 larva per plant. Our experimental levels may or may not be normal, but by using them we have demonstrated that predators are capable of suppressing *H. armigera* at high infestation levels. It could be suggested that high densities of prey may have arrested predators inside the control cages, and these increased predator densities could have led to overestimation of predation, however comparison of predator densities reported for control cages in Table 10.1 with those recorded concurrently in the bordering plot (Chapter 9) showed no difference.

Another shortcoming of the use of cohorts is that all individuals are of the same age, whereas in natural populations on cotton stages are largely mixed (Hogg & Nordheim 1983, Cock *et al.* 1990). This artificial age-structure may result in underestimation of the predation rate if predators are specific to certain stages of the prey. The predator complex on cotton consists predominantly of

ants and anthocorids, which show some degree of stage-specificity: anthocorids attack eggs and neonates, but not larger larvae of *H. armigera*, while *Myrmicaria* was regularly observed attacking larvae but not eggs (H. van den Berg, pers. observ.) and *Pheidole* attacks both eggs and larvae. Thus, the use of cohorts may have led to the underestimation of normal predation.

Predator exclusion studies that use manipulated prey or natural enemy numbers should be interpreted in relation to life table studies of the pest, so that the observed impact can be interpreted in relation to other mortality factors under local field conditions. The present study shows that predators have a great impact on *H. armigera* in cotton in terms of percentage predation. In the absence of predators, *H. armigera* levels were four to six times greater, and two-week exclusion had a significant effect on the numbers of damaged and undamaged fruiting parts of cotton, demonstrating the need to develop an IPM strategy for cotton that is based on the conservation and encouragement of natural enemies.

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11

Predation and parasitism on egg cohorts[1]

ABSTRACT - Egg cohorts of *H. armigera* on plants of cotton and sunflower were exposed in the field for 48 hours. In five trials on cotton, 12-65 % of the eggs were sucked by anthocorids, 8-27 % was lost due to chewing predators and abiotic factors, and 0-13 % of the initial number of eggs was parasitized. In seven trials on sunflower at another location, an average of 25 % of the eggs was lost after 48 hours, and there was no parasitism of eggs. Eggs on the stem and bud suffered more predation by anthocorids than those on the leaves. Seven species of anthocorids and seven species of egg parasitoids were found. The development period of eggs was measured on plants in the field concurrently with the trials, and was 4.3 days at 23°C on cotton, and 5.2 days at 20.5°C on sunflower.

Introduction

In East Africa, the African bollworm, *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) (=*Heliothis armigera*), is a pest problem on cotton and sunflower. Mortality of *H. armigera* mostly occurs during the early developmental stages, from the egg stage until the young larval stages (Chapter 5), but it has been largely unknown what factors are responsible. In Kenya, two groups of natural enemies are commonly found that attack the egg stage of *H. armigera*: egg predators of the family Anthocoridae (Heteroptera), and egg parasitoids of the families Trichogrammatidae and Scelionidae (Hymenoptera) (Chapter 4; van den Berg & Cock 1993).

Anthocorids are polyphagous predators that feed on soft-bodied prey such as thrips, mites and aphids, as well as eggs of Lepidoptera (Askari & Stern 1972, Evans 1976, Stoltz & Stern 1978). The main diet of some species may be plant pollen (Askari & Stern 1972, McCaffrey & Horsburgh 1986); some species have been shown to complete their development on a diet of pollen alone (Kiman & Yeargan 1985, Salas-Aguilar & Ehler 1977), and population increases commonly coincide with a period of pollen-shedding by host plants (Dicke & Jarvis 1962, Coll & Bottrell 1991, Chapter 5). In Africa, the role of anthocorids has already been recognized by Parsons & Ullyett (1934) and Peat (1935), who reported that *Orius* sp. destroyed 40 % of *H. armigera* eggs on cotton and maize. However, since then there have been virtually no reports of this predatory family attacking *H. armigera* in Africa.

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Egg parasitism of *H. armigera* has not been assessed in East Africa. In southern Africa, *Telenomus ullyetti* Nixon (Scelionidae) and *Trichogrammatoidea lutea* Girault have been documented as common parasitoids of *H. armigera*, sometimes causing important mortality (Parsons & Ullyett 1936, Jones 1937, van Hamburg 1981). In the event of multi-parasitism, the former species is generally the superior competitor over the latter (Kfir & van Hamburg 1988).

In this study we examine the impact of parasitoids and predators on *H. armigera* eggs on cotton and sunflower.

Materials and Methods

Field work was carried out at two research stations of the Kenya Agricultural Research Institute (KARI): the National Fibre Crops Research Station, Kibos, South Nyanza Province, which is a relatively hot and dry location with 'black cotton soil' in the Lake Victoria Basin, and the Western Agricultural Research Centre, Kakamega, Western Province, which is a relatively cool upland site, with high annual rainfall (1950 mm). At Kibos, cotton (var. BPA-75, spacing 90x30 cm) was planted during the long rains seasons of 1989 and 1990. In 1989, 0.15 ha of cotton was planted in replicated plots in a mosaic pattern with maize and sorghum. In 1990, 0.36 ha of cotton was planted in 9 sub-plots, each surrounded by a strip of arable land. At Kakamega, sunflower (var. Comet, spacings 75x30 cm) was planted during the short and long rains of 1989 and 1990. Each season, 0.15 ha of sunflower was planted in replicated plots in a mosaic pattern with maize and sorghum. In addition, a single 0.04 ha plot of sunflower was planted during the short rains of 1990/91.

For a realistic assessment of egg mortality, egg cohorts in our study were laid by moths rather than manually glued on plants, thus allowing for dislodgement by rain and wind (Nuessly 1986). Before oviposition, plants were manually searched for *H. armigera* eggs which were removed. Cages (LxWxH, 0.7x1x1.5 m, with 0.5 mm diameter nylon mesh and supported at each corner with a stick, each covered a 1 m row (i.e., 3 plants) of cotton or sunflower. Just before dusk, 6-12 moths of mixed sexes, from the laboratory culture supplemented with light-trap catches, were released inside each cage for oviposition. *H. armigera* oviposits primarily in the evening hours, from 18.30 to 23.00 hr (Topper 1987).

Next morning at 8 a.m., moths were caught, cages removed, and the eggs newly deposited on plants were marked by putting a small dot of liquid paper (typewriter correction fluid) at 0.5-1 cm distal to the egg. When more than 20 eggs were laid per plant, the surplus was removed so that the number of eggs per plant ranged from 1 to 20. The within-plant distribution of eggs deposited by caged moths on cotton was similar to that of natural *H. armigera* populations (Chapter 6), most eggs being laid on the leaves. On sunflower, the distribution of eggs on caged plants was similar to the natural situation, with most eggs deposited on the receptacle of the flower head, except caged moths oviposited

proportionally more on leaves than did natural populations. Hence, the number of eggs on the leaves were reduced to simulate a realistic distribution of eggs.

After a 48 hour-period of field exposure, the eggs were examined using a 10-fold hand lens, and the fate of eggs was recorded as lost, present, or (for studies on cotton only) sucked. An egg was recorded as lost if no egg was present 0.5-1 cm distal to the marking, even when egg-remains characteristic of feeding by chewing predators were found. Hence, lost eggs included disappearance due to predation and non-biotic factors. An egg was recorded as sucked if the chorion of the egg had collapsed, characteristic of feeding by predators with sucking mouthparts which ingest the egg contents but leave the chorion intact. Unfortunately at Kakamega, we did not record sucked eggs separately, but counted them as lost. Eggs present after 48 hours were reared individually in ventilated tubes in the laboratory until emergence of *H. armigera* larvae or parasitoids. Mortality due to parasitism was calculated as a percentage of the initial number of eggs exposed (apparent mortality).

Exposures of eggs were made on several occasions at crop stages attractive to ovipositing moths. At Kibos, three exposures were made in the 1989 long rains season, and two during the 1990 long rains season. At Kakamega, five exposures were made in the 1989 long rains, one in the 1989/90 short rains, and one in the 1990 long rains. Densities of predators were measured by careful visual inspection of 30 randomly-selected plants each week.

Because sucked eggs were not recorded separately in the trails on sunflower, we conducted a study specifically on sucking predators. With oviposition and exposure methods as described above, egg cohorts were laid on ten plants. Eggs were numbered by writing with a felt-tipped pen on the plant structure near the egg, and the position of the egg within the plant was recorded to determine the fate of eggs in different microhabitats. Two weeks prior to the experiment, plants were banded with a ring of insect-glue painted around the stem of the plants, about 15 cm above the ground, in order to prevent interference from ants and other crawling predators.

The developmental period of eggs was measured under natural conditions in the field, both on cotton at Kibos and on sunflower at Kakamega. Eggs were laid on caged plants as described above. Cages were removed the next morning, and all eggs were numbered as above. Both at Kibos and Kakamega, the study was conducted 14 weeks after planting. Starting from 3.5 days after oviposition, eggs were checked regularly - every 1½ hour at peak emergence to every 6 hours towards the end of the experiment - to record the time of hatching of neonates. Sucked eggs were not recorded separately, but were counted as lost eggs.

Results

On cotton at Kibos, predation and parasitism had a considerable impact on *H. armigera* eggs (Table 11.1). On average, 38 % of the eggs were sucked, 15 % lost and 6 % parasitized two days after oviposition, leaving 41 % of the eggs

surviving. On one occasion, survival was as low as 22 %, mainly due to the high percentage sucked.

The percentage sucked fluctuated greatly. In 1989, the percentage sucked increased with crop age, and with the density of anthocorids. Anthocorids reached levels of 3 adults and 13 nymphs per cotton plant on 18 July 1989. In 1990 however, the density of anthocorids was lower than in 1989, while predation was greater. Predation events were observed regularly in the field, both by anthocorid adults and nymphs. A complex of seven species of Anthocoridae were found (Table 11.2). The number of specimens in samples are shown to indicate the relative abundance of species at a site, but these numbers should not be used to compare the abundance of anthocorids between the two sites. Most common species at Kibos were *Cardiastethus exiguus* (Poppius), *Orius albidipennis* (Reuter), *O. tantillus* (Motschulsky), *O. thripoborus* (Hesse). At Kakamega, the anthocorid fauna was less diverse and only *O. thripoborus* was common.

The percentage of eggs lost after 48 hours due to chewing predators or abiotic factors ranged from 8 to 27 %. Beside anthocorids, dominant predators were ants (Hymenoptera: Formicidae); at Kibos, the ant community consisted of *Myrmicaria*, *Camponotus*, and *Pheidole* spp.; at Kakamega, *Pheidole* sp. dominated. Small *Pheidole* sp. ants were sometimes seen removing eggs and carrying them off to their nests. Although there was some rain in two trials at Kibos, this had no clear effect the percentage of eggs lost.

Table 11.1 Fate of egg cohorts of *H. armigera* exposed on cotton in the field. Kibos 1989-90. Rainfall during the 48 hour experiment is indicated. The 1989 crop was planted on 5 March, the 1990 crop on 16 March.

Occasion	n*	rain mm	% sucked**	% lost***	% parasitized****	% survival
6 June'89	114	0	12.3	27.2	12.7	47.8
5 July'89	52	3.4	15.4	11.5	8.4	64.7
18 July'89	89	0	40.4	12.4	4.3	42.9
17 July'90	85	0	64.7	8.2	5.1	22.0
24 July'90	60	3.0	55.0	13.3	0.0	31.7

* Number of eggs exposed
** Eggs consumed by predators with sucking mouth parts, predominantly Anthocoridae
*** Due to predation and other causes
**** Percentage of initial eggs parasitized

Table 11.2 Anthocoridae[1] and egg parasitoids[2] of *H. armigera* and found on cotton at Kibos, and on sunflower at Kakamega, western Kenya, 1989-90. For Anthocoridae, numbers of specimens in samples are shown.

Species	Kibos	Kakamega
Anthocoridae		
Blaptostethus sp.	4	-
Cardiastethus exiguus (Poppius)	59	-
Cardiastethus sp.	4	-
Orius albidipennis (Reuter)	35	3
Orius tantillus (Motschulsky)	20	3
Orius thripoborus (Hesse)	90	48
Orius sp. A (nr. *thripoborus*)	4	-
Scelionidae		
Telenomus ullyetti Nixon	+	+
Trichogrammatidae		
Trichogrammatoidea armigera Nagaraja		+
Trichogrammatoidea eldanae Viggiani	+	
Trichogrammatoidea lutea Girault	+	+
Trichogrammatoidea simmondsi Nagaraja	+	+
Trichogrammatoidea sp.	+	+
Trichogramma sp.		+

[1] Det. G.M. Stonedahl, IIE
[2] Det. A. Polaszek, IIE

Parasitism was low relative to predation. Since its level was calculated against the initial number of eggs, parasitism may be underestimated if eggs are first parasitized and then sucked or lost. Beside the specialist scelionid *Telenomus ullyetti*, we found a complex of trichogrammatids in association with *H. armigera* eggs (Table 11.2). *Trichogrammatoidea eldanae* Viggiani and *T. simmondsi* Nagaraja have not been found attacking *H. armigera* before, but *T. lutea* Girault has been commonly recorded from *H. armigera* in southern Africa (Chapter 3). *T. armigera* Nagaraja, only found at Kakamega, had not previously been recorded from *H. armigera* in Africa (Polaszek *in* Cock *et al.* 1991). Another *Trichogramma* sp. could not be identified to species because the taxonomy of this genus in Africa is in a confused state currently (Pintureau & Babault 1986, A. Polaszek, pers. comm. 1991).

Table 11.3 Fate of egg cohorts of *H. armigera* exposed on sunflower in the field. Kakamega, 1989-90. Rainfall during the 48 hour experiment is indicated. The 1989 crop was planted on 6 April, the 1990 crop on 22 March.

Occasion	n*	rain (mm)	% lost**	% parasitized
1 June'89	95	5.9	32.6	0
15 June'89	38	46.1	42.1	0
17 June'89	99	2.4	14.1	0
25 June'89	66	0.2	13.6	0
9 July'89	104	0.3	22.1	0
1 Dec'89	64	0	26.6	0
23 July'90	54	0	20.4	0

* Number of eggs exposed
** due to predation and other causes, including sucked eggs

Table 11.3 shows the fate of egg cohorts on sunflower at Kakamega, where survival of eggs was considerably greater than on cotton at Kibos (on average, 75 vs 42 %). The percentage of eggs lost due to predators (including sucking predators) and other causes varied from 14 to 42 %, and averaged 25 %. In none of the seven exposures did we encounter egg parasitism. However, regular sampling of the same plots showed parasitoids were present at low levels, and species are presented in Table 11.2. Percentage of eggs lost was greatest in those trials which coincided with greatest rainfall. On 15 June 1989, it rained 46 mm and 42 % of the eggs disappeared, which is about 20 % more than in trials without rainfall. In the absence of rain, the percentage eggs lost remained variable.

Fig. 11.1 shows the results of the 1989/90 study on sucking predators on sunflower. Shown are mean percentage sucked and lost per plant, and the s.e. between plants. On average, 13.8 % of the eggs were sucked and 9.2 % were lost (n=127 eggs); this corresponds with the levels of consumed and lost eggs of Table 11.2. The percentage sucked and lost differed considerably between plant-parts. Percentage sucked was higher on the bud and the stem (20-25 %) than on the leaves (5-10 %). Percentage of eggs lost, on the other hand, was largest on the upperside of leaves and on the stem.

The development period of *H. armigera* eggs on cotton at Kibos was 4.3 days (s.d. 0.34; n=52), at a mean temperature of 23°C. At Kakamega, egg development took 5.2 days (s.d. 0.53; n=79), at a temperature of 20.5°C. Fig. 11.2 shows the emergence and cumulative emergence of eggs at Kakamega.

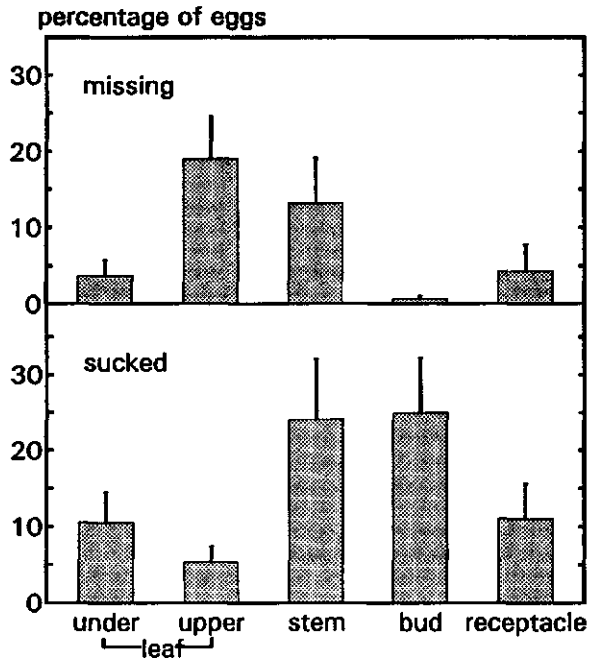

Fig. 11.1 Percentage of *H. armigera* eggs missing and consumed by sucking predators on different plant parts of sunflower. Kakamega, 1990/91.

Emergence started with a peak at noon of day 4. The last eggs emerged two days later. It was apparent that more eggs hatched during the day-time than after dark. Moreover it seemed that eggs exposed to the sun (e.g., on the upperside of the leaf) developed more rapidly than those in the shade (e.g., underside of the leaf)

Discussion

Our data show that natural enemies caused high mortality of *H. armigera* eggs on cotton at Kibos, but on sunflower at Kakamega the impact was considerably lower. Because anthocorids left a characteristic evidence of predation, their role could be assessed separately from other mortality factors. On cotton, anthocorids caused greater mortality than other predators or parasitoids. Surprisingly, in 1990, anthocorids caused greater mortality than in 1989 while they were less common (1.5 adult per plant). The 1990-crop suffered from drought-stress towards the end of the season, and plants had shed most of their fruiting parts. Because anthocorids often occur in the squares, flowers and bolls of cotton (Chapter 6), shedding of these parts may have caused anthocorids to forage more

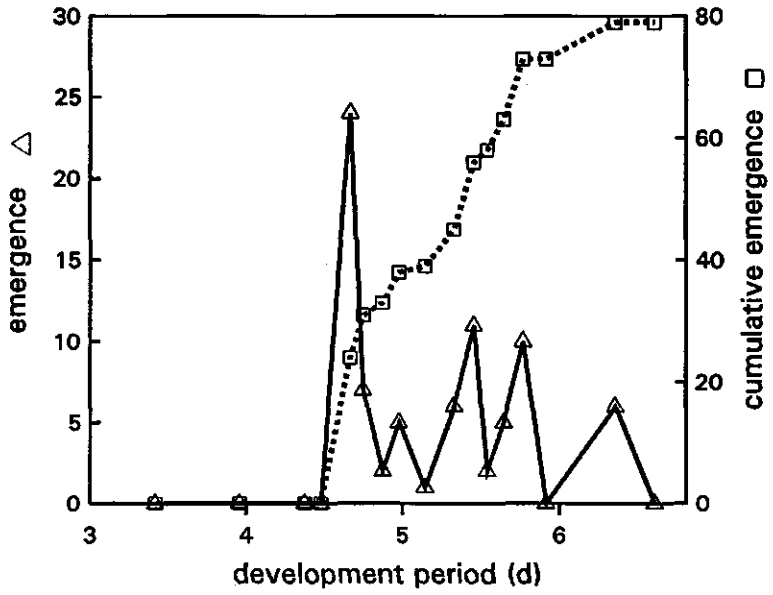

Fig. 11.2 Development period of a cohort of *H. armigera* eggs on sunflower in the field. Kakamega, 1990.

on other plant parts where *H. armigera* eggs are found, causing the high predation in 1990.

The percentage of eggs lost included those consumed by predators with chewing mouthparts. Ants were the most common group of chewing predators, and various species are known to remove eggs of Lepidoptera (Way & Khoo 1992); we observed *Pheidole* sp. removing eggs from sunflower and carrying them off to their nests. However, not all loss of eggs can be ascribed to predation. Our data from sunflower clearly indicate that more eggs were lost when it rained during a trial, although at most, rain dislodged about 20 % of the eggs. On cotton in Thailand, a two-hour rain storm reduced eggs of *H. armigera* by 80 % (Mabbett & Nachapong 1983). Nuessly *et al.* (1991) showed a relationship between the proportion of *Helicoverpa zea* (Boddie) eggs missing from cotton and the intensity of rain and wind, and developed a model to predict egg dislodgement. Their measure for rain intensity (in cm/h) is not applicable to our data, because it requires hourly rainfall records. They found that rain dislodged eggs at the tops of plants and on leaf upper surfaces more easily than eggs lower on plants or on other structures. This corresponds with our findings on sunflower (Fig. 11.1). Wind, on the other hand, dislodged eggs most easily at the bottom part of the plant and on the bolls. Once they drop, eggs are exposed to ground-dwelling predators and high temperatures on the ground surface and even if they do emerge, neonates may not be able to locate food plants (Fye 1972).

On sunflower, predation by anthocorids was greater on the stem and bud than on the receptacle and upper surface of the leaf. An earlier study on sunflower showed that anthocorids are predominantly found on the florets, receptacle, and on the bud (if anthocorids arrive early in the development of the crop), but rarely on the stem and leaves (Chapter 6). Thus the low percentage of sucked eggs on leaves may be attributed to the low incidences of anthocorids in this microhabitat. Although anthocorids are not often found on the stem, 24 % of the eggs were sucked in the upper part of the stem. Possibly, anthocorids leave the flowerhead briefly to forage on other parts of the plant.

Despite a rich complex of parasitoid species attacked the eggs of *H. armigera*, total parasitism of eggs was low.

We examined the fate of eggs during the first two days of development only. In reality, however, eggs take 4.2 days to develop at Kibos and 5.2 days at Kakamega. If the mortality rate due to predation, parasitism and other causes is constant during development, the proportion of eggs surviving (ϕ_t) until a certain age t is related to the mortality rate D as follows.

$$\phi_t = D^t$$

For example, if survival is 32 % over 2 days, D is 57 % per day, and survival over 4.2 days would be 9.1 %. At Kibos, measured survival rates over two days ranged from 22.0 to 64.7 %, which would be 4.2 to 40.1 % over the egg development period of 4.2 days. Similarly at Kakamega survival ranged from 0.58 to 0.86 % over 2 days, which is 24.2 to 67.4 % over the egg development period of 5.2 days.

However, mortality factors may not be constant during development of the eggs. The host-attack rate and host suitability of parasitoids may depend upon host age. For example, *Telenomus* spp. can complete development only when laid in young host eggs (Strand *et al.* 1986), although some Trichogrammid parasitoids may oviposit more in old than in medium-aged eggs, or show no preference in this respect (Pak 1986, Pak *et al.* 1986). Moreover, predators may prefer eggs of a certain age or find them more easily, and the rate of dislodgement may change during egg development because of a deteriorating attachment to the plant surface. Information about these relationships would improve mortality estimates, but is not available without further studies.

Egg infertility was not considered in this study, but parallel life tables indicated that the level of field-collected eggs that failed to hatch varied from 0 to 12 % (Chapter 5). In South Africa, van Hamburg (1981) reported that 3.7 to 15.3 % of the eggs were non-viable in trials on cotton.

Our data partly explain the high mortality of early developmental stages found in parallel life tables (Chapter 5), but major mortality may occur just after emergence when the first instar is in search of suitable sites for feeding (see Chapters 9 and 10). This was confirmed by Kyi *et al.* (1991), who followed the fate of *H. armigera* egg cohorts on cotton until the first instar and found that greatest mortality occurred just after emergence, which was attributed to a poor

establishment of hatchlings on the plant, and not due to predation. Similarly, a cohort life table from tobacco demonstrated that mortality during the first and second instars of *H. armigera* contributed most to generation mortality (Room *et al.* 1991). The survival of eggs (this Chapter) and the establishment of hatchlings (Chapter 9, 10) vary greatly between seasons and within seasons. This may explain why the relationship between initial levels of eggs and subsequent levels of larvae is often poor (van Hamburg 1981), and suggests that the use of egg counts for decision-making in integrated pest management may not always be reliable (Kfir & van Hamburg 1983, Matthews 1989).

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Part IV

Synthesis

12

When can natural enemies control the African bollworm?[1]

ABSTRACT - A three-year research project showed that natural mortality *H. armigera* was greater on maize and sorghum than on sunflower. Mortality on cotton was high, but varied largely between seasons. Key factor analysis showed that parasitism of *H. armigera* was negligible, that pathogens did not cause a high mortality, and that most mortality was attributable to predation and unknown mortality of eggs and larvae. Two predator groups were dominant, anthocorids and ants, but the first was generally poorly associated with their prey in time and space, especially on sunflower and sorghum. The contribution of predation and unknown mortality was evaluated by combining predator-exclusion methods and life-table studies. Ants sometimes caused important irreplaceable mortality of the pest, but their impact fluctuated between localities. Exclusion trials on sunflower showed little effect of crawling and flying predators on natural *H. armigera* infestation, largely because predators arrived too late in the season. On cotton, high background mortality masked the influence of predation, but concurrent cage studies and egg exposure studies, both with large cohorts of inoculated *H. armigera*, confirmed a strong impact of predation. Implications for improving control of *H. armigera* by measures that reduce oviposition by *H. armigera*, and enhance predation and parasitism are discussed.

THE AFRICAN bollworm, *Helicoverpa armigera* Hübner is one of the worst agricultural insect pests in Africa, attacking a variety of food and cash crops (Reed & Pawar 1982). Larvae feed mainly on the reproductive, harvestable plant parts. Despite its major pest status in the region, basic knowledge about the ecology and natural mortality of the pest remains highly inadequate. Even though there have been a number of studies evaluating parasitism (Chapter 3) quantitative data on the impact of natural enemies on pest numbers are generally lacking, particularly regarding predation (Fitt 1989). Such knowledge is essential for developing sustainable pest management, which is less dependent on chemical insecticides, but utilizes natural enemies by conserving and enhancing their populations (Greathead & Waage 1983).

In November 1985, an international workshop "Biological Control of *Heliothis*; Increasing the Effectiveness of Natural Enemies" was held in New

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Delhi, India (King & Jackson 1989) to document the importance of natural enemies attacking Heliothinae and to identify research needed for developing strategies to increase the effectiveness of natural enemies. The workshop concluded that "the ability to estimate and predict the impact of the natural enemy complex on Heliothinae populations, and of the crop losses caused by these, are essential for well-planned biological control and other integrated pest management action on crops". The workshop went on to recommend that further research is necessary and should be encouraged on, *inter alia*, identification, quantification, and assessment of the impact of predators, and identification of key species of predators, parasitoids and pathogens, through the use of life table studies. This workshop was a major step towards the formulation of the research programme described here.

Taking this basic guidance, a project was formulated by staff of the International Institute of Biological Control (IIBC), the Kenya Agricultural Research Institute (KARI) and the Overseas Development Administration (ODA) to assess the role of indigenous natural enemies in the population dynamics of the African Bollworm, *Helicoverpa armigera*. East Africa was chosen on the basis of long term interest in and research on the African Bollworm, principally as a pest of cotton. There was already substantial information available on the parasitoids attacking *H. armigera* in Uganda (Coaker 1959) and Tanzania (Reed 1965b, Nyambo 1990), but almost nothing was known about the predators and pathogens. There was little quantitative data on the population dynamics of *H. armigera* in Kenya, although the literature and local entomologists considered it a major pest of several crops.

The purpose of the present paper is to review the results of studies conducted in the western part of Kenya, bringing out the overall conclusions, lessons learned and suggestions for the future. Studies from central and eastern sites will be reported at a later date.

Incidence and mortality of the African bollworm

At seven experimental sites in different agricultural zones of Kenya the population dynamics of *H. armigera* and occurrence of natural enemies was studied on a combination of three smallholder crops of either sunflower, maize, sorghum or cotton (Chapter 4). *H. armigera* only occasionally achieved population densities sufficient to cause obvious damage to the crops, and was virtually absent from the coastal sites. The low incidence of larvae appeared to be widespread over all our sites studied, and light-trap data from Muguga, Kiambu District, 25 km East of Nairobi, show that annual *H. armigera* catches have fluctuated greatly during the past 20 years, but the last three years during which the project was run are at the minimum end of the range (ca. 10-times lower than the average of the preceeding 16 years) (Fig 12.1); there was no relationship between *H. armigera* numbers caught and rainfall.

Mortality levels varied greatly. *Trichogrammatoidea* spp. egg parasitoids, and *Linnaemya longirostris* (Macquart), a tachinid late-larval parasitoid, were the most common parasitoid species, but their impact was rather low. Anthocorids and ants (predominantly *Pheidole* spp., *Myrmicaria* spp. and *Camponotus* spp.) were potentially important predators of *H. armigera*, but their abundance fluctuated widely between sites. Pathogens were scarce and did not play a significant role.

More detailed studies were conducted in western Kenya. At Kakamega in Western Province, mono-crop plots of sunflower, maize and sorghum (host crops of *H. armigera*) were grown in four replicates (total area 0.4 ha) during two long rains and two short rains seasons from 1988 to 1990. About 50 km south of Kakamega, similar plots were grown at Kibos, Nyanza Province, with cotton, maize and sorghum during the long rains only. Weekly, 30 plants were sampled per crop at these two sites and all pest stages and predators were recorded. Pest organisms were reared for emergence of parasitoids. Recruitment of *H. armigera* was estimated with Southwood & Jepson's (1962) graphical method, and development periods of larval instars were calculated using data of Twine (1978). Because of darkening of eggs during development, we

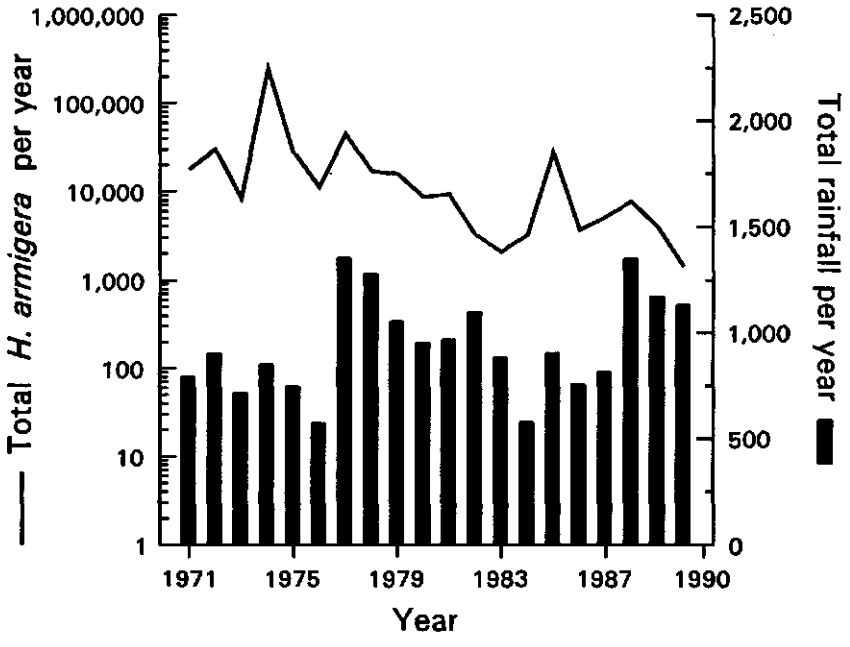

Fig. 12.1 Mercury vapour light trap catches of *H. armigera* (annual total) and rainfall (annual total) at IIBC Kenya Station, Muguga, Kiambu District, for 1971-1990 (by courtesy of KARI armyworm unit).

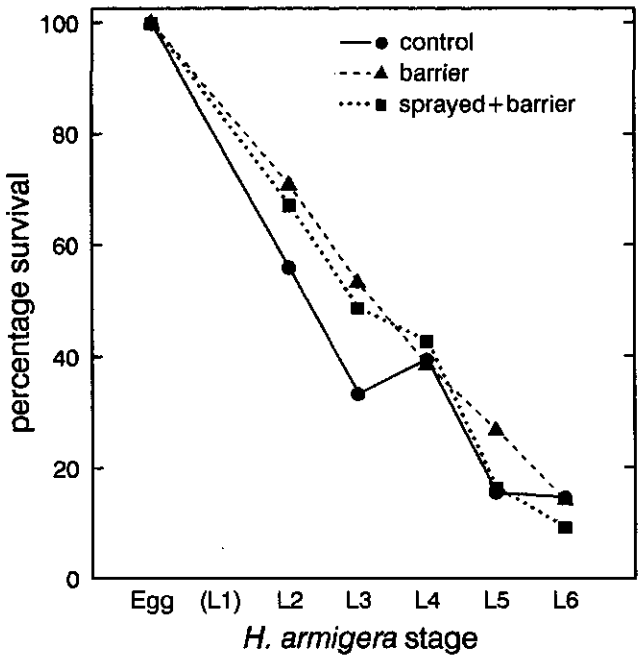

Fig. 12.8 Survivorship curve of *H. armigera* developmental stages in three predator-exclusion treatments on sunflower; Kakamega, 1990.

sunflower than on maize or sorghum, which may have contributed to the relatively high late-larval mortality on sunflower. Furthermore, ants were most common on sunflower plants with most larvae, indicating the recruitment of workers in response to *H. armigera* density.

Impact of natural enemies

Key factor analysis showed that most generational mortality was due to predation and unknown factors (Fig. 12.3), while parasitoids and pathogens were not important. To evaluate the relative roles of predation and other (abiotic or host-plant related) mortality factors, we studied the relation between predator abundance and pest mortality through correlative field data and manipulative experiments.

Earlier we showed that anthocorids were rather poorly associated with *H. armigera* eggs, which was mainly because they did not occur at the right time

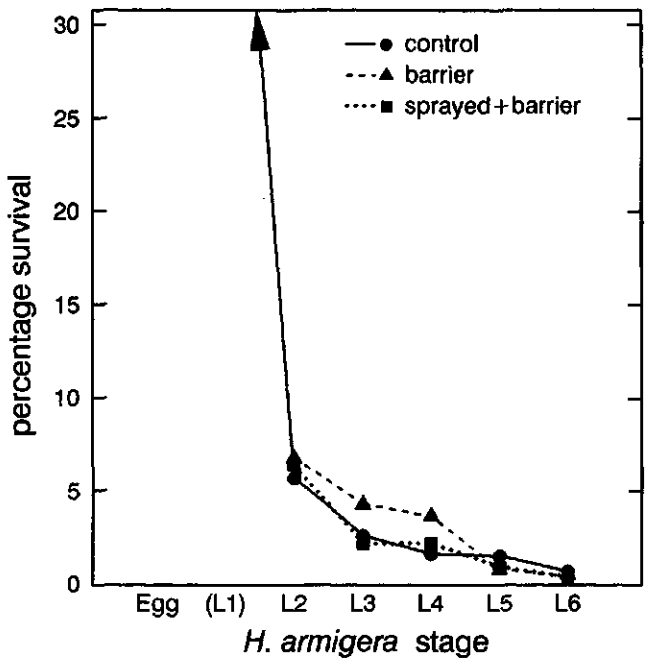

Fig. 12.9 Survivorship curve of *H. armigera* developmental stages in three predator-exclusion treatments on cotton; Kibos, 1990.

(Chapter 6). Yet, if we plot the occurrence of anthocorids during the period of availability of eggs against the survival of *H. armigera* eggs, there appears to be a relationship, as shown in Fig. 12.7 where the results of sunflower, maize and sorghum are combined. Data are from our western Kenya trials, and each data-point represents a site during the crop-season. When anthocorids were abundant, survival was low, but at low anthocorid levels, survival was high at several occasions. This suggests that anthocorids can suppress *H. armigera* when they are common concurrently with the egg stage. The large variation at low anthocorid densities indicates the influence of other mortality factors. On maize, survival was low irrespective of the occurrence of anthocorids.

Further, we studied the irreplaceable mortality caused by predators, by excluding specific groups of predators without directly affecting local *H. armigera* populations. Crawling predators, dominated by ants, were excluded from replicated sunflower plots by banding all plants in a plot with insect trap adhesive (Tanglefoot®), and development of natural *H. armigera* populations were followed in ant-exclusion and control plots. The role of ants was most obvious in our trial at Mwea Tebere, where *H. armigera* levels were almost seven times greater in the absence of ants than in control plots (Chapter 8). Flying predators,

dominated by anthocorids, were excluded by applying low concentrations of triazophos which killed anthocorids but did not affect *H. armigera*. In 1.4 ha trials, natural *H. armigera* populations were followed in replicated plots where crawling predators were excluded, in plots where both crawling and flying predators were excluded, and in control plots. Trials were conducted on cotton and sunflower.

Fig. 12.8 shows the survivorship curve of *H. armigera* stages in the three treatments on sunflower. Survival was greater than in earlier trials (see Fig. 12.2): 60-70 % of the eggs reached the second instar. Subsequent mortality declined steadily and less than 16 % reached the final instar. Survival in the control was slightly, but not significantly, lower than in the exclusions, indicating that natural enemies had no significant effect on *H. armigera* in this trial. Anthocorids, which mainly feed on the egg stage, appeared well after the oviposition peak of *H. armigera*. Moreover, the density of ants was very low.

On cotton, survival was extremely low this particular season (Fig. 12.9). In the control, only 6 % of the eggs reached the second larval stage. Survival was similarly low in the exclusions, indicating that high mortality was caused by factors other than predation. There were slight differences between treatments, but at such low levels of surviving larvae, there were no significant effects. It remains possible however, that young *H. armigera* stages were adversely influenced by the low concentrations of triazophos. The high level of background mortality appears to be related to host plant condition, because the crop suffered from moisture stress, and the number of suitable feeding sites for larvae had declined. Thus, we found no irreplaceable mortality by predation in sunflower or cotton. In the first case this was attributable to the lack of predators, in the second case high background mortality masked the effect of predation. Larval levels were low.

To obtain prey densities greater than field levels, we conducted a series of studies, in which we inoculated 4 x 2 m predator-exclusion and open control cages with large cohorts of *H. armigera* eggs. Two weeks after inoculation, larval levels in the exclusion were 4½ times greater than those in the control, indicating that natural enemies strongly reduce pest numbers. Again, background mortality was high (61-97 % in predator-exclusion cages), but egg numbers at inoculation were sufficiently large to measure significant differences in larval numbers. To evaluate mortality during the egg stage, we exposed marked egg cohorts, that were moth-deposited, on cotton plants in the field. The first two days after deposition, anthocorids sucked 12-65 % of the eggs; an additional 15 % of the eggs was lost and 6 % parasitized.

In conclusion, it is difficult to generalize about the impact of predation; the relative role of predation appears to be as variable as the level of background mortality. In some instances high background mortality suppressed the pest, in other instances survival was greater and the role of predation became more obvious. It is evident however, that locally occurring predator populations play an important role in suppressing the pest, and any control strategies should be based on conserving and encouraging their populations. The complex of

predacious ants is capable of suppressing the pest, but their role largely depends on their local abundance and whether they forage in the vegetation. However, their strategy of chemical communication and recruitment of workers may enable them to forage more effectively as pest densities increase, as we found at Mwea Tebere. Anthocorids can cause high egg mortality, and our results suggest that anthocorid abundance is related to high mortality of young *H. armigera* stages. However, anthocorids are generally poorly associated with the pest, mainly because they arrive too late in the season.

Our results indicated the importance of integrating life tables and natural enemy assessment methods. Evaluation of natural enemies under manipulated conditions can reveal the potential impact or marginal attack rate by the agent on the pest (Luck *et al.* 1988), and may be predicted based on density and functional response data. However, additional evaluation of natural enemies in the context of life tables is essential in order to elucidate the actual role of natural enemies in relation to other natural mortality factors (Jones 1982, Bellows *et al.* 1992), especially where these other factors have a large impact.

Implications for integrated pest management

The infestation level of *H. armigera* is determined mainly by two factors: the recruitment of eggs and the level of mortality during development. In turn, the recruitment of eggs into the crop depends on the presence of ovipositing moths and on the availability of other attractive host plants. Several studies support a long-range mobility of *H. armigera* in Africa and elsewhere (Farrow & Daly 1987), but low light-trap and pheromone-trap catches at our sites throughout the study period suggest that infestation was mainly caused by local populations, although low level immigration from other sources may have taken place.

In diverse agroecosystems, such as smallholdings in Kenya, suitable host plants are available to *H. armigera* during an extended period, which would favour resident populations. On the other hand, increasing crop diversity often reduces pest infestation (Risch 1983, Andow 1991), and ecological theory predicts that pests find plants more easily if the plants are concentrated in a monoculture than plants grown in polyculture (Root 1973). Although intercropping may not change the concentration of resources for *H. armigera* as the pest attacks a variety of crops in smallholdings, temporal differences in attractive periods would render crops less apparent when grown in polycultures. In our experiments, crops were grown in a mosaic of small 240-380 m^2 mono-crop plots, and hence the comparison between mono- and polycultures remains to be studied.

Preference for particular host plants may be utilized to distract moths from crops that are most vulnerable to *H. armigera* damage. On cotton, moths oviposit over an extended period of time, and the level of oviposition is rather constant. Consequently, two to three more or less overlapping generations can develop on the crop (Wardhaugh et al. 1980). In choice tests, Firempong &

Zalucki (1990) found that cotton is much less attractive to ovipositing moths than flowering sunflower and maize. Sorghum was not among the plants tested, but our results indicate that flowering sorghum is highly attractive to moths (Fig. 12.5).

Hence, interplanting with these crops may distract ovipositing moths from cotton. Maize has been used most commonly as a trap crop of *H. armigera*, and preference for maize can be so strong that cotton plots would remain almost clear of *H. armigera* eggs when bordered with a few rows of maize (Parsons & Ullyett 1934). However its relative attractiveness to ovipositing moths appears to be inconsistent (Parsons 1940b, Pearson 1958, Reed 1965b, Rens 1977, Coaker 1959, Chapter 4) and may be due to varietal differences of the host plant or behavioural differences among *H. armigera* populations.

Apart from the influx of eggs, the infestation level depends on the level of survival on crops. Survival of *H. armigera* is low on maize and sorghum, and when these crops are relatively attractive in the field they could act as a 'sink' of *H. armigera* infestations. In our trials, most mortality was attributable to factors other than natural enemies. Heavy rain and wind can cause large losses of eggs (Mabbett & Nachapong 1983), and prolonged rainy weather may soften the bond between eggs and the substrate (Nuessly *et al.* 1991), and in our trials occasional showers accounted at most for 20 % dislodgement of eggs (Chapter 11). The mortality level of *H. armigera* also depends on the host-plant condition. Our results from cotton suggested that mortality of *H. armigera* increased with the degree of moisture stress (Chapter 9, 10). Moisture-stressed cotton plants have fewer, and less suitable sites for larval feeding (Pearson 1958), and a low humidity may have a detrimental effect on egg hatching (Qayyum & Zalucki 1987).

Natural enemies sometimes caused important mortality and their role may be enhanced by manipulating their populations, for example by intercropping. In certain situations, an increased abundance and action of natural enemies in polycultures may be responsible for reduced pest levels (Russell 1989), but this would depend on the crop species, crop phenology and natural enemies involved. Our data suggest there are prospects to improve the impact of three groups of natural enemies: anthocorids, ants and parasitoids.

Since anthocorids and ants seem to be able to suppress the pest if they are sufficiently common at the right time at the right place, their impact on *H. armigera* (and other pests) may be enhanced by manipulating their populations. In cotton, *H. armigera* is present prior to flowering, which is earlier than anthocorid predators. Crops with distinct flowering periods strongly attract ovipositing moths and anthocorids simultaneously at flowering. If such crops are planted adjacent to or intercropped with young cotton, they could attract anthocorids and other, less common predators (see Chapter 4) early in the season, and at the same time distract ovipositing moths from cotton, as discussed above. Our data indicate that sorghum would be a better 'natural-control' crop than maize, because it attracts more anthocorids during flowering, and the level of oviposition by *H. armigera* is similar or higher. Moreover, sorghum varieties are

generally better adapted than maize to the dry climatic conditions where cotton is commonly grown. In North America, a study by Robinson *et al.* (1972a, 1972b) indicated that yields and predator populations (predominanlty coccinellids) in cotton were slightly greater if cotton was strip-cropped with sorghum than when strip-cropped with maize (or legumes). Detailed studies are required in East Africa on the prospects of 'natural-control' crops in cotton production, and on the movements of predators between crops.

Manipulation of ants is less straightforward, because the social biology of ants restricts their movements to a certain area around their nests, and colony sizes remain rather constant because ants store food for consumption at times of food scarcity (Carroll & Risch 1983). Nevertheless, ants could be augmented by providing carbohydrates, such as crushed sugar-cane or sprayed sugar solution (Hagen & Hale 1974), that arrest them in target plots and encourages them to supplement their diet with proteins obtained from arthropod prey (Carroll & Jansen 1973). More rigourously, nests could be transplanted into plots (Pavan 1979, Jones & Sterling 1979); at Kakamega, we tried transplanting several nests, but without any success of establishment. Further, existent soil-nesting ants such as *Myrmicaria* could be encouraged by allowing for non-cultivated borders around plots, or by conserving nest sites during land preparation.

Fig. 12.4 above demonstrated that the abundance of ants is not necessarily reflected in their foraging activity in the crop canopy, because workers strongly respond to the presence of food in the vegetation. On sunflower, the presence of sticky plant exudates was probably an important factor causing ants to visit the vegetation, since we commonly saw ants aggregated around the exudates on plants. Likewise on cotton, extrafloral nectaries and honeydew-producing *Aphis gossypii* Glover (Homoptera: Aphididae) attracted ants to plants, and may similarly provide food for other natural enemies.

Augmentative releases of trichogrammatids in the season may avoid early season application of insecticides, but might not be practical for control of *H. armigera* in Kenyan smallholdings (Ridgway & Morrison 1985). In South Africa, early attempts to mass release *Trichogrammatoidea lutea* Girault parasitoids against *H. armigera* on young cotton were unsuccessful, and failure of establishment was attributed to the scattered distribution of *H. armigera* eggs, a rapid dispersion of adult wasps, and to impediment of movements of wasps due a high degree of hairiness of the cotton variety used (Parsons & Ullyett 1936). In the Sudan however, recent augmentative releases of *Trichogramma pretiosum* against *H. armigera* on cotton were promising (Abdulrahman & Munir 1989), and deserve a continuing attention in a system which has been dominated by chemical methods of control.

Young larval parasitoids were almost absent at our sites, while in other regions, parasitoids of young larvae, such as *Campoletis chlorideae* Uchida, *Glabromicroplitis croceipes* (Cresson), *Hyposoter didymator* (Thunberg) and *Cotesia kazak* Telenga, often have a substantial impact on *H. armigera* or related Heliothinae (Messenger 1974, King *et al.* 1985, Carl 1989, Mohyuddin 1989).

Their introduction into East Africa might improve the overall level and reliability of biological control (Greathead & Girling 1982), without any cost to the farmer.

In East African agriculture, population dynamics of the pest and its natural enemies are not only influenced by contemporary crops as discussed above, but may also depend on the succession or rotation of crops. Nyambo (1988) suggested that increased growing of chickpea and tomato during the dry season provided food plants to *H. armigera* in the unfavourable period. Reed (1965b) postulated that build-up of *H. armigera* on early-sown maize in western Tanzania could be a cause of increased infestation in cotton. However, this would depend on whether maize acts as a source or sink for *H. armigera* populations. Our results show that survival in maize is very low (Fig. 12.2), which is supported by Parsons & Ullyett (1934) who observed lower survival in maize than in cotton. Moreover, an early-sown crop could encourage concurrent build-up of natural enemy populations (Reed & Pawar 1989).

In case natural enemies are not effective or have not yet built up in numbers high enough to control the pest, action may have to be taken against *H. armigera*. If farmers apply insecticides in the early crop, natural enemies, which might otherwise have built up and suppressed the pest, are killed, and farmers would rely more on insecticides for control. In this respect, development of effective biological insecticides such as *Bacillus thuringiensis* or *H. armigera* Nuclear Polyhedrosis Virus (NPV) would be an important component in a sustainable control strategy because they do not affect natural enemies. However, microbial insecticides are generally rapidly inactivated on foliage. Preliminary trials at Kakamega and Kibos with a new strain of *Bacillus thuringiensis* which showed extended persistence in the field, were promising in this respect (D.R. Dent, pers. comm., 1990).

On cotton, pests other than *H. armigera* may remain a problem, thus requiring additional methods of control. Pests that follow *H. armigera* in importance are Cotton Stainer, *Dysdercus* spp. (Heteroptera: Pyrrhocoridae), and Cotton Seed Bug, *Oxycarenus* spp. (Heteroptera: Lygaeidae), both appearing later in the season. The negative effect of insecticides on natural enemies may be limited by the choice of pesticide (Mullin & Croft 1985) and the timing of spraying (Hull & Beers 1985), but requires further study. In certain instances, the presence of pests may be advantageous to the crop. In fact, damage relations are poorly understood for most crop-pest combinations in East Africa. In China, Zhang & Chen (1991) concluded that it is better not to spray cotton against *A. gossypii* early in the season, because cotton can compensate for aphid feeding, while the aphids provide an important food source for coccinellid predators that allows the latter to build up.

Future plans

The programme emerged from a need to improve the understanding of the ecology and natural mortality factors of *H. armigera*, as a first step towards

developing integrated methods of control and to detect prospects for introductions of exotic agents. Although during our trials, *H. armigera* was generally not a major constraint to crop production, except in areas where cotton was grown, the pest may increase in importance because of agricultural intensification following a rapidly growing population in Kenya (Odingo 1988), and therefore, development of sustainable cropping practices will be of crucial importance. The results obtained would be applicable not only to *H. armigera* in Kenya, but to some degree also to related pests and in other countries in the region.

The three-year study showed that phenology and survival of *H. armigera* are variable between sites and between seasons, and thus a continuation of life table studies for one or two more seasons would be desirable, in particular in seasons with increased *H. armigera* populations in the region.

The methodology used in our studies was simple and based on visual recording in the field, which facilitated interpretation of our findings. These methods have been adapted to assist in IPM training of extension personnel and farmer groups in the National IPM programme of Indonesia, a system which could also be developed for the East-African smallholdings.

Various possible areas of follow-up work have been mentioned in the section above, focused on cotton. Of these, studies on intercropping are most promising and most feasible, firstly because crops as maize or sorghum may strongly affect the balance between natural enemy and pest populations, and secondly because such emphasis on conservation may stimulate sustainable agriculture in smallholdings. However, there will only be a brief period when the trap crop is attractive to ovipositing moths. A careful choice of varieties and planting dates might ensure the maximum effectiveness of trap crops in the case of sunflower. For cotton, where oviposition is extended over a period of three months (Chapter 9), planting of trap crops at regular intervals may be required, but a trap- or 'natural control' crop may be most crucial early in the season, because of its potential role to attract natural enemies into fields.

Follow-up work should be more site-specific and site-relevant, and should be holistic in its approach, in order to be accountable to farmers and their direct problems (Goodell 1984, Gallagher 1992). Pest management, or better, crop management, practices must be developed in close connection with farmers and extension personnel, and ideally, such studies would tie directly through the training system as 'training-driven' research (van den Berg 1992).

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Curriculum Vitae

On 24 July 1962 I was born in Ermelo, the Netherlands. In 1980 I graduated from the secondary school Chr. College Groevenbeek in Ermelo. The same year I started to study Biology at the Agricultural University, Wageningen, and passed the 'Kandidaatsexamen' in 1984. Afterwards, I started my graduate studies in Entomology and Animal Ecology. Four research subjects included 6-month research associates in Kenya and the Philippines to study indigenous and classical biological control of cassava green mites, and to assess the impact of natural enemies on early season pests of rice. The 'doctoraalexamen' (comparable with a Master of Science) was passed early 1988. Late 1987, I was employed as project entomologist by the International Institute of Biological Control (IIBC) to work on the population ecology of the African bollworm in smallholder crops, under the supervision of Dr M.J.W. Cock. During the first seven months I conducted preliminary work at the IIBC headquarters, Ascot, and the Natural History Museum, London. From 1988 until 1991, I was based at the IIBC Kenya Station at Muguga, Kenya, and worked mostly in the western part of the country, where the field research described in this dissertation was conducted. Early 1992, I joined the FAO National Integrated Pest Management Program for Rice-Based Cropping Systems in Indonesia to evaluate the impact of natural enemies on insect pests of non-rice crops (in particular soybean) in different parts of the country, to train extension workers to assess natural enemies, and to develop training methods for use at farmer field schools.