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The Biology and Ecology of *Heliothis armigera* (Hübner) and *H. punctigera* Wallengren (Lepidoptera : Noctuidae) in Australia: What do we know?

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Abstract

The taxonomy and identification of *Heliothis armigera* and *H. punctigera*, their distribution and host plants in Australia, the effect of host plant on reproduction and on the development and survival of immature stages, their movements, population biology and dynamics, and their control, are reviewed. Areas where further study is desirable include: the nature of host plant selection and host species preference; adaptability to new cultivars; effects of host plant on development; detailed life-table studies on different host plants; the contribution of predation, parasitism and disease to mortality; factors responsible for fluctuations in populations between years, including the origins of outbreak populations; and control strategies other than insecticide treatment.

Introduction

Heliothis armigera (Hübner) and *H. punctigera* Wallengren are arguably the most important pests, insect or otherwise, of field crops in Australia. They have attracted a great deal of research, especially since the development of resistance in *H. armigera*, firstly to DDT in the early 1970s and more recently (Anon. 1983) to synthetic pyrethroids. In the last 30 years there have been at least 183 publications dealing directly or indirectly with either or both species. These papers can be divided into one or more of the following categories: taxonomy, 6; basic biology, 31; ecology, 63; management and control, 125. Most research has been directed towards management and control. If we define an ecological paper to be one in which the aim of the paper was not management, then only 33 fulfil this criterion.

This review aims to appraise critically what is known about the biology and ecology of the main *Heliothis* species in Australia, and to identify areas which warrant further research. We shall restrict ourselves to the two economically important species, *H. armigera* and *H. punctigera*.

Taxonomy and Identification

The two pest species of *Heliothis* have attracted a plethora of common names (e.g. Broadley 1977*a*) including: cotton bollworm, bollworm, common bollworm, tobacco budworm, corn earworm, bean pod borer, tomato grub or worm, lucerne budworm, flower caterpillar, climbing cutworm and *Heliothis* worm or grub. Although this list of common names is colourful, suggestive of where these species feed, and highlights the extensive host range, it is misleading. For instance, tobacco budworm refers to both *H. armigera* and *H. punctigera* (e.g. Cunningham 1975). Although the two species are very similar, they are sufficiently different in phenology, host range and resistance status to warrant being separated at all stages. The history of the nomenclature and taxonomy of the genus *Heliothis* is full of controversy, which persists to this day (Nye 1982). Before the revision of the Australian members of the genus by Common

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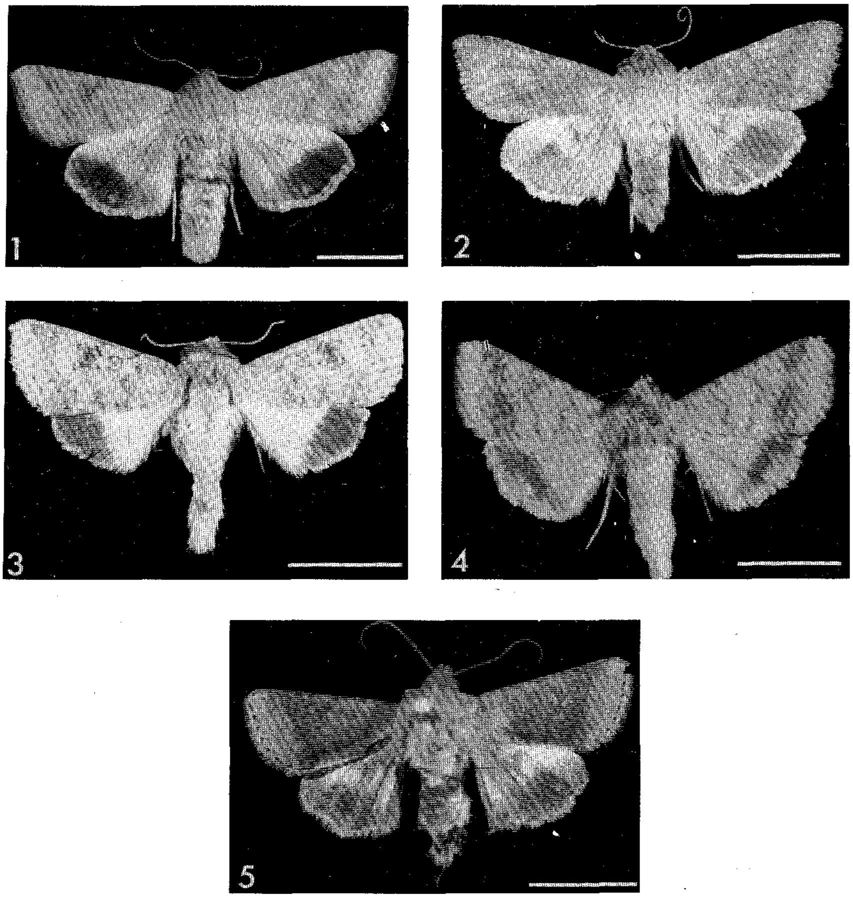
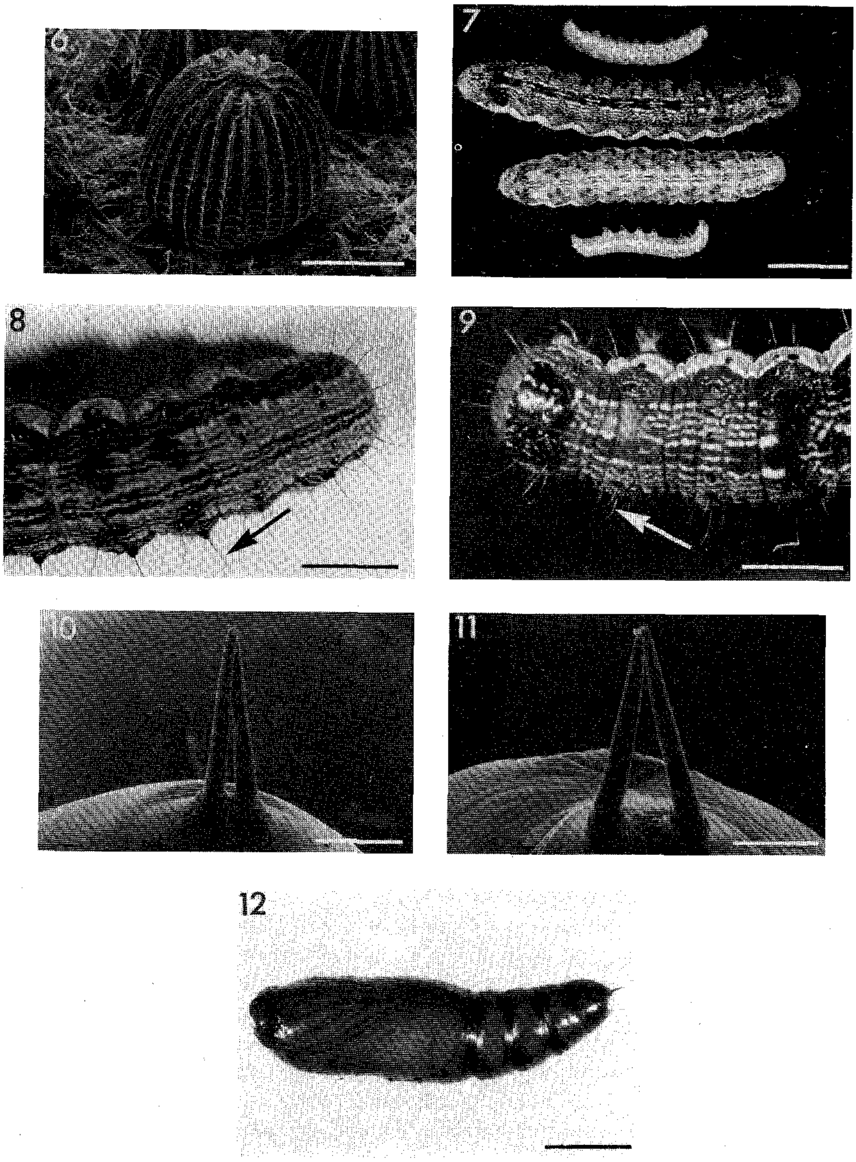
(1953), *H. punctigera* was confused with *H. armigera*, rendering previous work difficult to interpret or use.

The moth currently called *H. armigera* has been referred to as *Bombyx obsoleta* F., *H. obsoleta* (F.), *Noctua barbara* F., *Chloridea*, etc., by different authors (see Todd 1978). Hardwick (1965) suggested the generic name *Helicoverpa* and this has gained recognition mainly in the New World. Todd (1978) called for a revision of the specific names *armigera* and *punctigera* to *armiger* and *punctiger* to agree with the masculine gender of *Heliothis*. Nye (1980) requested the International Commission on Zoological Nomenclature to rule that the gender is feminine and this has been accepted (I.C.N.Z. 1985).



Figs 1–5. Adult specimens of Australian species of *Heliothis*: *1*, *H. armigera*; *2*, *H. punctigera*; *3*, *H. rubrescens*; *4*, *H. assulta*; *5*, *H. prepodes*. Scale lines, all 10 mm.

Common (1953) distinguished four Australian *Heliothis* species, namely: *H. armigera*, *H. punctigera*, *H. assulta* Guenée and *H. rubrescens* (Walker) (Figs 1–4). Recently Common (1985) described a fifth species, *H. prepodes* (Fig. 5). In the adult stage, *H. punctigera* can be distinguished from *H. armigera* by the presence of indistinct transverse lines on the forewings of both sexes. Both sexes of *H. punctigera* have an uninterrupted black terminal fascia in the hindwing; in *H. armigera* the black fascia has a pale patch between veins *M*3 and *Cu*2; also the bursa copulatrix is nearly symmetrical and the genital plate is cup-shaped (Common 1953, figs). Kirkpatrick (1961*a*) provided further notes on wing markings and colour, noting the variable nature of these in all four species. Wing markings are best used to identify newly emerged or unbattered specimens (Twine and Kay 1973); otherwise, genital characters should be used. Males have a long, backwardly pointed aedeagus, with a spur which is absent in *H. armigera*; females have an asymmetrical bursa copulatrix and genital plates with parallel ridges. Keys to the adult characters of all four species can be found in Common (1953) and Kirkpatrick (1961*a*). Although *armigera* and *punctigera* are morphologically very similar, there



Figs 6–12. Immature stages of Australian pest species of *Heliothis*: *6*, egg of *H. punctigera*; *7*, third and final instars of *H. armigera* (above) and *H. punctigera* (below); *8, 9*, head and thorax of *H. punctigera* (*8*) and *H. armigera* (*9*, note that setae are white); *10, 11*, cremaster spines of *H. punctigera* (*10*) and *H. armigera* (*11*); *12*, pupa of *H. punctigera*. Scale lines: *6, 10, 11*, 0·3 mm; *7*, 7 mm; *8, 9*, 3 mm; *12*, 5 mm.

is no evidence that they hybridise. Kirkpatrick (1962*a*) attempted to cross the species, and although he obtained eggs from four out of five crossing trials, none were fertile.

Kirkpatrick (1961*a*) compared the morphology of the immature stages of four *Heliothis* species and attempted to provide keys to separate them. Brown and Cantrell (1978) considered the keys to larvae unreliable, and concurred with Kirkpatrick (1961*a*) that *armigera* and *punctigera* were identical in all characters examined (Fig. 7). Stanley (1978) provided a method for separating larger larvae based on: (1) saddle markings on the dorsal surface of the first abdominal segment; (2) dark pigmentation, particularly on the legs. Both of these are present in *armigera*, but *punctigera* has no saddle markings and is lighter in colour. This method of separating larvae is in widespread use by field officers but has been shown to be unreliable (Daly and Gregg 1985). Cahill, Easton, Forester and Goodyer (personal communication) report success in separating third- and fourth-instar larvae of *armigera* and *punctigera* reared on an artificial diet by the saddle markings, and sixth-instar larvae by the colour of the dorsal anterior cervical shield hairs; these are white in *armigera* and black in *punctigera* (Figs 8, 9). Pupae can be separated reliably by measuring the distance between the outer edges of the cremaster spines at the junction with the cremaster ($>0\cdot22$ mm, *armigera*; $<0\cdot20$ mm, *punctigera*) (Figs 10–12) (Kirkpatrick 1961*a*; Cantrell 1981).

The inability to identify species at all stages has hindered ecological work undertaken in the field. The development of a quick and inexpensive serological technique for identification of species in field samples would greatly aid both management decision making and ecological work.

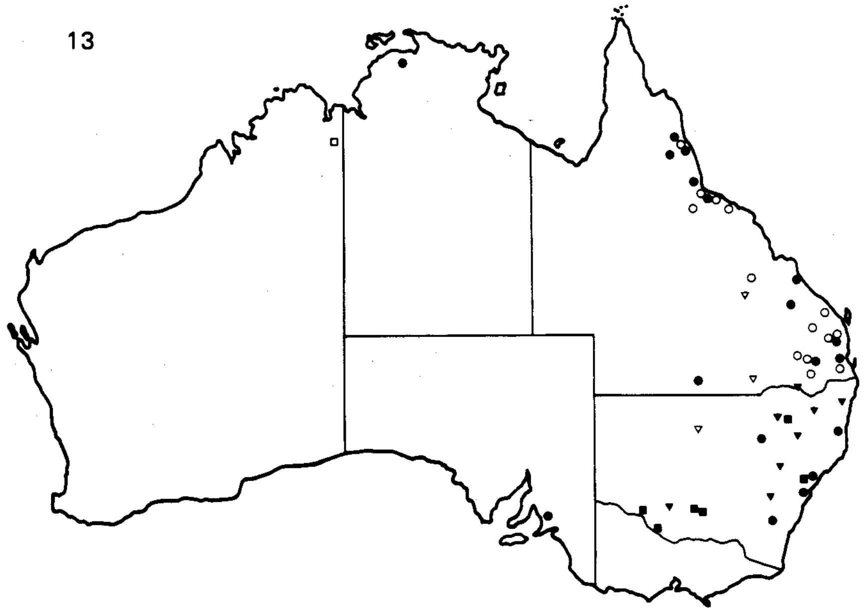
Daly and Gregg (1985) provided a method for separating the two species at any stage, including eggs and early instars. They used electrophoretic techniques, and found seven loci fixed for alternate alleles. For practical purposes, three enzyme systems (isocitrate dehydrogenase, phosphogluconate dehydrogenase, glucose-6-phosphate dehydrogenase) separated the species.

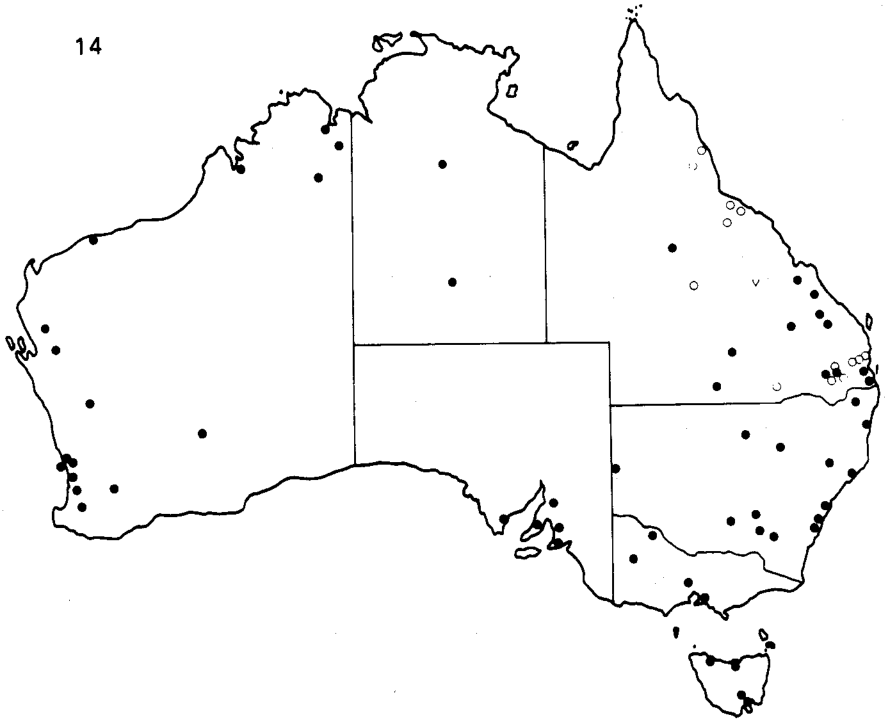
Distribution

The problem of identification of adult material before 1953 renders any earlier information on distribution of dubious value, unless supported by museum specimens. Common (1953) reviewed the distribution from collected material of both species in Australia. *H. armigera* (Fig. 13) predominated in coastal Queensland and New South Wales, and the Callide Valley of central Queensland. One specimen was recorded from Darwin in the Northern Territory and three from Adelaide in South Australia. These records were considered vagrants or accidental introductions with produce, as were the two females collected at Cunnamulla in far western Queensland, two specimens caught at a light trap near Trangie (inland New South Wales) and one at Canberra, A.C.T. *H. punctigera* was found throughout Australia (Fig. 14) except along the Queensland coast north of Brisbane. Kirkpatrick (1961*b*) clarified the distribution within Queensland (Fig. 14). *H. punctigera* can now be considered ubiquitous in Australia and *H. armigera* restricted to the coast and up to 100 miles inland.

Although Common (1953) noted that further collections were necessary to verify that *armigera* was not present in inland or in northern Australia, it became generally accepted that *armigera* was restricted to eastern coastal Australia and perhaps around Darwin in the Northern Territory.

The perceived distribution of a species may reflect the scale and intensity of collecting (and ability to identify) as much as it does the actual distribution. An equally plausible explanation for the distribution of *armigera* is that the species is normally present but rare in inland areas (see section on population dynamics) and hence difficult to detect. The expansion of agriculture, which supplies a sequence of suitable hosts over a wide area, along with certain management practices such as chemical sprays, may promote the abundance of *armigera*. Since Common's (1953) review *armigera* has been recorded frequently from non-coastal areas (Richards 1964, 1968; Wright and Nikitin 1964; Wright 1965*a*, 1965*b*, 1970; Goodyer and Greenup 1980; Hamilton and Muirhead 1981) (Fig. 13).





Figs 13, 14. Distribution records of: *13*, *H. armigera*; *14*, *H. punctigera*. ● Common 1953; ○ Kirkpatrick 1961*a*; ▽ Department of Primary Industries records; ■ Wright and Nikitin 1964; □ Richards 1964; ▼ Goodyer and Greenup 1980.

Questions about the distribution of a species are of more than academic interest because the answers can have a major bearing on population management. If, as we have implied, *armigera* is more widespread than at first thought, then do pest populations arise simply from an increase in abundance of local 'moths' because of a change in carrying capacity, or do such local demes become adapted to new hosts? Or has *armigera* extended its range by migration and become established in newly developed agricultural areas. If so, continuous reinfestation from source areas is an ever-present possibility. Knowledge about the origin of populations is crucial to management, particularly at a regional level (see, e.g., Knipling and Stadelbacher 1983; Mueller *et al.* 1984).

We shall return to this question of population origin. Clarification of the present distribution of *armigera* and *punctigera* would be a fruitful avenue of research. In particular, the status of these species in tropical inland regions and in non-agricultural situations should be established.

Questions about distribution of phytophagous insects are intimately related to: (1) the availability of suitable host plants; (2) the ability of the insect to locate, identify and use the hosts; (3) the effect of physical environmental constraints on development, survival and reproduction.

Host Plants

As the list of common names implies, larvae of both species feed on a wide range of agricultural crops. Both species also feed on a number of exotic and native 'weeds' (Table 1). Most research has centred on crops; 60% of all publications on ecology and management in the last 30 years deal with *Heliothis* species on crops, and only three include weeds or non-crop hosts. Of the papers concerned with *Heliothis* on crops, 49 relate to cotton; 14 to tobacco; three to maize; six to tomato; three to linseed; six to sunflower, seven to sorghum; three to soybeans, six to lucerne; 15 to the remaining field and horticultural crops; only six papers consider more than one host in one area. Although the concentration of research effort may reflect the pest status of *Heliothis* on certain crops (and the availability of research funds), this single-host approach ignores one of the basic features of the biology of both species, namely their highly polyphagous nature.

The published records of 'host plants' of both species are detailed in Table 1. The major work in this area is due to the extensive collecting and rearing by Kirkpatrick (1961*b*). The consideration of a plant as a host usually comes about when eggs and/or larvae are collected from the plant and subsequently reared (usually on an artificial diet) to adult for identification. Some simply identify larvae *in situ* (e.g. Wardhaugh *et al.* 1980), although this is highly unreliable with *Heliothis*.

The presence of immatures on a plant species does not necessarily imply that the plant is a host (e.g. Kitching and Zalucki 1983). For this to be so an insect must be able to complete development to the adult stage and be able to produce fertile offspring. Thus most of the 'hosts', especially non-crop plants, must be considered potential hosts. The presence of eggs does not mean that larvae will survive and develop; the presence of larvae does not mean these will develop into fertile adults or that the larvae arose from eggs laid on the plant in the first place.

Controversy even surrounds the pest status of the species on some crop hosts. Thus Twine (1973), working in south-eastern Queensland, collected *punctigera* eggs only from lucerne (see also Common 1953). Wardhaugh *et al.* (1980) and Wilson (1983) collected larvae of both species on this crop in the Narrabri area of New South Wales; *armigera* larvae were particularly frequent on irrigated lucerne in autumn (Wardhaugh *et al.* 1980). Similarly, Common (1953) considered *armigera* to be absent from linseed, although Kirkpatrick (1961*b*) recorded it on linseed in Queensland and Wilson (1983) notes that it occasionally occurs on linseed in the spring around Narrabri (one year in five).

Determination of whether a plant is a true host will require either: (1) rearing insects to

Table 1. **Host records of *Heliothis* spp. in Australia**

Host type: *W*, wild (uncultivated); *C*, cultivated (field, garden or horticultural crop); *e*, exotic; *n*, native. Reference: *1*, Common 1953; *2*, Cullen 1969; *3*, Department of Primary Industries; *4*, Kirkpatrick 1961*b*; *5*, Lea 1928; *6*, Richards 1968; *7*, Sloan 1940; *8*, Wardhaugh *et al.* 1980

Botanical name	Common name	Host type	Species recorded	Reference
Aizoaceae				
Trianthema pilosa	Pigweed	W, e	*punctigera*	6
T. portulacastrum	Black pigweed	W, n	*arm.* + *punct.*	4, 6
Zaleya galericulata	Hogweed	W, n	*punctigera*	6
Amaranthaceae				
Amaranthus interruptus	Amaranth	W, n	*punctigera*	6
A. viridus	Green amaranth	W, e	*Heliothis* spp.	7
Gomphrena globosa	Globe amaranth	W, e	*punctigera*	6
Asteraceae				
Arctotheca calendula	Capeweed	W, e	*punctigera*	2
Bidens pilosa	Cobbler's pegs	W, n	*Heliothis* spp.	7
Calendula sp.	Marigold	C, e	*punctigera*	2
Callistephus chinensis	Aster	C, e	*Heliothis* spp.	6
Calotis lappulaceae	Yellow daisy burr	W, n	*Heliothis* spp.	7
Carthamus lanatus	Saffron thistle	W, e	*armigera*	8
C. tinctorius	Safflower	C, e	*punctigera*	4
Conyza canadensis	Canadian fleabane	W, e	*Heliothis* spp.	7
Conyza sp.		W, n	*Heliothis* spp.	7
Dahlia pinnata	Aztec dahlia	C, e	*armigera*	3
Eupatorium adenophorum	Hemp agrimony	W, e	*Heliothis* spp.	3
Gerbera jamesonii	Gerbera	C, e	*armigera*	4
Gnaphalium japonicum	Cudweed	W, e	*Heliothis* spp.	7
Gnaphalium sp.		W, e	*Heliothis* spp.	7
Guizotia abyssinica	Niger seed	C, e	*punctigera*	6
Helianthus annuus	Sunflower	C, e	*armigera*	6
Helichrysum spp.	Everlastings	W, n	*punctigera*	5
Lactuca sativa	Lettuce	C, e	*arm.* + *punct.*	4, 6
L. serriola	Prickly lettuce	W, n	*Heliothis* spp.	7
Sonchus oleraceus	Common sowthistle	W, e	*punctigera*	3
Xanthium pinnata	Noogoora burr	W, e	*arm.* + *punct.*	3, 4
X. spinosum	Bathurst burr	W, e	*Heliothis* spp.	7
Zinnia elegans	Common zinnia	C, e	*punctigera*	6
Balsaminaceae				
Impatiens balsamina	Balsam	C, e	*punctigera*	6
Bignoniaceae				
Tecomaria capensis	Cape honeysuckle	C, e	*armigera*	3
Boraginaceae				
Echium plantagineum	Paterson's curse	W, e	*arm.* + *punct.*	2, 8
Brassicaceae				
Brassica campestris dichotoma	Brown sarson	C, e	*punctigera*	6
B. c. sarson	Yellow sarson	C, e	*punctigera*	6
B. c. toria	Toria	C, e	*punctigera*	6
B. juncea	Indian mustard	W, e	*punctigera*	6
B. napus	Rape	C, e	*arm.* + *punct.*	3, 6
B. nigra	Black mustard	C, e	*arm.* + *punct.*	3, 6
B. oleracea var. *botrytis*	Cauliflower	C, e	*punctigera*	6
B. o. var. *capitata*	Cabbage	C, e	*arm.* + *punct.*	4, 6
B. o. var. *italica*	Broccoli	C, e	*armigera*	3

Table 1. (*Continued*)

Botanical name	Common name	Host type	Species recorded	Reference
B. rapa	Turnip	C, e	*armigera*	3
Brassica sp.	Choisim	C, e	*punctigera*	6
Capsella bursa-pastoris	Shepherd's purse	W, n	*Heliothis* spp.	7
Lepidium hyssopifolium	Pepper cress	W, n	*Heliothis* spp.	7
Lepidium sp.	Pepper cress	W, n	*Heliothis* spp.	7
Matthiola incana	Stock, gillyflower	C, e	*punctigera*	6
Cannaceae				
Canna indica	Canna	C, e	*punctigera*	5
Caricaceae				
Carica papaya	Pawpaw	C, e	*armigera*	3
Caryophyllaceae				
Dianthus caryophyllus	Carnation	C, e	*arm.* + *punct.*	4
Chenopodiaceae				
Beta vulgaris	Beetroot	C, e	*arm.* + *punct.*	3
Chenopodium album	Fat hen	W, n	*Heliothis* spp.	7
C. polygonoides	Saltweed	W, n	*Heliothis* spp.	7
C. triangulare	Fishweed	W, n	*Heliothis* spp.	7
Rhagodia hastata	Berry saltbush	W, n	*Heliothis* spp.	7
Salsola kali	Soft roly-poly	W, n	*Heliothis* spp.	7
Cleomaceae				
Cleome viscosa	Tickweed	W, n	*punctigera*	6
Clusiaceae				
Hypericum perforatum	St John's wort	W, e	*punctigera*	1
Convolvulaceae				
Ipomoea? *aquatica*	Potato vine	W, n	*punctigera*	6
Ipomoea polymorpha		W, n	*punctigera*	6
Operculina turpethum	Onion vine	W, n	*punctigera*	6
Cucurbitaceae				
Citrullus lantanus	Melon	C, e	*arm.* + *punct.*	3
C. lanatus var. *caffer*	Watermelon	C, e	*punctigera*	4
Cucumis melo cantalupensis	Rock melon	C, e	*punctigera*	6
C. sativus	Cucumber	C, e	*punctigera*	6
Cucurbita moschata	Squash	C, e	*punctigera*	6
C. pepo	Pumpkin	C, e	*punctigera*	6
C. p. medullosa	Marrow	C, e	*punctigera*	6
Euphorbiaceae				
Acalypha hispida	Chenille plant	C, e	*arm.* + *punct.*	6
A. wilkensia	Copper-leaf	C, e	*arm.* + *punct.*	6
Leptopus decaisnei		W, e	*punctigera*	6
Ricinus communis	Castor-oil plant	W, e	*armigera*	6
Fabaceae				
Alysicarpus vaginalis	Alyce clover	W, n	*punctigera*	6
Arachis hypogaea	Peanut	C, e	*arm.* + *punct.*	6
Cajanus cajan	Pigeon pea	C, e	*arm.* + *punct.*	3, 6
Centrosema pubescens	Centro	C, e	*armigera*	3
Cicer arietinun	Chick pea	C, e	*arm.* + *punct.*	6
Dolichos minima	Rhynchosia	W, n	*Heliothis* spp.	7
Glycine max	Soybean	C, e	*arm.* + *punct.*	6
Lablab purpureus	Lablab bean	C, e	*arm.* + *punct.*	3, 6
Lathyrus odoratus	Sweet pea	C, e	*armigera*	3
Lupinus angustifolius	N.Z. blue lupin	C, e	*punctigera*	6
Lupinus sp.	Lupin	C, e	*arm.* + *punct.*	1
Macroptilium lathyroides	Phasey bean	C, e	*arm.* + *punct.*	6

Table 1. (*Continued*)

Botanical name	Common name	Host type	Species recorded	Reference
Medicago polymorpha	Burr medic	C, e	*armigera*	4
M. sativa	Lucerne	C, e	*arm. + punct.*	3, 4
Phaseolus vulgaris	French bean	C, e	*arm. + punct.*	4, 6
Pisum sativum	Garden pea	C, e	*arm. + punct.*	6
Sesbania cannabina	Sesbania pea	W, n	*arm. + punct.*	6
S. campylocarpa	Sesbans	W, n	*punctigera*	6
S. erubescens	Sesbans	W, n	*punctigera*	6
S. simpliciuscula	Sesbans	W, n	*arm. + punct.*	6
Stizolobium deeringianum	Velvet bean	C, e	*punctigera*	6
Stylosanthes humilis	Townsville lucerne	C, e	*punctigera*	6
Trifolium alexandrinum	Berseem clover	C, e	*punctigera*	6
T. repens	White clover	C, e	*punctigera*	3
Vicia benghalensis	Purple vetch	W, e	*punctigera*	6
V. sativa	Common vetch	W, e	*punctigera*	6
V. villosa	Russian vetch	W, e	*punctigera*	6
Vigna sesquipedales	Snake bean	C, e	*punctigera*	6
V. unguiculata	Cowpea	C, e	*armigera*	3
Geranaceae				
Pelargonium rodneyanum	Geranium	C, e	*punctigera*	5
Pelargonium sp.	Pelargonium	W, n	*punctigera*	5
Iridaceae				
Gladiolus sp.	Gladiolus	C, e	*arm. + punct.*	4
Lamiaceae				
Lamium amplexicaule	Deadnettle	W, e	*punctigera*	2
Origanum vulgare	Wild marjoram	C, e	*armigera*	3
Salvia reflexa	Mintweed	W, e	*punctigera*	3
Stachys sp.	Stachys	W, e	*punctigera*	5
Liliaceae				
Asparagus officinalis	Asparagus	C, e	*punctigera*	5
Linaceae				
Linum usitatissimum	Linseed	C, e	*arm. + punct.*	1
Malvaceae				
Abelmoschus esculentus	Okra	C, e	*arm. + punct.*	4, 6
A. ficulneus	Native rosella	W, n	*punctigera*	6
Abutilon indicum	Indian lantern flower	W, n	*punctigera*	6
A. otocarpum	Desert Chinese lantern	W, n	*punctigera*	6
A. oxycarpum	Flannel weed	W, n	*punctigera*	6
Althaea officinalis	Marsh mallow	W, e	*punctigera*	5
Gossypium hirsutum	Cotton	C, e	*arm. + punct.*	4
Hibiscus cannabinus	Kenaf hibiscus	C, e	*arm. + punct.*	3, 6
H. rosa-sinensis	Hibiscus	C, e	*punctigera*	4
H. sabdariffa	Rosella	W, e	*armigera*	3
H. trionum	Bladder ketmia	W, e	*armigera*	3
Sida cordifolia	Flannel weed	W, n	*armigera*	3
S. retusa	Paddy's lucerne	W, n	*Heliothis* spp.	7
S. spinosa	Spiny sida	W, n	*punctigera*	6
Meliaceae				
Owenia acidula	Emu apple	C, e	*punctigera*	5
Mimosaceae				
Neptunia monosperma	Native sensitive plant	W, n	*punctigera*	6
Moraceae				
Ficus platypoda	Fig	W, n	*punctigera*	5

Table 1. (*Continued*)

Botanical name	Common name	Host type	Species recorded	Reference
Musaceae				
Musa acuminata	Cavendish banana	C, e	*armigera*	4
M. paradisiaca	Banana	C, e	*punctigera*	6
Musa sp.	Banana	C, e	*armigera*	3
Myoporaceae				
Eremophila gilesii	Green turkey bush	C, n	*punctigera*	3
E. longifolia	Berrigan	C, n	*punctigera*	5
Myrtaceae				
Melaleuca incana	Teatree	C, n	*armigera*	3
Nyctaginaceae				
Boerhavia diffusa	Tarvine	W, n	*punctigera*	3
Oxalidaceae				
Oxalis pes-caprae	Soursob	W, e	*punctigera*	2
Paperveraceae				
Papaver nudicaule	Iceland poppy	C, e	*punctigera*	3
P. somniferum	Opium poppy	C, e	*punctigera*	6
Passifloraceae				
Passiflora edulis	Passion fruit	C, e	*armigera*	3
Pedaliaceae				
Josephina eugeniae	Josephina burr	W, n	*punctigera*	6
Sesamum indicum	Sesame	C, e	*arm. + punct.*	3, 6
Poaceae				
Brachiaria sp.		W, n	*Heliothis* spp.	7
Hordeum vulgare	Barley	C, e	*armigera*	3
Oryza sativa	Rice	C, e	*punctigera*	5
Panicum miliaceum	French millet	C, e	*armigera*	4
Panicum sp.	Panicum	C, e	*armigera*	3
Saccharum officinarum	Sugar cane	C, e	*punctigera*	5
Sorghum bicolor	Forage sorghum	C, e	*arm. + punct.*	3
Triticum aestivum	Wheat	C, e	*arm. + punct.*	3, 6
Zea mays	Maize	C, e	*arm. + punct.*	4, 6
Polygonaceae				
Rumex sp.	Dock	W, n	*punctigera*	5
Portulacaceae				
Portulaca grandiflora	Rose-moss	W, e	*punctigera*	6
P. filifolia	Pigweed	W, e	*arm. + punct.*	6
P. tuberosa	Pigweed	W, e	*punctigera*	6
Portulaca sp.	Pigweed	W, e	*punctigera*	3
Proteaceae				
Macadamia integrifolia	Macadamia nut	C, n	*armigera*	3
M. tetraphylla	Queensland nut	C, n	*arm. + punct.*	3
Resedaceae				
Reseda luteola	Wild mignonette	C, e	*armigera*	8
Rosaceae				
Fragaria × ananassa	Strawberry	C, e	*arm. + punct.*	4
Malus domestica	Apple	C, e	*punctigera*	5
M. sylvestris	Crab apple	C, e	*punctigera*	5
Prunus persica	Peach	C, e	*punctigera*	5
P. domestica	Plum	C, e	*punctigera*	5
Rosa sp.	Rose	C, e	*punctigera*	1
Rutaceae				
Citrus limon	Lemon	C, e	*armigera*	3
C. sinensis	Orange	C, e	*armigera*	4

Table 1. (*Continued*)

Botanical name	Common name	Host type	Species recorded	Reference
Scrophulariaceae				
Antirrhinum majus	Snapdragon	C, e	*arm. + punct.*	1, 3
Verbascum virgatum	Mullein	W, e	*armigera*	8
Solanaceae				
Capsicum frutescens	Capsicum	C, e	*punctigera*	6
Datura leichhardtii	Native thornapple	W, n	*arm. + punct.*	6
Lycopersicum lycopersicum	Tomato	C, e	*arm. + punct.*	1
Nicotiana tabacum	Tobacco	C, e	*arm. + punct.*	1
Nicotiana sp.	Wild tobacco	W, n	*Heliothis* spp.	7
Petunia × *hybrida*	Petunia	C, e	*arm. + punct.*	3
Physalis minima	Wild gooseberry	W, n	*Heliothis* spp.	7
P. peruviana	Cape gooseberry	W, e	*arm. + punct.*	3
P. virginiana	Ground cherry	W, n	*Heliothis* spp.	7
Solanum echinatum		W, n	*punctigera*	6
S. melongena	Eggplant	C, e	*punctigera*	6
S. tuberosum	Potato	C, e	*arm. + punct.*	3
Tiliaceae				
Corchorus olitorius	Jute	W, e	*punctigera*	6
Urticaceae				
Urtica sp.	Stinging nettle	W, e	*punctigera*	5
Verbenaceae				
Verbena bonariensis	Purpletop	W, n	*Heliothis* spp.	7
V. officinalis	Common verbena	W, n	*Heliothis* spp.	7
Vitaceae				
Vitis vinifera	Grape	C, e	*armigera*	4
Zingiberaceae				
Zingiber officinale	Ginger	C, e	*armigera*	3
Zygophyllaceae				
Tribulus terrestris	Caltrop	W, n	*Heliothis* spp.	7
Zygophyllum sp.	Twinleaf	W, n	*Heliothis* spp.	7

the adult stage on the plant (preferably intact, growing plants and not excised parts: see Hoque 1985); or (2) collecting pupae (of larvae completing development on the plants) from the field and testing the fertility of subsequent adults.

Notwithstanding the incomplete nature of the records, *punctigera* seems to be found predominately on dicotyledonous plants, whereas *armigera* occurs on both di- and monocotyledons (Table 1; Wardhaugh *et al.* 1980; Wilson 1982). Of the 159 species of plant (in 49 plant families) recorded as host for either species, 32 were used exclusively by *armigera*, 84 by *punctigera* and the remainder (43) by both. A wider range of plant families seems to be used by *punctigera* (39) than by *armigera* (29). The bulk of the hosts are exotic (125) only three native hosts being recorded for *armigera*, 25 for *punctigera*, and six being shared.

Much work remains to be done on the host plants of *Heliothis*. However, given the range of hosts already recorded, it would seem that the distribution of neither species is limited by host plants. We will next consider the effect of host plant on reproduction, immature development and survival.

Reproduction and Host Plant Choice

Eggs of both species are about 0·5 mm in diameter, nearly spherical (height and diameter equal), slightly flattened at the base and summit, and pearly white when newly laid. The chorion is visibly ribbed and the micropyle on top of the egg is surrounded by a smooth ribless area

(Fig. 6). Eggs are laid singly on various plant structures—leaves, buds, flowers, fruit and stems (Kirkpatrick 1961*a*; Cullen 1969).

Cullen (1969) provides the only study of reproduction in *punctigera* to date. He studied the effects of mating, temperature, humidity and food supply on adult female fecundity, egg fertility and adult longevity in the laboratory and field. Eggs are not developed at adult emergence. Females mate within 1–2 days and continue to mate (up to six times in field-collected moths) and produce mature eggs throughout their adult life (*c.* 2 weeks, depending on temperature). At the two temperatures studied, 19° and 24°C, the mean (±SE) number of eggs per female lifetime were similar: 1395 ± 160 and 1437 ± 229 respectively. Maximum lifetime fecundity was 2899 (at 24°C) with a maximum egg production on one day of 691 (average 112 eggs per female per day at 24°C over 12·8 days longevity, and 83 eggs per female per day at 19°C over 16·8 days). Mating stimulated oviposition, and food availability affected fecundity and fertility. Lack of food (sugar solution) greatly decreased fecundity and mating frequency.

No studies equivalent to Cullen's (1969) work have been published for Australian *armigera* (but see Adjei-Maafo 1980); and the effects of host plant on the size, potential fecundity and fertility of either species have not been investigated. Most Australian studies rely on overseas results for *armigera*, even though the responses to hosts are known to differ within continents (e.g. Coaker 1959).

Although adult moths can be active (feeding and ovipositing) during the day (e.g. Common 1953; Cullen 1969; personal observations), most activity occurs at night, particularly in the 3–4 h after and including dusk (Cullen 1969; Persson 1976). Persson showed that *punctigera* females were relatively more abundant or active (as assessed by light traps) in the first part and males in the later part of the night. In *armigera* both sexes became more abundant after midnight, at least in subtropical Queensland.

Egg-laying in *armigera* showed a bimodal distribution during the night, with the initial peak larger than the later one (Persson 1974). Moonlight strongly depressed egg-laying, either preventing the start of oviposition or causing it to stop once begun. However, an underlying endogenous rhythm was also implicated (Persson 1974). Peak female activity coincided with peak oviposition (Cullen 1969; Persson 1974) and most mating was thought to take place around and after midnight. Female moths in both species produce pheromones which attract males (Rothschild 1978; Rothschild *et al.* 1982).

The phenology of *Heliothis* oviposition on its host plants is complex. Most authors comment on the coincidence of peak egg-laying with, or its occurrence just before, peak flowering and nectar production (Cullen 1969; Wilson *et al.* 1972; Wilson 1976, 1981*a*; Adjei-Maafo 1980; Broadley 1980; Wardhaugh *et al.* 1980; Adjei-Maafo and Wilson 1983). However, 'considerable' oviposition occurs on pre-flowering soybeans (Richards 1968; Wardhaugh *et al.* 1980), cotton (e.g. Wardhaugh *et al.* 1980; Wilson 1981*a*) and tobacco (Broadley 1978*b*). To a lesser extent eggs are also laid on the leaf-whorls of seedling sorghum (Passlow 1973; Wilson 1976), leaves of sunflowers at any stage (Broadley 1980), tomatoes and lucerne at any stage (Cullen 1969), and pre-tassled maize (Wardhaugh *et al.* 1980).

The distinction between the apparent attractiveness of flowering crops and the suitability of sites for oviposition led Cullen (1969) to consider oviposition to consist of two distinct stages: (1) concentration of ovipositing moths within an area; (2) selection of a particular oviposition site. Cullen (1969) considered chemical cues, the presence of food, and humidity to be relatively unimportant to an ovipositing female selecting a specific oviposition site, and suggested that the type of surface texture was the principal cue used. Hairy or rough-textured surfaces attract more oviposition (Hassan 1985) and the tarsi of *punctigera* seem to play a pre-eminent role in such site selection. However the presence of chemoreceptors on the ovipositor of *punctigera* (Hoque and Rice, personal communication) suggests that chemical cues may also be important.

The clumped distribution of eggs of *Heliothis* species within cotton crops (Wilson and Room 1982; Hassan 1985), which are theoretically of uniform genetic quality, age and condition, suggests that females use many cues to locate suitable oviposition sites. These may include subtle variation in plant quality (secondary chemicals, nutrients) (e.g. Mabbett and Nachapong 1983), size, nectar production and plant morphology; individual females may also vary in their responses to these cues.

Cullen (1969) attributed the increase in oviposition on flowering peas and lucerne to the chemical attractiveness of such crops. Females would be attracted to such areas and concentrate their activities, thus resulting in higher numbers of eggs. The close correlation between oviposition (between plants), oviposition site selection (within plants) and extra-floral nectar production in two cotton cultivars led Adjei-Maafo and Wilson (1983) to suggest that the presence of extra-floral nectar *per se* attracted oviposition. Adjei-Maafo (1980) found a 28–45% reduction in oviposition by *Heliothis* species on nectariless compared with nectaried cotton. The absence of extra-floral nectar reduced mating in *punctigera*, and fecundity and fertility in both species. Adjei-Maafo (1980) suggested that the timing of oviposition in the field was determined by the phenology of nectar production by cotton by means of its influence on fecundity. The presence of adequate nectar also seems to induce more sedentary behaviour in adults, leading to local concentration of moths (Adjei-Maafo 1980; Wardhaugh *et al.* 1980). However, egg-laying peaks also occur on: (1) crops, including cotton, before flowers and nectar are available; (2) crops where nectar is not produced or is inaccessible (e.g. tobacco, sorghum, maize); this suggests that other cues, including chemical attractants, are involved. Wardhaugh *et al.* (1980) attribute anomalies such as the apparent absence of *Heliothis* infestations on seemingly attractive hosts to asynchrony in time and/or space of ovipositing moths.

Perhaps the obvious question, which no one has yet addressed, is: do demes (local populations) of *Heliothis* species show similar preferences for host plants? How much variation is there between individual female moths in oviposition preferences? Most workers have had no choice but to assume that moths were identical throughout their geographic range, despite circumstantial evidence that there may be geographic differences (see also pp. 784–9). Miller *et al.* (1979) found that soybean crops suffered more damage outside cotton-growing areas than when grown adjacent to cotton. This was attributed to an oviposition preference for cotton. *H. punctigera* was considered to be the major economic species attacking cotton in south-western Queensland (Davis *et al.* 1963), but did not infest cotton in the Callide region of central Queensland (Common 1953), although present in that area. Geographic differences in individual preferences for host plants could be influenced by many factors, including: (1) genetically determined preferences; (2) adult experience of host availability in the local area, which will in turn be influenced by adult movement and age. The apparent increase in *armigera* and *punctigera* oviposition on cotton in various geographic localities (e.g. the Ord, Namoi) after a number of years could imply a change in preference due to genetic adaptation to new hosts. Common (1953) suggested that the failure of insecticide treatments to increase cotton yields in the Ord and central Queensland was possibly related to the fact that *punctigera* does not normally attack cotton (in the Ord) and that *armigera* was not a serious pest on this crop in central Queensland (see also Passlow 1958, 1959). Since the 1950s both *Heliothis* species have come to be considered the major pests of cotton wherever it is grown. This could reflect changes in agronomic practices as much as changes in host preferences. Since the 1950s the area grown to cotton has increased, thereby increasing the frequency of contact between insect and plant.

Methods of growing cotton have also changed. Most cotton is irrigated and heavily fertilised with nitrogen. Both practices increase the attractiveness of the crop (Wilson *et al.* 1972; Wardhaugh *et al.* 1980) and heavy use of pesticides may promote populations, because predation is reduced. A worthwhile area of research would be to examine the nature of host-plant selection and host species preferences in both *Heliothis* species. Such studies should include a representative collection of hosts rather than one or a few species, as understanding of the nature of polyphagy is essential. Host-plant resistance is a major tactic for pest management (Thompson and Lea 1980), but it is still unknown whether *Heliothis* is able to adapt to monocultures of 'new' cultivars.

Immature Development and Diapause

An essential component of any population-ecological study of an insect species is a knowledge of its physiological time-scale, which is mediated in part by temperature. It is now commonplace for ecologists and entomologists to record the effects of temperature on the rate of development. Kirkpatrick (1962*b*) recorded the time spent in the egg, larval and pupal stages by four species of *Heliothis* over 1 year. Records were made inside an insectary, and development times related to mean monthly temperatures. Samples were small and in some months records are missing. The diet used is not clear but may have included cut French beans (Kirkpatrick 1962*a*). Under these conditions *armigera* and *punctigera* showed similar changes in generation times (summing the time in the egg, larval and pupal stages) over the year. In midwinter (May–July) with temperatures averaging 16–18°C, *Heliothis* took about 73 days (in the absence of a pupal diapause). In summer (December–January) with temperatures of about 28°C, both species took about 34 days from egg to adult.

Cullen (1969) studied the effects of constant temperatures (ranging from 9·5° to 40·0°C) on the development of all stages of *punctigera* reared on chopped French beans. He found that at 19·4°C females developed significantly faster than males (30·7 and 32·5 days respectively; $P<0\cdot01$). Twine (1978*a*) found no sex differences in the development of *armigera*, at least in those reared on artificial diets. Development was optimal at *c*. 35°C for all stages of *punctigera*, and a development threshold of 10°C was estimated for larvae (visual extrapolation from a temperature–development curve).

Twine (1978*a*) reported the effects of constant temperatures on the development of larvae and pupae of *armigera* reared on an artificial diet. A developmental zero of 11°C was estimated for the combined larval and pupal stages, with a development time of 475 day-degrees. The rate of development was maximal at 33·9°C. A developmental threshold of 11·7°C and thermal constant of 43·3 day-degrees were determined for the egg stage of *armigera* by Kay (1981*a*). The rate of development was also maximal at 33·9°C for eggs. Wilson *et al.* (1979) studied the effects of constant temperatures on pupae (field-collected as late-instar larvae in autumn). They reported a developmental threshold temperature of 12°C, calculated from a curve fitted by eye to the inverse of median time taken to develop to the adult stage. Foley (1981), on the other hand, reported a developmental zero of 14·8°C ± 1·0°C for non-diapausing pupae of *armigera*, and a development time of 160 day-degrees, compared with 200 d° (Wilson *et al.* 1979) and 211 d° (Twine 1978*a*).

Room (1983) used the data of Twine (1978*a*), Kay (1981*a*) and Cullen (1969), obtained at constant temperatures, to derive expressions relating temperature to percentage development per day of eggs, larvae, pupae and adult females (to 50% oviposition) against temperature. He used Pradhan's equations (Pradhan 1946), with an optimum developmental temperature of 35°C for all stages; this was to allow for the reduced development rates at temperatures above the optimum. The same expressions were used for both species, because their responses to constant temperatures were similar. Room (1983) also calculated the times taken to develop through various stages, using screen temperatures recorded in the Namoi Valley, New South Wales, transformed to temperatures experienced by eggs and larvae of *Heliothis* species on cotton (and pupae in the soil). The predicted generation times agreed with field observation of peak egg counts and peak light trap catches in the Narrabri area (Wardhaugh *et al.* 1980). The expressions have also been used to project egg and larval development over 1–2 days as part of a computer-based management system (Room 1979*b*; Hearn *et al.* 1981). Generation times of *Heliothis* species in the Narrabri area, as estimated from peak light catches and/or egg counts in summer (December–February) are of the order of 35–45 days. Wilson *et al.* (1972) estimated a generation time of 6–7 weeks in the Ord area, W.A.

Although Room's (1983) temperature-driven model seems to work, it is possible that factors other than temperature are also involved. A slowing of development at high temperatures was *assumed* to be due to supra-optimal temperature effects, and Pradhan's equation fitted. However, Kay (1981*a*) did not evaluate temperatures higher than Room's (1983) estimated optimum of 35°C, and Twine (1978*a*) had only one constant temperature higher than 35°C, although larvae failed to complete development at this temperature (38·4°C). Similarly, Cullen (1969) did not obtain results at temperatures above 35°C for pupae and eggs, as very few larvae survived at 40°C. More studies in the range 30–45°C are clearly needed. Also all constant-temperature work has used larvae fed chopped beans or artificial diets. Development tends to be faster in individuals reared on artificial diets (e.g. Pretorius 1976) than in those fed plant material. Duration of larval development in *armigera* is very variable, and can be extended to six or seven instars instead of the more normal five or six. Twine (1978*b*) suggested that the additional moults, and consequently a longer developmental period, are determined by diet, temperature and 'vigour'. Kay *et al.* (1979) showed that the addition of even low concentrations of gossypol, a terpenoid pigment found in cotton, greatly extended larval development times in both species of *Heliothis*. Generation times may therefore be influenced by host-plant factors as well as temperature. A major area requiring careful experimental work is determination of the effects of various host plants and temperature on *Heliothis* development. The effects of fluctuating temperatures also need to be considered. Foley (1981) showed that development of *armigera* pupae is speeded up by fluctuating temperatures. In addition, the temperatures actually experienced by the insect in the field and its relationship to development, as opposed to temperatures measured in a Stevenson screen, needs to be carefully considered (see, e.g., Gregg 1981).

Both species of *Heliothis* exhibit a facultative pupal diapause. The factors inducing diapause in *punctigera* have been studied in the laboratory by Cullen and Browning (1978) and by Browning (1979, 1981). Diapause was induced in most (*c.* 90%) pupae when both pupae and larvae were exposed to a temperature of 19°C and 12L : 12D photoperiods. If eggs and developing larvae experienced a shortening photoperiod, diapause was more likely and more pronounced (Cullen and Browning 1978). Diapause does not occur if temperatures after feeding ceases and before pupal ecdysis are 28°C or over. In both species diapausing pupae can be recognised by the persistence of 'eye spots' in the post-genal region. The time taken for diapausing pupae to complete development has been recorded by Kirkpatrick (1962*b*), Cullen (1969), Cullen and Browning (1978) for *punctigera*, and by Kirkpatrick (1962*b*), Wilson *et al.* (1979), Foley (1981) and Kay (1982*a*) for *armigera*.

Diapausing pupae took about 69–318 days to develop, with those pupating later in the season taking less time (Kay 1982*a*) in south-east Queensland. Foley (1981) recorded a threshold of 15·4–17·3°C for post-diapause development, which was higher than the 12°C reported by Wilson *et al.* (1979). The percentage of pupae entering diapause varied from year to year, maximum percentage diapause of 88, 94 and 100% being recorded in 1976, 1977 and 1978 respectively in the Brookstead–Cecil Plains area of Queensland (Kay 1982*a*). Wilson *et al.* (1979) recorded an average of 80% pupae diapausing between late April and May in the Namoi region of New South Wales.

In northern Australia, the percentage of diapausing individuals is much lower and *Heliothis* species are active all the year round. Wilson *et al.* (1972) found no evidence for diapause on the Ord, and *Heliothis* spp. are active all the year in the Mareeba district of northern Queensland (Broadley 1977*b*; Currie *et al.* 1982) and in central Queensland (D. Murray, personal communication). However, detailed information on levels of diapause is not available for these regions. Adults of both species emerge from diapause over a protracted period during spring and early summer. Wilson *et al.* (1979) and Cunningham *et al.* (1981) showed that the time taken to break diapause in *armigera* could be described by a geometric distribution with a long 'tail' for pupae which took a long time for this.

Immature Survival

Few life-table studies of *Heliothis* on its various host plants have been published. Most studies on immature survival have been observational, with mortality factors inferred by authors. Evenson and Basinski (1973), Bishop and Blood (1977), and Room (1979*a*) catalogued insect predators and parasitoids found on cotton and associated with *Heliothis* survival. Tables 2–4 detailed the records of natural enemies of *Heliothis* on various hosts

Table 2. Natural enemies of *Heliothis* spp.: parasitoids

Key to references: *1*, Bishop 1979; *2*, Bishop 1984; *3*, Bishop and Blood 1977; *4*, Bishop and Holtkamp 1982; *5*, Broadley 1981*a*; *6*, Broadley 1981*b*; *7*, Broadley 1984; *8*. Cooper 1979; *9*, Cullen 1969; *10*, Evans 1985; *11*, Evenson and Basinski 1973; *12*, Forrester 1981; *13*, Kay 1982*b*; *14*, Learmonth, in Hopkins 1981; *15*, McLaren and Rye 1981; *16*, Michael 1973*a*; *17*, Michael 1973*b*; *18*, Miller *et al.* 1979; *19*, Poinar 1975; *20*, Pyke 1981; *21*, Richards 1968; *22*, Room 1979*a*; *23*, Samson and Blood 1980; *24*, Shepard *et al.* 1983; *25*, Sloan 1940; *26*, Tcakle *et al.* 1983; *27*, Titmarsh 1985; *28*, Twine 1973; *29*, Wilson 1983; *30*, Wilson and Greenup 1977; *31*, Wilson *et al.* 1972; *32*, Wright and Nitikin 1964. ? Not positively identified

Taxon	Cotton	Sunflower	Lucerne	Maize	Tomato	Tobacco	Linseed	Lupin	Peanut	Potato	Safflower	Sorghum	Soybean	Grain legumes
Diptera														
Tachinidae														
Anamastax braueri (Hardy)		5												
Anamastax sp.						27								
Carcelia noctuae Curran	3,22,30	12										26,29		
Carcelia sp.		5,7,13				27								
Chaetophthalmus biseriatus Malloch	3,22?	7?12?	9?	13								29		
Chaetophthalmus sp.		5	2,8										10	
Compsilura concinnata (Meigen)		7												
Cuphocera sp.		7												
Exorista curriei Curran	31											26		
Exorista sp.		7				27								
Goniophthalmus australis (Baranov)	11,21,31	7,12									21	26	10	24
Goniophthalmus sp.						27								
Palexorista sp.			2											
Sisyropa sp.			2											
Tritaxys heterocera (Macquart)		5												
Unidentified species	22		9											

						Hymenoptera								
Braconidae														
Cardiochiles sp.	22													
Chelonus sp.		5,7												
Microgaster sp.												17		
Microplitis demolitor Wilkinson			2									26	10	24
Microplitis sp.	3,22,30	5,7,12,13				27							10	
Pristomerus sp.		7												
Rogas sp.			2											
Unidentified species	22													
Chalcidae														
Brachymeria sp.	21													
Ichneumonidae														
Charops sp.													10	
Heteropelma scaposum (Morley)	3,22,30	5,7,12,13		13		27						29	10	24
Ichneumon promissorius Erichson														
= *Pterocormus promissorius*	3,22,30											29		
Lissopimpla excelsa (Costa)	3,11,22,32											29		24
Netelia producta (Brulle)	3,11,22, 30,32		2,4									29	10	24
Netelia sp.		7												
Ophion sp.			8											
Unidentified species			9			27								
Pteromalidae														
Unidentified species	22		28											
Scelionidae														
Telenomus sp.	3,22,28		2,8,28	28		28		28	28	28				
Trichogrammatidae														
Trichogramma australicum Girault	28		8,28	28	28		28					17		
Trichogramma ivelae Pang & Chen					15									
Trichogramma sp.	3,22	14										16,26		
Trichogrammatoidea flava Girault			2,28				28							
Trichogrammatoides rara Girault	25													
Trichogrammatoides sp.	3,22													

Table 3. Natural enemies of *Heliothis* spp.: predators

For key to references, see Table 2

Taxon	Cotton	Sunflower	Soybean	Lucerne	Linseed	Safflower	Grain legumes
Dermaptera							
Labiduridae							
Labidura riparia truncata Kirby	3,22,29	6,12	10	4			24
Orthoptera							
Tettigoniidae							
Conocephalus sp.	22						
Heteroptera							
Nabidae							
Nabis kingbergii Reuter = *Tropiconabis capsiformis* (Germar) = *Nabis capsiformis* Germar	3,11,20,22, 23,32	6,12	10				
Pentatomidae							
Cermatulus nasalis (Westwood)	3,11,22,30,32	6,12	10,18	4,8			24
Oechalia schellenbergii (Guérin-Méneville)	3,11,22,30,32	6,12	10,18	4,8	21	21	24
Lygaeidae							
Geocoris lubra (Kirklady)	3,20,22?	12	10	4			24
Oxycarenus luctuosis (Montrouzier & Signoret)	22	6,12	18	4			
Miridae							
Deraeocoris signatus (Distant)	3,20,22	6,12	10	4			
Reduviidae							
Coranus sp.			10				
Neuroptera							
Chrysopidae							
Chrysopa ramburi Schneider	3			8			
Chrysopa signata Walker	3,22?23			4,8			
Hemerobiidae							
Micromus tasmaniae Walker	3,22,23	6,12		4,8			

Coleoptera					
Coccinellidae					
Coccinella repanda Thumberg	3,11,20,22,32	6,12	10,18	4,8	24
Diomus notescens Blackburn	3,20,22	6,12	10	4	24
Harmonia arcuata (F.) = *Coccinella arcuata* F.	3,20	12	18		24
Micraspis frenata (Erichson)	3,11,20,22,32	6,12	10,18	4	24
Cantharidae					
Chauliognathus pulchellus Macleay	3,22	6	10	4	24
Carabidae					
Calosoma schayeri Erichson	22	12	10	4	24
Helluo insignis Sloane	22				
Unidentified species			10		
Melyridae					
Dicranolaius bellulus Guerin	3,20,22	6,12	10	4	24
Araneida					
Lycosidae					
Lycosa sp.	3,22				
Clubionidae					
Chiracanthium diversum Koch	1,3,22,30	12			24
Clubiona notabilis	1,3?				
Salticidae					
Bianor concolor (Keys)	1,3				
Hasarius obscurus L. Koch	22				
Oxyopidae					
Oxyopes amoenus L. Koch	1,3				
Oxyopes elegans Koch	22			4	
Oxyopes mundulus L. Koch	1,3	6?	10	4	24
Theridiidae					
Achaearanea veruculata (Urquhart)	3,22,30	6?,12			
Thomisidae					
Diaea variabilis L. Koch	3		10		

in different locations. Bishop and Blood (1977), using direct observation and laboratory rearing, identified 18 predators, 10 parasitoids and three diseases of *Heliothis* in south-eastern Queensland (Tables 2–4). Room (1979*a*) used direct observation, laboratory petri-dish studies and field radiotracer studies (see Room 1977) to identify 19 predators and 16 parasitoids of *Heliothis* in the Namoi Valley (Tables 2, 3). Relatively few natural enemies were listed for the Ord region (Tables 2, 3) by Evenson and Basinski (1973), Michael (1973*a*, 1973*b*) and Wilson *et al.* (1972). No comprehensive list of potential beneficials has been published for other cotton-growing areas. Natural enemies of *Heliothis* have been listed for other hosts (Tables 2, 3), including soybeans (Evans 1985), sunflowers (Forrester 1981; Broadley 1981*a*, 1984) and tobacco (Titmarsh 1985).

Observations of predators feeding, or parasitoids emerging, provide little information on their influence on population dynamics of *Heliothis*. Bishop and Blood (1980) recorded arthropods in the ground strata of cotton, and considered that a number of species could play a significant predatory role, including *Labidura riparis truncata* (Dermaptera), *Lycosa* sp. (Araneida), and some of the Carabidae. Similar information has been obtained for two spiders, two neuropterans and one nabid (Samson 1977; Samson and Blood 1980; Bishop and Blood 1981) and for hemipterans (Awan 1981). Two species of spider showed a direct numerical response to the abundance of *Heliothis*, although this was not sufficient to prevent loss of production in the cotton crop (Bishop and Blood 1980). Samson and Blood (1980) showed that, in the laboratory at least, third-stage *Chrysopa signata* (Neuroptera) and adult female *Tropiconabis capsiformis* (Heteroptera) were voracious predators of *punctigera* eggs and larvae. Second-instar *C. signata* was more efficient than third-instar *T. capsiformis* when searching for *punctigera* eggs.

Although no detailed life-tables have been published for *Heliothis* on cotton, Room (1979*b*) provided some indication of the level of mortality (losses) over a season in unsprayed cotton in the Namoi. Compared to the number of eggs laid (white eggs), very few small larvae (instars II and III) became established on plants and even fewer completed development (i.e. to the large larval stage). Room attributed these losses to predators and competition. It has been commonly observed that high densities of eggs on cotton early in the season (i.e. on pre-squaring, seedling cotton) yield very few second- and third-instar larvae establishing, whereas later in the season their number increases (Passlow 1959; Wilson and Greenup 1977; Room 1979*b*). The heavy early mortality is often attributed to harsh environmental conditions (Wilson and Greenup 1977; Wilson 1982) and predation. The increase in establishment over the season has been attributed to declining searching efficiency of predators as plants increase in size (Wilson and Greenup 1977). Kay (1981*a*) found that eggs failed to develop and survive constant temperatures of 39·4°C, and Twine (1978*a*) showed larvae would not develop beyond instar IV at 38·4°C. This does not necessarily mean that heavy mortality on seedling cotton is due to fluctuating high temperatures. Predation, cannibalism and host-plant incompatibility could all play a role. Only detailed life-table studies and experimental work in field and laboratory can answer these and other questions associated with *Heliothis* survival.

Titmarsh (1985) provides the only Australian life-table study of *Heliothis* species (on tobacco). Broadley (1978*b*) had earlier found that survival rates of eggs (mean *c.* 103 per sample) to early-instar larvae were below 10%. Titmarsh (1985) was able to show that dislodgment of eggs and larva–host plant incompatibility accounted for a large proportion of the mortality in the egg and first-instar stages. On maize, larval cannibalism of eggs and larvae is considered to be the major mortality factor (Sloan 1940; Twine 1971, 1974); this may also occur on sorghum and sunflower, where very few larvae result from initial high numbers of eggs (see Sloan 1940; Twine 1971; Passlow 1973; Twine *et al.* 1983). However, Twine's (1971) laboratory studies on cannibalism restricted larvae to closed containers, preventing escape. In the field, larvae can respond to crowding by moving (see below), although cannibalism of eggs may be important at high population densities. Predation and parasitism may also be important on sorghum (Michael 1973*b*; Twine *et al.* 1983) and soybeans (Evans 1985). Cullen (1969) recorded very high mortality (*c.* 97%) of *punctigera* on lucerne, where disease was considered to be the main cause of mortality in larvae.

Stanley (1978) studied the competitive interactions between larvae of both species, in the laboratory on a semi-synthetic diet, and on cotton plants in the glasshouse. She found that, although cannibalism occurred in *punctigera*, larvae were tolerant of increasing density and tended not to act aggressively when encountering others. In contrast, *armigera* was more aggressive, cannibalism increasing with density. Survival of *punctigera* was depressed in the presence of *armigera*.

Parasitism levels vary greatly among different host plants, seasons and geographic locations. Egg parasitism was relatively unimportant on tobacco in north Queensland (Titmarsh 1985). Twine (1973) found a mean of 8% parasitism in collections of eggs of *Heliothis* species from various hosts and locations in south-east Queensland. Parasitism ranged from 0 (usually in *armigera* on maize) to 65% on potatoes. The major egg parasitoid was *Telenomus* sp. nr *triptus* Nixon (Scelionidae) (92·7% of all parasitoids reared). Three other parasitoids (trichogrammatids) were also recorded. Sloan (1940) recorded egg parasitism levels of 18–58% during November–March in the Callide Valley, and Waite (1981) reported 60% egg parasitism in unsprayed cotton around Emerald, Qld. In the Ord, Michael (1973*b*) and Robertson (1977) recorded over 50% and >99%, respectively, parasitism in *Heliothis* eggs on sorghum. They found that larvae were also heavily parasitised by *Microgaster* sp. (Braconidae). Wilson and Greenup (1977) recorded up to 30% parasitism levels in *Heliothis* larvae on cotton in northern New South Wales over three seasons, parasitoids emerged from both the larval stages (braconid, *Microplitis* sp.) and the pupal stage (three ichneumonid species and one tachinid). Broadley (1984) recorded similar levels of larval parasitism by a complex of 11 species on sunflowers in south-east Queensland, but Forrester (1981) recorded only five parasitoids on this host plant in northern New South Wales.

Table 4. Pathogens identified from *Heliothis* species

Pathogen	Reference
Virus	
Nuclear polyhedrosis virus	Bishop 1984; Bishop and Blood 1977; Cooper 1979; Teakle 1973*a*, 1973*b*, 1977
Granulosis virus	Bishop and Blood 1977; Cooper 1979; Teakle 1974, 1977
Unidentified	Cullen 1969
Fungi	
Beauveria bassiana	Bishop 1984; Teakle 1977; Wilson and Greenup 1977
Nomuraea rileyi	Teakle 1977
Protozoa	
Nosema heliothidis	Bishop and Blood 1977; Teakle 1977; Titmarsh 1985
Nematoda	
Heterorhabditis bacteriophora	Poinar 1975

Kay (1982*b*) found that in south-eastern Queensland, three parasitoids entered diapause along with their host during winter, and Wilson (1983) reported similar findings for three parasitoids in the Namoi Valley. Some parasitoids, such as *Heteropelma scaposum* (Ichneumonidae), seem to be associated with *Heliothis* over a wide geographic range (Table 2) and many host plants. Others seem to be restricted to certain host plants. The influence of host plant on the number of beneficial species is shown in Table 2. Studies by Adjei-Maafo (1980) and Ampofo (1981) demonstrate the dramatic effect that differences in plant variety may have on the insect communities found on cotton.

As with parasitism, the contribution of diseases (Table 4) to the mortality of the immature stages of *Heliothis* seems to vary seasonally, geographically, and with host plant. Titmarsh (1985) recorded very few (only three out of 3585) larvae on tobacco killed by disease.

Cullen (1969) considered disease to be the major cause of mortality of *punctigera* population on lucerne in South Australia. Teakle (1973*a*) records 'large populations of *Heliothis* larvae . . . frequently destroyed by disease in southern and central Queensland in the spring', and found that a nuclear-polyhedrosis virus was the main cause of death, although a granulosis virus also infected about 10% of larvae on lucerne. Similar high levels (60–80%) of disease-induced mortality in *Heliothis* species were recorded by Bishop (1984) on lucerne in the Hunter Valley, N.S.W. Twine *et al.* (1983) noted that the incidence of disease outbreaks in *Heliothis* on sorghum is 'quite high'. Wilson and Greenup (1977) record disease incidence in larvae over three seasons on cotton in the Namoi, ranging from 0 to 64%, with 20% of overwintering pupae killed by *Beauveria bassiana*, a fungal disease. Wilson *et al.* (1972) did not detect polyhedrosis virus in *Heliothis* on cotton in the Ord. Teakle (1977) recorded five diseases associated with *Heliothis* in Queensland (Table 2) and Cooper (1979) recorded three diseases in South Australia. A parasitic nematode, *Heterorhabditis bacteriophora*, has also been recorded from *punctigera* in South Australia (Poinar 1975; Cooper 1979).

In general, disease levels become substantial only when conditions are moist or humid and population densities are high. Under these conditions disease transmission is rapid and numbers crash. Diseases may be expected, therefore, to be important mortality agents on irrigated crops within the subtropical and tropical areas of Australia. The (potential) role of predators, such as *Nabis tasmanicus* (= *N. kingbergii*) (Heteroptera) (Beekman 1980) and *Oechalia schellenbergii* (Heteroptera) (Cooper 1981) in assisting disease transmission (NPV) should not be overlooked. The NPV remains viable in the gut of these predators which have fed on infected larvae, and may be excreted elsewhere on plants or even be transported to other crops. Even low levels of virus intake by *Heliothis* larvae may be sufficient to initiate an epizootic in the population (Teakle 1977; Cooper 1979).

Accurate assessment of survival rates and mortality factors is perhaps most difficult for the pupal stage. This stage is often not included in studies, or at best, the incidence of disease and parasitism is measured and used as an indicator of losses. Such an approach ignores the potentially important regulatory role that polyphagous soil predators (e.g. staphylinid larvae, carabid larvae and adults, ants, earwigs, etc.) could have on *Heliothis* pupae, although Wilson (1983) considered these to be unimportant.

In summary, further work is required on the survival of immatures (and adults) of *Heliothis*. In particular, accurate life-tables for *Heliothis* species on different hosts need to be developed. Such studies, supported by field experimentation, are required if we are to know the relative contribution made by the various hosts to the local adult population pool. The roles of various mortality agents (weather, predators, parasitoids, diseases, competitors, host plants) need to be assessed if management decisions are to be based on sound research information.

Heliothis is only one part of the community of insects and other organisms that occur in any one location. Enumeration of what is there is the essential first step of an ecological study. The interactions within such communities (i.e. the relationships between the organisms) can then be studied. Between-generation life-tables will help quantify the regulatory role of a particular mortality agent in long-term population fluctuations. Such life-tables cannot ignore any stage of the life cycle and should be drawn up in various geographic regions.

Movements of Adults and Immatures

An understanding of the movement process is central to life-system studies of most species (Gilbert *et al.* 1976). The feeding patterns (and consequently the distribution of damage on economic hosts) of lepidopteran larvae are in part a function of how the larvae move over their host while locating suitable feeding sites. Such movements may be within and between plants of the same and different species. Larvae need also to locate suitable pupation sites. Adult females must be able to locate suitable habitats in which to lay eggs, and males need to locate females. Movement by adults is central to the spatial population structure and dynamics of a species (Taylor and Taylor 1977) and to the question of where pest populations originate.

Movements of *Heliothis* larvae *en masse* have been commented on by a number of authors (Lea 1928; Veitch 1938; Sloan 1945; Wasson 1946). In general, these movements seemed to originate when the initial host plant dried off in early summer and larvae moved to locate other plants on which to complete development. These movements may appear spectacular because of the numbers involved; not as noticeable but equally important to survival are the extensive movements of individual larvae, both within and between plants. Broadley (1978*b*) found eggs on leaves of all ages of pre-flowering tobacco, but larvae tended to move up the plant towards the reproductive structures. The locations of feeding larvae on cotton have been well described (Ampofo 1981; Wilson and Waite 1982; Hassan 1985). Wilson and Waite (1982) concluded that the seasonal differences in abundance between *punctigera* and *armigera* are largely attributable to changes in the abundance of preferred feeding sites (fruit structures). Older larvae feed selectively on older fruit. Many bolls are attacked during a larva's lifetime, and larvae usually leave bolls after eating only part of them (Ampofo 1981).

There is some indication that on sunflowers larvae move from flower to flower. Wardhaugh *et al.* (1980) found most large larvae on young heads, and supposed that they had moved from older heads. In general *Heliothis* has been described (by, e.g., Broadley 1977*a*; Wilson and Waite 1982) as preferentially feeding on buds, flowers and fruit on most hosts. However, larvae may not always be able to feed on the plant structure on which they hatched, or continue feeding once they have started, if plants respond to feeding by mobilising secondary metabolites. Brier and Rogers (1981) showed that it is difficult for young *armigera* to establish on soybean pods. When young larvae were transferred to pods after feeding on foliage for *c.* 4–6 days they suffered high mortalities. Older larvae handle pods well and seem to prefer these structures as feeding sites (Evans 1985). The biochemical basis of host-plant use and larval movement have not been investigated, although the mixed-function oxidase system has been studied in older larvae (Collins and Hooper 1984*a*, 1984*b*; 1985). This detoxification system presumably enables *Heliothis* to use varied host plants and host-plant parts.

The preference for fruiting structures and the tendency to move from one fruit to another, often without consuming each fruit, result in extensive damage even when the number of large larvae is relatively low. Many questions on the feeding patterns of *Heliothis* on its various host plants, and why larval movement is so extensive, remain unanswered. Larvae may be moving to avoid plant secondary chemicals, predators and/or competitors, or to locate more nutritious feeding sites.

The movement behaviour of adults within areas and the movement between areas have not been well documented. An understanding of the former is essential to determine how extensively a female distributes her eggs. Between-area movements determine the amount of gene flow and may influence the origins of pest infestations in crops.

Little is known about how *Heliothis* moths locate host plants or the extent of female movement within and between patches of host plants. Wardhaugh *et al.* (1980) noted that hosts with a short flowering period (e.g. sorghum, wheat, sunflowers, rape, linseed) could not support more than one generation, and adults emerging from them would need to disperse. Crops with a prolonged flowering period (cotton) or with suitable foliage and flowers (tobacco, lucerne, soybeans, tomato) attract moths and support *in situ* breeding. The presence of nectar results in fewer long-distance movements by adults (Adjei-Maafo 1980; Wardhaugh *et al.* 1980). If there are many host plants at various stages of development (as occurs in irrigated areas in late spring and summer) then extensive intercrop movements may be expected—although this has yet to be shown.

Evidence for the scale and level of long-distance movement is extensive, but circumstantial. *H. punctigera* has been taken at lights in New Zealand (Fox 1978) and both species have been caught on Norfolk I. (Holloway 1977), although neither species is reported to breed in these areas. Farrow (1984) found *armigera* on Willis I. in the Coral Sea. Anomalies in light-trap catch patterns are often taken to indicate migration (e.g. Persson 1976; Morton *et al.* 1981; Wilson 1983). When higher-than-expected numbers are caught, prevailing wind directions are used to indicate the likely direction of movement. Drake *et al.* (1981) used radar to detect movement of adult *punctigera* across Bass Strait; such movements were associated with warm anticyclonic airflows ahead of cold fronts. Drake *et al.* (1981) inferred the origins of these moths by backtracking to south-western New South Wales and north-western Victoria. Studies such as these need to be extended Australia-wide, and the scale and origins of movements identified.

Other evidence for extensive movements is the occurrence of insecticide resistance in areas where the insecticide in question has supposedly not been used (Wilson 1974; Goodyer and Greenup 1980). From a detailed study of light-trap catches of both species in the Namoi, Morton *et al.* (1981) suggested that *punctigera* is intrinsically more mobile than *armigera* (see also Wardhaugh *et al.* 1980; Wilson 1982). This notion of relative mobilities could in part explain the development of insecticide resistance in *armigera* but not in *punctigera* (e.g. Twine and Kay 1973; Wilson 1974; Goodyer *et al.* 1975; Kay 1977)—due, presumably, to the continuous influx of individuals of the latter species from unsprayed populations. However, Daly and Gregg (1985), using gel electrophoresis, showed that the genetic distance between widely separated localities is low in both *armigera* and *punctigera*, and concluded that significant gene flow occurs in both species. Thus, although *punctigera* may be more mobile tham *armigera*, and is perhaps an obligatory migrant, movement in *armigera*, probably a facultative migrant, may also be extensive.

Population Biology and Dynamics

There are no long-term studies on the population dynamics of *Heliothis* species on a regional basis in either an agricultural or a non-agricultural situation. Damage and heavy infestations are generally sporadic, though there are reports of occasional plague years when damage was widespread. Common (1953) collated records of such outbreaks of one or both species in some Australian States in the following years: 1911, 1913–14, 1924–25, 1927–28, 1944–45 and 1949–50. More recently, major outbreaks of *armigera* have been recorded in the Ord in 1970 (see Wilson *et al.* 1972) and the Namoi in 1972–73 and 1977–78 (both species) and 1980–81 (*punctigera*) (light trap data: Wilson 1983).

Most population studies have made use of light traps and have used the catches as indicators of population phenology and relative abundance. The longest series of catches are those at Turretfield, S.A. for *punctigera* (24 years) and at Myall Vale in New South Wales for both species (1972–85). Persson (1976) used light traps to monitor activity of noctuids in south coastal Queensland, the trap being operated continuously for $1\frac{1}{2}$ years; both species occurred throughout the year, although numbers were low in winter; *H. punctigera* captures peaked in spring and early summer and *armigera* in late summer or early autumn. Overall, *punctigera* catches were twice those of *armigera*. Of the total catch of Noctuidae, *punctigera* made up only 4% and *armigera* only 2·3% (see also Brown 1978).

Further south, *punctigera* is even more abundant relative to *armigera*. Around Narrabri from September to April *punctigera* is on average eight times more abundant than *armigera* (Wilson 1983, table 2), and around Adelaide *armigera* is absent. Further north the situation is reversed and *armigera* outnumbers *punctigera*, at least in the Ord (see Wilson 1982). However the latter is probably due to cropping practices and insecticide usage. Both species were rare before irrigated cotton was grown, and Wilson (1982) suggests that *armigera* became more abundant after sorghum was introduced in 1969.

From an analysis of light-trap catches from 1973–74 to 1980–81 in the Narrabri region, Wilson (1983) concluded that 'the pattern of catches of the two species was . . . fairly constant'. In 2-monthly intervals from September to April, *armigera* made up 10, 10, 6 and 60% of the total catch. Both species showed population peaks in November–December, and *armigera* showed a further, smaller peak in March–April, by which time *punctigera* had declined. This temporal pattern—*punctigera* early, *armigera* later in the season—has been noted by many authors, at least in northern subtropical and southern inland regions (Persson

1976; Wardhaugh *et al.* 1980; Morton *et al.* 1981; Wilson 1983). In South Australia, where *armigera* does not seem to occur, *punctigera* is also abundant early and disappears later in the season (Cullen 1969). This seems to rule out interspecific competition as a cause for the change in species composition, although this process may be locally important in other areas on shared hosts (Stanley 1978). Cullen (1969) proposed that the decline of *punctigera* in South Australia was due to the fertility, fecundity and longevity of adult moths declining with the availability of nectar over a dry summer. However, the decline also occurs in subtropical and tropical regions with summer rainfall, and Wardhaugh *et al.* (1980) suggested that *punctigera* may disperse to some unknown host. The dramatic decline of *punctigera* populations on several

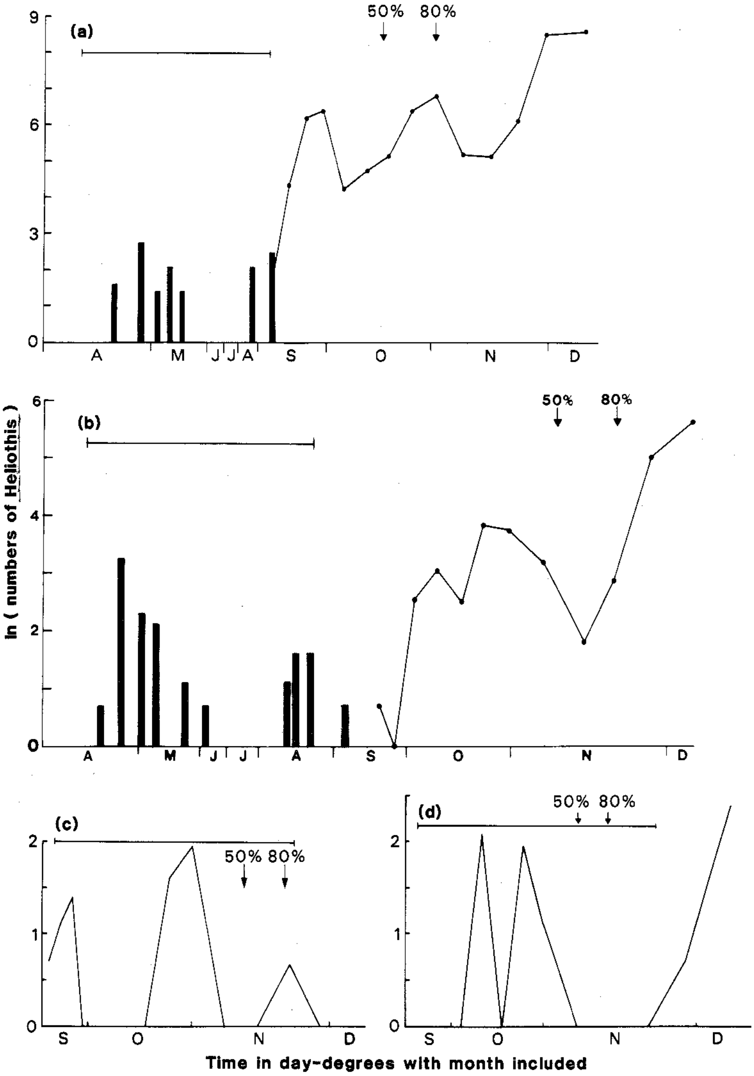


Fig. 15. Abundance of *Heliothis* adults caught at light traps (———), 50% and 80% cumulative emergences from diapausing pupae (arrows), and newly emerged adults from non-diapausing pupae (bars), on a log scale plotted against time in day-degrees (months indicated) in the Namoi Valley, N.S.W.: (*a*) *H. punctigera*, 1981; (*b–d*) *H. armigera*, 1975 (*b*), 1974 (*c*) and 1976 (*d*). Horizontal line above each graph indicates generation time on day-degree scale. Sources: Wilson *et al.* 1979; Cunningham *et al.* 1983; Wilson 1983; unpublished light-trap data from Myall Vale.

hosts (e.g. maturing cotton, sunflowers, lucerne) suggests that these hosts may no longer be suitable for oviposition or survival of *punctigera*, or perhaps that this species is suppressed by *armigera* with its superior competitive ability, at least on cotton (Stanley 1978).

Cullen (1969) was unable to determine the source of the large early spring population of *punctigera*, as numbers of diapausing pupae derived from the autumn generation were low. Cullen and Browning (1978) were unable to demonstrate whether diapause could extend over 1 year in the large spring population of pupae. It is possible that the spring moths are immigrants, which raises the question of where they come from.

The most extensive regional studies of *Heliothis* populations in terms of phenology and relationships to crop availability have been conducted in the Namoi Valley (Wilson *et al.* 1979; Wardhaugh *et al.* 1980; Wilson 1983). In this review we will concentrate on overwintering and spring population phenologies of *Heliothis* species presented in the above papers. Not all pupae formed in late autumn enter diapause (Figs 15*a*, 15*b*). Some moths emerge in April–May and others in August. Presumably the late autumn moths will attempt to locate hosts for oviposition. Eggs and larvae could develop, because fluctuating temperatures and heliothermic warming could speed up development beyond the linear day-degree model of Fig. 15 in favourable years (when frosts are rare). Wright (1969) provides the only published data of *Heliothis* activity over winter in the Namoi. In 1966–67 and 1967–68 the light trap was operated year-round; catches in May–June and July–August were 136 and 136 in the first year and 30 and 372 in the second. Unfortunately the two species were not separated. These values indicate that moths are not uncommon during winter in the Namoi, but it is not known where they come from.

Relationships between peak light-trap catches and emergence from diapausing or non-diapausing pupae are not clear (Figs 15*a*, 15*b*) for either species. Non-diapausing *punctigera* emerge in late August and/or early September, whereas the first light-trap peak falls in late September (Fig. 15*a*). These moths could not be the offspring of the August emergence, unless the latter adults do not respond to light for 4 weeks. Further, most (75%) diapausing moths emerge by the second week of October, yet the next light trap peak is about 2 weeks later. Similarly, for *armigera*, peak light-trap catches are out of step with the recorded emergences from diapause (Fig. 15*b*). Wilson (1983) attempted to explain the early anomalies in the abundance of *punctigera* by immigration or early emergence of the non-diapausing fraction, although his own data do not support the latter. One of the inherent problems in such interpretations of population origins is the use of field cages and/or burial of pupae after pupation. Both methods may delay emergence (see Mueller *et al.* 1984).

Wilson (1983) provided some evidence that population abundance of *armigera* may be correlated with areas of susceptible crops in the Namoi Shire, although this assumes a largely local origin for this species (but see pp. 800–2). The early abundance of *punctigera* could in part be related to autumn population levels in the Namoi cropping area (Wilson 1983).

Clarification of the origins of infestations is essential before area-wide management practices can be considered. Understanding the factors responsible for population fluctuations between years, and in particular the origin of outbreak populations, is also essential.

Population Management: Past, Present and Future

The pest status of *Heliothis* species on their various crop hosts was reviewed for all Australia by Common (1953) and more recently for Queensland by Broadley (1977*a*). Neither author provided an objective economic measure of lost production and/or the cost of control of these pest species. Alcock and Twine (1981) estimated the economic costs of *Heliothis* in Queensland to be $16 million (range $8–28 million). Wilson (1982) in a review of *Heliothis* management in Australia, expanded Alcock and Twine's (1981) results to an Australia-wide context and estimated the cost of *Heliothis* control in 1980 dollars to be about $23·5 million.

To date, most effort has been directed towards insecticide trials and the recommendation for their use on various crops such as cotton (Passlow 1958, 1959; Davis *et al.* 1963; Wright

1965*a*, 1965*b*, 1970; Shedley *et al.* 1969; Wilson 1969; Wilson *et al.* 1972, 1983; Michael 1973*c*; Turner and Rigby 1976; Arends and Campion 1980; Hamilton 1980; Waite 1981; Waite and Murray 1981), linseed (Passlow *et al.* 1960; Passlow and May 1960; Bourke and Campbell-Smith 1967), lucerne (Hooper 1958; Bourke 1963; Berg 1980; Turner and Franzman 1981), sorghum (Passlow 1973; Keefer 1981; Twine and Kay 1982), sunflowers (Broadley 1978*a*, 1980), maize (Hamilton and Muirhead 1980, 1981), tobacco (W. A. Smith 1953, 1961; Edwards, 1957; Smith and Saunders 1961; Davis and Saunders 1963; Cunningham 1971, 1975; Broadley 1977*b*, 1979; Broadley *et al.* 1979), tomatoes (Gellatley and Braithwaite 1962; D. Smith 1978; Hargreaves and Cooper 1979, 1982; Hamilton and Wright 1980) and various other field and horticultural crops (e.g. Broadley 1977*a*; Turner 1978; McKay 1981; Franklin and Hughes 1982; McKay *et al.* 1983; Swaine and Ironside 1983).

Other concerns have been with the efficacy of certain chemicals or combinations of sprays (Braithwaite 1957; Clift 1976, 1979; Kay 1981*b*; Wilson 1981*b*) and spray formulations (MacQuillan *et al.* 1976; Davies *et al.* 1982). Associated with these spray trials and recommendations has been the necessity to monitor the development of resistance, most notably to DDT (Twine and Kay 1973; Wilson 1974; Goodyer *et al.* 1975; Kay 1977; Kerr 1977; Goodyer and Greenup 1980). Recently resistance has been detected to synthetic pyrethroids in various localities in Queensland and New South Wales (Anon. 1983; Gunning *et al.* 1984). This situation was monitored closely and has led to a strategy restricting the use of pyrethroids to one *Heliothis* generation area-wide throughout the two States. In reducing the use of the pyrethroid group of insecticides, the strategy attempts to introduce the concept of insecticide management. Although commercial control of the *Heliothis* complex relies heavily on the use of insecticides, such a management strategy is one of the few ways of prolonging their useful life. However, insecticides are not a long-term solution to pest problems. The failure of chemical control in the Ord led to the virtual abandonment of cotton growing (Michael and Woods 1980). Ultimately the cost of chemical control to the producer and society will force the use of alternative tactics and strategies (Perkins 1982). This process is most likely to occur in the cotton industry.

Management of *Heliothis* species (and other pests) on cotton has moved away from the regular application of protective broad-spectrum sprays (but see Wilson *et al.* (1983) and the 'toxic carpet' approach) and bases treatment on: (1) the use of scouts to ascertain the level of insect infestation, relative to some threshold (Wilson 1981*a*); (2) the use of sequential sampling plans to categorise populations (Sterling 1976); (3) more recently, a computerised 'on-line' decision-making package called SIRATAC—an acronym for CSIRO and New South Wales Department of Agriculture tactics for growing cotton (Room 1979*b*; Hearn *et al.* 1981; Ives *et al.* 1984; Pyke 1985).

SIRATAC was used to synthesise the results of research work on crop growth, insect pests, insecticide efficacy and economic injury levels into a tactical management program. The important pest management principles which have been incorporated into SIRATAC include the use of natural mortality, 'softer' insecticides whenever feasible, the natural fruiting habit of the cotton plant, and economic thresholds.

The prototype management system was constructed by Room (1979*b*) and has been progressively updated as further research results have become available. Initial gaps in knowledge were filled by commonsense intuitive values; these have since been replaced by research results or modified by experience. Inclusion of subjective elements was unavoidable because without them the system would never have been implemented.

Several entomological aspects of SIRATAC warrant further extensive research. These include the methodology and reliability of sampling insect pests of cotton, the need for short-term prediction of *Heliothis* oviposition, and the role and importance of natural mortality, particularly that relating to predators. For monitoring, Sage and Gregg (1985) have recently investigated the efficacy of four designs of pheromone traps for monitoring *Heliothis* populations in cotton.

Management packages such as SIRATAC could well be developed for other crop systems, e.g. sorghum, oilseeds (sunflowers, soybeans, linseed), tobacco, tomatoes, maize. This would put decision-making for individual farmer's fields on a rational basis. However, SIRATAC is not a panacea for all pest management problems. Even if every cotton farmer were using SIRATAC, pesticide resistance could still develop in *Heliothis*, because of the polyphagous and migratory tendencies of the genus. The necessity for a regionally based approach to *Heliothis* population management was recognised when the pyrethroid resistance spraying strategy was implemented.

Although alternating insecticides of different groups and minimising reliance on single types of insecticides will increase the useful lifetime of chemicals, other or supplementary control strategies need to be researched and integrated into existing management programs. These alternatives include the use of host-plant resistance, pathogens, natural enemies and behavioural control (by means of semiochemicals). The breeding of resistant varieties by conventional means is slow, and work in Australia has been restricted mainly to cotton (Mungomery *et al.* 1977; Kay *et al.* 1979; Adjei-Maafo 1980; Thomson and Lee 1980; Ampofo 1981; Hassan 1985), sorghum (Wilson 1976), soybeans and navy beans (Rogers 1981). The use of genetic engineering techniques offers an exciting prospect for speeding up the development of resistant varieties.

Although *Bacillus thuringiensis* and nuclear polyhedrosis virus have been used commercially with mixed success (Rogers *et al.* 1981, 1983), the potential role and importance of pathogens and natural enemies in regulating the abundance of *Heliothis* is not well established. Even though the prototype of SIRATAC attempted to maximise mortality due to natural enemies (Room 1979*b*), the role of these enemies remains poorly researched. Despite this, egg parasitoids (trichogrammatids) have been used in inundative releases to control *Heliothis* populations on sorghum and cotton in the Ord (Michael 1973*a*, 1973*b*; Grim and Lawrence 1975; Woods 1981), tomatoes in Victoria (McLaren and Rye 1981) and cotton on the Darling Downs in Queensland (Twine and Lloyd 1982). The first two of these trials produced good results, but the last was unsuccessful. Pathogenic nematodes that attack the mature larval stages in the soil offer a further possibility for biological control.

Biocontrol could be augmented by inundative releases on individual farms (Blood *et al.* 1980) but such releases would perhaps be most effective when co-ordinated on a regional level. The aim of such a management scheme would be to reduce the overall level of the population within a region (on all hosts) such that economically damaging levels would rarely be reached. Other potential tactics for any regional (area-wide) scheme would include: (1) destruction and/or management of alternative hosts early in the season (where applicable); (2) disruption of mating behaviour by the use of pheromones which have been developed for Australian *Heliothis* species (Rothschild 1978; Anon. 1980; Rothschild *et al.* 1982); (3) the release of sterile males (Hooper 1981).

The polyphagous nature of *Heliothis* dictates the adoption of an area-wide approach to its management, as recently suggested by Knipling and Stadelbacher (1983). The effectiveness of such an approach will depend on the relative contributions of 'local' and immigrant moths to the 'local' population (i.e. how big is area-wide) and on the role of density-dependent mortality factors, alternative hosts, etc. (Mueller *et al.* 1984). An area-wide approach does not rule out the use of on-farm integrated pest management practices. Ideally population management would take a two-tiered approach: (1) minimisation of the *Heliothis* population overall; (2) SIRATAC-type programmes for within-farm crop-based management, should the need arise. However, implementation of such a management package requires a basic understanding of the *Heliothis* life system. As our review indicates, we are a long way from such an understanding.

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