1. Pest Control By Arthropod Predators

1.1 Introduction

The reproductive capacity of any plant or animal species gives it the theoretical potential to rapidly fill the world if unrestrained (Darwin, 1859). That this does not occur can ultimately be explained by the restricted distribution of a finite quantity of suitable resources. However, even within regions which appear to offer all the fundamental requirements, species do not always reach population densities which would directly exhaust those resources. The reasons populations fail to reach the carrying capacity of their environment are particularly important because they may explain how to predict or utilise natural phenomena to reduce pest species in agricultural systems. The activity of predatory arthropods may explain or contribute to the containment of these pest populations. This possibility forms the basis of the work described in this thesis.

The literature review (Chapters 1 & 2) discusses the theoretical background of the contribution of natural mortality factors to pest control. This leads to discussion of the role of predators in controlling pest populations, and the experimental methods for determining the impact of predators. In particular, the discussion focuses on whether *Helicoverpa* spp. can be controlled by endemic levels of native generalist predators in Australian cotton crops.

The experimental sections of this thesis explore the impact of endemic levels of predatory arthropods on *Helicoverpa* spp. populations. It is clear that these predators remove individuals from pest populations. What is not known is whether this mortality is considerable, additional (to that which would occur without predators) or predictable. Therefore I have endeavoured to measure the impact of endemic predatory arthropods on *Helicoverpa spp*. using laboratory and field cage predation experiments as well as comparative population studies of predator and prey species.

1.2 The Great Debate Over Population Regulation

The factors which affect the size and variability of populations have received considerable attention (Nicholson 1933, Solomon 1949, Andrewartha and Birch 1954). These include intraspecific and interspecific competition for resources, predation or disease, and environmental extremes. However in most cases the relative contribution of each factor has remained obscure because their impact has been difficult to quantify. This has led to over eighty years of strongly contested debate, essentially arguing the relative importance of the abiotic environment verses the biotic environment in the regulation (or at least limitation) of animal populations. Several major concepts have dominated the debate, including density dependence, biotic and abiotic factors, equilibrium or balance, and regulation. It is impossible to proceed without some clear definitions of these.

Definitions:

Density dependence: A factor is density dependent if its effect (rate) varies with the density of the population being affected (Andrewartha and Birch 1954). The opposite is *density independence*.

Regulation: The maintenance of a population size, above which density dependent forces conspire to cause negative feedback, and below which these forces are relaxed allowing the population to return to an equilibrium position (Berryman 1982).

Biotic: Biological factors such as natural enemies, plant defences and intra and interspecific competition. The opposite is *abiotic;* non-biological factors such as weather and climate (Solomon 1949). The close interaction between physical and biotic elements has caused difficulties in clearly assigning factors to these categories and this has often confused the debate.

Balance: Although 'the balance of nature' is readily and popularly understood as a model of how populations are governed, ecological scientists do not agree about the causes or even the existence of this 'balance'. That this debate continues is testimony to just how difficult it is to define 'balance', and to collect conclusive evidence showing the extent to which various factors might produce 'balance'.

Balance to Nicholson (1933) meant regulation and therefore 'control'. He defended the existence and importance of balance by portraying it as the regulation that acts on a population even within a 'sea' of buffeting and often highly destructive density independent processes. He clearly believed that only density dependent forces can exert regulation and that, for practical purposes, the abiotic environment is density independent and therefore cannot impose regulation on populations. He therefore regarded natural enemies as the most important factor for population control.

Nicholson (1933) reiterated Chapman's (1928) analogy of a cork's tortuous path as it is carried down a stream and focussed on the balance displayed within the turmoil. The cork's altitude (population level) is often greatly affected by waves and whirlpools (the density independent effects). However the cork is continually 'balanced' (position relative to the water surface) by its displacement of the water (density dependent regulation).

Although a degree of 'balance' is illustrated in this analogy, it is the relative importance of these balancing influences which is questioned by the critics. Ecologists (especially those concerned with pest management) are interested in the absolute population level and the relative importance of the various mortality factors including density independent ones. That is, in the terms of the cork analogy, they are interested in whether waves and whirlpools have a more important influence on cork altitude than buoyancy.

Nicholson (1933) pointed out that very small balancing forces might be responsible for regulating populations even where large density independent effects are occurring. For example, the environment may be responsible for 90% of the mortality of a certain pest. Survival of the remaining 10% would lead to a substantial population increase and may represent a severe pest problem. Natural enemies may reduce survival to less than 2% and therefore be a critical element causing a population decline. If the impact of the environment is reliable but that of the natural enemies variable then the latter is the critical factor. This explains how a relatively small density dependent influence can be a key factor in pest control. However, it is also conceivable that density independent factors can be highly effective at reducing a pest population, regularly and on their own. This would represent density independent control but would not occur if abiotic conditions were consistently favourable for the pest. In such cases, the density-independent effects of regular applications of pesticides can offer this sort of 'control'. This is often only a short-term solution because it selects for pest

populations with insecticide resistance (Dent, 1995). In these cases, natural enemies may be a crucial factor in pest management.

In opposition to Nicholson, Andrewartha and Birch (1954) argue that the environment can act in a density dependent way and therefore truly regulate populations. An example is that of a habitat in which there are a limited number of shelters. The impact of an adverse weather event would depend on the proportion of the population able to occupy these shelters. That is, there would be a large proportion killed at high population densities but only a small proportion killed at low population levels even though the same number of individuals can find shelter.

Although climatic events may be density dependent in effect, the timing of the event is not closely related to the population level. Storms do not occur because aphids have reached a certain threshold, although the seasonal patterns of population growth and adverse weather may tend to coincide. The weather events which inflict severe mortality may or may not occur, and are generally no more probable as the population of the pest increases. Natural enemies, however, might be expected to be more intrinsically linked to the time of the prey increase. This suggests that they might be more reliable regulators.

Workers influenced by these considerations have widely assumed that regulatory factors are biotic by definition, and this has brought considerable emphasis upon natural enemies as the most likely key factors for controlling pest populations. Therefore, the debate over density dependence has also pivoted around the relative importance of biotic or abiotic factors in containing populations. Solomon (1949) provides a comprehensive review of these issues, many of which remain relevant today.

The opposing points of view are essentially:

1) That density dependence is the only possible source of 'regulation' and therefore biotic factors are usually the most important agents of population control. This is commonly partnered by the acceptance of the 'general equilibrium theory' which asserts that population densities reach a relatively stable equilibrium governed by the upward exploitation of a habitat by a certain species and the downward pressures of other species exploiting them. 2) That density independent factors (generally abiotic) are the most important influence on population levels, frequently containing populations in a way which appears regulatory. This is commonly accompanied by the suggestion that population size is bounded by resource availability at high levels and a reduced probability of mortality at low or near extinction levels. Considerable instability is exhibited between these boundaries, so the 'general equilibrium theory' receives little support.

1.2.1 Importance of Regulation to Pest Control

Regulation theories have often argued that most natural populations are or can be 'controlled' by natural factors. However, this does not necessarily mean that natural causes of mortality will operate to maintain a pest population at or below the level of an economic threshold. The economic threshold is the population level at which projected economic losses justify the costs of intervention by the manager. Effective pest control consists of keeping the pest population below this level (Metcalfe and Luckmann 1994). Therefore pest management obviously defines a population level which is considered damaging, but this may have little relevance in biological population dynamics. This is where the importance of regulation verses limitation of a population has confused the population balance debate. 'Control' to the natural population biologist is regulation, but to a pest manager it is maintenance below a threshold level.

Regardless of the theoretical arguments about the relative importance of biotic or abiotic factors, predatory insects are commonly put forward as being capable of imposing control.

1.3 The Impact of Predators

1.3.1 General Lack of Conclusive Evidence

Conclusive measurements which show the predatory impact of one insect upon another in real situations are rare. Complaints about this situation are common throughout the literature on insect predation (Seymour and Jones 1990, Titmarsh 1992). Generally the goal of confidently and accurately assigning the magnitude of a reduction in a pest population to an accompanying population of predators has not been achieved, in all but a few instances where the evidence is overwhelming (eg. Frazer and Gilbert 1976). However, the possibility that predators could be key factors in the reduction of pest populations to below action thresholds remains plausible and appealing.

Attitudes on the importance of the impact of predators to pest control are also loosely divided into two. They are that:

1) Predators commonly regulate pest populations to below economic thresholds. When experimental evidence does not show this, it is because it is very difficult to demonstrate. For example, when confronted with a review by Dempster (1983) of nine life table studies of Lepidoptera of which only one gave any indication of regulation by predators, Hassell (1985 and 1987) replies that delayed density dependence (the indicator used here for natural enemy activity) is a very difficult feature to demonstrate. Lack of evidence, however, leaves the question unanswered and certainly does not support the theory that natural enemies are usually important.

2) Predators exploit prey populations to an extent consistent with ensuring the survival of the predatory species (O'Neil and Wiedenmann 1987). This may or may not contribute appreciably to prey regulation and may or may not be useful from a pest control standpoint. This view is commonly partnered by an expectation that once populations are viewed over a long enough time frame, high variability is apparent, equilibrium theory looks less convincing and abiotic factors appear more important.

Again, the persistence of these alternative views is largely due to the absence of definitive measurements of predatory impact. In the light of these difficulties researchers have focussed considerable efforts on the techniques and interpretation of predation studies.

The resurgence of pest populations following the removal of natural enemies by broad spectrum insecticides has often been cited as evidence for a considerable regulatory effect by parasites and predators over pest populations (Ridgway *et al.* 1967, Leigh 1985, Wilson and Morton 1993). In some instances, where the effect of parasites can be quantified or dismissed, a significant effect of predators has been clearly demonstrated (van den Berg and Cock 1993).

Generally however, acts of predation in the field are sufficiently brief, hidden and scattered over space and time, to make direct surveillance extremely difficult (Sterling 1989). Also, predatory insects usually leave no readily recordable evidence of their activities (Greenstone and Morgan 1989). These properties have challenged the detective skills of many entomologists and resulted in a variety of methods intended to quantify predation. Unfortunately, in an effort to achieve quantitative measurements, artefacts of variable and often unknown influence have usually been created. Therefore the interpretation of many experiments involves subjective assumptions, many of which meet uneasy acceptance, especially if one method is used on its own (Greenstone and Morgan 1989, Hagler *et al.*, 1992). Titmarsh (1992) points out that the impact of predation is commonly overestimated by presuming that all unexplained disappearance of prey is due to predation. This has happened primarily in life table studies but also in radioactive labelling work (McDaniel and Sterling 1981, Hogg and Nordheim 1983).

1.3.2 Measurement of Predation

The evidence of a substantial suppression of insect pests by predation is largely circumstantial (Titmarsh, 1992), however many remain convinced that predators, even at endemic levels, regulate pest populations to below economic thresholds (eg. Sterling 1989, Hassell 1985 and Berryman 1982).

Experimental techniques to measure predation include: i) Augmentation, removal or introduction of natural enemies; ii) Field cages and other inclusion-exclusion techniques; iii) Prey enrichment; iv) Direct observation; and v) Chemical evidence of natural enemy feeding (see reviews by Kiritani and Dempster 1972, Luck *et al.* 1988 and Sunderland *et al.* 1988).

More technologically advanced methods for detecting predation use immunological assays or radioisotopes to detect the remains of prey amongst the gut contents of suspected predators (*eg.* Room 1977, McDaniel *et al.* 1978, McDaniel and Sterling 1979 and 1982, Sunderland *et al.* 1987, Greenstone and Morgan 1989 and Hagler *et al.* 1994). There have been cases where the amount of radioactivity in the predator was detected with discrete enough quantities to allow the estimation of the number of prey taken (Sunderland 1988). However,

these methods remain largely qualitative due to difficulties with unknown variables which influence the source or quantity of marker or antigen. These problems include; the unknown time of feeding; unknown size of the meal; variation in decay and discharge rates of digesta under variable digestion conditions; and the possibility of shared or secondary predation (Sunderland 1988, Lovei *et al.* 1990). Quantifying serological assays is potentially possible by the simultaneous assessment of two or more antigens from the same prey source which have different rates of degradation (Sunderland 1988). A simpler approach is possible if it is realistic to assume that a positive response represents a single attack. This is only applicable to systems with low prey density. Sunderland (1988) considered that perhaps the major limitation of labelling techniques is the disturbance to the prey populations during labelling and redistribution before sampling. Serological techniques are superior from this point of view because the system need not be disrupted prior to the collection of the predators (Stuart and Greenstone 1990).

The difficulties in assessing predator impact have led to an abundance of research on predatory systems which are more easily studied, especially under laboratory conditions or in restricted field situations, *eg.* the predation of aphids by coccinelids (Hagen *et al.* 1962, Baumgaertner *et al.* 1981). Often in these systems predators exhibit an overwhelming impact because the prey is dominant and abundant and there are relatively low or readily definable effects from alternative causes of mortality. Therefore, the theories of predation and the methods of assessing predatory impact have been developed mainly from laboratory studies on limited aspects of predator behaviour in thé absence of definitive measurements from more difficult field systems. Many natural or agricultural systems do not display such overwhelmingly clear predator to prey relationships. Features of these systems not often present in laboratory studies include:

- A fluctuating but relatively low density of a suite of endemic generalist predators.
- Major changes in predator populations due to factors other than target prey availability.
- Low population densities of pests with low economic thresholds.
- The possibility of high mortality of pest populations from confounding alternative factors, such as plant defenses and environmental factors.
- Fluctuating and relatively abundant alternative prey.
- A reduced dependence on prey if predators also feed on plant material.

General predation theory fails to offer approaches which are relevant in these situations. Coccinellids feeding on abundant aphids would represent a system where the predator appears to have little need to compromise between energy used in searching and energy for other needs. This balancing of resource allocation has been critical for developing optimal foraging theory and may be a dominant factor in many low prey density situations, especially considering the importance of natural selection through times of extremely low prey availability (Stephens and Krebs 1986).

1.4 Classical Functional & Numerical Response Theory

Empirical studies have provided an extensive traditional basis for experimentation on predator behaviour by introducing the concepts of functional and reproductive numerical responses. These analyses, however, have suffered from a general lack of empirical validation and have concentrated on the consumptive aspects of predator behaviour (Solomon 1949, Holling 1959b and Hassell *et al.* 1977).

1.4.1 Functional Responses

The functional response describes the rate at which an entomophage consumes or kills its prey relative to the density of that prey (Trexler *et al.* 1988). It generally takes one of four forms: Type I, an increasing linear relationship (density independent); type II, a decelerating curve (negatively density dependent); and type III, a sigmoidal relationship (positively density dependent). Type IV describes a type II response in which the predation rate decreases after reaching a maximum (Trexler *et al.* 1988, Holling 1959a and b).

The type of response has been considered to be an intrinsic property of a particular entomophage and may give an indication of its potential to regulate a pest population. Type III is the only response which shows a species is independently capable of imposing negative feedback; a condition necessary for population regulation (Franz 1972). That is, the greater the prey density the greater the proportion of prey destroyed by the predator.

This approach has come under considerable criticism on two levels:

a) Critics consider that the arena is too artificial to give meaningful results because 'many vital aspects of the field relationship may be completely overlooked in the laboratory' (Frazer and Gilbert 1976). The combined evaluation of a comprehensive series of papers collated by Baumgaertner *et al.* (1981), which extended the studies of Frazer and Gilbert (1976), strongly criticised the classical laboratory approach when used in isolation from general biological studies in the field.

b) Usually the prey densities tested are grossly higher than those the entomophages would encounter in real situations (O'Neil 1989).

Therefore, when a predator is evaluated solely on its functional response, many factors which may affect its overall performance, such as predator/prey relationships, temperature, lifecycle, response of the prey, and the architecture of the real environment are ignored (Frazer and Gilbert 1976). This aspect is discussed in greater detail in a later section on difficulties with measurement and interpretation.

1.4.2 Reproductive Numerical Responses

The reproductive numerical response is the relationship of the rate of predator reproduction to the number of prey consumed (Hassell 1976). The most common response is where a greater number of prey attacked leads to a greater rate of increase by the predator. Models which incorporate the functional and numerical responses to predict the impact of parasitoids have been more successful than those for predators (Hassell 1976) because parasitoids are generally highly specific to their prey (host) and have reproductive rates more directly correlated to their attack rates. The ability to regulate a pest can therefore be inferred from their relative rates of population increase.

In a situation where a pest species is colonising a crop we might expect low initial numbers of both the pest (prey) and the predator species. If the predator is sufficiently specific then the rate at which each individual predator attacks the prey over a range of prey densities (functional response) multiplied by the rate at which it can reproduce by feeding on those prey (numerical response) gives the overall predation rate. Within this simplified scenario it is clear

that unless the overall rate of prey attacked can increase at a greater rate than the population increase of the pest then limitation of the pest population cannot occur. For this to happen either the functional response (for each individual predator) must exhibit a region of increasing rate of attack as pest density rises (positive density dependence), or the rate of predator reproduction must be greater than that of the pest. In reality the pests usually have greater rates of natural increase, that is, they are more 'r' selected (Macarthur and Wilson 1967) than predators. Therefore considerable attention has been directed at establishing whether a predator species shows a progressively increasing rate of attack as pest density increases (*ie.* a type III functional response).

1.4.3 Difficulties with Measurement and Interpretation

The relative ease with which an estimate of the functional response can be gained in petri dish styled consumption trials has led to an abundance of this kind of data. However the more difficult to measure numerical response is seldom estimated. Therefore, demonstrating that a predator has a type III functional response has dominated the thinking of many researchers, and a great deal of the literature has been devoted to establishing the underlying shape of these response curves (*eg.* Livdahl and Stiven 1983, Houck and Strauss 1985 and Williams and Juliano 1985). Generally it appears that predators exhibit type II responses in petri dish trials or very close to it (eg. Asante 1995).

The validity of these responses has drawn severe criticism when determined in unrealistic conditions especially from petri dish style feeding trials. A serious criticism is that the functional and numerical responses are measured at greatly exaggerated prey densities (Kiritani and Dempster 1972, O'Neil 1989). O'Neil (1989) presents a diagram (Figure 1.1) to emphasise how inappropriate these test prey densities usually are. The main effect of unrealistic prey densities is that the searching or survival behaviour of the predator cannot be realistically displayed. Field cage trials have commonly given a different functional response category than trials using the petri dish arena (eg. Stark and Whitford 1987, O'Neil 1989). A common field cage functional response is a horizontal to moderately increasing linear response across a realistic range of prey densities (type I) (Stark and Whitford 1987, O'Neil 1989). Some predators show quite constant and low rates of prey consumption, that is, a nearly horizontal functional response (O'Neil and Stimac, 1988). Prey handling time, which pervades

the explanations of the limits to predation rate found at high prey densities in petri dishes, becomes insignificant at realistic prey densities of some pests. In many studies the calculation of handling time from functional response data has been grossly overestimated (Chow *et al.* 1983, Wiedenmann and Smith 1993). Therefore it is an oversimplification to rank predators on the shape of their functional response curves alone. As early as 1976, Fraser and Gilbert pointed out that temperature and several aspects of insect biology such as reproductive state, aestivation and reproductive diapause can alter the predictions of this simplistic approach.



Figure 1.1 Reproduced from O'Neil (1989) to illustrate the gross difference between the prey densities commonly used to determine the functional responses of generalist entomophagous insects in the laboratory and those encountered in the field. The field range is indicated by the small box in the bottom left hand corner of the diagram. Extrapolation of the curve generated from the remaining unrealistically high values is of questionable validity.

The importance of the reproductive numerical response has possibly been overemphasised. Other numerical responses which could result in overwhelming numbers of predators at the site of pest infestations might include the redistribution of the existing population of predators to the concentrations of the pest either regionally or at the canopy level (Frazer and Gilbert, 1976). Predators may also exit a site as prey levels decline, releasing their constraint on the pest population (Ives, 1981). The series of papers to which the latter two references belong is a landmark attempt to apply the basic principles of classical functional and numerical response theory. They concluded 'that no mathematical function, involving only the

current densities of predator and prey, can predict the true predation rate' (Frazer and Gilbert, 1976). These studies place considerable importance on the pest (pea aphid, *Acyrthosiphon pisum* Harris) and coccinellid predator (several species of coccinellid) densities, although the latter were particularly difficult to obtain, but highlighted the possibility of overwhelming effects by temperature, prey age distribution and predator-prey biology and behaviour on predation rate. These studies revealed three distinct differences between predator behaviour in the field and the laboratory: i) The distribution of prey affected the predation rate in laboratory trials but not in the field, ii) Predators in the laboratory were more active than in the field. Perhaps the lack of hiding spaces in the laboratory arena induced continual movement, and iii) Temperature had an overriding effect which may not be noticed under constant laboratory conditions.

Moreover, the conclusions of Fraser and Gilbert (1976) question the existing theories of equilibrium stability. They considered their system to be resilient but remarkably unstable in that either the prey population rapidly increased (outbreaks), or the predators drove them rapidly towards extinction before leaving when prey was too scarce to meet the predators maintenance requirements. Leaving corresponded to 0.3 aphids per stem but was dependent on the age distribution of the aphids (Ives 1981). Therefore the functional response of the predators was destabilising and stability was only restored by the predators numerical response.

There are many other studies which show that environmental and other intrinsic factors can seriously affect the level or shape of functional responses. Chow *et al.* (1983) showed that temperature and level of hunger of a predatory bug (*Geocoris bullatus* (Say)) on a herbivorous bug (*Lygus* spp.) affected the functional response. As the temperature was increased from 15 to 35° C maximum predation rates (i.e. the plateau section of the type II response) increased from 0.4 per hour to 2.5 per hour. At high prey densities (20 prey offered in 15.5cm dia. x 6.5cm high plastic containers) the rate of attack decreased by about 37% over 12 hours, indicating an effect of hunger. Furthermore, in all these cases the predicted handling time grossly over estimated the observed handling time. Therefore not only does this work demonstrate factors which would increase the complexity of predicting field predation rates from basic functional responses, but it also questions the common conclusion that handling time predominantly explains limitations on attack rate.

Differences in the morphology of cotton varieties have also been shown to alter predator efficiency. Treacy *et al.* (1987) showed that greater densities of trichomes reduced the mobility of lacewing larvae (*Chrysopa rufilabris* (Burmeister)) and therefore reduced their overall functional response curve on *Helicoverpa zea* (Broadie) eggs.

Chesson (1989) points out that the presence of alternative prey may simply reduce the amount of time a generalist predator spends in pursuit, capture or consumption of a target species, thereby lowering the functional response. The existence of preference for the alternative prey would be expected to further reduce the response. He demonstrates that prey preference and prey size affected the functional response of the aquatic bug *Notonnecta hoffmani* (backswimmers) predating *Culex pipiens* larvae (mosquito) (Chesson 1989). Although he had previously (Chesson 1984) shown that notonectids could significantly reduce the density of mosquitoe larvae, in the presence of alternative prey (in this case *Drosophila* sp. trapped on the water's surface) predation of mosquito larvae virtually ceased. This author considered handling time was important in this system because of the high density of the prey used. He also raises the possibility that the functional response might be altered by using a more complex search arena or the presence of other species of predators introducing interspecific competition.

Therefore, alternative sources of food, whether prey or plant, might alter the impact of predators especially where the target species are at low prey densities. Generalist predators may already be present in effective numbers before the pest species arrives. Resident predators may remove colonising levels of the pest. This is due, ironically according to Murdoch *et al.* (1985), to their generalist nature which is commonly considered a disadvantage for effective pest control.

Luff (1983), in reviewing the potential of predators for use in pest control, redirected the emphasis to the overall rate of prey removal. Although predators or parasites with type III functional responses and rapid intrinsic rates of increase can impose density dependent regulation, the emphasis on only these distracts attention from other attributes or behaviour which may combine to produce an overall density dependent response. Murdoch (1973) demonstrated that predators deemed to be type II can exhibit an overall density dependent response as they become larger. Although they may exhibit a type II response at any particular developmental stage, as they grow they move to the greater attack rates of a higher type II curve.

1.5 Behaviour for Survival, and the Implications for Biological Control

Siddique and Chapman (1987) reported that the Pacific Damsel bug, *Nabis kinbergii* (Reuter) reached maximum longevity when fed only 1 aphid (*Acyrthosiphon pisum*)/day. Egg production was proportional to the predation rate but the maximum predation rate was 2 aphids per day. The predator could survive up to 2 weeks without feeding on an insect and 2 months when fed 1 aphid every 4 days, demonstrating a low food requirement. This case may illustrate a principle put forward by O'Neil and Wiedenmann (1987): a predator which continues to actively search for prey after collecting some subsistence amount at low prey densities reduces its chances of survival. The alternatives would be to sit and wait for the prey density to increase or to leave that area and search another for higher prey densities. The latter behaviour may be over a small or large scale. Movement has been clearly demonstrated in response to low prey densities for *Coccinella* spp. (*C. californica* Mannerheim and *C. trifasciata* Mulsant) on pea aphids (*Acyrthosiphon pisum*)(Ives 1981).

The life span of some predators, being in the order of months, suggests that a 'sit and wait' strategy may be advantageous under some conditions. If so, where very low pest levels are required for economic control, as with *Helicoverpa* spp. on cotton, the most effective predators may be those which cannot 'afford' to sit and wait for higher prey densities but also cannot move away. Unfortunately, according to O'Neil and Wiedenmann (1987) these would not be expected to survive at low prey densities and inundative releases would be necessary to ensure they were present at the most appropriate time. Conservation of predators or classical biological control would probably be ineffective. Insects which are predatory as juveniles are possibly better candidates because of their limited powers of dispersal and more urgent nutritional requirements for development. This may predispose them to avidly search for prey regardless of prey densities. A case which would fit this description is the larvae of *Chrysopa* spp. (the green lacewing) predating on *Heliothis* spp. in inundative releases on cotton (Ridgway and Jones 1968).

1.6 Are Predators Good Biological Control Agents?

The predators which inhabit cotton crops are usually generalists and many authors continue to assert that it is this lack of specificity which suggests predators are unlikely to be good biological control agents. However, Murdoch (1969) reminds us that it may be just this generalist nature which gives them an advantage over more specific agents. Whereas specific agents (mainly parasitoids) may take several generations to re-establish the numbers required to impose a controlling influence over a pest, a population of generalists persisting on alternative prey, possibly even plant feeding, may be sufficiently large to curb the initial pest increases and thereby avoid outbreaks. So, although predators are rarely introduced in modern classical biological control programs, this should not be regarded as evidence that they are unimportant in biological control in the broader sense. Frazer *and* Gill (1981) however, question the merit of introducing exotic species of predators because they expect that the introduced effect would only compensate for those of the native species in the systems they studies. In any case the generalist nature of most predators would make it extremely difficult to introduce predators because of the requirement for target specificity (Carver, 1989).

1.6.1 Survival of Predators in Agricultural Systems

Prey consumption by a predator is a major requirement for its survival and therefore the type, rate and amount of prey consumed could all be expected to be major components of a model which explains which behaviour better equips predators for survival. The importance of high prey consumption rates has been questioned by O'Neil and Wiedenmann (1987). After finding major discrepancies between functional response theory and their field results they suggested an alternative approach to laboratory functional responses and concentrates on realistic field conditions.

The functional response approach has generally reported insect predators to be of type II. Therefore the predominant general description of predatory behaviour has been that increasing numbers of prey are attacked per day as prey density increases and that this is limited by handling time at high prey densities. Pooling the conclusions of several studies, which measured predation rates in realistic environments on field pest densities, found that several of the predatory species studied in soybeans maintained a low and relatively constant rate of attack (ca. 0.4 prey per day) over a wide range of realistic prey densities in the field (O'Neil and Wiedenmann 1987, O'Neil and Stimac 1988, O'Neil 1989, Wiedenmann and O'Neil 1992). Not only was the functional response flat but the rate of attack was much too low for handling time to be considered an influential factor on overall predation rate. Their studies re-establish the importance of searching behaviour to explain predation rates. Unfortunately the design of most functional response experiments intrinsically deny the expression of the searching behaviour as well as offering enormously unrealistic prey densities.

O'Neil and Wiedenmann (1987) follow up their cage studies of predation rates with studies of the survival of the predator species. They found that at various levels of food intake the predator compromised reproductive potential in order to maintain longevity. Therefore they theorise that these predators maintain longevity as a more effective means of survival compared to maintaining reproductive output. This would provide a mechanism for surviving periods of low prey availability and is probably indicative of the environments in which these species have evolved. O'Neil and Wiedenmann (1987) suggest that this predisposes such species to colonise annual agricultural systems because they have the ability to establish populations where prey density is initially very low. Therefore the predators we should expect to establish in annual agricultural systems are those with this approach to prey.

Unfortunately this is probably not the sort of agent we can expect to rapidly contain an outbreak or major influx of a pest, but one which will almost certainly be present when the pest arrives. Therefore the predators we find in annual cotton crops are present because they can survive at low prey densities. They do this by efficiently allocating their energy or nutrient resources gained through predation to growth, reproduction and longevity to maximise the chances of survival - they have to survive the bad times, not the good.

1.7 Conclusion

The classical approaches to studying predation have formed the basis of scientific discussions about the potential of natural enemies for many years. Unfortunately the components of consumption described in these laboratory styled studies include such a low proportion of the potentially important variables and measure them in such a simplified

environment that the importance of other factors or the possibility of major interactions (as difficult as they may be to measure) is not exhibited. The cases in which the classical approach has best described real situations are where reality best mimics the laboratory environment, ie. with one species of predator amongst one exceedingly abundant prey species, such as with coccinellids and aphids. Even so the most comprehensive field study addressing this failed to validate the classical approach (Baumgaertner *et al.* 1981).

When attention, as in this thesis, is directed towards assessing the impact of a suite of generalist predators on a relatively minor (in abundance) prey species; further complicated by abundant alternative prey, open systems, weather and unsynchronised populations, the classical component approach appears grossly inadequate. Where so many variables have large and probably interacting effects, understanding the impact of predators will probably require assessing the completely assembled and functioning system.

The theoretical assessment of predator behaviour in the final sections of this chapter suggest that the predatory species predisposed to colonisation of annual agricultural habitats are those which are not likely to reduce a target prey species to the very low densities required for the control of *Helicoverpa* spp. in cotton.

2. The Prospect of Controlling *Helicoverpa* spp. by Predators in Australian Cotton Crops

2.1 Introduction

Discussing the possibility that endemic predator species can control *Helicoverpa* spp. in Australian cotton crops requires an overall appreciation of how predators can contribute within the practices and goals of this agricultural system. Therefore this chapter provides a description of the Australian cotton industry, emphasising the practices and aspirations of the growers regarding pest control. The biology and behaviour of the pest is also presented as a basis for discussing aspects which might be beneficial or detrimental to efforts to use predators to contribute to control.

For convenience the discussion of the effectiveness of predators is simplified by comparing studies of similar predators on Heliothine pests from several countries. However since the transfer of the *Helicoverpa armigera* and *Helicoverpa punctigera* from the *Heliothis* genus to *Helicoverpa* it has become difficult to write generally of this group of Heliothine pests which was previously so conveniently grouped as *Heliothis*. The group of major pest species generally under discussion throughout this thesis are; *Helicoverpa punctigera* and *Helicoverpa armigera*, both natives of Australia and the old world and; *Helicoverpa zea* (Boddie), and *Heliothis virescens* (F.), natives of the new world.

2.2 The Australian Cotton Industry

The cotton industry in Australian is technologically advanced. The crop is intensively grown, mostly under flood irrigation, using a high level of inputs including fertilisers, pesticides, machinery and labour. Yields are amongst the highest in the world at 1200 to 1700 kg lint/hectare. Most of the production (ca. 90%) is exported as unprocessed lint. The average variable cost of production is A\$1400 per hectare including A\$370 per hectare for insect pest

control (Fitt 1994). Cotton is considered a high value crop, but with such high variable expenses and in the absence of government subsidies, yield expectations are high. The relevance of this to pest control is that economic thresholds are particularly low (ca. 1 larva per metre of row). A well established research base has developed to support the Australian cotton industry, especially for the development of higher yielding plant varieties, optimal cultural practices and non-chemical pest control strategies (Fitt 1994).

The climates suitable for cotton in Australia are those of the summer rainfall areas of midwestern New South Wales and Queensland. These provide long, hot and wet summers for rapid growth but also dry harvesting conditions during March and April. Access to irrigation water is essential for intensive production. This is applied by flooding the furrows of the fields and therefore requires a self sealing soil such as the heavy cracking clays (red and black earths) of midwestern New South Wales and Queensland. These areas were almost exclusively used for wheat, beef and sheep production prior to the 1970s, before the development of water storage on the major western flowing rivers including the Condamine, Macquarie, Namoi and Gwydir. With access to water these areas adopted irrigation cropping in which cotton has dominated because of its high potential returns. Development of cotton growing regions from Emerald (23.5^oS in Queensland) to Tandou (32.5^oS in southern New South Wales) has led to a record of 270,000 hectares sown to cotton at its peak in 1992 (Fitt 1994). In recent years production has suffered from low water allocations due to prevailing drought conditions.

2.3 Helicoverpa spp. as Key Pests of Australian Cotton

In many regions of the world, the key pests of cotton are larvae of Heliothine moths of the genera *Helicoverpa* and *Heliothis* (Vaissayre 1995). In all cotton growing regions where this situation exists, pest management is a difficult and complex business. Fitt (1989) notes a number of ecological characteristics which contribute to the pest status of *Helicoverpa* spp:

(1) High mobility (Gregg *et al.* 1995) and high rates of increase mean that *Helicoverpa* spp. are capable of overwhelming any functional or numerical response of the predators (Fitt 1989). Numbers which would elicit control can appear over one night.

(2) *Helicoverpa* spp. are multivoltine with a facultative diapause. Therefore 4-5 generations can develop each season in the Namoi area of New South Wales, and 6-7 generations at Emerald in the northern reaches of the cotton areas in Australia (Forrester *et al.* 1993).

(3) The large size and rapid development of the larvae leads to high levels of plant damage by individual caterpillars. Combined with direct feeding on the yielding structures means that thresholds for *Helicoverpa* spp. are extremely low in comparison to other pests which are amenable to biological control. Typical Australian thresholds are five eggs or one larva per meter, early to mid season. However, the natural mortality of *Helicoverpa* spp. during the egg and early instar stages (up to III) is usually very high (Zalucki *et al.* 1986), and although the contribution of the various mortality factors including predators remains unclear (Kyi *et al.* 1991), there are situations where damaging larval populations fail to develop from substantial egg numbers.

(4) Insecticide resistance is a major problem with Heliothines throughout the world. In Australia there is substantial resistance in *Helicoverpa armigera* (but not *H. punctigera*) to most groups of insecticides (Forrester *et al.* 1993). The present insecticides are still effective if used against neonate larvae because resistance is not strongly expressed in neonates (Daly *et al.* 1988). Later instars are also more protected from insecticides because they move to lower positions in the canopy and are likely to be feeding internally (i.e. in the fruiting structures). Therefore insecticides are usually applied before high levels of natural mortality can be exhibited or exploited.

(5) *Helicoverpa* spp. have a wide host range, encompassing 172 species in 40 families for *H. punctigera*, and 101 species for *H. armigera* (Zalucki *et al.* 1986). These hosts include some alternative crops to cotton which are frequently grown in Australian cotton areas, and many native plants and weeds. This means that *Helicoverpa* spp. can build up on other crops and then move to cotton, and that by utilising a sequence of hosts they can remain in an area for many generations. On the other hand, it also opens possibilities for trap cropping, especially since cotton seems to be one of the less attractive hosts (Zalucki *et al.* 1986).

2.3.1 Helicoverpa Ecology and Control in Australian Cotton

The production of cotton in Australia has relied heavily on the use of broad spectrum insecticides to control two key pests, Helicoverpa punctigera and Helicoverpa armigera. These pests cause considerable damage in relatively low densities and are estimated to cost A\$60-70 million dollars in direct production losses and A\$90 million in control (insecticides and crop scouting costs) (Fitt 1994). H. punctigera arrives on continental winds from inland Australia, including western Queensland and the Great Victorian and Simpson deserts (Gregg 1995). *Helicoverpa armigera* are considered to be much less migratory and many (though not all) can originate from local overwintering sites where hosts, including soybean, corn, sorghum and cotton, were grown in the previous year (Wardhaugh et al. 1980). Helicoverpa spp. are particularly attracted to flowering hosts and although cotton is not the most preferred host (Zalucki et al. 1986), it is often the most commonly available host in flower when the Helicoverpa spp. adults arrive or emerge because of its indeterminent habit (Wardhaugh et al. 1980). The adult female Helicoverpa spp. oviposit within the upper third (top 20cm) of the plant canopy (Dillon and Fitt 1995). Each is capable of laying about 200 eggs per day during its 5 to 7 day life span. These are usually placed singularly and separately on leaves and fruiting structures (Cullen 1969). The larvae hatch in about 3 days and move to the terminal leaves or squares and begin feeding (Dillon and Fitt 1995). Most mortality (often over 90%) occurs during the egg to 2nd instars, at least on tobacco (Titmarsh 1992). Larvae develop through five to six instars over two to three weeks causing a variety of plant damage from leaf chewing to 'tipping' (i.e. removal of the terminal growing points which causes the development of several new apices) early in the season, and direct damage to fruiting structures later in the season when squares, flowers or bolls are present (Wilson and Waite 1982). The larvae move further down the plant as they develop.

Fully developed larvae descend the plant and burrow into the soil to a depth of up to 10 cm and form a naked pupa (i.e. without a chrysalis) within an excavated chamber (Pyke and Brown 1996). Emergence from the pupal stage occurs after two weeks if the temperature is sufficient and day lengths are increasing. If the pupae experience reducing daylength and cooler temperatures, typical of the approaching winter, many enter diapause until the increasing temperatures and day lengths of the following spring (Fitt 1989). The length of the life cycle, when not affected by quiescence, is determined by temperature but usually requires about five

weeks. The Namoi season supports four to five generations per year whereas the more northerly areas with a longer season can support six to seven generations (Forrester *et al.* 1993).

The failure of insecticides due to the rapid development of resistant *H. armigera* populations has been dramatically demonstrated by attempts to grow cotton in the Ord River Scheme of north-western Australia (Michael and Woods 1980). Here the dependence on organochlorins and organophosphates against *Helicoverpa armigera* led to the complete collapse of cotton production in this area over a three year period. This illustrates a lesson which has been learned in cotton growing regions throughout the world (Luttrell *et al.* 1994): the use of any particular insecticide chemistry without alternative strategies represents an unstable situation for cotton production. The migratory behaviour of *H. punctigera* appears to have caused enough genetic dilution of resistant biotypes to avoid appreciable problems with this species.

The possible impending loss of two insecticide groups, synthetic pyrethroids and endosulfan, because of resistance developing in *H. armigera* together with environmental concerns has rekindled the search for ways of utilising alternative sources of pest mortality, especially those considered to be environmentally benign. Environmental and human health concerns have already led to the removal of some insecticides from Australian cotton, for example, chlordimeform and chlorfluazuron. Chlorfluazuron (Helix[®]) was a recently developed insecticide designed to disrupt chitin formation in arthropods. This insecticide was used in the experiments conducted during this thesis because it was considered to be potentially less destructive to predatory insects. However, Mendal *et al.* (1994) found that chlorfluazuron prevented the eggs of a predatory coccinellid (*Chilocous bipustulatus*) from hatching whether the chemical was contacted by the female directly or via feeding on treated prey.

Residues of chlorfluazuron appeared in Australian beef late in 1994; by January 1995 it was voluntarily removed from use on cotton by the Australian cotton industry. Subsequently the authorities allowed its provisional registration to lapse. Contamination of the meat is believed to have occurred through the practice of offering cotton trash (mill waste) to cattle or the grazing of abandoned cotton crops during the drought (R. Schulze, pers. comm. 1996). These occurrences have again focussed research on finding environmentally acceptable alternatives, of which the contribution of endemic predatory arthropods is one.

2.3.2 Non-Chemical Alternatives for Pest Management in Cotton.

Resistant Plant Varieties

Cotton varieties have generally been selected on a direct appraisal of improvements to yield and fibre quality. Concomitant inclusion of pest resistance traits has produced varieties suited to contemporary pest control practices. For example the much reduced leaf area (per leaf) of the Siokra variety is conducive to effective insecticide application by allowing superior penetration of the canopy by the insecticide to give better coverage (Thompson and Lee 1980). However the Okra-leaf varieties also provide a less suitable habitat for mites which leads to considerably reduced mite populations compared to the delta-leaf varieties (Wilson 1994). Overall, shorter season varieties have predominated in overseas selection programmes which avoid, rather than resist, pest attack. However, shorter season varieties often have lower yields under Australian conditions, and these types are not widely used. A large gene base exists which includes *Helicoverpa* resistant characteristics of both chemical and morphological origin but none of these characters have been deliberately introduced to the varieties currently being used (Fitt 1994).

Transgenic Cotton

Recent developments have enabled the production of transgenic cotton varieties. Sections of DNA from the bacterium, *Bacillus thuringensis* (Bt), have been successfully introduced into the cotton genome enabling the plants to synthesise the CryIAc protein that is a Bt toxin (Peacock and Llewellyn 1996). Many variants of the Bt toxins are naturally available from these bacterium and therefore it has been possible to introduce selectivity by using those which are specific to Lepidopterans. However, the prospect of the complete Australian cotton crop expressing mortality for *Helicoverpa* spp. for long periods of the season is expected to impose tremendous selection pressure for resistant biotypes and therefore raises serious considerations about the rapid development of resistance, especially in *H. armigera*. The potential resistance problems may be avoided by rotating with different Bt toxins in subsequent crops. Resistance may also be reduced by planting combinations or mixtures of Bt and normal (*Helicoverpa* spp. susceptible) varieties. It is proposed that some proportion of the cropping area be sown to non-Bt cotton (as refugia). This could produce enough Bt-susceptible insects

which, upon mating with insects surviving on the Bt-plants, could dilute the resistant gene pool and maintain a very high proportion of the Bt-susceptible insects. This is based on the assumption that insects with the heterozygote combination of genes for resistance are susceptible (Roush 1994).

The introduction of transgenic plants may reduce the use of broad spectrum insecticides. Arthropod predator populations might increase under these conditions and add a considerable contribution to the mortality of the remaining *Helicoverpa* spp. However, the prospect of other insects, especially the green mirid (*Creontiades dilutus* (Stal)), becoming key pests in the absence of insecticides presently being applied to control *Helicoverpa*, has raised concern. The role of predators in this very different situation may bring future pest populations and their economic thresholds much closer to a biologically controllable solution than presently appears to be the case for *Helicoverpa* spp. in Australia.

Cultural Control

Cultural control has mainly been directed at locally overwintering pupae and therefore mostly affects *H. armigera*. Post harvest tillage is known as 'pupae busting' and breaks the life cycle of the Helicoverpa spp. by directly damaging the pupae, collapsing the emergence tunnels or exposing the pupae to other mortality factors such as predation or parasitism. This practice is especially important to insecticide resistance management because the proportion of resistant insects within the population increases towards the end of each cotton growing season. For example, in an area such as the Namoi-Gwydir (around Narrabri and Moree, N.S.W.) in 1989-90, December (mid season) proportions of Helicoverpa armigera surviving a discriminating dose of endosulfan rose from less than 10% to 20-30%. For synthetic pyrethroids, resistance frequency started at 25-30% and rose to 70-75% (Forrester 1993). Therefore a reservoir of mostly resistant pupae accumulates to overwinter beneath the crop, and has the potential to greatly increase the levels of resistance in following years. Pupae busting has generally occurred as a consequence of the usual tillage practices to prepare the soil for the next crop. However in recent years the adoption of practices to maintain permanent seed beds in order to improve soil structure and cut production costs, has reduced the prevalence of postharvest tillage. This raises concerns about the survival of these resistant pupae particularly with the introduction of Bt cotton varieties.

Trap cropping has received some attention but has not been generally adopted in Australia. There are no crops which offer a high enough potential return to allocate land which is suitable and prepared for cotton. Proportionally small areas of lucerne, as strip crops, have been tested in experimental trials and it has been suggested that it increases the numbers of beneficial insects in the cotton while attracting another pest, mirids (*C. dilutus*) away from the crop (R. Mensah, pers. comm. 1994).

Parasites

There has been limited work done on importing parasites to Australia for biological control of *Helicoverpa* spp. in the classical sense. Several exotic parasites have been introduced to Australia including, *Trichogramma pretiosum* Riley, *Cotesia marginiventris* (Cresson), *Cotesia kazak* (Telenga), *Campoletis chorideae* (Uchida) and *Hyposoter didymator* Thunberg (Michael 1989). However, there has been no demonstrated impact on the pest status of *Helicoverpa* spp. in cotton.

Trichogramma spp. (micro-Hymenoptera) are tiny egg parasitoids of Lepidoptera which have been used with highly variable results. Russian reviews claim effective control (Sugonyaev 1994) but researchers in the USA could not confidently predict the effects of using *Trichogramma* (Ridgway and Morrison 1985). Problems cited have been, misidentification of the parasitoid, possible inefficiencies due to rearing on an alternative host, and the unsuitability of the new environment. *Trichogramma* spp. have also been studied for their potential for biological control in Australian cotton, but have so far been of limited value (Murray *et al.* 1994, Scholz 1990 and 1992).

Pathogens

Results using nuclear polyhedrosus viruses (NPV's) have also been variable (Teakle 1989). Elcar®, the commercially available version of NPV, has not been commonly used on cotton because of its low activity. Problems include the deactivation of the virus by UV light, and attempts have been made to increase the durability of the virus with protective coats or different formulations. Also, differences in climatic conditions, especially humidity appear to have a marked effect on the success of NPV. There is a requirement for an environmentally

acceptable tactic which imposes immediate high mortality to take the place of synthetic insecticides and it is most likely that a pathogen will fulfil this role. Recent research on improving the activity and stability of pathogens offers considerable promise (Watkinson 1995).

2.4 How Can Predators Be Included in Control Programmes?

There are basically four methods of using biological control agents: conservation, augmentation, inoculation and inundation.

Conservation simply relies on the natural establishment of endemic predators to contribute to pest control. Practices which destroy or discourage predators are minimised. Reducing the use of broad spectrum insecticides is an example of this.

Augmentation is the encouragement of greater than endemic predator levels by practices which remove the most limiting of the predator's requirements, such as providing more overwintering habitats or alternative or supplementary food sources. One metre wide strips of perennial grasses were maintained in wheat fields in England (beetle banks) to provide overwintering sites for rove beetles (Hickman *et al.* 1992). This produced a much greater population of rove beetles which subsequently disperse into the wheat crop imposing control of aphids in the following spring. Hagen (1971) developed food sprays which attract and arrest predatory species. The inclusion of tryptophan in a spray formulation of lacewing food greatly enhanced their fecundity from 50 to 600 eggs per female (Hagen 1976). Renewed interest in food sprays by Mensah and Harris (1995) in Australia has demonstrated reduced numbers of *Helicoverpa* spp. in the presence of (Envirofeast®) food spray.

Mensah (1996) recorded considerable suppression of *Helicoverpa* spp., particularly *H. punctigera*, to oviposit on plants treated with Envirofeast®. He has also included lucerne strips through cotton crops, aimed at manipulating the position and abundance of arthropod pest and predators within the cotton crop. The extent to which the lucerne strips and/or food sprays, via predator manipulation or oviposition deterrency, contribute to the decline in *Helicoverpa* spp.

is not clear. Overall, however, fewer insecticide applications have been required under these trials to control the pest.

Classical inoculative releases involve the introduction of an exotic insect, usually from the original native range of the pest, to the new region of the pest problem. The control agent hopefully establishes and proceeds to reach an effective abundance. The control of cottony cushion scale by the coccinellid *Rodolia cardinalis* (Mulsant) in orange groves in California is a renown example (Caltagirone 1981). However exotic predators are generally considered to be poor candidates for classical biological control because they are usually polyphagous and therefore likely to pose an unacceptable environmental risk to native fauna in the new range (Carver 1989).

Inundative releases involve the mass release of control agents in sufficient numbers to provide immediate control of the pest. Although desirable, the continuing impact from subsequent generations of the natural enemy from these releases is not of prime importance here. An example is the experimental mass release of *Chrysoperla carnea* onto cotton by Ridgway and Jones (1969). Although apparently effective it has not been widely accepted in practice, probably due to difficulties of insect rearing and application technology.

Helicoverpa as a Target of Biological Control

The traditional textbook examples where predators and prey show closely related, delayed 'boom and bust cycles', may not be particularly relevant to the dynamics of predators and *Helicoverpa* spp. in cotton (Varley *et al.* 1973). Here the pest may be a very small proportion of the available prey with very little influence over the abundance of the predators. Therefore *Helicoverpa* spp. probably contributes a relatively small amount to the reproductive or other numerical responses of the general group of predators encountered in Australian cotton fields. Predators which appear to be more strongly linked to the presence of lepidopteran larvae may be an exception. Such as, the large Pentotomid, *Oechalia schellenbergii* (Güerin-Meneville), but this species rarely reaches appreciable populations in Australian cotton (Awan 1985, and this thesis, Chapter 5).

Therefore the following sections address two questions: Firstly at a theoretical level; Are *Helicoverpa* spp. good targets for biological control?, and secondly; What might we expect of an effective predator? The ecology and behaviour of the pest is paramount to its susceptibility to biological control practices. Generally however, native, direct pests with low economic thresholds, which immigrate in damaging numbers to annual crops would not be expected to be good targets for biological control. Such pests would be expected to be more amenable to biological pesticides, inundative releases or resistant plant varieties.

2.5 Prospects for Controlling Helicoverpa spp. with Predators

2.5.1 International Comparisons

The degree of optimism regarding predators in reviews from the different nations appears to reflect the severity of the Heliothis/Helicoverpa abundance and persistence within the areas concerned. The positive review by Sterling (1989) is appropriate for Texas, particularly the Texas high plains (latitude about 35°N, non-irrigated, short season), and to a lesser extent parts of Mississippi, Alabama, Georgia and South Carolina with similar latitude where Heliothis/Helicoverpa are in relatively low abundance. However, in Southern Texas, for example the Rio Grande valley (latitude 30°N) the Heliothis spp. egg abundance is similar to that which occurs on irrigated cotton in Australia and scepticism about predators remains strong. Conversely, in Uzbekistan (latitude about 40°N) egg pressures are again low and optimism about beneficials is high. Sugonyaev (1994), when reviewing cotton production in the Commonwealth of Independent States, presented entomophage efficiency levels (EEL) which were used to adjust pest economic thresholds. The economic threshold for Heliothis in these areas is 1 to 2.5 larvae per meter. If the EEL is 1.0 -1.5 predators per plant the economic threshold for the pest remains unchanged but if the EEL reaches 2.5 -3.0 then economic thresholds are increased by 50%. However he also remarks that in favourable years outbreaks of *H. armigera* occurred once in every three years even if predator numbers reached the EEL.

Difficulties also arise with these broad comparisons where the Heliothine complex is not an exact ecological parallel. In the comparison between Australia and the US, there appears to be a simple comparison with two similar species in each complex. The US has *Helicoverpa zea* and *Heliothis virescens*, whereas Australia has *Helicoverpa armigera* and *Helicoverpa punctigera*. Compared to *Heliothis virescens*, *Helicoverpa zea* is larger, probably more damaging and more fecund. Likewise *Helicoverpa armigera* parallels *Helicoverpa zea* in a similar comparison with *Helicoverpa punctigera*. *Helicoverpa armigera* and *Helicoverpa armigera* and *ecologically very similar* and probably the most damaging species in each complex. From the point of view of control using pesticides, both complexes have a generally susceptible species and a resistant species. Unfortunately for Australia the most damaging species, *Helicoverpa armigera* is also the resistant species. In the US, *Heliothis virescens* is resistant but less damaging, while the most damaging species, *Helicoverpa zea*, is controllable with insecticides. In the presence of insecticides this may account for much of the difference in Heliothine egg abundance noted in each region.

The predators which inhabit Australian cotton fields are usually of the same genera to those which inhabit annual, herbaceous crops, such as lucerne, soybean and cotton, throughout the temperate to subtropical areas of the world (for example, Byerly *et al.* 1978, Bechinski and Pedigo 1982, Evans 1985, King and Coleman 1989, van den Berg and Cock 1993, Sugonyev 1994 and Kabissa 1995). These generalist predators include: coccinellids, nabids, anthocorids, pentatomids, geocorids, reduviids, neuropterans, Formicidae and a suite of spiders, especially Oxyopidae and Salticidae. These predators probably fulfil similar niches in each of their native countries, but many years of separated evolutionary selection may well have produced quite divergent behaviours in species which appear superficially similar. Differences in the agricultural practices, climatic conditions or the uniqueness of the particular native pest may also alter the effectiveness of predators in a particular country or situation.

The number of species of arthropod predators in cotton crops has been suggested to be in the order of 600 by US reviewers (Whitcomb and Bell 1964, as cited by Room 1979a). However, only 10 to 15 families, each represented by only one to five species have been consistently prevalent and abundant enough to be considered important to *Helicoverpa* spp. control. Predators identified in Australian cotton fields are estimated by Room (1979a) to include more than 41 species, but again only 10 or so are likely to be important. In general, the American species have been the most thoroughly studied. In many cases both laboratory and field predation rates have been measured along with general biology and behaviour studies (for example; Tamaki and Weeks 1972, Frazer and Gilbert 1976 and Ables *et al.* 1978). Inundative releases and behaviour modifying compounds have also been demonstrated to be effective (Ridgway and Jones 1969, Hagen *et al.* 1971). Inaction thresholds, that is levels of *Heliothis* spp. populations relative to the abundance and efficiency of the available predators which indicate that no insecticide intervention is necessary, are being applied in areas of southern USA. The predators are weighted according to their consumption efficiencies, via computer aided decision packages such as TEXCIM (Sterling 1995).

Sterling (1989) considers that native polyphagous predators often contribute regulatory and irreplaceable mortality to pests on cotton. He calculates that, for 95% of the time, cotton crops in Texas are growing without the protection of insecticides and considers that this, in conjunction with results from radio tracer studies, indicates considerable removal of *Heliothis* spp. eggs by predators. He suggests that the introduced 'red imported fire ant', *Solenopsis invicta* Buren, in particular contributes considerably to the maintenance of *Heliothis* spp. below economic thresholds (McDaniel and Sterling 1982).

In contrast, very little has been done to evaluate the impact of the predatory arthropods on *Helicoverpa* spp. in the Australian crops. Therefore the contribution to the control of *Helicoverpa* spp. by endemic predatory arthropods in Australia is largely unknown. A cautionary approach was adopted by Fitt (1989) who, referring to the Australian cotton situation, suggested that; 'the evidence of a regulatory function of beneficial organisms at the regional level is sparse for polyphagous insects in general, but especially for *Helicoverpa* spp.'. He concluded that, as with many other 'r-selected' pests, it seems probable that the regional abundance of *Helicoverpa* spp. is determined more by climatic (abiotic) factors, which act directly on the insects or indirectly through effects on host plant abundance and quality, than by biotic factors. He continued to say that, at the field scale, predators are not generally seen to be effective.

These two views remain internally consistent for the areas and situations they refer to, but the first view has been repeatedly put forward in reviews clearly meant to imply that this could well be the situation in many countries of the world if insecticides were used more appropriately (King and Coleman 1989, Sterling 1989). A wealth of information has been produced in the southern states of the U.S.A. to show that relatively high levels of the American species of generalist predators occur in cotton which experiences relatively low influxes and/or limited persistence from *Helicoverpa/Heliothis* spp. In rain grown cotton (with relatively low yield expectations), predators are usually sufficient to impose acceptable control (Lingren *et al.* 1968, Ridgway and Jones 1969, McDaniel and Sterling 1979, 1981 and 1982, King and Coleman 1989). If the Texan situation is similar to that in Australia, the Australian cotton industry might be using insecticides because it is using insecticides. That is, it is on an insecticide treadmill due to the destruction of natural enemies by the insecticides directed at the pest. If the Texan situation is not similar to Australia, possibly because the Australian pests species are more abundant and/or more destructive or that their natural enemies are less abundant and/or less effective, then insecticides might be an appropriate measure.

Reviewers commonly raise the point that predators have been shown to regulate pests in some agricultural systems and that this is therefore possible, even likely, with *Helicoverpa/Heliothis* spp. (Sterling 1989, King and Coleman 1989). However it is important to establish whether predators have the ability to reduce the pest to below an artificially determined satisfactory level, not the ability to regulate *per se*. Regulation to five insects per row-m, would represent extremely good biological control of an indirect pest with a high economic threshold, but represents extremely poor control of *Helicoverpa* spp. given current Australian yield expectations of around seven bales per hectare. Halving the yield expectations would considerably improve the prospects of achieving biological control without altering the biological prospects for regulation but this is a bit unrealistic, to say the least!

The situation in Australia could be different from that in Texas in several important ways apart from higher yield expectations. These include: i) *Helicoverpa* spp. infestations may be more abundant and more prolonged in Australia, ii) Australian predators may be naturally less abundant or less effective than their American counterparts, and iii) Australian *Helicoverpa* species may be more resilient to climatic effects, be more damaging or even have more effective anti-predator ploys. Some of these suggestions may be quite speculative, but they raise the possibility that small differences between species might have a large overall influence on the prospects for biological control, especially when very small changes in absolute pest density are economically important. Therefore the prospects for biological control of *Helicoverpa* spp. by predators in Australia will depend on the seasonal abundance and the effectiveness of the particular predators available.

Estimates of *Heliothis* spp. egg density have been recorded as high as 12 eggs per rowm in Oktibbeha County, Mississippi, USA (Hogg and Nordheim 1983). Hutchison and Petri (1983) used between 1.6 and 5 eggs per row-m to represent realistic field levels in their experiments, also in Mississippi. This appears to be low compared to those recorded in Australia. Egg densities of up to 40 eggs per row-m have been recorded in soft-option insecticide treated cotton at Moree, and up to 19 eggs per metre in organically grown cotton at Boggabilla N.S.W. (this thesis). There are anecdotal reports of *Helicoverpa* egg densities of several hundred per row-m in the Ord river area of Western Australia (P.C. Gregg, pers. comm. 1996). The appearance of *Helicoverpa* also appears to be more prolonged in Australia than reported by studies in the southern USA. Ridgway and Jones (1969) in Texas, were able to follow a single influx and decline of *Heliothis* spp. over the duration of their lacewing inundative release studies.

The frequent and widespread use of insecticides in Australian cotton growing areas prevents the estimation of how many predators might inhabit the crops in the absence of these treatments. An isolated insecticide-free plot might be indirectly affected by regional spraying because source areas are depleted or population movements are disrupted. The first application of a broad spectrum insecticide each season on a crop is possibly the most destructive to the predatory fauna. It has been suggested by Sterling (1989) that it takes between two weeks to two years for predator components to re-establish. Delaying pesticide use, particularly the organophosphates, for as long as possible has been commonly recommended by US agricultural advisory agencies for many years (King 1986). This period before the first insecticide is applied each year, in crops where seed treatments are not used, may give some indication of the capacity of predators to control pests. However only low numbers of predators are typically present at this time as the crop canopy is small.

Fitt (1989) suggests that in Australian cotton, predators of *H. armigera* and *H. punctigera* cannot be relied upon for control, since they never approach the ratios of 0.5-1.0 predators per egg or larva suggested in reviews such as King (1986) as necessary. However, in Australia both the predator and *Helicoverpa* spp. abundance are likely to alter under a reduced insecticide regime. Would the predator numbers increase relative to the pest if insecticide use was not so prevalent? The studies in this thesis (Chapter 5) would suggest that there are frequently periods where ratios of this magnitude, at least in absolute terms, occur in Australian

cotton fields, particularly when *Helicoverpa* spp. are around threshold levels (ca. 1 per row-m). However, using these ratios at the higher levels of *Helicoverpa* spp. pressure, of around 10-40 per m, would theoretically require 10-40 predators per row-m to cope with them. Predator abundance of this magnitude was not recorded in the conventionally treated or soft-option crops surveyed during this thesis but was, at least occasionally, possible in isolated unsprayed cotton crops. A modified version of predator-prey ratios which included limits to the size of the pest population or the time during the season that they are considered effective might be more suitable to the Australian situation.

The sections devoted to the impact of predators in a review by King and Coleman (1989) covered several papers which together appear to show that predators have often been the predominant mortality factor controlling *Helicoverpa/Heliothis* spp. in the southern states of the USA. However, on closer inspection of the cited literature the evidence appears less convincing.

Perhaps the best evidence offered by King and Coleman (1989) was one of the few published cases where insecticides have been shown to cause *Helicoverpa* spp. resurgence (Ridgway *et al.* 1967). Two experiments comparing the number of predators and *Helicoverpa* spp. eggs and larvae were conducted under different systemic insecticide treatments. The results were variable. The first experiment reported two of five insecticide treatments giving significantly higher *Heliothis* egg and larval populations than the control (no insecticide). Only one of these was associated with a significant reduction in predatory insects, and if spiders are included there was probably no reduction in predators across all of the treatments. The second experiment showed a significant reduction of spiders in two of four insecticide treatments. Although the differences were not statistically significant, the *Heliothis* eggs present in the control plot averaged 20.3 per 100 terminals whereas in the insecticide plots it was 34.7 to 50 per 100 terminals. It is therefore difficult to attribute the lower *Heliothis* spp. larval infestation that followed to greater removal by predators, or lower initial oviposition.

Some insight to the contributions made by the different predators might be indicated by this study. The predatory bugs such as *Geocoris* spp. (mostly *G. punctipes*), *Orius tristicolor* (White), *O. insidiosus* (Say) and *Nabis alternatus* (Parshley), were clearly shown to be the most seriously affected by the systemic insecticides. Therefore, if the reductions in *Heliothis*

spp. infestations were due to predation, this group appeared to be responsible and therefore the most efficient of the predators. Spiders were possibly less effective because their abundance did not appear to relate with the *Heliothis* spp. abundance, but this is difficult to ascertain because the species composition and size of the spiders were not reported.

King and Coleman (1989) also rely heavily on the radiotracer work of McDaniel and Sterling (1979, 1981 and 1982) for demonstrated cases of predator imposed control. In experiments where radioactively labelled prey (P^{32}) were distributed throughout test plots of up to 20 hectares of insecticide free cotton, several predators were convincingly identified as consuming *Heliothis* spp. Furthermore, by introducing their predicted predation rates into life table analysis, they claimed to have identified predation as responsible for 99.3% of the mortality of the pest. The impact of predators is supported further by demonstrating that removing the considerable predation of the egg stage allowed only 0.02% greater survival to the 5th larval instar, due to compensatory predation on later stages.

A portable geiger counter was used to locate the prey in the this study and all the prey which were not located by this means were presumed to have been predated. The possibility that many of these disappearances were due to other factors is unconvincingly dismissed by reference to a previous study (Lincoln *et al.* 1967) suggesting that missing eggs can probably be attributed to predation. More recent studies have shown that large numbers of eggs can be dislodged by the wind (G. Dillon pers. comm. 1994). Therefore the certainty of the contribution to mortality due to predators is not substantiated and this seriously questions the conclusions.

A common criticism of predation studies is that the methods used fail to identify exclusive or additional mortality. The destruction of even a large proportion of a pest population may not necessarily change the net survival of a pest because that destruction may simply replace another mortality factor (Kirtani & Dempster 1972). Therefore the records of radioactivity from predators collected by McDaniel and Sterling (1981) may have represented prey which had already died or had a high probability of dying from some other factor shortly afterwards. Control plots using some form of predator exclusion method are necessary to identify the level of mortality which is exclusive to the predators. Therefore the conclusions by McDaniel and Sterling (1981) that the overall field mortality was due to predation were not conclusive. That some combination of natural factors caused this level of mortality is undeniable, but the useful contribution made by predators remains obscured. Notwithstanding this, the high rate of labelling observed over a short period after prey release, especially for ants, certainly suggests the potential of predators to exert controlling influence.

Sunderland (1988) also questions the ability of radiolabelling methods to clearly indicate the number of prey items taken by a predator. This would be particularly true for the study of McDaniel and Sterling (1981), given the low number of predators they used to base their estimates (sometimes only one individual). However, even with these limitations, the number of prey consumed per predator per day was not high and appeared to be consistent with the suggestions from field cage studies that less than 1 prey item per day was common across a range of predatory arthropod species (O'Neil & Wiedenmann 1987, O'Neil & Stimac 1988, O'Neil 1989, Wiedenmann & O'Neil 1992). The exceptions were an individual spider (*Chiracanthium inclusum* (Hentz)) which appeared to have taken 2.9 larvae and an ant species (*Solenopsis invicta* Buren) which was usually attributed less than 0.1 of a larva per day each (n=600). However the lack of reported details about the densities of unlabelled *Heliothis* spp. of field origin, reduces the validity of this estimation. The numbers of predators. however, were reported and ranged from 11.1 to 23.5 per row-m. This is considerably more than was present under conventional or soft-option insecticide treatments in Australia but possible in untreated plots (Chapter 5, this thesis).

The general conclusion of the review by King and Coleman (1989) regarding the impact of predators is that a ratio of 2 predators to 1 pest egg or larva is sufficient to contain *Heliothis* spp. to below economic thresholds for raingrown cotton in the Southern states of the USA. The basis for this comes essentially from generally observed practices and has not been convincingly substantiated with experimentation. However it is important to note that the experiments do not show that predators are not effective, only that their impact is difficult to measure and therefore at this stage unknown and unpredictable.

2.5.2 Which Predators Consume Helicoverpa spp.?

There are many species of predators which consume *Helicoverpa* spp. This has been clearly demonstrated by radiotracers and field observations. They are non-specific (though probably with various degrees of prey preference) and therefore regarded as generalists. Some species consume any or all of the life stages, but many take only eggs and young larvae which are easier targets and fall into the prey range of smaller predatory species. The impact on later instar larvae or pupae is also important to reduce future populations which may have been exposed to insecticides and therefore harbour elevated frequencies of insecticide resistance genes. The later instar larvae may have more effective defensive reactions, or be hidden within bolls and therefore often avoid or thwart attacks. Larger larvae are preferred as prey by some larger predators such as *Oechalia schellenbergii* in Australia or *Podisus maculiventris* (Say) in the USA (Lopez *et al.* 1976, Awan 1985).

Some phytophagous insects have been identified as predators of Helicoverpa spp. In the USA, McDaniel and Sterling (1982) implicated cotton fleahopper adults and nymphs (Pseudatomoscelis seriatus Reuter) as the second most likely arthropod to have consumed Helicoverpa eggs even though it is primarily considered a sap sucking pest. Likewise, there is some confusion as to the status of the apple dimpling bug (Campylomma livida Reuter, Hemiptera: Miridae) in Australia. It appears to cause damage to the crop and is generally considered a sucking pest, however, Room (1979a) showed that it also feeds on considerable numbers of Helicoverpa eggs in petri dishes (3.9 eggs/predator/day) and by radiotracer identification in the field. The convenient application of the terms 'phytophagous' or 'entomophagous' to describe the arthropods found in cotton crops can be a misleading oversimplification in many cases. Plant feeding has been noted for several 'predatory' species, particularly hemipterans such as Orius insidiosus (Kiman and Yeargan 1985), Nabis spp. and Geocoris punctipes (Stoner 1970 and 1972). The application of in-furrow (sidedress) systemic insecticides has been reported to reduce Orius, Nabis and Geocoris which might suggest supplementary plant feeding. However, the path of acquiring a lethal dose of the insecticide, via plant or prey, or if indeed the reduction was not simply due to the removal of available prey was not established (Ridgway et al. 1967).

2.5.3 Measurements of Predation Rates on Helicoverpa spp.

Scientific studies of biological systems range from broad overall measurements to detailed analysis of their components. The overall approach describes the possible outcomes, whereas the component approach may give some insight into the action of the parts and therefore aid interpretation. However the latter approach often lacks predictive power as a result of errors (due to interactions between sub models) which are introduced as the overall model of the system is reconstructed. Both approaches have been used to evaluate the predation rates of predators.

The Holistic Approach

Holistic studies include chemical or mechanical exclusion experiments which attempt to measure the overall effect of the predator complex on *Helicoverpa* spp. in the field with minimal interference.

Sterling (1989) has stated that because 'most insects are limited to a major extent by natural enemies, exclusion studies provide little new information except to add another species to the list of animals limited by natural enemies'. He continues to say that the current goal is to find out how natural enemies achieve this, in order to improve the prediction of their effect. This is clearly meant to imply that *Heliothis* spp. has already been added to this list of regulated pests, but exclusion experiments have not shown that natural enemies usually limit *Heliothis* or *Helicoverpa* spp. in cotton, nor that the often considerable levels of predation that do occur are irreplaceable. Typically the results are highly variable and confounded by the mortality contributed by other factors.

A recent study showing these difficulties of interpretation was conducted by van den Berg and Cock (1993 and 1995) on cotton in Nairobi, Kenya. Using exclusion cages they demonstrated a strong effect of predation on the survival of *Helicoverpa* spp. to 1.3 larvae per row-m compared to 6.1 larvae per row-m, 14 days after initial infestations of 150-400 viable eggs/cage (4m long cages with 24 plants per cage). The predator cages (controls) in this study were not sealed but were open at the base to allow predator movements. This allowed more natural behaviour of the predators, especially of ants whilst maintaining a similar environment to the exclusion cages, which were sealed at the base. There were high numbers of predators involved during the prey reductions. For example night active spiders or ants which had left the cages prior to the counting procedures might have been missed. Another difficulty with these trials is that survival of the pest and/or predators may have been increased under the caged conditions due to factors such as reduced wind speeds, higher humidity and increased shading. Measurement of survival in an open area similarly infested with the pest near the field cages can be used to indicate whether the survival of pests in the open predator cage mimics that of the open field (Titmarsh 1992). This could show if the level of mortality attributed to the predators is irreplaceable. A later study by van den Berg and Cock (1995) which addresses this question, used chemical exclusion to avoid the effect of cages. This study recorded high rates of natural mortality (96.4-99.7%) regardless of the presence of predators and therefore showed no irreplaceable mortality due to predation. They offered two ways in which their trial might have underestimated the effect of predators. Firstly that the insecticide used to remove predators might also have caused high mortality of the pest in the exclusion plot. However preliminary experiments suggested that this treatment did not effect Helicoverpa spp. The second possibility was that the few predators which were present in the exclusion plot were as effective as the large numbers of predators in the control, possibly because they had less competition for those prey. However, studies of other predators (not necessarily ants) at various predator densities have generally shown very low and linear rates of prey consumption per predator over realistic field densities of the pest, (O'Neil and Weidenmann 1987, Stark and Whitford 1987). The question this poses is that, if mortality of such a high degree is commonly exhibited, what is the relative importance of abiotic factors and predators to total mortality? This remains unknown because, as with the studies of van den Berg and Cock (1993 and 1995), a thoroughly convincing experiment has not been conducted. Demonstrations of moderate to high predation rates have not included methods that show the mortality is irreplaceable.

The Component Approach

This approach selects potentially effective predators for detailed evaluation. Particulars of the consumptive behaviour are studied in relatively simplified environments to facilitate measurement which invariably removes many attributes of the whole system. Confidence accrues with repeatable results but the problem remains that the system being measured might be severely altered by the isolation process. Nevertheless some studies have attempted to extrapolate these results to the field by including suspected important variables such as alternative prey, to investigate more realistic settings (for example, Ables *et al.* 1978).

Lacewing larvae (Neuroptera: usually *Chrysoperla* spp.) have received as much attention as any predatory species on cotton for the control of *Heliothis* spp. It is instructive to collect the available information on these species as an indication of how the impact of these predators has been evaluated.

Lacewing larvae are logical candidates for investigation because they are found in many cotton growing areas of the world and some exhibit a tolerance to systemic insecticides which might be useful in IPM progammes (Ridgway and Jones 1969). Average field abundance in unsprayed cotton using absolute sampling methods ranged from 0.31 to 3.50 larvae per row-m in California (Gonzalez *et al.* 1977). Byerly *et al.* (1978) usually found about 2 per row-m but on one date recorded about 20 per row-m in the Southern San Joaquin Valley of California. In contrast at Narrabri (Australia), Wilson and Room (1982) reported a three season average of only 0.002 per row-m for *Mallada signata* (Scheider) larvae (= *Chrysopa signata*, the Australian counterpart to *Chrysoperla* spp.) on cotton. Even allowing for the probability that the sampling method was not as thorough as the US studies, it seems likely that the abundance of lacewings is much lower in Australian cotton.

Direct observations (Room 1979a) and radio tracers (one individual by McDaniel and Sterling 1982) have confirmed *Chrysoperla* larvae as predators of *Heliothis* or *Helicoverpa* spp. in the field. Field cage studies (Ridgway and Jones 1969) and laboratory studies (Lingren *et al.* 1968 and Room 1979a) have also shown they are capable of consuming *Heliothis* spp. eggs and larvae, but in confined, and therefore possibly forced, situations.

Laboratory predation rates for *Chrysoperla carnea* (the American species) averaged 42.7 eggs or 48.8 first instar *Heliothis* spp. larvae per day for each predator. For third instar *Chrysoperla* this was 95.7 eggs or 62 first instar larvae per day per predator. Room (1979a) showed 13.6 eggs per day per Chrysopid larva (*Chrysopa ?signata* Walk = *Mallada signata* the Australian counterpart). However, when tested in field cages these rates reduced considerably to less than 1 egg per predator per day even at higher than realistic prey densities (Stark and Whitford 1987). Ridgway and Jones (1968 and 1969) released inundative numbers of *C. carnea* larvae into large field cages and later onto open cotton. They showed 73.8 to 99.5% reductions in *H. virescens* survival in the field cages and 75% reductions in field

releases using 25 to 100 larvae per row-m. In 5 of 7 cases where they released into the cages *H. virescens* were reduced to below economic thresholds (0.49 to 0.62 larvae / row-m). Eight days were required to achieve this with synchronised pest and predator populations. In the two cases where control was not achieved the initial *H. virescens* densities were 5 to 10 times higher than field populations normally encountered (14.8 larvae / row-m), and accompanied by extremely high levels of alternative prey (aphids)

Thresholds used in Australia are similar if not slightly more relaxed than this (around 1-2 larvae / metre) but the level of initial infestation would commonly reach the levels considered in the US work to be uncontrollable by inundative releases of up to 10 predators per plant.

A type 1 functional response was exhibited by *Chrysoperla rufilabris* on seedlings with 2 to 10 *Heliothis* spp. eggs per seedling (1.6 to 5.3 eggs taken) which was much higher than field rates (Nordlund and Morrison 1990). 1.3 to 4.2 larvae were consumed at densities of 2 to 10 per seedling. Treacy *et al.* (1987) found similar results. Nordlund and Morrison (1990) also showed that handling time did not change significantly with the number of successful encounters. This implied that learning was not improving the response of these predators. Handling times on *Heliothis* spp. eggs were 217 secs by 2nd instar predators to 71 secs for 3rd instars; on larvae, 437secs by 2nd instar predators to 205 secs for 3rd instars. They described it as a voracious feeder but one which might only be useful for inundative releases due to its type 1 functional response. Lopez *et al.* (1976) studied *Chrysoperla carnea*, in laboratory and field cages and showed different predation rates at different levels of complexity of the search arena. They demonstrated control of *Heliothis* spp. in cages with 27 *Chysoperla carnea* per metre (on cotton terminals) but cautioned against extrapolating these results to the field due to lack of alternative prey, small search arena and exaggerated predator density.

Ridgway and Jones (1969) again showed that inundative releases of *Chrysoperla carnea* eggs or larvae can reduce *Heliothis* spp. to below threshold and consequently give a three fold increase in yield. Two releases occurred of 20.1 larvae per row-m and, one week later, at 45.5 per row-m bringing an infestation of 6 *Helicoverpa/Heliothis* spp. eggs per row-m to virtually nil survival. The control area had larval infestations up to 4.1 per row-m following this egg influx. A concurrently run field cage trial implied 50,000 *C. carnea* eggs per acre could be adequate to reduce a 17 eggs per row-m *Helicoverpa/Heliothis* spp. infestation to below threshold. Within the modified environment of the cage, the control (no

per acre could be adequate to reduce a 17 eggs per row-m *Helicoverpa/Heliothis* spp. infestation to below threshold. Within the modified environment of the cage, the control (no predators) gave an 85% mortality (egg to large larvae) which under these high *Heliothis* spp. pressures (17 eggs per row-m) allowed 2.5 larvae per row-m to survive. This was therefore above a threshold quoted by these authors in (1968) of 0.5 larvae per row-m. Interestingly, overall mortality of eggs between the three *C. carnea* densities of 10,000, 50,000 or 200,000 per acre in the cages were 93%, 96.5% and 99% respectively and the mortality of larvae was 52%, 85% and 96% respectively. Within the 6% difference in overall survival between the 10,000 and the 200,000 per acre treatments, the final infestation varied from 1.1 (well over threshold) to 0.16 larvae per row-m. This emphasises the small difference in percentage mortality between successful control and severe crop losses and the large number of predators which might be required to impose control in the absence of other contributing factors.

In the field release trial, intercepting this single *Helicoverpa/Heliothis* influx caused a three fold increase in yield (albeit a low yield by irrigated cotton standards ~ 455 kg per acre). Therefore, although control has been demonstrated to be possible by inundative releases in this experiment, it required very large numbers of predators (greater than has been recorded in Australia) in a situation where the *Helicoverpa/Heliothis* spp. pressure was moderate, 6 eggs per row-m, and not prolonged. The control area recorded a much lower mortality than shown in many other experiments where field mortality minus predators has been recorded, possibly because particularly mild conditions over the period of this experiment produced unusually low abiotic mortality. The presence of alternative prey was not reported.

Thead *et al.* (1987) showed low rates of predation in field cages. They combined radiotracing and cage predation rates to show how various predators at various densities impact on *Helicoverpa* eggs and larvae. Prey consumption of up to 1 egg or larva per 48 hours was normal for all predatory species they tested. A predator to prey ratio of 5:1 only caused a 12.1% pest reduction and only 8% of the predators recovered had fed on *Heliothis* spp.

This is the state of the knowledge for the most thoroughly studied species and unfortunately it is sufficient only to imply that control may occur at high predator abundance in the absence of extraneous circumstances. The underlying theme is one of unpredictability at the present level of understanding.

2.5.4 Prospects For Improving Predator Efficiency

The possibility of increasing predator numbers by behavioural manipulation has been clearly demonstrated for lacewings via the food sprays of Hagen *et al.* (1971). These attract adult lacewings to a crop and increase their fecundity. This tool might also allow some control over the movement and levels of predators, but it has not been adopted for control practices, despite the excellent results achieved by Hagan (1971) during experiments. Problems such as the cost and timing of producing the insects and the incompatibility of this with insecticides as well as the complications of requiring a greater level of understanding by growers have combined to extinguish its use.

In their review of the prospects for the biological control of *Helicoverpa/Heliothis* spp. Jackson *et al.* (1989) highlight the need to improve the effectiveness of natural enemies in general because they often do not maintain populations below acceptable levels. The prospect of increasing the efficiency of predators using chemicals has developed from observations that carnivorous insects commonly use volatile cues to locate more promising areas for searching or oviposition or to directly locate the prey. These cues are volatiles associated with the prey or its damage (Awan 1985). The complexity of such chemical factors has been demonstrated by the ability of some species of plants to generate specific volatiles throughout undamaged tissues in response to specific insect damage and thereby attract a specific parasitoid (Takabayashi and Dicke 1996). With predators, such volatiles can elicite an increased searching activity and therefore increase the chance of finding the prey. Hagen *et al.* (1976) demonstrated considerable potential to attract *Chrysoperla* sp. using 'food' sprays which mimic the honeydew of the prey species (in this case aphids). Tryptophan, a component of the spray, was also found to have a considerable effect on the fecundity of the adult lacewings leading to 12 fold increases in oviposition (from 50 to 600 eggs per individual).

Recent work by Mensah and Harris (1995) has demonstrated that the abundance of many endemic predators can be increased by applying food sprays to cotton crops in Australia. The mechanisms of these sprays are largely unknown but the possibility of altering the predators feeding behaviour by maintaining the insects in a 'hunting mode' could improve the prospects of predator impact. The prospect of this compound also possessing an oviposition deterrency for *H. punctigera* presents an intriguing dimension. It may involve interactions

between cues exploited by the herbivore to locate good feeding sites (and possibly avoid predators), the predators to locate the prey, and the plants to elicit predators to protect themselves. Chemicals which imply the presence of other prey, predators, or damaged plants may also deter oviposition (Vet and Dicke 1992).

2.5.5 How Predators Might Be Incorporated into IPM

How might predators be incorporated in future IPM systems, especially if we knew more about their behaviour and impact? The monitoring of pests could be extended to incorporate the counting of predators. The number of predators relative to the number of pests adjusted for plant stage, prevailing weather and time of the season could be incorporated to give a likely risk of *Helicoverpa/Heliothis* damage and therefore affect an insecticide decision. King and Coleman (1989) cite a peg board example where the discovery of a predator during pest monitoring counteracts the movement of the pest counting peg towards the action line (i.e. a one to one predator to pest ratio).

The compatibility of predators with other pest management tactics varies considerably between applications. Insecticides are generally detrimental to biological control but where pest resistance occurs it may be possible to rely on natural enemies early in the season and introduce the insecticides at the latest possible moment. This would reduce the selection pressure on early pest populations and allow predator populations to establish. Although the insecticides would cause considerable disruption to the predators this may be minimised by using more selective chemicals or those to which certain predators may have demonstrated some tolerance. A greater impact on the pest than its natural enemies may be possible by judicious placement and/or timing of insecticide applications.

Predators as a secondary source of mortality could be of particular importance to impact on later season populations which are likely to contain a large proportion of resistant genotypes. For example late season survivors of Bt insecticide applications or Bt plant varieties may be reduced by predators.

There are several cases where predators have synergistic interactions with direct hostplant resistance or may even be the reason a plant variety appears to be resistant to a pest (indirect-host plant resistance). For example, Treacy *et al.* (1987) found that high trichome density obstructed the mobility and therefore predation rate of *Chrysoperla rufilabris* (Burmeister) larvae on *Helicoverpa zea* eggs as a possible explanation for higher survival of *Heliothis* on pilose cotton varieties. However it is possible for a characteristic conveying direct host-plant resistance on a pest, such as a toxic secondary plant metabolite, to also reduce the effectiveness of a natural enemy via transferred toxicity or reduced prey supply. In such a case the two mortality factors are not synergistic and a compromise may be necessary to benefit from the stability and retarded resistance development which are features of multifactor control systems (van Driesche and Bellows 1996).

2.6 Conclusions

Although there are examples of arthropod pest populations which are clearly reduced to non-pest status by natural enemies (for example, mites and scales), the situation on cotton with *Heliothis* or *Helicoverpa* spp. is potentially different. In this situation the pest has an extremely low economic threshold, can arrive in numbers greater than action thresholds by immigration overnight, and is a very small proportion of the available prey. All these features could greatly alter the importance of generalist predators to the overall mortality of this pest. The impact of predators on *Helicoverpa* spp. in Australia, despite the efforts of many researchers, remains largely unknown. The evidence does however provide partial answers to some important questions.

(1) Do generalist predators feed on *Helicoverpa* spp.?

Individual species have been identified which at least occasionally predate on *Helicoverpa* spp. This information has been obtained for many of the commonly encountered predatory genera by direct observation, prey marking in the field (McDaniel and Sterling 1979, Room 1979a), in field cages (Stark and Whitford 1987, van den Berg and Cock 1993, Titmarsh 1992) and in laboratory consumption experiments (Room 1979a).

(2) What are the predation rates on *Helicovera* spp.?

Generally, predation rates have not been convincingly established. The best estimates are those gained in field cages, although these are fraught with interpretational difficulties regarding climate manipulation and possible differences from the larger field scale. Field prey marker experiments are not affected by these problems but suffer from the typical markrecapture requirements especially those regarding realistic prey redistribution. It is abundantly clear however that laboratory consumption rates grossly overestimate the prey consumption which occurs in the field, and at worst might even indicate prey which is not taken in the field. The per predator rate of consumption of prey appears to be in the vicinity of 1 meal per day for most types of generalist predators inhabiting the cotton system.

(3) Can predators reduce Helicoverpa spp. to below economic thresholds?

Field population studies consistently fail to provide conclusive evidence that this is occurring. Abiotic factors or plant mortality factors provide an alternative explanation, especially when it has been established that these factors alone can result in mortalities of 96.4 to 99.7% (van den Berg and Cock 1995).

Component experiments have often given much higher rates of predation than holistic trials. Although several factors have been identified as influencing predation rates, confident models of field predation rates have not been possible. The practical approaches to the use of predators (via the inclusion of predator/ prey ratios in decisions during crop scouting) have therefore progressed without scientific confidence and are based on results from experiments of limited explanatory power and circumstantial or anecdotal evidence of field experiences.

Sterling (1989) has suggested that in Texas, with high populations of ants and with moderate yield expectations, and low *Helicoverpa/Heliothis* spp. pressure, the amount of predation (mainly by ants) is considerable, and possibly controls *Heliothis* spp. In other areas, such as Australia, where ants are not prevalent, and not likely to be so because of irrigation practices, and where yield expectations are greater and *Heliothis/Helicoverpa* spp. pressure is higher and more prolonged, the impact of predators may only rarely contribute significantly to the other natural mortality factors.

However, it remains distinctly plausible that the conservation of predators, by intervention or non-intervention, contributes appreciably to pest mortality, and is worthy of further investigation. The conclusions merely reflect the difficulties involved in demonstrating this and therefore highlights our lack of scientific evidence about the impact of predators and therefore our inability to apply our knowledge to confidently include predators in pest management decisions.

3. General Materials and Methods: Including the list of arthropod species collected during the study.

3.1 Introduction

For the studies described in this thesis, several cotton crops were chosen in which the managers were using quite different insecticide programmes to control *Helicoverpa* spp. Some of these insecticide treatments were expected to be less damaging to potentially beneficial insects such as predators. Therefore they provided an opportunity to study *Helicoverpa* spp. populations in areas of relatively high and low predator abundance. Differences in the abundance or distribution of *Helicoverpa* spp. at these sites were expected to give an indication of the impact that predators might have.

When looking at the potential for endemic species of predators to control pests it is important to know the range of arthropods inhabiting the crop. Recognising potential predators is obviously important, but it is also useful to know the broad suite of insects present and how abundant they are at different times in the season. This helps with understanding the possible roles of alternative prey or natural enemies (of both *Helicoverpa* spp. and the predators) which might influence the predator/prey relationships at the focus of the study and is essential for formulating rational integrated pest management programmes (Evans 1985).

Monitoring the cotton crops required an extensive survey method which was general in its ability to collect different species from all parts of the habitat of interest. In this case suction sampling of the complete cotton canopy for a short section of row was chosen. The expectations and results of this method are explored and discussed in the next chapter (Chapter 4), but the general materials and methods used to collect arthropods are described here to avoid repetition in several later chapters. Where the methods have been modified for a particular reason there will be additional explanation in the materials and methods section of those chapters.

3.2 The Study Sites

The locations of the study sites in N.S.W. in relation to the major towns in the northern N.S.W. are presented in Figure 3.1 and 3.2.



Figure 3.1 The study sites were situated in the cotton growing areas of mid western N.S.W. about 530 km NNW of Sydney. The 'Midkin' property, managed by Auscott Pty Ltd., was 20 km north of Moree, N.S.W. The 'Alcheringa' property, managed by Dave Coulton, was 5km south of Boggabilla N.S.W. The 'Wilby' property, managed by Ben Coulton, was 1km north of North Star.



Figure 3.2 A regional map showing the study sites in relation to one another. The 'Midkin' sites were 20 km north of Moree N.S.W. on the Mungindi Road. Boggabilla is 115km north of Moree on the Newell Hwy. The 'Alcheringa' site was 5km South of Boggabilla N.S.W. North Star is approximately 100 km North of Moree and 26 km east of the closest Newell Hwy. intersection to North Star. The 'Wilby' site was 1km north of the North Star township. All distances are in kilometers.

3.2.1 Midkin 1992/3

Auscott Pty Ltd, a corporate farm at 'Midkin', 20 km north of Moree, NSW (29^o 28'S, 149^o 51'E) was, at the time of these studies, investigating the prospects of growing cotton in the absence of two insecticide groups, endosulfan and the synthetic pyrethroids. Therefore two cotton fields of realistic commercial sizes were being managed under different insecticide strategies, one using insecticides which were thought to be less damaging to predators (hereafter called "soft-options") and the other using the conventional broad spectrum insecticides common in commercial practice at that time. Auscott provided these treatments over two seasons (1992/3 and 1993/4: see chapter 5, Tables 5.1 to 5.2 for rates and application methods). Regular suction samples were taken over these years at this property. The cage trials (Chapter 7) were also conducted on this farm in the area shown in Figure 3.3.



Figure 3.3 A schematic diagram of the 'Midkin' site over the 1992/93 growing season. Field 1 was treated with Soft-Option insecticides (those considered to be less destructive to beneficial insects) and field 2 with conventional insecticides (the current industry practices, based mainly on endosulfan and synthetic pyrethroids). Four suction samples were collected from each plot frequently throughout the cotton growing season. 'D.S.' are the sites used for the diurnal sampling experiments in 1992/3; the 1st experiment was located near plot 5 and the 2nd and 3rd experiments between plots 3 and 4. The area used for the cage trials in 1993/4 is shown to the east of Field 1. This area was wheat stubble during the 1992/3 season but sown to cotton in 1993/4.

Two adjacent fields were sown to cotton. Field 1 was 150 hectares sown to cv. CS 50 at a rate of 16 plants per meter. Field 2 was 72 hectares sown to cv. Siokra L22 at a rate of 14 plants per meter. Four subplots, each of 0.5 hectares, were established in each field, where suction and visual sampling were conducted (Figure 3.3).

3.2.2 Midkin 1993/4

Two adjacent fields were again selected for the trial. However in contrast to 1992/3, both the insecticide treatments were applied to each field (Figure 3.4). Two sub-plots were established in each field, one in the conventional and the other in the soft-option ends of each field. The cotton variety used in both fields was Siokra L23 sown "skip-row" (that is, leaving one row in every three unplanted) at a rate of 10 plants per meter to conserve the soil moisture.



Figure 3.4 The 'Midkin' site in 1993/94. The soft-option insecticides (mainly *Bacillus thuringiensis*, thiodicarb and chlorfluazuron) and conventional insecticides (endosulfan and synthetic pyrethroids) were applied to different areas of the same field. This was on the opposite side of Carole Creek and 2km north-west of the 1992/93 site in figure 3.3. Plots 1,2,3 & 4 represent the 0.5 hectare subplots where suction samples were collected on a weekly basis. The boarder between the soft-option and the conventional treated area was 400m from the end of each field. The surrounding land use is presented to aid discussion of possible source areas of pests and predators.

3.2.3 Alcheringa 1993/4

The 'Alcheringa' site was a 250 hectare field of irrigated organically grown cotton (cv. Siokra L23 at 13 plants/meter). Eight row wide strips of Sorghum (8m) were present every 200 rows of cotton. Sixteen rows of cotton on the far eastern side of the field were left untreated with insecticide as a control plot. This control area was adjacent to a bordering 8 metre wide sorghum strip (Figure 3.5).



Figure 3.5 A schematic diagram of the 'Alcheringa' site in 1993/4, 3 km south of Boggabilla N.S.W. Field 5 was irrigated cotton treated with organically certified compounds presented in Tables 5.3 and 5.4. Plots 1 and 2 represent the 0.5 hectare plots where four suction samples were collected on a weekly basis with the Macvac and a fortnightly basis with the Bigvac. Sorghum strips 8 meters wide (8 rows) were present every 200 metres of cotton. A 16 meter wide 'control' plot was established at the eastern end of the field between the sorghum and the organically grown cotton which received no direct applications of the organic treatments for arthropod pest control.

At the time of this study, Coulton Farming Pty Ltd were exploring the prospects of growing cotton organically. During 1993/4 access was available to two of their farms, 'Wilby' at North Star, NSW (28^o 56'S 150^o 24'E), and 'Alcheringa' at Goondiwindi, Qld (28^o 33'S 150^o 18'E), to compare the predator abundance under these practices. Although no synthetic

insecticides were used on these farms, natural products including pyrethrins, *Bacillus thuringiensis* and garlic were used. However, plots where no insecticides of any kind were applied were also available at these sites.

3.2.4 Wilby 1993/4

The 'Wilby' site was a 145 hectare field of rainfed, organically grown cotton (cv. Siokra L23 at 7 plants/meter). This also had sorghum strips of 8 rows wide every 200 rows of cotton crop, and a control site of 16 rows of cotton adjacent to the sorghum border (Figure 3.6).



Figure 3.6 A schematic diagram of the 'Wilby' site in 1993/4, 1 km north of North Star, N.S.W. Field 6 was a 145 hectare area of rain grown cotton (Siokra L23). 1 and 2 are the plots where suction samples were collected on a weekly basis using the Macvac and on a fortnightly basis using the Bigvac (see Section 3.3 for sampling methods). 8 metre wide strips of sorghum were established every 200 metres of organically treated cotton. A 16 metre wide 'control plot, which received no direct applications of the organic treatments, was established at the western end of the field between the sorghum and the organically grown cotton.

3.3 Sampling Methods

Suction sampling was the major means of collecting arthropods throughout this study. Three methods of using suction samplers were employed in order to collect from different sized plants and to allow comparisons with protocols being used by contemporary researchers. Experiments to determine the efficiency of these suction methods are described in chapter 4. Visual counts were used very early in the growing season to survey predators on very small seedlings and continued throughout the season for estimating *Helicoverpa* spp. egg and larval abundance. A very limited amount of pitfall trapping was conducted to explore the ground dwelling fauna.

3.3.1 Visual Counts

These were visual inspections of 5 adjacent plant terminals in 6 locations along a 30 meter transect. The number of insects in 30 terminals were counted as described by the entomoLOGIC 1992 protocols; entomoLOGIC is a computer decision support system for cotton pest management in Australia (Anon 1995). *Helicoverpa* spp. eggs and larvae were recorded according to the entomoLOGIC guidelines. Predatory arthropods and mirids (*Creontiades dilutus*) were also recorded.

3.3.2 Small Electric Suction Sampler ("Elecvac")

An electrically powered suction device (hereafter termed the "Elecvac") was built to collect insects from small cotton plants (i.e. of approximately 10 to 20 cm tall). An automotive heater-fan motor was the basis of this design which generated an air velocity of 6.5 m/s through a 7.2 cm diameter intake. During sampling the unit was carried like a backpack while the intake nozzle, on a flexible hose, was directed up one side, across the top and down the other side of each cotton plant in a 10 meter interval of cotton row. The nozzle was moved forward one nozzle width with each pass. A nylon stocking was used as the collecting net. This was secured to the intake nozzle using an elastic band. The lip of the nozzle brushed against the cotton plants during sampling, penetrating the canopy to approximately 2 cm. Immediately

after the sampling distance had been vacuumed, the catch was quickly enclosed by twisting the open end of the net and clasping it with a bulldog clip. The clips were bolted to a numbered clip board to keep the catches in order. A tent peg attached to a 10 m length of cord was pushed into the ground at the start of the sample interval. The cord was allowed to unreel during sampling and therefore stopped the operator at a distance of 10 m. This avoided marking out areas prior to sampling, which might have disturbed the arthropods being sampled.

3.3.3 Large Petrol Suction Sampler ("Bigvac")

A 70cc petrol motor driven mistblower (Solo® Mistblower Port 423; 7032 Sindelfinger 6, Postfach 60 01 52, Federal Republic of Germany) was modified for use as a suction sampler. This unit, hereafter called the "Bigvac", developed a 16 m/s air speed through a 16 cm diameter intake. It was based on the 'D-vac' suction sampler developed in the U.S.A. by Dietrick (1961) and was carried as a backpack. Nets made from polyester (woven mesh with 9 square holes / mm², each hole 0.2 mm across) were fitted to the intake with a large elastic band. As with the Elecvac, the intake was directed up one side, across the top and down the other side of the cotton plants in a 10 meter interval of row, moving one intake width further with each pass. The intake brushed against the leaves and terminals as it passed, penetrating the canopy to approximately 5 cm. The catch was secured by tying a knot in the top of the net whilst the motor was still operating at a speed capable of holding the catch in the base of the net.

3.3.4 Small Petrol Suction Sampler ("Macvac")

This was a 20cc, petrol motor driven vac/blower (MacCulloch Superairstream VI, imported to Australia by 'Masport®' Crn. Boundary Rd. & Industrial Dr., Braeside, Victoria, 3195) used in the vacuum cleaner mode. It created an airspeed of 9.5 m/s through a 11cm diameter intake. This unit is hereafter called the "Macvac". Nets were made of knitted voile (mesh with 9 triangular holes ranging up to $0.1 \text{ mm}^2/\text{ mm}^2$). The method of using the Macvac was considerably different to the other two vacuum units. The operator paced a distance of approximately 20 meters. The intake of the unit was directed downwards towards the top of the cotton plants and a single straight pass of 20 seconds duration was made with the intake clipping the tops of the plants. The nozzle was pointed slightly backwards so that the lowest

lip did not scoop up plant material. The catch was secured by tying off the opening of the nets with short pieces of string. The arthropods were subdued with chloroform before cleaning and sorting as for the Bigvac.

The Macvac was used because similar machines were in general use by other researchers and consultants to sample predators in commercial cotton crops at the time of the study. The sampling method used was a standard recommended for this purpose during Australian Cotton Research and Development Corporation workshops (D.A.H. Murray 1992, pers. comm.). Although it was judged likely that the Macvac used in this way would be less efficient than the Bigvac, it was considered necessary for this project to have some means of comparison with contemporary studies. The relative efficiency of the Macvac is described in Chapter 4.

3.3.5 Arthropod Sample Processing

The samples were transferred to 70% ethanol and sorted under a binocular, dissecting microscope (12 x magnification). The initial transfer to ethanol occurred in two ways. During the first growing season (1992/3) a 12 volt portable suction device was built which held the sample against a screen whilst large pieces of leaf or flower were removed. Plant parts were lightly brushed with a soft 2.5 cm wide paint brush to return insects to the screen, then an aspirator was used to transfer the insects into ethanol filled vials. The screen was made of the same material as the sampling nets. This method was developed mainly to help collect large numbers of living predators for serological analysis. In the second season (1993/4) the catches and nets were returned to the laboratory in a cooled "Esky" (portable ice chest) and the insects subdued using chloroform. The contents of each net were tipped into a one litre plastic beaker from which the large plant material was removed manually. Insects adhering to the plant material were returned to the beaker by brushing with a soft 2.5 cm wide paint brush. After a thorough secondary cleaning using a binocular microscope and tweezers to remove the remaining plant material, insects were identified and counted.

3.4 Arthropod Species

3.4.1 Specimen Identification

The species collected from cotton crops in northern N.S.W. were very similar to those collected by Evans (1985) from soybeans in southern Queensland. The genera were similar to those reported from many herbaceous crops in the subtropical to temperate areas of the world (for example, Bechinski & Pedigo 1982, Evans 1985, King & Coleman 1989 and Jackson *et al.* 1989). The first priority for this study was to identify the predatory arthropods. Many of these, such as the Coccinellidae, Nabidae and Melyridae have been previously identified and were readily recognised to species by reference to field guides, particularly Room (1979b). Several of the phytophagous insects were well known pests and were therefore also easily identified from commonly available sources (Room 1979b, Forrester & Wilson 1988 and Pyke & Brown 1996). There remained, however, a vast array of less common and less easily identifying them, and their likely importance to the aims of the project. Samples of arthropods in these categories were taken to the Australian National Insect Collection (ANIC, CSIRO Division of Entomology, Canberra) for further identification. Voucher specimens of unusual species have been lodged at ANIC.

3.4.2 Species Collected

The scientific and common names of the insects collected in various groupings on the data sheets used to record results are shown in Table 3.1. Also shown is the functional group (predators, parasitic or phytophagous), and the source of identification or the taxonomist who identified representative specimens of them. Although every arthropod in the samples was counted and ascribed to a category, the identifications which follow the grouped categories , such as 'Other Hymenoptera' and 'Diptera' are by no means conclusive.

Table 3.1 The Species Collected from Australian Cotton Fields. The taxonomists who assisted or identified specimens are acknowledged following the arthropods they identified. Scientific and common names follow Naumann (1993) and CSIRO (1991).

Data Sheet Grouping	Genus & Species	Family	Common Name	Functional group	Taxonomist
					or source of
					identification
Coleoptera					
Coccinella transversalis	Coccinella transversalis (Fabricius)	Coccinellidae	Transverse ladybird	Predatory	Room (1979b)
Harmonia conformis	Harmonia conformis (Boisduval)	Coccinellidae	Common spotted ladybird	Predatory	Room (1979b)
Micraspis frenata	Micraspis frenata (Erichson)	Coccinellidae	Striped ladybird	Predatory	Room (1979b)
Diomus notescens	Diomus notescens (Blackburn)	Coccinellidae	Two spoted ladybird	Predatory	Room (1979b)
Dicranolaius bellulus	Dicranolaius bellulus (Guérin Meneville)	Melyridae	Red and blue beetle	Predatory	T. Weir
Anthicus spp.	Anthicus australis (King) Anthicus ?pallidus (Macleay)	Anthicoridae		Scavenger	A. Calder
Mictolestodes macleayi	Mictolestodes macleayi (Csiki)	Carabidae		Predatory	A. Calder
Carpophilus spp. Adults	Carpophilus spp.	Nitidulidae	Cotton flower beetle	Pollen feeder	Room (1979b)
Other Coleoptera	Corticaria hirtalis (Broun)	Lathridiidae		Fungi feeder	A. Calder
	Monolepta spp.	Chrysomelidae		Phytophagous	A. Calder
	Arispoda spp.	Chrysomelidae		Phytophagous	A. Calder
	Stethorus nigripes (Kapur)	Coccinellidae		Predatory	T. Weir
	Ditropidus sp.	Chrysomelidae		Phytophagous	T. Weir
	Chaetocnema sp.	Chrysomelidae		Phytophagous	T. Weir
	Unidentified-Several species	Chrysomelidae		Phytophagous	T. Weir
	Unidentified-One species	Corylophidae:		Fungus feeder	A. Calder
	Unidentified- Several species	Curculionidae		Phytophagous	CSIRO (1991)
Collected in Pitfall traps	Sepedophilus sp.	Staphylinidae,		Possibly predatory	T. Weir
Collected in Pitfall traps	Mesomorphus sp.	Tenebrionidae		Scavenger	T. Weir
Collected in Pitfall traps	Agrypnus spp.	Elateridae		Phytophagous	T. Weir
Collected in Pitfall traps	Paederus cruenticollis Germar	Staphylinidae	Whiplash rove beetle	Possibly predatory	T. Weir
Collected in Pitfall traps	Scymnodes spp. 2 species	Coccinellidae		Predatory	T. Weir
Hemiptera					
Geocoris sp.	Geocoris sp.	Lygaiedae	Big-eyed bug	Predatory	T. Weir
Germalus sp.	Germalus sp.	Lygaiedae	Green big-eyed bug	Predatory	T. Weir
Nabis kinbergii Reuter	Nabis kinbergii (Reuter)	Nabidae	Pacific damsel bug.	Predatory	M. Malipatil

Table 3.1 con't.					
Data Sheet Grouping	Genus & Species	Family	Common Name	Functional group	Taxonomist
				_	or source of
					identification
Oechalia schellenbergii	Oechalia schellenbergii (Guérin-	Pentatomidae	Predatory shield bug	Predatory	Room (1979b)
	Meneville)				
Orius spp.	Mostly Orius tantillus Motschulsky	Anthicoridae	Minute pirate bugs	Predatory	T. Weir
Nysius vinitor Bergroth	Nysius vinitor (Bergroth)	Lygaeidae	Rurtherglen bug	Phytophagous	T. Weir
Nysius clevelandensis Evans	Nysius clevelandensis (Evans)	Lygaeidae	Grey cluster bug	Phytophagous	T. Weir
Oxvcarenus luctuosus	Oxvcarenus luctuosus (Montrouzier	Lvgaeidae	Cotton seed bug	Phytophagous	Room (1979b)
	and Signoret)				
Nezara viridula	Nezara viridula (Linnaeus)	Pentatomidae	Green vegetable bug	Phytophagous	Room (1979b)
Other Pentatomidae	Unidentified-Several species	Pentatomidae	shield bugs	Phytophagous and	CSIRO (1991)
				? Predatory	
Taylorilygus pallidus	Taylorilygus pallidus (Blanchard)	Miridae	Broken backed bug	Phytophagous and	Room (1979b)
				Predatory	
Campylomma spp.	Campylomma leibknechti (Girault)	Miridae	Apple dimpling bug	Phytophagous and	M. Malipatil
				Predatory	
1	Campylomma seminigricaput	Miridae		Phytophagous and	M. Malipatil
	(Girault)			Predatory	
Creontiades dilutus	Creontiades dilutus (Stal)	Miridae	Green mirid	Phytophagous and	M. Malipatil
				Predatory	
Austroasca viridigrisea	Austroasca viridigrisea (Paoli)	Cicadellidae	Green vegetable jassid.	Phytophagous	M. Fletcher
Brown Cicadellids ¹	Orosius argentatus (Evans)	Cicadellidae	Common brown jassid.	Phytophagous	M. Fletcher
	Limotettix incertus (Evans)	Cicadellidae		Phytophagous	M. Fletcher
	Phaconeura froggatti Kirkaldy	Meenoplidae		Phytophagous	M. Fletcher
	Balclutha rubrostriata (Melichar)	Cicadellidae		Phytophagous	M. Fletcher
	Zygina ? melanogaster (Kirkaldy)	Cicadellidae:		Phytophagous	M. Fletcher
	Ausroagallia torrida (Evans)	Cicadellidae	Spotted leafhopper	Phytophagous	M. Fletcher
Juvenile Cicadellidae ²	All juvenile cicadellids-Several spp.			Phytophagous	CSIRO (1991)

¹ This category was overwhelmingly Orosius argentatus

² Overwhelmingly a combination of the juveniles of both *Austroasca viridigrisea* and *Orosius argentatus* Early instars of these species are not readily distinguishable in rapid sorting.

Table 3.1 con't.					
Data Sheet Grouping	Genus & Species	Family	Common Name	Functional group	Taxonomist
	-				or source of
					identification
Large Leaf hoppers:	Oliarus lubra (Kirkaldy)	Cixiidae		Phytophagous	M. Fletcher
	Batracomorphus angustatus (Osborn)	Cicadellidae	Large green jassid	Phytophagous	M. Fletcher
	?Batracomorphus angustus (Osborn)	Cicadellidae	Large green jassid	Phytophagous	M. Fletcher
	(Nymphs)				
Aphis gossypii	Aphis gossypii (Glover)		Cotton aphid	Phytophagous	M. Carver
Aleyrodidae:	Unidentified -? No. of species	Aleyrodidae	Whiteflies	Phytophagous	CSIRO (1991)
Psyllidae	Unidentified-? No. of species	Psyllidae		Phytophagous	CSIRO (1991)
Alydidae	Unidentified- 2 species	Alydidae		Phyophagous	CSIRO (1991)
Scutelleridae	Unidentified-Several species	Scutelleridae	jewel bugs	Phyophagous	CSIRO (1991)
Tingidae	Unidentified-2 species	Tingidae	lace bugs	Phytophagous	CSIRO (1991)
Striped femur bug	Coridromius sp.	Miridae		Phytophagous	M. Malipatil
	Plinthisus sp.	Lygaeidae		Phytophagous	T. Weir
Psocoptera					
	Unidentified One species	Various	booklice	Phytophagous	CSIRO (1991)
Neuroptera					
	Mallada signata (Scheider)	Chrysopidae		Predatory as Larvae	T. New
	Micromus tasmaniae (Walker)	Hemerobiidae	Brown lacewing	Predatory as larvae	T. New
Lepidoptera					
Helicoverpa spp.(larvae)	H. armigera (Hübner)	Noctuidae	Cotton bollworm	Phytophagous	Room (1979b)
	H. punctigera (Wallengren)	Noctuidae	Native budworm	Phytophagous	T. Edwards
Earias huegeli (larvae)	Earias huegeli Rogenhofer	Noctuidae	Rough bollworm	Phytophagous	T. Edwards
Chrysodeixis spp. (larvae)	Chrysodeixis spp.	Noctuidae	Tobacco loopers	Phytophagous	Room (1979b)
Bucculatrix sp.	Bucculatrix gossypii Turner	Lyonetiidae	Cotton leaf perforator	Phytophagous	T. Edwards
Bucculatrix sp. (larvae)	Bucculatrix gossypii Turner	Lyonetiidae	Cotton leaf perforator	Phytophagous	T. Edwards
Other Lepidoptera:	Category for the remaining				
	Lepidoptera. Unidentified				

Table 3.1 con't.					
Data Sheet Grouping	Genus & Species	Family	Common Name	Functional group	Taxonomist
Data Sheet Grouping				r unenonai group	or source of
					identification
Hymenoptera					Identification
Chelonus sp	Chelonus sp	Braconidae		Parasitic	L Naumann
Telenomus spr	Telenomus spn	Scelionidae ³		Parasitic	I. Naumann
Trichogrammatidae	Mostly Aphelinoidea sp	Trichogrammatidae		Parasitic	M Carver
menogrammatiaue	some Ufens sp.	i nonogi uninatidado		T drushie	
Microplitis demolitor	Microplitis demolitor Wilkinson	Braconidae		Parasitic	I. Naumann
Gonatopus sp.	Gonatopus sp.	Dryinidae		Parasitic	I. Naumann
Bethylidae	Goniozus sp. & Rhabdepyris sp.	Bethylidae		Parasitic	I. Naumann
Ichneumonidae large	Netelia producta (Brulle)	Ichneumonidae	Orange caterpillar parasite	Parasitic	I. Naumann
	Heteropelma scaposum (Morley)	Ichneumonidae	Two-toned caterpillar	Parasitic	I. Naumann
			parasite		
	Lissopimpla excelsa (Costa)	Ichneumonidae	Orchid dupe	Parasitic	I. Naumann
	Pterocormus promissorius (Erichson)	Ichneumonidae	Three banded caterpillar	Parasitic	I. Naumann
			parasite		
Formicidae:	Unidentified - many spp	Formicidae	Ants	Predatory	CSIRO (1991)
Other Hymenoptera	Anacharis zealandica Ashmead	Figitidae		Parasitic	I. Naumann
	Callitula sp.	Pteromalidae		Parasitic	I. Naumann
	Apostocetus sp.	Eulophidae		Parasitic	I. Naumann
	Dierinous sp.	Chalcididae		Parasitic	I. Naumann
	Perilopinpus sp.	Perilampidae		Parasitic	I. Naumann
	Isoplatoides sp.	Pteriomalidae		Parasitic	I. Naumann
	Dinoarmus sp.	Pteriomalidae		Parasitic	I. Naumann
	Podagunion sp.	Torymidae		Parasitic	I. Naumann
	Podagrionella sp.	Torymidae		Parasitic	I. Naumann
	Anastatus sp.	Eupelmidae		Parasitic	I. Naumann
	Spilomicous sp.	Diapriidae		Parasitic	I. Naumann
	Euderus sp.	Eulophidae		Parasitic	I. Naumann
	Euplectrus sp.	Eulophidae		Parasitic	I. Naumann

³ A Sceionidae: *Telenomus* sp. was found to parasitise *Mallada signata* (Neuoptera) eggs.

Table 3.1 con't.					
Data Sheet Grouping	Genus & Species	Family	Common Name	Functional group	Taxonomist
					or source of
					identification
Hymenoptera con't.	Hemiptarsenus varicoris (Girault)	Eulophidae		Parasitic	I. Naumann
	Apostocetus sp.	Eulophidae		Parasitic	I. Naumann
	Agathis sp.	Braconidae		Parasitic	I. Naumann
	Microgastrinae ? no. of species	Braconidae		Parasitic	I. Naumann
	Mymar sp.	Mymaridae		Parasitic	I. Naumann
	Gonatocerus sp.	Mymaridae		Parasitic	I. Naumann
	Stephanodes	Mymaridae		Parasitic	I. Naumann
	Unidentified Agaonids	Agaonidae		Fig parasitoid	I. Naumann
	/ No. of species	Caalianidaa		Democitie	I. Noumonn
	species	Scenomdae		Farastic	I. Naumann
	Unidentified Encyrtids	Encyrtidae		Parasitic	I. Naumann
	? No. of species				
	Unidentified Ichneumonids - several species	Ichneumonidae		Parasitic	I. Naumann
Diptera ⁴					
	Unidentified - 2 species	Culicidae	Mosquitoes	Predatory (vertebrates)	D. Colless
	Unidentified - 1 species	Dolichopodidae	Long-legged flies	Predatory	D. Colless
	Unidentified - 1 species	Lauxaniidae		Scavengers	D. Colless
	Unidentified - 1 species	Agromyzidae		Phytophagous	D. Colless
	Tephritinae - 3 species	Tephritidae	Fruit flies	Phytophagous	D. Colless
	Ephydridae - 2 species	Ephydridae		Algal feeders	D. Colless
	Chloropidae - 2 species	Chloropidae	Grass flies	Scavengers	D. Colless
	Drosophila (Scaptomyza) sp.	Drosophilidae	Ferment flies	Phytophagous	D. Colless
	Isodrapetis sp.	Empididae:	Dance flies	Predatory	D. Colless
	Unidentified - 1 species	Pipunculidae		Parasitic	D. Colless
	Unidentified - 1 species	Ceratopogonidae	Sand flies	Predatory (vertebrates)	D. Colless
	Unidentified - 1 species	Scatopsidae		Scavengers	D. Colless
	Rivellia sp.	Platystomatidae	Boatman flies	Scavengers	D. Colless
Syrphidae	Unidentified ? No. of species	Syrphidae	Hover flies	Predatory	D. Colless

⁴ All diptera except Syrphidae were included in this category. Culicidae were separated on occassions particularly in the diurnal experiments (Chapter 4.4).

Table 3.1 con't.					Taxonomist or
Data Sheet Grouping	Genus & Species	Family	Common Name	Functional group	source of
					identification
Thysanoptera ⁵	Franklinella schultzei Trybom	Thripidae		Phytophagous ⁶	L. Bauer
	Thrips imaginis (Bagnall)	Thripidae		Phytophagous ⁶	L. Bauer
	Thrips tabaci Lindeman	Thripidae		Phytophagous ⁶	L. Bauer
	Thrips australis (Bagnall)	Thripidae		Phytophagous	L. Bauer
	Haplothrips varius	Tubulifera		Phytophagous	L. Bauer
	Haplothrips robustus	Tubulifera		Phytophagous	L. Bauer
	Haplothrips frogatti	Tubulifera		Phytophagous	L. Bauer
	Desmothrips propinquus?	Aeolothripidae		Phytophagous	L. Bauer
	Desmothrips tenuicornis?	Aeolothripidae		Phytophagous	L. Bauer
Acrididae					
Acrididae	Unidentified several species	Acrididae	Grasshoppers & locusts	Phytophagous	CSIRO (1991)
Juvenile Acrididae	Unidentifed juvenile acridids	Acrididae	Grasshoppers & locusts		
Grillidae	Unidentified few species	Gryllidae	Crickets	Phytophagous	CSIRO (1991)
Collembolla	Unidentified several species	Various	Springtails	Phytophagous	CSIRO (1991)
Arachnida ⁷					
Salticidae	Unidentified - 1 species	Salticidae	Jumping spiders	Predatory	M. Gray
Oxyopes spp	Oxyopes - 3 species	Oxyopidae	Lynx spiders	Predatory	M. Gray
Chiracanthium sp.	Chriracanthium sp.	Clubionidae	Yellow night stalking spider	Predatory	M. Gray
Theridiidae.	Unidentified ? No. of species	Theriodiidae	Combfooted spiders	Predatory	M. Gray
Diaea spp.	Diaeae spp. ? No. of species	Thomisiidae	Flower spiders	Predatory	M. Gray
Araneus spp.	Araneus spp. ? No. of species	Aranaeidae	Orbweaver spiders	Predatory	M. Gray
Other spiders	Unidentified several species	Various		Predatory	M. Gray
Acarina					
Tetranychidae	Unidentified ? No. of species	Tetranychidae	Mites	Phytophagous	Room (1979b)

⁵ All Thysanoptera, adult and juveniles were pooled in this category.
⁶ Also facultative predators of mites.
⁷ Spiders were arbitrarily divided into large and small categories depending on their head capsule width, < 1mm or > 1mm