PREDATOR INTERACTIONS WITHIN A TROPHIC LEVEL: *PHALANGIUM OPILIO* L. (ARACHNIDA: OPILIONES) AND MITES (ARACHNIDA: ACARI)

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This study investigated commensal feeding interactions between the European harvestman (*P. opilio* L.) and the predatory mites *Balaustium* spp. and *Anystis baccarum* L. It also investigated the feeding behaviour of *P. opilio*. Experiments were conducted in the laboratory using standardised temperature, humidity, photoperiod and experimental arenas, with eggs of the brown blowfly (*Calliphora stygia* F.) as prey facsimiles. Due to initial difficulties in obtaining enough predatory mites, mite feeding was manually simulated piercing blowfly eggs with a minuten pin.

P. opilio consumed significantly more freeze-killed than live blowfly eggs, indicating that freezing induced chemical and/or physical changes to blowfly eggs that are detected by *P. opilio*. Significantly more manually pierced eggs were consumed by *P. opilio* compared with unpierced ones, demonstrating that piercing caused a chemical and/or physical to the egg and increased the feeding rates of *P. opilio*.

Different densities of eggs had no effect on the numbers eaten by *P. opilio* and placing single pierced eggs next to groups of unpierced eggs also had no effect on the numbers of unpierced eggs eaten. These results suggest that *P. opilio* does not exhibit klinokinesis or orthokinesis to intensify its search for prey around the area where previous prey were located.

P. opilio ate significantly more brown blowfly eggs that had previously been fed on by mites, demonstrating that a short term commensal interaction existed. However, further work is required to demonstrate if the relationship is commensal in the longer term. A comparison between hand-pierced and mite-pierced eggs showed that *P. opilio* ate

significantly more of the former indicating that mite and hand piercing were quantitatively different.

The potential for, and importance of, other commensal or mutual relationships between predators in agroecosystems is discussed. The lack of klinokinesis and orthokinesis in *P. opilio* is compared with other predators and parasitoids that do exhibit these behaviours. The means by which prey are detected by *P. opilio* are discussed in relation to interpreting behaviours such as prey inspection. Concerns about the effect of pre-treatment and handling of sentinel prey and the problems of using prey facsimiles are raised.

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Chapter 1: Introduction

This thesis examines feeding interactions between two soil-surface dwelling arthropod predators of agroecosystems; harvestmen (Arachnida: Opiliones) and mites (Arachnida: Acari). It also investigates harvestmen feeding behaviour in relation to prey condition, density and spatial arrangements. It then considers the value of this information for biological control in agroecosystems.

This introduction briefly reviews wider trends in agriculture and their relationship with biological control. It then reviews in more detail the literature on predatory arthropods in agroecosystems. A discussion of ecological theory concerning interspecific interactions between predators and parasitoids is also provided. The introduction finishes with a statement on the stimulus for beginning this study and its specific aims.

1.1 Global trends in agricultural production and pest management

Among the key characteristics of agricultural production in the last decade of the 20th century were rapidly increasing concerns about the effects of the intensification of agriculture and the use of agrochemicals on the environment and human welfare (Dahlberg 1996; Barbosa 1998; Ehler 1998; Anon. 1999). Some sectors of the public and scientific establishment, for example, the 'organic' movement and wildlife conservation groups, have called for a change in the direction of agriculture from the production maximisation focus that has existed since the second world war, to a focus on long term ecological, social and economic sustainability of both agricultural and wider biological systems (Fry 1991; Nychas 1995). This has begun a shift towards production and pest control systems that are more reliant on ecological understanding, the introduction of biological control agents and the manipulation of agroecosystems, than intervention with chemical-based biocides (Barbosa 1998). These changes have been driven by a number of factors, including consumer pressure and increasing scientific understanding of ecological systems and the impact of the intensification of agriculture (Bridgewater, Walton *et al.* 1996; Richards 1997).

1.2 Biological control in agroecosystems

Biological control of pests, both animals and plants, by natural enemies can be divided into three types; 'classical', 'augmentation', and 'conservation' (DeBach 1964; Dent

1991; Dent 1995; Barbosa 1998; Ehler 1998; Gurr & Wratten 2000). Most early attempts, and successes, in biological control were of the 'classical' type where a natural enemy is introduced to control a pest (normally exotic). An example, is the control of *Opuntia* spp., a serious cactus weeds of Australian grazing land, by *Cactoblastis cactorum* (Berg) (Johnston & Lloyd 1982). 'Augmentation biological control' is a more recent development. It works by regularly releasing often large numbers of the biological control agent in the area where it is needed. Augmentation has been highly successful in protected cropping situations. For example, the regular release, during the growing season, of the predatory mite *Phytoseiulus persimilis* (Athias-Henriot) to control the pest mite *Tetranychus urticae* (Koch) is a well established and highly effective practice for food crops such as cucumbers (*Cucumis sativus* L.) (Jarosik 1990; El Laithy 1996). 'Conservation biological control' is a relatively recent development within the biological control scientific framework. However, it has been practised by farmers for centuries. For example, as early as 900 AD, Chinese growers placed nests of the predaceous ant *Oecophylla smaragdina* F. in mandarin trees to reduce the populations of foliage-feeding insects (Sweetman 1958; Doutt 1964; Simmonds, Franz *et al.* 1976). Conservation biological control focuses on manipulating aspects of the ecosystem to conserve and enhance populations of natural enemies so that pest problems are reduced (Barbosa 1998; Gurr & Wratten 2000). For example, the different plant communities in field boundaries (e.g., hedges, grassy swards) can support widely varying populations and species of beneficial organisms. Some types of margins support populations of 'beneficials' that can achieve economic levels of pest control in the adjacent crop, while other margins do not (Wratten 1988). Some flowering plants, e.g., *Phacelia tanacetifolia* (Benth.) and buckwheat (*Fagopyrum esculentum* Moench) can attract and provide food for the adult stages of predators and parasitoids, such as hoverflies (Syrphidae) and the leafroller parasitoid *Dolichogenidea tasmanica* Cameron (Braconidae) (Wratten & Van Emden 1995; Stephens, France *et al.* 1998; Irvin, Wratten *et al.* 1999). Therefore, by creating and maintaining the types of field boundaries that support populations of beneficial species and or sowing plants that produce sufficient nectar and pollen to enhance populations and efficacy of 'beneficials', pests can be maintained below economic thresholds. For example, Wratten and Van Emden (1995) calculated that the establishment of 'beetle banks' and associated crop loss for a 20 ha winter wheat field would cost about UK £150, while savings from reduced pesticide use could amount to £300 and prevention of a 5% yield loss due to aphids a further £660.

Savings would be greater in following years as £85 of the first year cost was the establishment of the 'beetle bank'.

Conservation biological control therefore, has a number of advantages for farmers. Once a technique is devised, the 'technology' is easy to make available to farmers. Implementation is often inexpensive, requiring minor modifications to agricultural practices and / or the introduction of particular flowering plants, which often then become self-sustaining (Ehler 1998). Farmers have more control over, and can reverse most, if not all, the effects of the changes, if problems arise. In comparison, reversal is not an option with 'classical biological control'. Also conservation biological control does not require the regular purchase and introduction of 'beneficials' from commercial suppliers, often at considerable cost, as is required for 'augmentative' biological control (Ehler 1998).

1.3 Conservation biological control research in agroecosystems

There is an increasing literature on conservation biological control in agriculture (Barbosa 1998). These include studies looking at techniques that can be implemented by farmers, for example, the formation of 'beetle banks' as refuges for beneficial invertebrates (Wratten & Van Emden 1995) and more fundamental work investigating individual aspects of single species, for example, laboratory-based predator feeding rates (Dennis & Wratten 1990). Such work has ranked potentially useful predators that can help control pests (Wratten, Bryan *et al.* 1984). These include mites (Acari), spiders (Araneae), harvestmen (Opiliones), beetles (Coleoptera), flies (Diptera) wasps and ants (Hymenoptera) and lacewings (Neuroptera) (Holland 1999).

For example, Sunderland and Vickerman (1980) dissected the gut of c. 12,000 polyphagous predators taken from ten spring barley fields in the UK. Sixteen species of ground beetles (Carabidae), three species of rove beetles (Staphylinidae) and one species of earwig (Dermaptera) were found to have consumed aphids. By multiplying the proportion of individuals that contained aphids by the predators' mean density, a predation index could be established. However, this study could not assess the impact of fluid feeders such as spiders. Serological techniques, which are more complex and costly, are required to identify whether such species, have consumed particular prey species, as shown for example, by the work of Ashby (1974).

Studies of field boundaries have shown them to be important reservoirs of predatory arthropod species (Wratten 1987; Sunderland 1988). Further work established that long matted grasses commonly found at the base of hedges themselves rather than the hedges were responsible for the increased numbers of ground-dwelling epigeal beetles and other beneficial arthropods (Sotherton 1985; Greaves & Marshall 1987). This led to the deliberate creation of such habitats using grasses such as cocksfoot (*Dactylis glomerata* L.), to increase the populations of some beneficial arthropods (Thomas, Wratten *et al.* 1991).

Other studies have researched the effects of providing floral resources such as *Phacelia tanacetifolia* Benth., mustard (*Sinapsis alba* L.), coriander (*Coriandrum sativum* L.) and buckwheat (von Klinger 1987; Bowie, Wratten *et al.* 1995; Stephens, France *et al.* 1998; Platt, Caldwell *et al.* 1999). These provided shelter for ground beetles (Carabidae) and rove beetles (Staphylinidae) (Barbosa & Benrey 1998). More importantly they provided pollen and nectar for the adult stages of predators and parasites such as hoverflies (Syrphidae) and hymenopteran parasitoids (Hagley & Barber 1992; Hickman & Wratten 1996; Barbosa & Benrey 1998).

However, for such conservation biological control techniques to be more easily expanded, a sound theoretical and empirical understanding of beneficial and pest behaviour and populations is important. To be useful, theory should be able to identify species of predators and parasitoids that have potential to control pests, and predict how they will perform in a given ecosystem (Barlow & Wratten 1996). Also, using the principles of conservation biological control in classical biological control could increase the success rates of the latter type of biological control (Gurr & Wratten 1999).

1.4 Predation and parasitism theory

The global trends described in Section 1.1 have put increasing demands on science to supply biological rather than chemical solutions to pest and disease problems (Anon. 1999). However, understanding and manipulating biological and ecological processes is much more difficult than identifying chemicals with potential for pest or disease control. As Slobodkin (1988) pointed out, “Ecology has deep rooted characteristics that make its problems more difficult to solve than, for example, those of physics”. Theoretical, rather than descriptive, advances in ecology are often hard won. Even when such general principles (e.g., the Lotka-Volterra equations or Game Theory (Poundstone 1992)) are discovered that underlie ecological behaviour, it is difficult to

find examples where the predictions of the theory are not disguised by stochastic or other external interactions to the point of severely limiting the predictive power of the theory (Mackauer, Ehler *et al.* 1990). Even when general principles are adapted to a particular ecological system, or a direct simulation of the system is made, it by no means guaranteed that model and system will behave in the same way. Despite these difficulties, it is important to identify and model the underlying dynamics of ecological systems to facilitate better predictions, thereby improving efforts to use biological control agents or ecological manipulation to achieve pest control with reduced use of biocides (Barlow & Wratten 1996). Theoretical advances are also important in forming broad concepts or paradigms that guide research (Wolpert 1992). An example is, the concept of a metapopulation, introduced in 1969 by R.A. Levins (Hanski & Gilpin 1997).

The dynamics of predators, parasitoids and their prey is one of the more extensively studied areas of ecological dynamics. This is particularly true for insects, due to their significant impact on global food production and human health and because their short life cycles and small size make them highly amenable to laboratory study (Taylor 1984).

These studies have addressed both ends of a scale from general theory to simulations that incorporate considerable detail of the interactions of a single predator or parasitoid, their prey and their environment. A few include multiple predators or parasitoids and prey species, often with prey switching, e.g., (Sullivan, Krebs *et al.* 1994). General theory has attempted to distil the key common components of predator and prey systems, while simulations are frequently designed to enable accurate predictions of future populations, particularly when an artificial change is made to the system, for example, culling.

Despite the large amount of knowledge and data amassed and the considerable efforts to develop a theoretical basis for biological control theory is still little used by biological control practitioners (Beddington, Free *et al.* 1978; May & Hassell 1988; Waage 1990; Wratten & Gurr 2000). Suggested reasons for this include the following:

1. disparity in the questions being asked by modellers and practitioners (Kareiva 1990);
2. the strategic focus of many models is of limited use when deciding on tactics (Barlow & Goldson 1993);

3. the mismatch between biological control, which needs only to maintain pests below economic thresholds, and theory which focuses on near complete host suppression (Barlow 1993);
4. often several beneficials are introduced to control a single pest, so one species does not have to achieve control by itself (Goldson, Phillips *et al.* 1994);
5. the stability of beneficial populations is not critical for success. They can fluctuate to the extent that extinctions occur in local populations but still produce effective biological control. This is due to metapopulations that act as sources of beneficials that re-populate areas where the local population have become extinct (Barlow & Wratten 1996; Helenius 1997; Letourneau 1998).

If theory is of limited use when dealing with single pest and prey organisms (a common situation in classical biological control (Gurr & Wratten 2000)) then it is likely to be of even less help when addressing the more complicated dynamics of conservation biological control. This has led to the situation where competing suggestions on how to advance conservation biological control are made. For example, Barbosa and Benrey (1998) noted that the traditional approach in biological control, that of studying single factors, then studying combinations of factors, assuming an additive effect, may not be justified, while Ferro and McNeil (1998) suggested the creation of a database of the biology of natural enemies which can be used to predict which natural enemies have potential to control pests. In contrast, Herzog and Funderburk (1986) identified a need for a systems level approach, due to the impossibility of studying all possible combinations of pest, natural enemy, crop and cultural practice.

Therefore, while there is a critical need for conservation biological control solutions as discussed in Section 1.3, theory is still of limited help in achieving them. This particularly related to under-studied groups, such as the Arachidea.

1.5 The roles of mites and harvestmen as predators in agroecosystems

Both mites and harvestmen belong to large taxa, with world-wide distribution. There are about 40,000 named species of Acari and an estimated total of 500,000 to one million species (Barns 1989; Groombridge 1992). Opiliones are estimated to number 3500-5000 species (Hillyard & Sankey 1989). Of the two, mites have received more attention, as some mite genera are plant or animal pests or parasites (Walter & Proctor

1999). Harvestmen, in contrast, are polyphagous predators and scavengers (Hillyard & Sankey 1989) and their direct impact on humans, crops and livestock is limited.

Mites are also important predators of agricultural pests, including other mites (Walter & Proctor 1999). Early successes in 'augmentative' biological control, as identified in Section 1.2, involved mites. Their role in agroecosystems, compared with larger predatory arthropods such as beetles, is less well understood. However, there are numerous examples where natural populations of predatory mites have been shown to play a significant role in limiting pest numbers, for example, Sorensen, Kinn *et al.* 1976; Balazs, Molnar *et al.* 1997; Croft, Pratt *et al.* 1998; van Lenteren & Loomans 1998; Raut & Bhattacharya 1999. Studies that focus on harvestmens' role in reducing the numbers of agricultural pests are very limited. Most studies focus on a single pest species and the range of predators, including harvestmen, that prey on it, or they research a particular crop and its arthropod fauna which may include harvestmen, for example, Ashby 1974; Wratten & Pearson 1982; Leathwick & Winterbourn 1984; Butcher 1986; Chiverton 1987; Dixon & McKinlay 1989; Drummond, Suhaya *et al.* 1990; Dennis, Bentley *et al.* 1996; Sivasubramaniam, Wratten *et al.* 1997. While such studies are not specifically looking at harvestmen their results do indicate that harvestmen may be achieving levels of pest control of significance to agricultural production.

1.6 Mite and harvestmen: trophic interactions in New Zealand

A small number of empirical studies of beneficial arthropods in New Zealand agricultural ecosystems have been undertaken to establish densities, species and habitat preferences, for example, Wratten & Pearson 1982; Berry, Wratten *et al.* 1995; Berry, Wratten *et al.* 1996; Berry 1997; Chapman, Simeonidis *et al.* 1997; Sivasubramaniam, Wratten *et al.* 1997. These have frequently shown marked differences in the populations and species of arthropods between the margins and centres of fields and between different boundary vegetation types. Berry (1997) also attempted to quantify predation rates of carrot rust fly (*Psila* rosae F.) eggs by soil-surface predators using Indian meal moth (*Plodia interpunctella* Hubner) eggs and to correlate this with predator activity and distribution. Berry also studied the predation of both Indian meal moth and brown blowfly (*Calliphora stygia* F.) eggs in different field boundary types using time-lapse video.

From the video-recording work, Berry (unpublished data) suspected that the predation of brown blowfly eggs by mites increased the predation of the same eggs by the European harvestman (*Phalangium opilio* L.). Unfortunately, this could not be quantified from the original observations as the resolution of the video image was too poor to allow accurate measurement of mite feeding. Furthermore, eggs were clumped, making differentiation of individual eggs difficult. Currently no work in any agroecosystems exists that demonstrates that the feeding activity of one predator species can increase the predation activity of a second. Examples do exist of such commensal interactions in aquatic habitats, i.e., where the activities of species 1 has a beneficial effect on species 2 without any detrimental effect on species 1 (Hodge & Wallace 1996). For example, increased numbers of larvae of two species of helodid beetle *Prionocyphon discoideus* Say and *Helodes pulchella* Guérin-Meneville, in water-filled tree holes in central Pennsylvania, USA, increased the numbers of the ceratopogonid midge *Culicoides guttipennis* Coquillett, due to the beetle's shredding / chewing feeding behaviour, with consequent increases food availability for the deposit-feeding midge (Paradise & Dunson 1997). Similarly in the pitchers of the insectivorous plant *Sarracenia purpurea* L., the growth of mosquito larvae *Wyeomyia smithii* Coquillett was enhanced by increased numbers of larvae of the midge *Metriocnemus knabi* Coquillett, because the midges feed by chewing on solid material while the mosquito filter-feeds on particles. In contrast, larger numbers of the mosquito had no effect on the numbers of midge larvae (Heard 1994).

If commensalism between different predator species, or a suite of predators, exists in agroecosystems it could increase the extent of biological control by predators above that achieved by the same predators acting without such an interaction. Commensalism and mutualism also have implications for theoretical models, and extrapolations of laboratory based feeding studies to field situations. If such interactions were common, there will be a need to take account of them in both general and detailed ecological models and theory, and when extrapolating laboratory-derived predator feeding rates to natural situations.

While there are no examples of commensalism or mutualism between two different species of predators in agroecosystems, there are many examples of commensalism and mutualism, both between predators and other species and interspecific relationships that do not involve predators at all. A classic example involving a predator and a herbivore is the ant-aphid relationship, which can be commensal or mutual; see for example, Roy

1994; Bauer & Nieto 1998; Hopkins & Thacker 1999; Muller, Adriaanse *et al.* 1999; Volkl, Woodring *et al.* 1999. The practice of intercropping, where two crops grown together yield more than if the same area had been cropped but the crops grown separately (Theunissen 1995), is another example of mutualism; see also, Vandermeer, Schultz *et al.* 1990; Anderson & Sinclair 1993; Bulson, Snaydon *et al.* 1997.

1.7 Arthropod predation behaviour and video recording techniques

The means by which arthropod predators and parasitoids locate their prey, and also avoid attacking the same prey twice, e.g., superparasitism (Field & Keller 1999), is an increasingly rich field of study. For example, volatiles released by both plant pests and the damaged plants are attractants for predators of the pest (Nealis 1986; Schutte, Baarlen *et al.* 1998; Shimoda & Dicke 1999). Many predators will intensify their pattern of searching to the immediate area where prey was last located (Murdie & Hassell 1973; Sabelis 1981; Mols 1986; Casas 1988; McEwen, Clow *et al.* 1993; El Kareim 1998; Rao, Vinson *et al.* 1999). For example, Vinson *et al.* (1978) noticed an increase in the turning rate of females of the parasitoid *Microterys flavus* Howard when it came into contact with honeydew secreted by the brown soft scale *Coccus hesperidum* L. Such studies require very detailed data, much of which has to be obtained by continual observation. The use of video recorders allows such continual observation, without which the costs and demands on research staff would be excessive. Video techniques can also overcome some of the problems of traditional data collection, such as pitfall traps or vacuum sampling. For example, Halsall & Wratten (1988) used video to assess the efficiency of pitfall trapping on seven carabid species, by measuring the proportion of encounters with the edge of a pitfall trap which resulted in capture for each species. This demonstrated that the proportion of carabids caught varied between species. Video also allows for the collection of data such as detailed analysis of the timing of predator activity, the recording of a wider range of behaviours and the identification of unknown behaviours (Varley, Copland *et al.* 1994; Wratten 1994).

There are also potential problems associated with video recording of arthropods. Many of these involve artificial lighting which may, for example, cause an increase in the temperature of the arthropod and its environment resulting in altered behaviour. Light intensity and direction can also influence arthropod behaviour. Ideally artificial lighting should simulate natural conditions to the point where the behaviours being recorded are

unaffected (Varley, Copland *et al.* 1994). Laboratory-based experiments on arthropods often require the use of limited sized arenas which can influence arthropod behaviour. The design and shape of such arenas are also critical. For example, predatory mites tended to walk around the perimeter of circular arenas, because of their tendency to follow leaf edges (Berry & Holtzer 1990).

Therefore, laboratory-based video recording of polyphagous predators must ensure that laboratory conditions simulate natural conditions as far as possible to ensure that the behaviours being measured are as close as possible to those in the natural state.

1.8 Study aims

This study aims to establish if predatory mites feeding on blowfly eggs increase the likelihood of the same eggs being eaten by the European harvestman *P. opilio*. It will also investigate the dynamics of the interaction, analysing the feeding rates of *P. opilio*, the effects of spatial distribution of eggs and *P. opilio* searching behaviour.

The specific aims of each experiment are identified in their respective Sections in Chapter 2: Rationale for Experimental Design and Materials & Methods.

Chapter 2: Rationale for Experimental Design and Materials & Methods

2.0 Acclimatisation of *P. opilio* for experiments

A group of between 20-60 *P. opilio* was kept in a vivarium in a controlled environment room that also housed the experimental arenas. This acclimated *P. opilio* to the temperature, relative humidity and photoperiods of the experiments and standardised the pre-experimental conditions they experienced.

The vivarium comprised a transparent Perspex tank 510 mm wide and deep, and 560 mm high. A single opening 300 mm square in the centre of one side provided access. The opening was covered with a fine-mesh white nylon cloth to allow air exchange and was secured to the tank with 'Velcro'. The floor was covered with a 50 mm deep substrate consisting of a mixture of sand, grit and fine grade tree bark. This provided a substrate similar to that found in the natural habitat of *P. opilio* (Sankey 1949), and it absorbed water without losing its structure or becoming sticky. The substrate was kept moist to maintain a relative humidity of between 60% to 80% within the tank at 15° C (with a 5° C range), the temperature of the controlled environment room. This is considered an optimum temperature and the preferred humidity for ground dwelling harvestmen such as *P. opilio* (Todd 1950). Seven cardboard tubes, 30 mm in diameter and approximately 200 mm in length acted as resting / hiding places for *P. opilio*. These were kept off the ground by means of upturned 90 mm diameter Petri dish bases to keep the cardboard tubes dry. Between five to fifteen broad bean plants *(Vicia faba* L.*)* (cv. Evergreen), one to three weeks old, grown in peat and bark potting mix with slow release fertiliser granules in a 150 mm plant pot placed in a water filled saucer, were placed in one corner of the tank. The bean plants supported a high numbers of pea aphids (*Acyrthosiphon pisum* Harris) as prey for the predators. This was to ensure that *P. opilio* was fully satiated prior to pre-experiment starvation. The bean plants were replaced as they senesced.

The photoperiod was 16/8 light/dark. During the photophase light was provided by 6 fluorescent bulbs consisting of three 'Osram L30W/11-860 Lumilux Plus Daylight' and three 'Osram L30W/77 Fluora. These created daylight-equivalent spectra, and were situated 150 mm above the top of the vivarium. They produced 72.7 µ moles photons/m^2/second at the vivarium floor. During the scotophase a 40 watt, clear glass,

incandescent bulb situated 1.2 m above the vivarium, provided illumination producing 0.24 µ moles photons/m^2/second at the vivarium floor.

To ensure that all *P. opilio* individuals were used only once in any experiment they were collected at the Biological Husbandry Unit (BHU), Lincoln University, and were released after the experiment at a domestic dwelling approximately 8 km away. The BHU has been under organic (Anon. 1998) management for 22 years (R. A. Crowder, pers. comm.). *P. opilio* was found predominantly under thick wooden planks over irrigation valve access pits, with the exception of the only two mature males collected, which were found on fence posts surrounded by tall grass. Slightly more male than female *P. opilio* were collected. All males collected, with the exception of two, were immature and were without the characteristic exceptionally large apophysis on the distal segment of the chelicerae. Males ranged from 2-4 mm in body length with the exception of the mature males the body length of which measured 6 mm. Females ranged from 2-5 mm in body length.

2.0.1 Pre-experimental work

Preliminary trials were conducted to help refine the experimental designs used. These trials considered the range of behaviours to be recorded, arena design, handling procedures, number of eggs to be used, and the method and duration of starvation.

Harvestmen are cannibalistic (Bristowe 1949; Sankey 1949). Cannibalism was observed in the starvation containers and vivarium and occurred between *P. opilio* individuals of similar and different sizes. Therefore, individuals were isolated during starvation.

Preliminary tests were carried out in which the periods of starvation ranged from one to six days. The mean number of brown blowfly eggs eaten for each starvation period was recorded hourly (Figure 1). Although the number of trials run at each starvation period differed (two to six trials per period), the mean number of eggs eaten by *P. opilio* per trial indicated that egg consumption increased with up to three days of prior starvation. *P. opilio* mortality during starvation periods first occurred after four days and increased progressively from then. A starvation period of three days was therefore chosen as a compromise, ensuring that *P. opilio* consumed sufficient eggs while minimising mortality during this period.

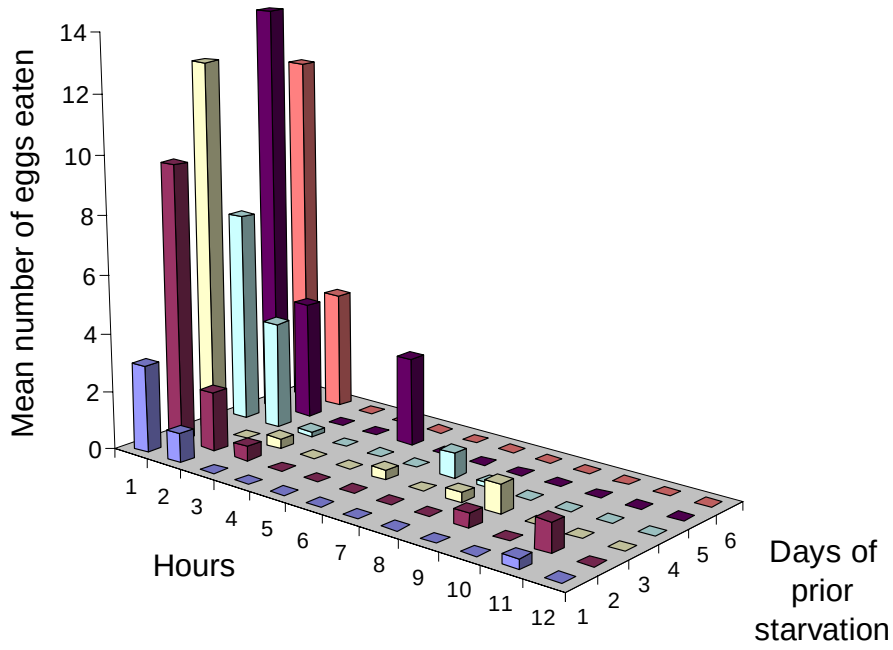

Figure 1. Mean number of blowfly eggs eaten over a 12 h period by *P. opilio* individuals that had been subjected to one to six days of starvation.

During the photophase *P. opilio* frequently hid for several hours in the corners of the experimental arenas after transfer from the starvation containers. A circular arena prevented this behaviour and also reduced the surface area of the arena, therefore, increasing the rate of encounters with the Petri dish containing blowfly eggs; (see Section 2.3 for details of arena design).

P. opilio individuals often displayed catalepsy (appearing to be dead) when being moved, especially if this involved shaking or tapping to remove them from their resting places. Individuals would become completely immobile and remain so for several minutes, then instantly become fully active again. The only sign that they were alive in this state of immobility was the reflex of the tarsi of the last pair of legs to grasp an object, such as a thin stick, that was placed under the legs and then lifted. It was considered unlikely that neither catalepsy, nor the other tendency to run around very rapidly after being moved, would affect feeding behaviour in the experiment. However, as a precaution a 40 5 50 mm long piece of medium-density polyethylene (MDPE) pipe was used to transfer *P. opilio* from starvation containers to the arena to minimise such effects.

Initially, a six by six grid comprising 36 brown blowfly eggs was tested. This was later reduced to sixteen eggs in a four by four grid. This ensured that the random distribution of the experimental treatments among the eggs did not produce a pattern that was too

ordered there was an even number of eggs to facilitate statistical analysis, and that the amount of data collected was not excessive.

Previous observations of arthropods in agroecosystems using video recording techniques, e.g., (Berry 1997, Navntoft unpublished data) recorded a range of behaviours, including prey consumption, prey inspection, prey removal, time spent by arthropods in an arena, total number of arthropods, etc. A number of these behaviours were clearly irrelevant for a highly controlled experimental situation because a known number of *P. opilio* was used in experiments and their movements were restricted by the arena design. Behaviours recorded during the first few trials included the number of blowfly eggs eaten, eggs inspected, eggs moved, inspection of the places where eggs had been removed or eaten and *P. opilio* movement across the video image . It quickly became apparent that recording of *P. opilio* movement, in contrast with studies in natural habitats, provided no data relevant to the aims of this study, given the labour requirements of the extra work.

P. opilio occasionally picked up an egg, moved it and deposited it uneaten. This occurred so infrequently that the behaviour was not recorded. A record was kept of any eggs that were moved but uneaten in case they were eaten later. A more frequent behaviour was that *P. opilio* partially ate an egg and then either returned the remains to exactly same place where the egg was found or deposited it elsewhere. Where this occurred, only the first partial eating was recorded and any further interactions with the egg were ignored. More problematic in assessing the behaviour of inspecting eggs or of places where eggs had been eaten was the very frequent behaviour of eating the contents of an egg and chewing the shell into a very small ball and depositing it either exactly where the egg was found or elsewhere (Figure 2). *P. opilio* would then often detect and eat these egg shells at a later time. It was clear from the first trials that *P. opilio* would both inspect areas where eggs had been eaten and where there had never been any eggs. As chewed eggs shells were not visible on the video image against the peat substrate (they could be seen only against a substrate of matt black card), it meant that the recording of any behaviour that was not clearly associated with a whole egg could be influenced by chewed egg shells. The data, therefore, included eggs inspected, eggs eaten and eggs uneaten. The discovery of the wide range of behaviours exhibited by *P. opilio* while feeding is a good example of the value of video techniques to both raise new questions as well as address existing ones (Wratten 1994).

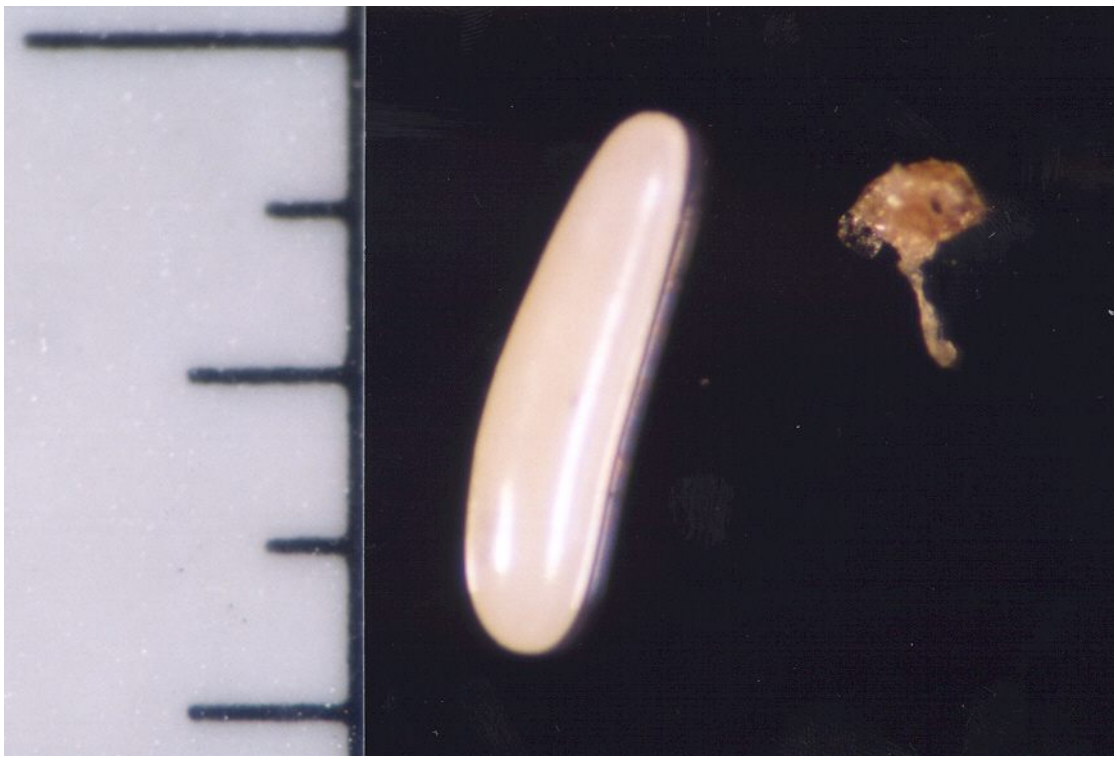

Figure 2. Live uneaten brown blowfly egg and predated egg shell after being eaten by a *P. opilio* individual. One graduation = 0.5 mm.

Initially only one *P. opilio* was used in the pre-experimental trials; however, some individuals failed to eat any blowfly eggs. The use of two *P. opilio* per arena increased the chance of predation occurring by more than half, because not only were there twice the number of *P. opilio*, but the active *P. opilio* almost always encountered the inactive one, causing it to become active. This minimised the chance of no predation.

2.0.2 General experimental design

The experimental designs used for the experiments had a large number of common elements, such as the arena used and the environmental conditions. This Section describes those elements.

Two Perspex tanks, identical to the vivarium tank described in Section 2.1, each comprised an experimental arena. The same substrate as was used in the vivarium was placed on the floor of the tanks to a depth of 50 mm. It was heated to 80° C for 18 h, prior to placement in the tanks, to kill any invertebrates or their eggs that may have been present to ensure that they did not breed and provide an alternative food source for *P. opilio*.

Circular arenas were created within the tanks by a sheet of 3 mm thick polycarbonate formed into a cylinder, 320 mm in diameter and 150 mm high. This removed corners in which *P. opilio* tended to hide, and prevented *P. opilio* escaping from the arenas. Matt

black card was glued to the outside of the Perspex cylinder to minimise external visual stimuli.

To facilitate the placement of brown blowfly eggs in the arena, they were placed on Petri dish lids or bases (either 50 mm or 90 mm in diameter) that were filled level with the rim with damp “Yates Black Magic” peat-based, seed-raising mix, that had been sieved to <500 μm. This provided a uniform background to maximise the contrast of blowfly eggs for the video camera and removed debris that may have affected the ability of *P. opilio* to detect the eggs. The peat was moistened to prevent egg desiccation.

When a single Petri dish was used, it was buried in the centre of the arena with the rim level with the substrate surface. The edge of the Petri dish was covered with a thin layer of the substrate to minimise the tendency of *P. opilio* to track the edge of the dish.

Before *P. opilio* individuals were used in experiments, they were kept in the vivarium for a minimum of four days to acclimatise. They were then starved for 72 h in individual semi-transparent, 80 mm wide by 90 mm high plastic pottles with 30-40 holes approx. 1 mm in diameter, punched in the lid to allow air exchange. Heat-treated substrate was placed in the bottom to a depth of 30 mm and moistened to create a high humidity. A 40 mm diameter by 50 mm long piece of medium density polyethylene (MDPE) pipe was placed on top of the substrate in the pottle to provide a resting / hiding place for *P. opilio*. The pottles were then placed on a shelf next to the vivarium. The MDPE pipe was also used to transfer *P. opilio* into the arena to minimise the disturbance caused by transferring individuals from pottle to arena. The two pieces of pipe were left in the arena for the duration of the experiment, on opposite sides of the arena and about 50 mm from the arena’s edge. Two *P. opilio* (one of each sex) 3-5 mm in body length were used for each replicate (Figure 3 and Figure 4). Larger females and mature males were not used in experiments.

Figure 3. Immature female *P. opilio*.

Figure 4. Immature male *P. opilio*.

The photoperiod and lighting equipment was the same as described in Section 2.1. The photoperiod was chosen to simulate a summer day, the time of year when *P. opilio* are more active and abundant. The scotophase started one and a half hours after the start of the experiment. *P. opilio* feed at all times of day and night but it is generally believed that consumption and activity increases at night (Phillipson 1960; Williams 1962; Hillyard & Sankey 1989). This was corroborated by casual observations of *P. opilio* activity in the vivarium. During the photophase most *P. opilio* were found in the cardboard tubes. During the scotophase they were often to be found among the bean plants, moving across the floor and aggregated in the corners of the vivarium. During the photophase light levels were 11.17 µ moles photons/m^2/second at the arena surface.

During the scotophase light levels were 0.28 µ moles photons/m^2/second at the arena surface produced by an incandescent bulb. These values differ slightly from the vivarium due to the arenas being located in a different part of the controlled environment room. Field work by Berry, (1997) and Navntoft (unpublished data) used infra-red light for illumination in the field. This is considered the most suitable for film and video studies of invertebrates (Varley, Copland *et al.* 1994). However, in this study, a low level of background light was required to simulate natural night time light levels such as moonlight. Such low light also provided sufficient light for the video cameras.

The activity of *P. opilio* in the Petri dishes was recorded for 12 h using Bischke CCDm50 12P and Burle TC300E high-resolution, monochrome, low-light surveillance cameras attached to Hitachi time lapse video recorders. The cameras were mounted approximately 400 mm above the Perspex tanks, i.e., 960 mm above the Petri dish.

2.1 *P. opilio* 'preference' for pierced or unpierced, freeze-killed blowfly eggs

The work of Berry (1997), that was the impetus for this study, used freeze-killed brown blowfly eggs as prey facsimiles. These were eaten by a wide range of predators, including harvestmen. It was important therefore to continue to use brown blowfly eggs to ensure that Berry's suggestions of a commensal interaction between mites and *P. opilio* were addressed. Eggs were purchased from the New Zealand Pastoral Agriculture Research Institute Limited (AgResearch) Wallaceville Insectary and preserved in a freezer at -80° C. A four by four grid of the freeze-killed eggs was placed 15 mm apart in a grid on the surface of a 90 mm Petri dish base filled with moist sieved seed mix as described in Section 2.3.

Due to difficulties in getting enough predatory mites of the species found in agricultural field margins studied by Berry, (1997) and Navntoft (unpublished data), it was decided to simulate the feeding behaviour of the mites on the blowfly eggs by manually piercing them. Eight randomly chosen eggs were therefore pierced with a minuten pin (a very small pin used by entomologists for mounting specimens), with a tip diameter of 20 µm, so that some of the contents of the egg could escape. The hole was made as small as possible to minimise the amount of the egg contents that escaped. For each replicate, a new random selection of eight eggs was pierced.

One male and one female *P. opilio* that had been starved as described in Section 2.3 were released into the arena for 12 h.

The following data were collected: for each egg eaten or inspected, its treatment (pierced, unpierced), position on the grid and the time from the start of the experiment of egg consumption or inspection.

Data were analysed using paired *t*-tests, comparing the number of pierced eggs with unpierced eggs consumed, and the number of pierced eggs with unpierced eggs inspected.

2.2 *P. opilio* 'preference' for live or freeze-killed blowfly eggs

During periods of warmer weather (a daily maximum of 20° C or more) eggs often hatched during transport from Wallaceville to Lincoln. Therefore, A colony of blowflies was established from eggs originally supplied by Wallaceville. The colony was kept in a controlled environment room at Lincoln University at 25° C with a day: night photoperiod of 16:8 hours.

While there was no discernible difference between live or freeze-killed blowfly eggs to the human eye, it was not known whether *P. opilio* could detect differences. As discussed in Section 2.4, Berry (unpublished) had used freeze-killed eggs while other researchers, expanding on her work used fresh eggs as bait (Navntoft, unpublished data). Therefore, it was considered important to verify if *P. opilio* reacted differently to freeze-killed compared with fresh blowfly eggs.

The same experimental design, equipment and data analysis were used as described in Section 2.4 except for the treatment of the eggs. In each replicate, half the blowfly eggs were freeze-killed, and had been stored at -80° C in a freezer, and the other half were live eggs that had been stored in a refrigerator at 4° C with a 2° C range.

2.3 *P. opilio* 'preference' for pierced or unpierced live blowfly eggs

The experiment described in Section 2.5 showed a clear 'preference' by *P. opilio* for freeze-killed compared with live eggs. This suggested that the experiment comparing the 'preference' of *P. opilio* for pierced rather than unpierced eggs (Section 2.4) should

be repeated using live eggs in place of freeze-killed eggs. It was also considered important to use live eggs for future experiments as these were closer to the state that eggs would be found in the field.

The same experimental design, treatments, equipment and data analysis were used as in Section 2.4 except that live eggs, which had been stored in a refrigerator at 4° C with a 2° C range, were used.

2.4 *P. opilio* 'preference' for live pierced and unpierced blowfly eggs, with egg replacement

A weakness of the experimental design used in Sections 2.4, 2.5 and 2.6 was that egg numbers were continually being depleted (Holling & Arditi 1982). No information could be obtained on the total numbers of eggs that could be consumed if eggs were replaced after consumption. It was also possible that the rapid depletion of the 'favoured' egg type was increasing the rate of consumption of the 'less favoured' egg type. To address these issues the experiment described in Section 2.6 was repeated, with the modification of replacing the peat filled Petri dish and all the blowfly eggs. These were replaced at intervals of one, two, four, six and nine hours from the start of the experiment. The same random arrangement of pierced and unpierced eggs was used for the replacement eggs in each replicate, with a new random arrangement being used for each replicate. To reduce the disturbance to the *P. opilio* in the arena and to facilitate the changing of the Petri dishes, the edges of the dishes were not covered with the substrate, as they had been in previous experiments.

The following data were collected: for each egg eaten, its treatment (pierced, unpierced), position in the grid, and the time from the start of the experiment of egg consumption.

Data were analysed using paired *t*-tests to compare the number of pierced and unpierced eggs eaten, and the change in the number eaten on an hourly basis.

2.5 Rate of egg consumption, percentages of blowfly eggs eaten and mean number eggs eaten

By recording the time from the start of the experiment for each inspection and consumption of eggs, an analysis of the rate of egg inspection and consumption over time could be made. For the first three experiments described in Sections 2.4, 2.5 and

2.6, the number of eggs eaten and inspected for both types of egg was plotted on an hourly basis; for the fourth experiment the recording of egg inspection had been discontinued (see Section 4.1.2 for explanation), so only consumption of both egg types was analysed. Also, for the first four experiments, the total number of eggs eaten from all replicates expressed as a percentage of the total eggs available was calculated, as well as the mean number of eggs eaten in each replicate.

2.6 *P. opilio* 'preference' for blowfly egg position in a four-by-four grid

A criticism of the previous experiments was that the use of a four-by-four grid of eggs forced *P. opilio* to walk over the outside twelve eggs before they were able to detect the centre four eggs. To determine whether *P. opilio* showed a 'preference' for eggs on the periphery compared with the centre of the grid a *post hoc* analysis of the data from experiments in Sections 2.4, 2.5 and 2.6 was carried out. For each replicate from each experiment, the number of unpierced eggs eaten was divided by the number of pierced eggs eaten from both the centre four eggs and the peripheral 12 eggs. The resulting set of ratios was analysed with paired *t*-tests.

2.7 Effect of the proximity of pierced to unpierced blowfly eggs, on predation of unpierced eggs by *P. opilio*

P. opilio showed a greater 'preference' for pierced eggs than for unpierced eggs. This raised the question whether the 'preference' was due to *P. opilio* being able to locate the pierced eggs more easily rather than finding them more attractive as food.

Numerous studies have demonstrated that predators (and parasitoids) intensify their search for prey around the area where previous prey was located; for example, (Murdie & Hassell 1973; Hassell, Lawton *et al.* 1977; Sabelis 1981; Mols 1986; Casas 1988; McEwen, Clow *et al.* 1993; El Kareim 1998). This behaviour was observed in *P. opilio* during previous experiments, although it was intermittent. *P. opilio* was as likely to arrive in the field of view, eat one egg and then leave, as arrive and eat several eggs in succession or walk over the eggs without detecting them. No quantitative measurements were taken of these behaviours and the use of two *P. opilio* in the

experiments precludes analysis of these data, as it was impossible to identify which individual ate which eggs.

Berry (1997) studied the effect of aggregated eggs on the rate of egg inspection and consumption by harvestmen in the field. Brown blowfly eggs were placed in eight clusters, two of ten eggs, four of five and two sets of single eggs, on a soil-filled Petri dish. Of the eggs consumed, 68% were taken from clusters of ten, 24% from clusters of five and 8% from the single eggs. Measurements ceased after 25 eggs had been removed as the cluster sizes became similar. Harvestmen and predatory mites accounted for almost all the consumption of eggs. This indicates that either harvestmen can detect aggregated prey more easily or can intensify their searching after locating prey.

If *P. opilio* find pierced and unpierced eggs equally attractive as food, but have difficulty locating unpierced eggs, then if a pierced egg is placed immediately next to unpierced ones *P. opilio* should also eat the unpierced eggs due to the localised nature of their searching behaviour. The clumping of the unpierced eggs should also enhance this effect. If *P. opilio* find the unpierced eggs less attractive than pierced eggs then there should be no difference in the consumption of unpierced eggs, whether they have a pierced egg next to them.

To explore the above, two experiments were run, the first at 5 mm egg spacing. The results indicated that there was no increase in consumption of unpierced eggs next to pierced ones. However, the eggs may still have been too dispersed so a second experiment was run with the eggs 1 mm apart, the minimum distance possible without their touching.

The standard experimental set up was used as described in Section 2.3. Four 50 mm diameter Petri dish lids were filled with moist, sieved peat. On each Petri dish nine brown blowfly eggs were placed in the centre on the surface of the peat, arranged in a three-by-three grid. In the experiment at the 5 mm spacing, two dishes were randomly chosen and in each of the dishes one egg was randomly selected and pierced with a minuten pin. In the experiment at the 1 mm spacing, two dishes were randomly chosen and in each of these, one position in the 3 by 3 grid was randomly chosen and an extra egg was then placed in that position and pierced with a minuten pin. If the additional egg was placed in the centre of the grid the other eggs were moved to ensure that a 1 mm gap existed between all the eggs. If the additional egg was placed in one of the peripheral grid positions it was placed 1 mm outside the existing eggs. An additional

egg was used in the 1 mm spacing experiment to avoid having to use ratios in the statistical analysis.

The four dishes were placed in the arena to form the corners of a square 140 mm apart. Two *P. opilio* were put into the arena for 6 h.

For each eaten and uneaten egg, their treatment and grid position were recorded. Data were analysed using paired *t*-tests.

2.8 The effect of distance between blowfly eggs on the total consumption of, and 'preference' for, pierced and unpierced eggs by *P. opilio*

The overall percentage of eggs eaten in the experiments described in Section 2.10 varied considerably between the two egg spacings. At the 5 mm spacing 6% of eggs were eaten while 21% of eggs were eaten at the 1 mm spacing. However, as the two experiments were run separately and, therefore, not randomised no valid statistical comparison could be made. Results did strongly indicate, however, that decreasing the spacing between the eggs (i.e., increasing their density or degree of aggregation) was contributing to increased consumption rates. This differed from the results of experiments which showed that unpierced eggs were no more likely to be eaten when in proximity to a pierced egg than they were when they were not next to pierced eggs, for either the 5 mm or 1 mm spacings. *P. opilio* was, therefore, consuming the pierced egg but then ignoring the neighbouring unpierced ones, indicating that proximity of eggs had no effect on the consumption of eggs by *P. opilio*.

To analyse this conflicting evidence further, an experiment was designed to measure consumption rates for eggs that were spaced widely apart or close together. It was decided to test close spacings of 15 mm and 1 mm against the widest (60 mm) spacing that could be accommodated in the arena.

The experiments also compared the 'preference' of *P. opilio* for pierced and unpierced eggs both within and between treatments to investigate the effect of spacing on 'preference' for the two types of eggs.

In both experiments and all treatments the Petri dishes were filled with moist sieved peat and a total of sixteen eggs, arranged in a four by four grid, was used for each replicate. The widely spaced eggs were 60 mm apart on the square, and placed in sixteen separate 50 mm diameter Petri dish lids. For the 15 mm spacing, the lid of a

90 mm diameter Petri dish was used and for the 1 mm spacing a 50 mm lid was used. In each replicate, half the eggs were randomly selected and pierced with a minuten pin. The allocation of replicates to arenas and the order in which the replicates were completed were fully randomised. One male and one female *P. opilio* were put in each arena for 6 h, at which point, for each eaten and uneaten egg, its treatment (pierced, unpierced), grid position, grid spacing and egg spacing were recorded.

Differences between pierced and whole eggs for the same size grid was analysed using paired *t*-tests. Differences between the rate of egg consumption for pierced, unpierced and total eggs were analysed with an independent *t*-test.

2.9 *P. opilio* 'preference' for blowfly eggs previously pierced by mites

To determine whether mite feeding on blowfly eggs increased consumption of eggs by *P. opilio*, in comparison with the manual piercing that had been used in previous experiments, considerable numbers of mites had to be collected and maintained in the laboratory. High numbers were required to ensure that eggs could be pierced by mites within an hour of the start of the experiment. This was because 'attractiveness' of mite-pierced eggs to *P. opilio* may decrease over time due to the loss and drying of any escaped egg contents.

2.10 Mite collection

Mites were initially collected from August 1999 onwards with a suction sampler similar to that of Arnold (1994), pitfall traps 8 cm wide and 9 cm high with a piece of galvanised tin placed 5 cm above the trap to exclude rain were also used, as was extraction of mites from plant debris using a Berlese funnel. A number of sites were sampled including:

The Lincoln University Dairy Farm;
The Heinz Wattie's Australasia Ltd. / Lincoln University Organic Farm ('Kowhai Farm'), Canterbury, New Zealand (This is in first year of conversion to certified organic production (Anon. 1998);
Hart's Creek Farm, Leeston, Canterbury, New Zealand, a mixed cropping farm (certified organic (Anon. 1998) for 13 years (Chamberlain, T. P., pers. comm.);
The cropping farm of R. H. Hawkins, Ladbrooks, Canterbury, New Zealand.

Numerous studies have show that field boundaries, particularly those with perennial grass species contained more predators, including mites, than did field centres or field boundaries consisting of a fence without non-crop vegetation (Wallin 1985; Coombes & Southerton 1986; Wallin 1986; Duelli, Studer *et al.* 1990; Thomas & Wratten 1990; Thomas, Wratten *et al.* 1991; Thomas 1991; Kromp & Steinberger 1992; Kajak & Lukasiewicz 1994; Berry 1997) Navntoft (unpublished data). Therefore, at the farms described above, collection was restricted to field boundaries with hedges or other non-crop vegetation. Suction sampling was done as close to the boundary as vegetation would allow. Pit fall trapping collected very few mites and was abandoned after four weeks. Berlese funnel extraction produced much lower numbers of mites than did suction sampling, because only limited quantities of plant debris could be put in the Berlese funnels whereas suction sampling could more quickly extract mites from a much larger volume of plant material. The numbers of mites collected was between zero and 20 during a 30-minutes suction sampling period. The mite species captured included a number of species that were phytophagous or did not predate fly eggs. Three genera of mites that were considered to have the potential to be predators of blowfly eggs were identified. These included the genus *Anystis*, the so-called whirligig mites, that are highly active predators of phytophagous mites and other microarthropods (Sorensen, Kinn *et al.* 1976); *Balaustium* spp. (Acari: Eryraeidae) which are generalist predators and also feed on pollen (Zhang, Z. Q. pers. comm.), and mites of the *Macrocheles* genus which are specialist feeders on fly eggs (Wade & Rogriguez 1961). Suction sampling was conducted on a number of occasions from August 1999 to March 2000.

With the limited numbers of suitable mites collected and with a lack of success in culturing suitable mites in the laboratory, alternative approaches to get sufficient mites, of suitable types, to feed on blowfly eggs for experiments were investigated.

2.10.1 Anystis baccarum L.

During late December 1999 large numbers of *Anystis baccarum* were found on Algerian ivy (*Hedera canariensis* L.) growing as an understory below silver birch trees (*Betula pendula* Roth.) on the western side of the Burns Building, Lincoln University, New Zealand. This site was approximately 150 m from Kowhai Farm where Berry (1997) had completed some of her video recording research. In early January, mites were collected by pooter (Southwood 1984) and kept individually in 50 mm diameter Petri dishes to prevent cannibalism, which occurred frequently when the mites were kept in

groups. A 1.5 cm^2 piece of filter paper was moistened and placed in each Petri dish with the mite. On this was placed one brown blowfly egg that had been freeze-killed at -80° C. The piece of moistened filter paper prevented desiccation of the eggs and provided water and a low humidity for the mites. *A. baccarum* was adversely affected by high humilities, and if larger areas of moistened filter paper were used mites frequently died. The Petri dishes were kept in a controlled environment room at 20° C with a 3° C range with a dark:light photoperiod of 8:16 hours.

Despite the wide prey range of *A. baccarum* not all mites fed on the freeze-killed blowfly eggs (Table 1). Those that did consumed only about 1.5 eggs each before they died. The mites that did eat eggs lived for an average of about six days, and depending on whether immature pea aphids were used as supplementary food (Figure 5). Therefore, only about 20% of mites would feed on a freeze-killed egg on any one day. Considerable numbers of mites were, therefore, required to produce enough pierced eggs for experiments.

The requirement for live eggs in experiments caused further problems as live blowfly eggs hatched in less than 24 h at the experimental temperature, which further reduced the number of pierced eggs. Mites fed on both live eggs and newly hatched blowfly larvae, showing that they were acceptable prey. This low level of feeding was complicated by a large population decline of *A. baccarum* at the collection site in early January 2000. Several species of mites in the genus *Anystis* have cyclical populations (Mostafa, DeBach *et al.* 1975; Sorensen, Kinn *et al.* 1976). Aphids were included in the diet in an attempt to extend the life of the remaining mites; however, this increased the length of survival only from an average of 4.6 to 7.1 days (Figure 5). However, these data, and all of those in Figure 5 and Table 1 need to be treated with caution, as there was no randomisation and as the data were collected over three weeks, the mites were likely to have been at different developmental stages.

Table 1. Proportion and number of *A. baccarum* that ate blowfly eggs and the mean number of eggs eaten ±SE in a no-choice or choice test with an immature pea aphid.

	Proportion of mites that ate eggs	Number of mites	Mean number of eggs eaten	SE
No Choice	0.60	51	1.57	0.220
Choice	0.54	14	1.64	0.439

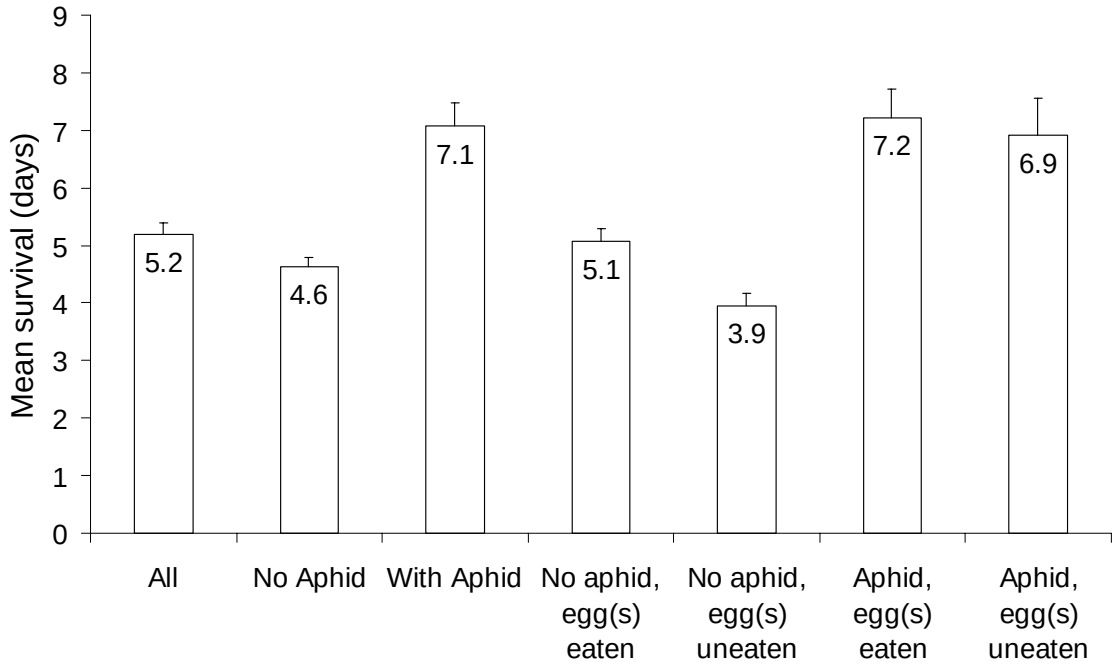

Figure 5. Mean (±SE) survival of *A. baccarum* kept in individual Petri dishes. Mites were fed one freeze-killed blowfly egg a day and some were given immature pea aphids as food. Mites were kept at 20° C with a 3° C range with a dark:light photoperiod of 8:16 hours.

Other researchers have raised *Anystis* species in the laboratory. Mostafa *et al.* (1975) raised *A. agilis* (Banks) in a laboratory for up to 45 days, feeding it the thrip *Scirtothrips citri* (Moult.) and the mite *Panonychus citri* (McG.). Only those provided with *S. citri* oviposited. Sorensen (1976), in laboratory studies, found that the mean development time of *A. agilis* to the adult stage was 48.9 days. Adults consumed an average of 39 adult females of the mite *Tetranychus urticae* (Koch) or 6 nymphs of *Erythroneura elegantula* (Osb.) per day. Zhang Z. Q., (pers. comm.) also raised *Anystis* species on *T. urticae*. It therefore seems that while blowfly eggs and aphids are eaten by *A. baccarum* they are insufficient on their own. It is noted, however, that as the *A. baccarum* collected were adults nearing the end of their life, and the population on the ivy very rapidly declined at the same time as did that of the mites in captivity, the mites kept in the laboratory may not have lived any longer had they been provided with other prey types.

2.10.2 *P. opilio* 'preference' for *A. baccarum*-pierced freeze-killed or unpierced live, blowfly eggs

Due to the difficulties of getting enough live eggs that had been pierced by *A. baccarum*, an experiment was completed using freeze killed eggs fed on by this species.

Freeze-killed brown blowfly eggs were placed on moistened 1.5 cm^2 pieces of filter paper and placed in 50 mm Petri dishes with a single *A. baccarum* for 24 h. Eggs that had been fed on by the mites over this period were collected and stored on the original moist pieces of filter paper, in a 50 mm Petri dish in a refrigerator at 4° C with a 2° C range for a maximum of 48 h. Eggs were considered to have been fed on if the egg was reduced in volume. Eight mite-pierced eggs and eight live blowfly eggs were randomly arranged in a four-by-four grid, spaced 15 mm apart on the square and placed on a 90 mm Petri dish filled with moist sieved peat. The rest of the experiment used the standard experimental design.

For each eaten and uneaten egg, its treatment (pierced, unpierced), and grid position were recorded and data were analysed using paired *t*-tests.

2.10.3 Macrochelid mites

Small numbers of macrochelid mites were collected using a suction sampler from the farms described in Section 2.13 that had livestock. Macrochelid mites are considered to be effective predators of eggs of the house fly (*Musca domestica* L.) (Wade & Rogriguez 1961) and are associated with animal dung, particularly where livestock are kept under cover and manure is allowed to build up (Cicolani 1992). Macrochelid mites use phoresy on flies to disperse. Mites were collected by two means: extraction from compost and manure, and trapping flies.

Samples of manure and compost were collected from the Lincoln University Dairy Farm, Harts Creek Farm and the researchers domestic garden, all situated in Canterbury New Zealand. The samples were placed in Berlese funnels for a period of one to three days. All extracted invertebrates were collected in dry plastic beakers, that were emptied daily. Mites were then removed individually, using a fine, moistened, paint brush.

Five fly traps were built using clear 1.5 l polycarbonate drink bottles and flower pots. Approximately the top third of a bottle was cut off and inserted, with the neck innermost, into the bottom third of the bottle. The open end was then placed over the base of a flower pot. The pots had a basal diameter of about 8-10 cm to ensure a tight fit on the bottle. Four holes, approximately 1-2 cm in diameter, were made in the sides of the pot, about five cm above the rim. 1-3 g of fresh meat was placed inside a small 100 ml plastic container and covered with water. This was then placed on the ground and the inverted flower pot and drink bottle was secured in place over it.

The trap was emptied by lifting both parts of the bottle off the pot, placing it in a transparent polythene bag and then separating the two halves and vigorously shaking. The bag was then placed in a refrigerator at 4° C with a 2° C range for about five minutes to reduce the activity of the flies and allow the mites to be easily separated. Traps were placed in a number of locations in the vicinity of the researcher's dwelling. A range of livestock including cattle, sheep, horses, and chickens were kept on surrounding properties, ensuring that there were plenty of flies in the area.

Mites were kept in pottles measuring 80 mm wide by 90 mm high, with a lid comprising a 90 mm diameter Petri dish lid with a 50 mm hole cut in it covered with fine nylon gauze. These were filled with a substrate consisting of a mixture of 9 g of dried, finely ground, fresh cow manure, 1 g of soya flour, and 20 ml of water. This substrate was developed by Wade & Rodriguez (1961) to maximise the number of offspring of macrochelid mites. The substrate was kept moist by daily addition of water. Freeze-killed brown blowfly eggs were added on a daily basis as food. The pottles were kept in the laboratory under ambient lighting conditions, with temperatures ranging from 13-27° C. The mites were transferred to new pottles with fresh substrate every three to five days due to rapid mould growth and sporolation.

Two species of mites, *Glyptholaspis americana* (Berlese) (Macrochelidae) and *Pergamasus* sp. (Berlese) (Parasitidae) were collected from both fly traps and manure. Many were dehydrated and thrived on the moist substrate. However, they failed to consume brown blowfly eggs. To confirm this, three mites of each species were confined in a 50 mm diameter Petri dish, with half the area of the dish covered with moist filter paper. Five blowfly eggs were placed on the other half of the Petri dish. After four days the eggs were uneaten; however, one of the *Pergamasus* sp. mites was eaten. *G. americana* is reported to feed on house fly eggs (Afifi 1988). Despite the rapid reproduction of macrochelid mites observed by Wade & Rodriguez (1961) and Rodriguez *et al.* (1962) no reproduction was observed in the captive mites over a three week period. The mites were therefore considered unsuitable for the study.

2.10.4 Balaustium spp.

In early March 2000, *Balaustium* spp. appeared in large numbers in the mown grass strip next to the macrocarpa (*Cupressus macrocarpa* Gordon) hedge boundary in field A5 of Kowhai Farm. This is one of the sites used by Berry, (1997) for her time-lapse video recording. The mites were collected from the grass strip with a suction sampler.

They were then extracted by first sieving between 1 mm and 250 µm aperture soil sieves, and then manually removing them with a moistened fine paint brush or pooter (Southwood 1984).

In the laboratory *Balaustium* spp. would rapidly attack and consume blowfly eggs (Figure 6) . There was no evidence of cannibalism by *Balaustium* unlike *A. baccarum*. This allowed *Balaustium* spp. mites to be kept *en masse* in small clear plastic containers 45 mm wide, 55 mm high, with a 20 mm diameter hole, covered with a fine nylon gauze, in the lid. A mixture of nine parts plaster of Paris and one part carbon power was mixed with enough water to form a paste and made into small tablets of assorted sizes. These were then allowed to set, baked at 50° C for 12 h and then soaked in water. The tablets were then placed in the containers with *Balaustium* spp. to provide water and a suitable relative humidity. Previous work had found that the mites died after approximately 24 h if the humidity was too high or after two to three days if it was too low and if no water was available. The containers were kept in the laboratory at ambient temperatures between 13-27° C under ambient lighting conditions. The mites were not fed, apart from giving them the eggs used in experiments.

Figure 6. *Balaustium* spp. feeding on a live brown blowfly egg. One graduation = 0.5 mm

2.10.5 Experimental design

Balaustium spp. were prepared for preying on eggs by removing the water-soaked tablets from the mites' containers 15 h before the start of the experiment. The amount of feeding on eggs by *Balaustium* spp. increased considerably if they had been deprived of water and food. Live brown blowfly eggs were kept in a 50 mm Petri dish, on moist filter paper, in a refrigerator at 4° C with a 2° C range for a maximum of 48 h. Using a fine damp paint brush eggs were transferred to dry clean filter paper to dry them, then placed on a glass coverslip and placed in the container holding the mites for 15 minutes. This was sufficient time for the mites to feed on most of the eggs without completely draining the contents. At the same time more blowfly eggs were dried, placed on another cover slip and then placed in an empty container, identical to that which housed the mites, for 15 minutes. After this period both sets of eggs were retrieved and the mites shaken off. The eggs were then handled using a piece of 10 amp fuse wire, rather than a paint brush, to avoid transferring or diluting any egg contents that may have been released by mite feeding. The intermediate step of drying the eggs on clean filter paper prior to placing them on the coverslips was necessary to stop the eggs sticking to the glass which would of made them impossible to remove using the fuse wire.

The same experimental design as described in Section 2.4 was used with the exception that live eggs were used and blowfly eggs were pierced by mites, not by hand. For each egg eaten or uneaten, its treatment and grid position were recorded. Data were analysed using paired *t*-tests.

2.11 *P. opilio* 'preference' for live mite-pierced or manually pierced brown blowfly eggs

As most experiments had used manual piercing of eggs due to difficulties in obtaining sufficient mites, it was considered appropriate to compare the consumption of eggs that had been pierced by mites with those pierced manually. Also the results of the experiment described in Section 2.13.5 indicated that while *P. opilio* did eat more mite-pierced eggs than unpierced eggs, the mean numbers eaten were much lower than were those for hand-pierced eggs. This difference meant that it was vital that a comparison was made between hand-pierced and mite-pierced eggs. The same experimental design and data analysis as described in Section 2.13.5 was used with the exception that whole

live eggs were substituted with eggs manually pierced with a minuten pin as described in Section 2.4.

Chapter 3: Results

3.1 *P. opilio* 'preference' for pierced or unpierced, freeze-killed blowfly eggs

P. opilio ate significantly more pierced eggs than unpierced eggs (paired *t*-test, $t = -4.30$, 9 df, $P < 0.001$, Figure 7). However, the number of eggs that were inspected did not vary between the two types ($P > 0.05$, Figure 7), nor was there any significant difference between the number of inspections of pierced and unpierced eggs ($P > 0.05$, Figure 7). 'Eggs inspected' means the number of eggs, of each type that were inspected one or more times. 'Egg inspections' means the total number of times that *P. opilio* inspected eggs of each type. Therefore, with eight eggs of each type available to *P. opilio*, the maximum number of eggs inspected is limited to eight, while the number of egg inspections is theoretically unlimited, but in practice constrained by the amount of *P. opilio* activity and the duration of the experiment.

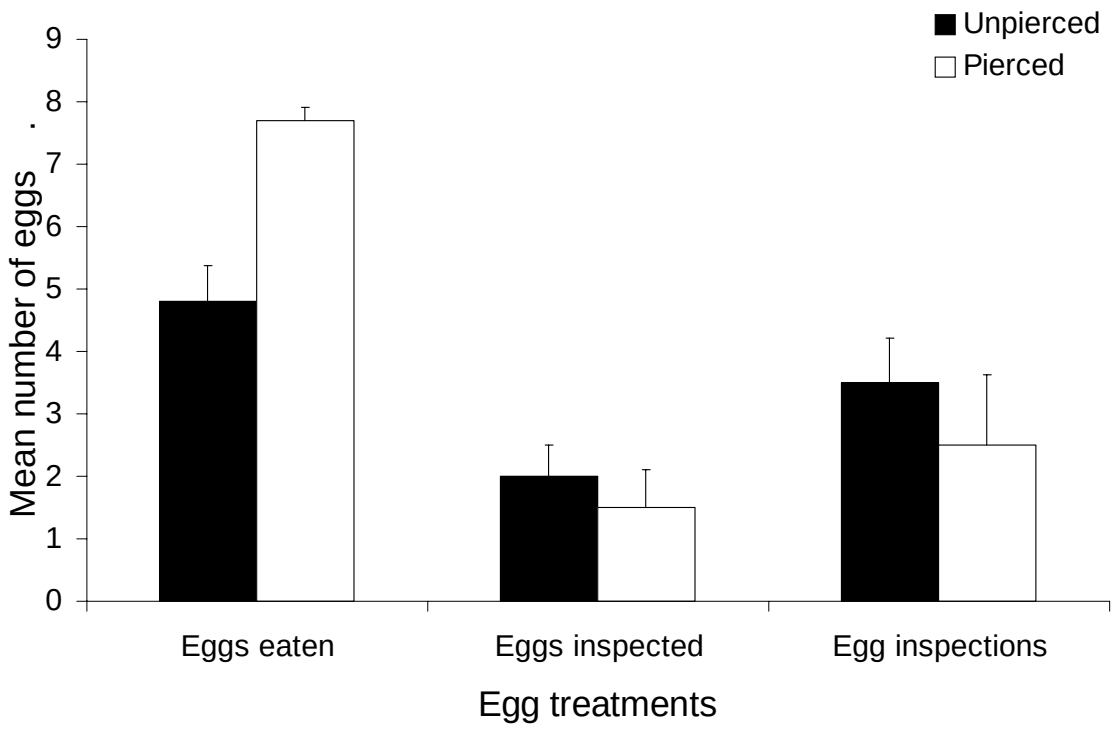

Figure 7. Mean number (+ SE) of pierced and unpierced, freeze-killed blowfly eggs eaten or inspected by *P. opilio*; see Section 3.1 for definitions.

3.2 *P. opilio* 'preference' for live or freeze-killed blowfly eggs

P. opilio clearly 'preferred' to eat freeze-killed rather than live blowfly eggs, consuming over 11 times more freeze-killed eggs (paired *t*-test, $t = -17.18$, 9 df, $P < 0.001$, Figure 8). They also inspected over four times more freeze-killed eggs than fresh eggs (paired *t*-test, $t = -2.70$, 9 df, $P = 0.024$, Figure 8). Egg inspections were just significant with 6 times more freeze-killed eggs being inspected than live eggs (paired *t*-test, $t = -2.34$, 9 df, $P = 0.044$, Figure 8). The larger P value for egg inspections compared with numbers of eggs inspected indicates that a minority of eggs were receiving the majority of inspections by *P. opilio*.

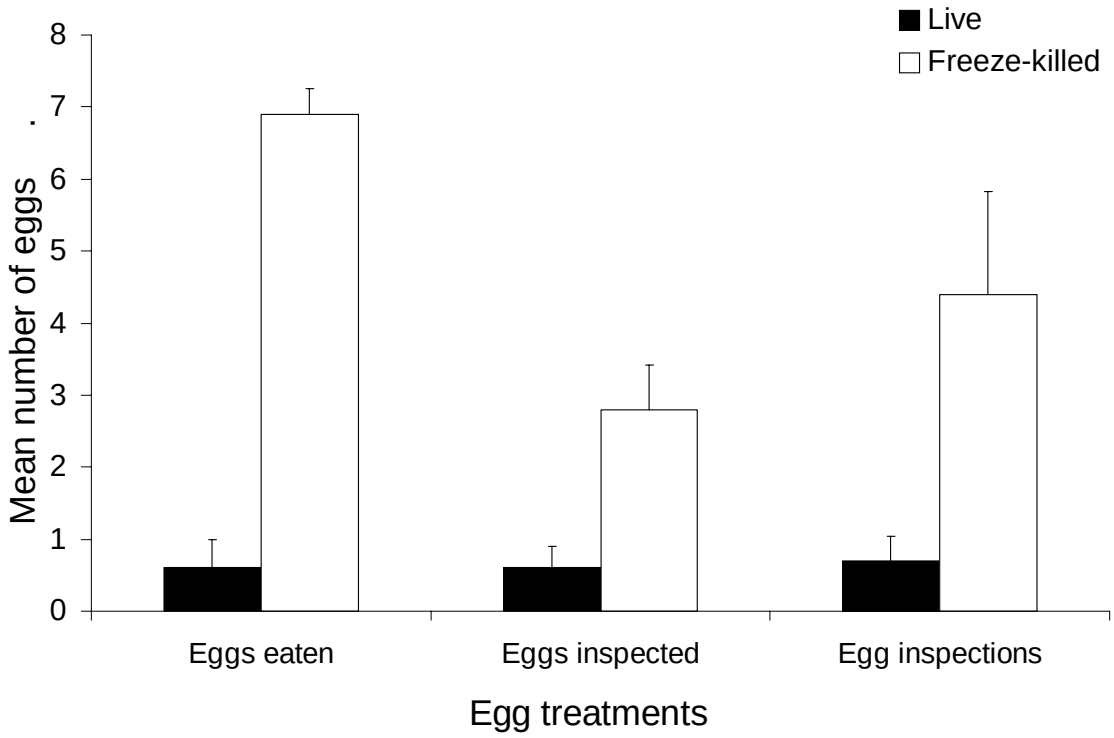

Figure 8. Mean (+SE) number of freeze-killed and live blowfly eggs eaten or inspected by *P. opilio*.

3.3 *P. opilio* 'preference' for pierced or unpierced live blowfly eggs

P. opilio again showed a very clear 'preference' for egg type, eating 62 times as many pierced eggs than unpierced eggs (paired *t*-test, $t = -47.35$, 7 df, $P < 0.001$) (Figure 9). However, in contrast with the previous experiment (Section 3.2) there was no significant difference ($P > 0.05$) between the number of eggs inspected (Figure 9) or the number of egg inspections by *P. opilio* for the two egg types (Figure 9).

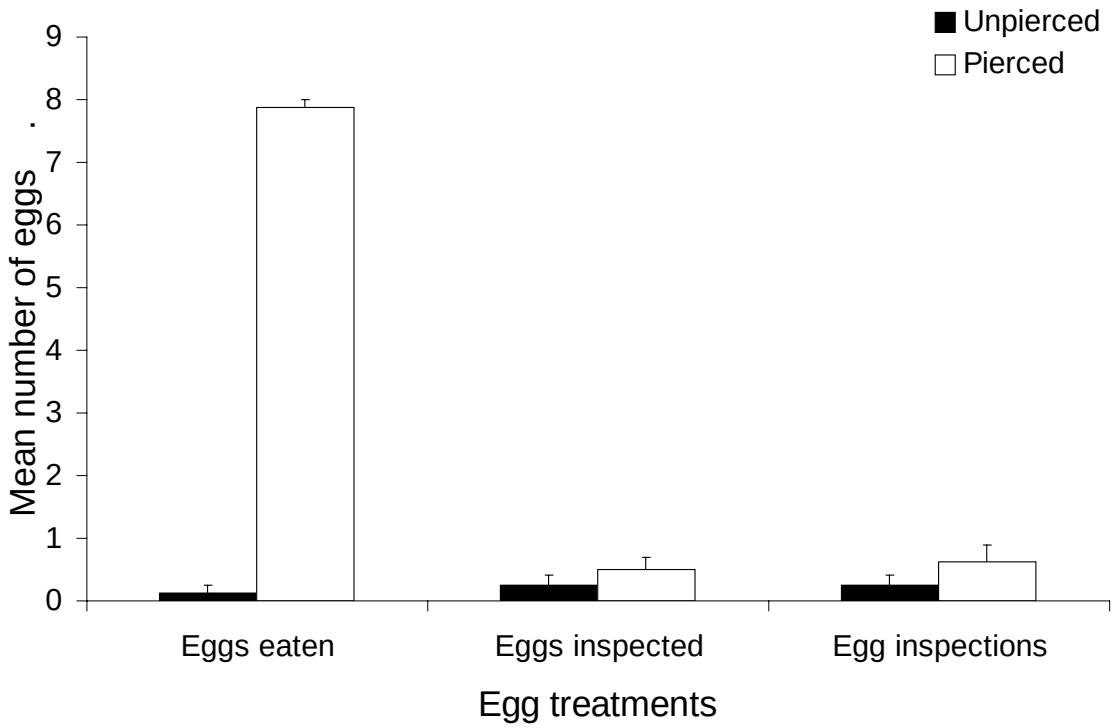

Figure 9. Mean numbers (+SE) of pierced and unpierced, live blowfly eggs eaten or inspected by *P. opilio*.

3.4 The effect of egg replacement on *P. opilio* 'preference' and consumption of pierced and unpierced live blowfly eggs

3.4.1 'Preference' for pierced and unpierced live blowfly eggs

Egg replacement accentuated the 'preference' of *P. opilio* for live pierced eggs rather than for live unpierced eggs, with 26 times as many pierced eggs being eaten (paired *t*-test, $t = 12.67$, 4 df, $P < 0.001$, Figure 10).

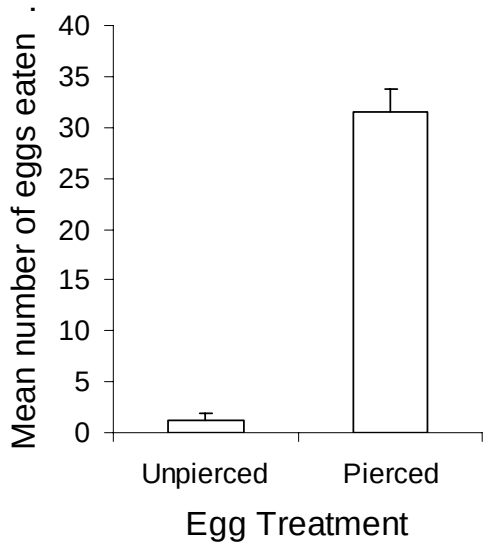

Figure 10. Mean number (+SE) of pierced and unpierced blowfly eggs eaten by *P. opilio* with replacement of all eggs at intervals of one, two, four, six and nine hours.

3.5 The effect of egg replacement on consumption of live blowfly eggs

Previous experiments (Sections 3.1, 3.2, and 3.3), while primarily analysing *P. opilio* 'preference' for the two egg types being tested, also recorded the length of time from the start of the experiment to when eggs were eaten and / or inspected. The majority of eggs were eaten or inspected in the first two hours of the experiment (Figures 11, 12 and 13).

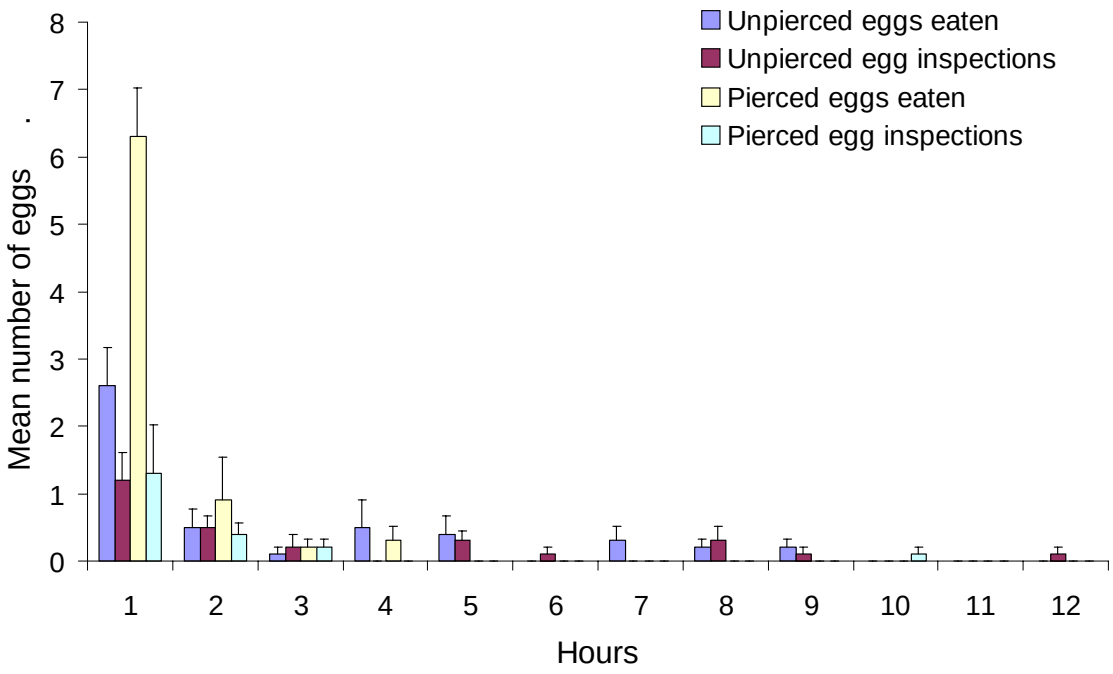

Figure 11. Mean numbers (+SE) of pierced and unpierced, freeze-killed blowfly eggs, eaten or inspected by *P. opilio* over a 12 h period. Scotophase started at hour two and ended at hour ten.

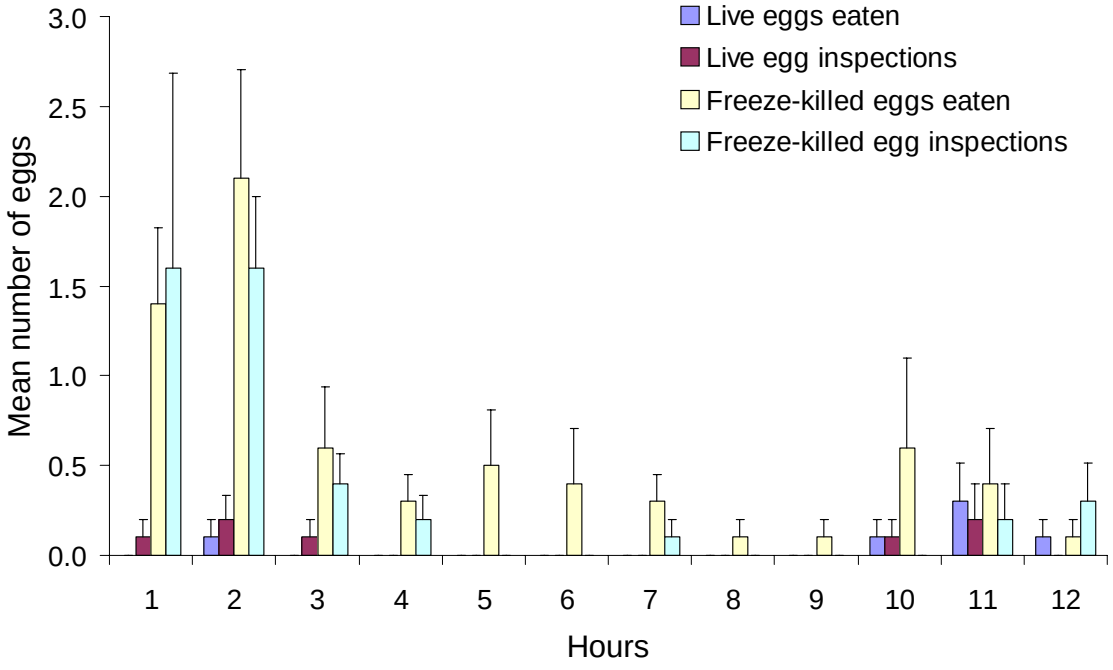

Figure 12. Mean numbers (+SE) of live or freeze-killed blowfly eggs, eaten or inspected by *P. opilio* over a 12 h period. Scotophase started at hour two and ended at hour ten.

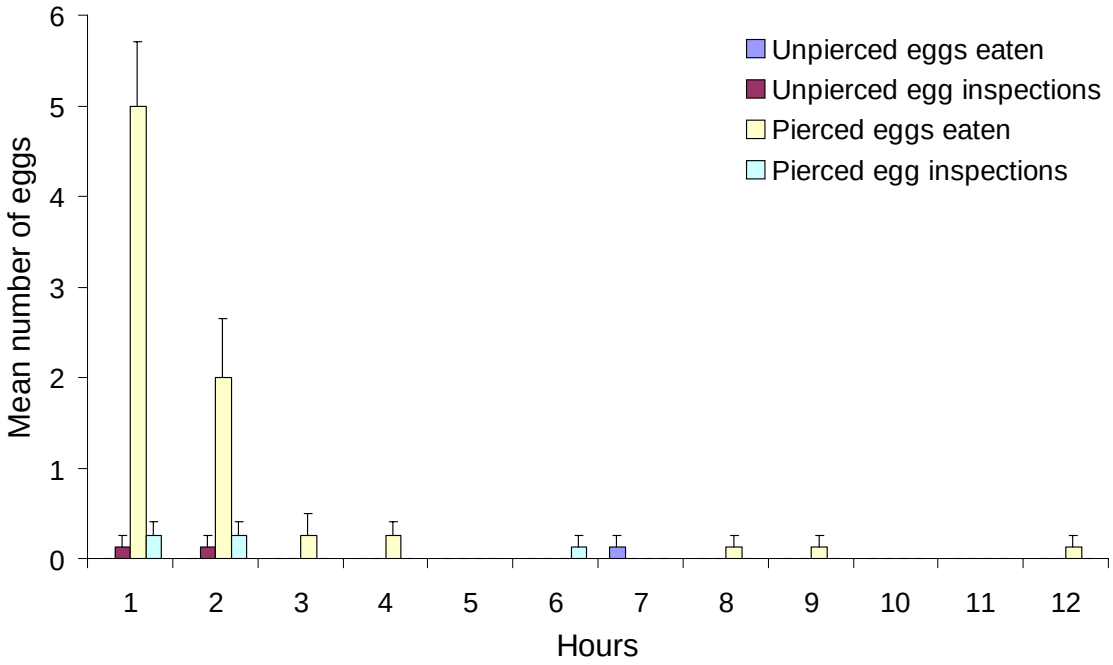

Figure 13. Mean numbers (+SE) of pierced or unpierced live blowfly eggs, eaten or inspected by *P. opilio* over a 12 h period. Scotophase started at hour two and ended at hour ten.

In comparison, the pattern of egg consumption by *P. opilio* when eggs were replaced was different over time (Figure 14). The majority of eggs were no longer eaten in the first two hours. Consumption continued at higher, though declining, rates throughout the experiment. There was, however, only one significant difference between the number of eggs eaten from any one hour and the next. That was between hours two and three (paired *t*-test, $t = 3.07$, 4 df, $P = 0.04$). The rest of the changes from hour to hour were not significant ($P > 0.05$).

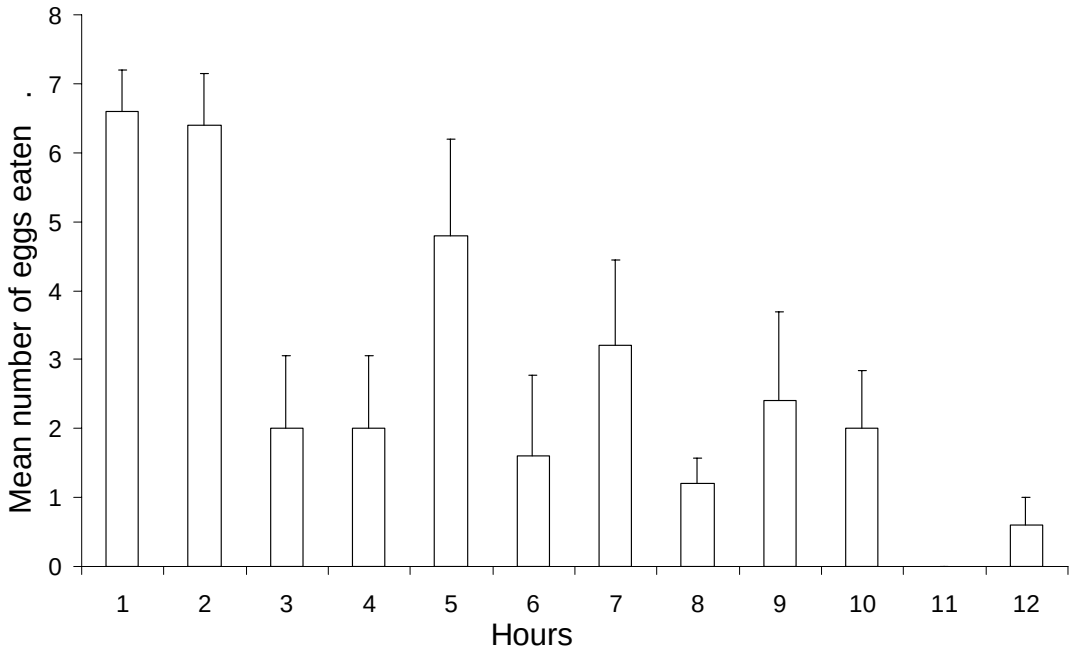

Figure 14. Mean numbers (+SE) of pierced and unpierced live blowfly eggs eaten by *P. opilio* over a 12 h period with eggs replaced at intervals of one-two-four-six and nine hours. Scotophase started at hour two and ended at hour ten.

A comparison of the number of eggs eaten, expressed as a proportion of the total number of eggs available in the experiments, showed that replacing eggs produced the lowest proportion of eggs eaten, while the experiment using pierced and unpierced freeze-killed eggs had the highest proportion eaten (Table 2).

Table 2. Proportion of eggs eaten, with one SE, out of the total number of eggs used in the experiment.

Experiment	Proportion of eggs eaten	SE
Pierced and unpierced, freeze-killed eggs	78	3.4
Live and freeze-killed eggs	47	4.1
Pierced and unpierced, live eggs	50	1.2
Pierced and unpierced live eggs with egg replacement	34	2.2

An analysis of the mean number of blowfly eggs eaten in each replicate for the four experiments discussed above showed that between 2.5 and 4.1 times as many eggs were eaten when eggs were replaced than when they were not (Figure 15).

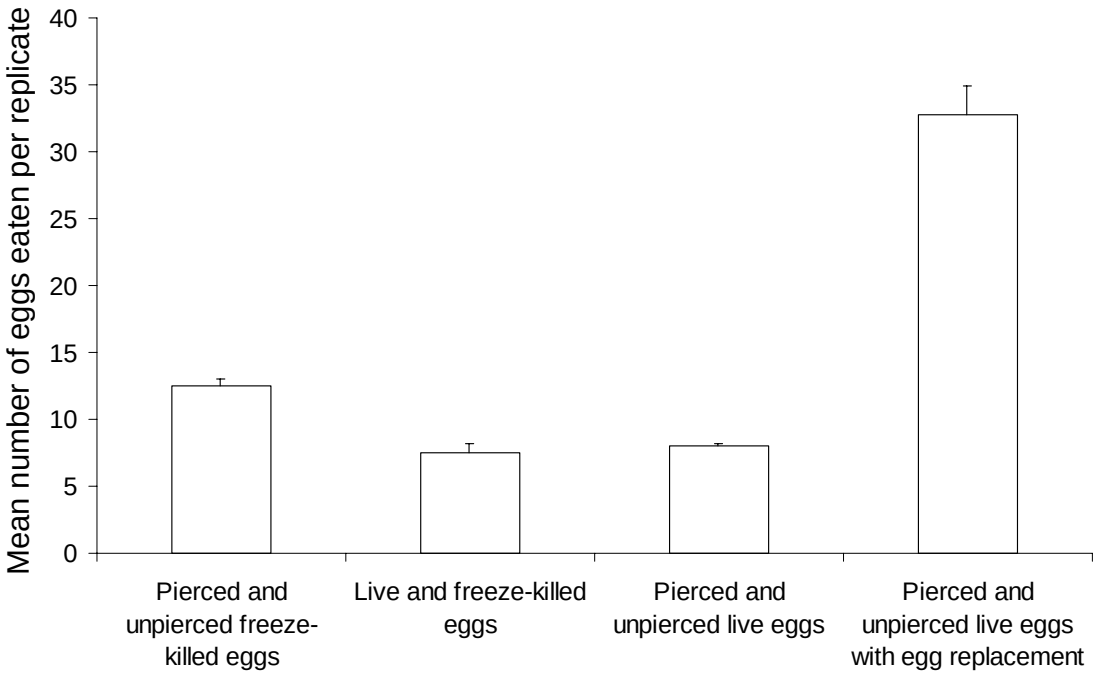

Figure 15. Mean numbers (+SE) of blowfly eggs eaten per replicate for four experiments.

No analysis of egg inspections or eggs inspected was made because these measurements had been discontinued from the experiment analysing the effect of replacing eggs (Section 3.4). See Section 4.1.2 for explanation and discussion.

3.6 *P. opilio* 'preference' for egg positions in a four-by-four grid

P. opilio showed no significant 'preference' ($P > 0.05$) for the twelve eggs that were on the periphery of the four-by-four grid compared with the four eggs in the centre (Figure 16).

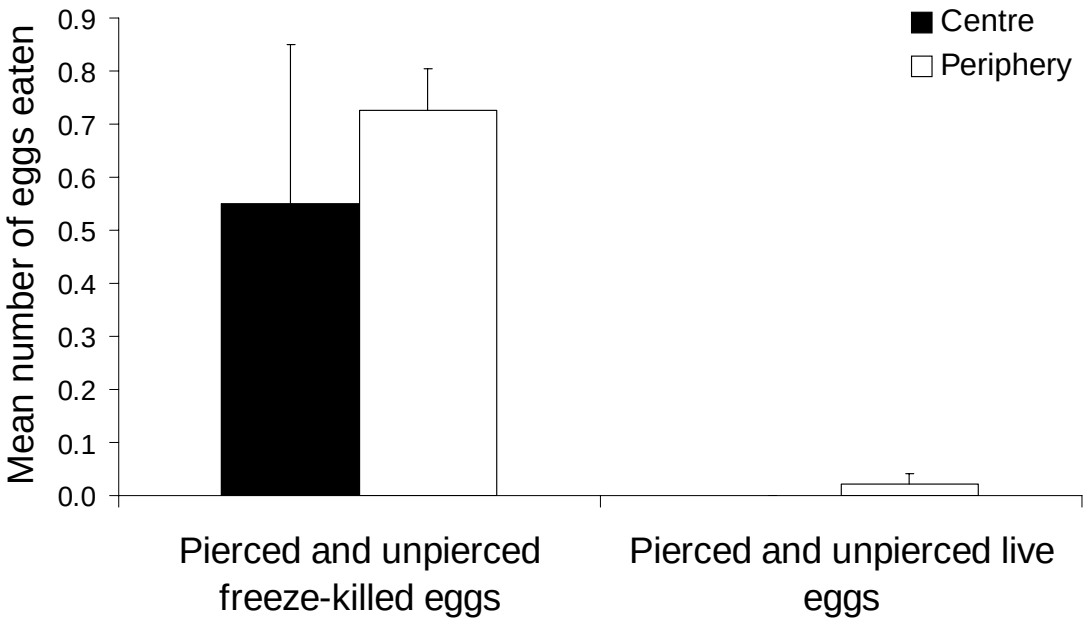

Figure 16. Mean (+SE) number of unpierced and pierced eggs eaten by *P. opilio* from the centre four eggs or 12 peripheral eggs in a four-by-four grid.

3.7 *P. opilio* 'preference' for unpierced eggs with or without a pierced egg in close proximity

P. opilio individuals consumed no more unpierced live eggs whether there was a pierced live egg next to them or not, at either 5 mm or 1 mm spacing between the eggs ($P > 0.05$, Figure 17 and Figure 18). Different scales are used for the two figure because ratios were used in the analysis of the 5 mm-spaced experiment while they were not required for the 1 mm-spaced eggs.

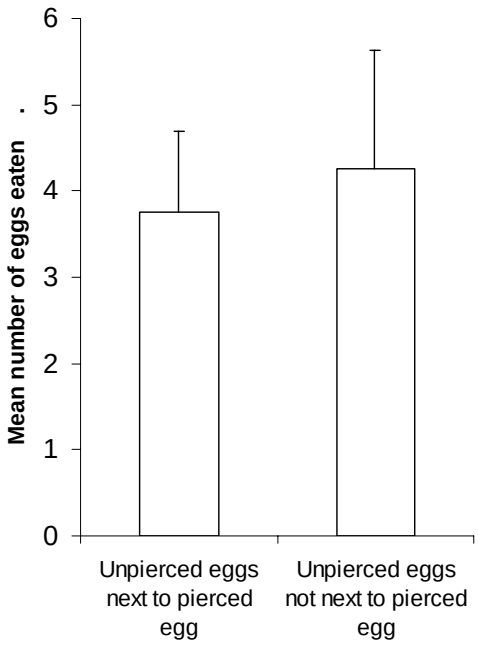

Figure 17. Mean numbers (+SE) of unpierced eggs spaced 1 mm apart eaten when a pierced egg either was, or was not, placed 1 mm away.

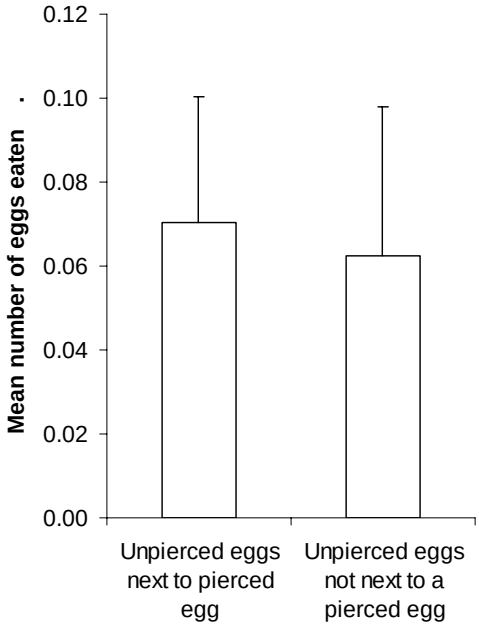

Figure 18. Mean numbers (+SE) of unpierced eggs spaced 5 mm apart eaten when a pierced egg either was, or was not, placed 5 mm away.

A *post hoc* analysis revealed that at the 1 mm spacing, 21% of the eggs were eaten, while at the 5 mm spacing only 6.3% were eaten. This indicated that decreasing the distance between the eggs increased the numbers of eggs eaten.

3.8 The effect of distance between blowfly eggs on consumption of, and 'preference' by *the predator*

In the experiment with 15 and 60 mm spacings between the eggs, *P. opilio* continued to display greater preference for pierced eggs compared with unpierced ones at both the 60 mm (paired *t*-test, $t = 8.49$, 3 df, $P = 0.003$, Figure 19) and the 15 mm egg spacing (paired *t*-test, $t = 7.13$, 3 df, $P = 0.006$, Figure 19).

However, *P. opilio* did not eat significantly ($P > 0.05$) different numbers of eggs (of both types) between the 60 mm and 15 mm spacings (Figure 19). There was also no significant difference ($P > 0.05$) between the numbers of pierced or unpierced eggs eaten at the two spacings (Figure 19).

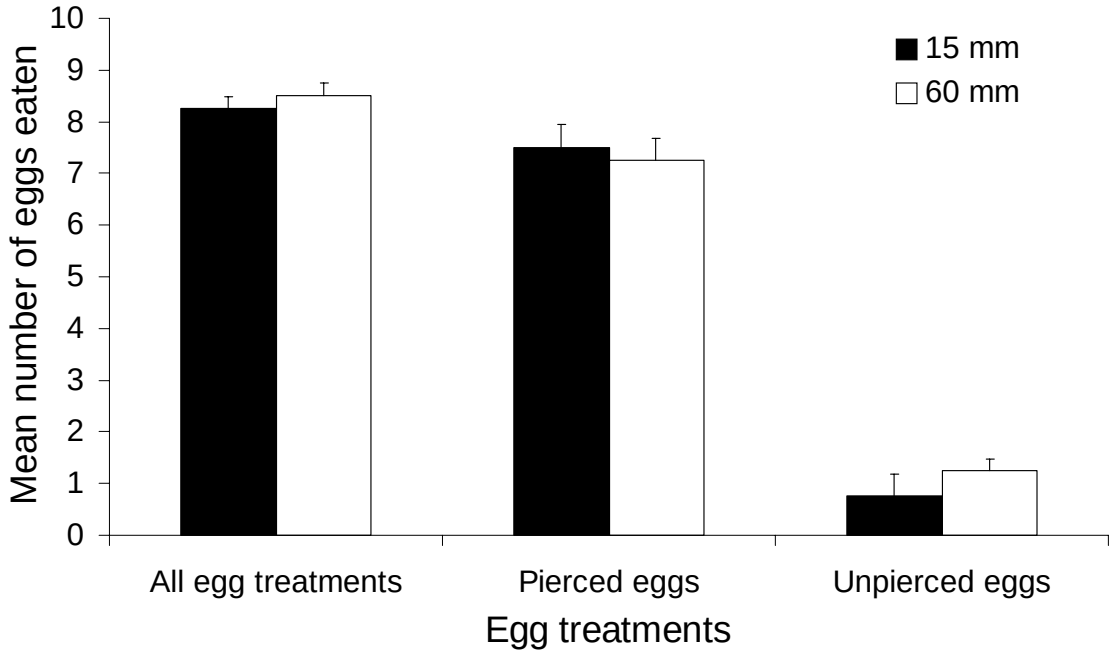

Figure 19. Mean numbers (+SE) of pierced and unpierced blowfly eggs, spaced at either 15 or 60 mm, eaten by *P. opilio*.

Unusually, in the second experiment at 1 and 60 mm egg spacings there was no significant difference ($P > 0.05$) between the number of unpierced eggs eaten compared with pierced eggs at the 60 mm egg spacing (Figure 20). *P. opilio* did eat more pierced eggs at the 1 mm spacing (paired *t*-test, $t = 7.17$, 4 df, $P < 0.001$, Figure 20).

There was no significant difference ($P > 0.05$) between the number of eggs eaten (of both types) by *P. opilio* between the 60 and 1 mm egg spacings (Figure 20). There was also no significant difference ($P > 0.05$) between pierced or unpierced eggs eaten at the two spacings (Figure 20).

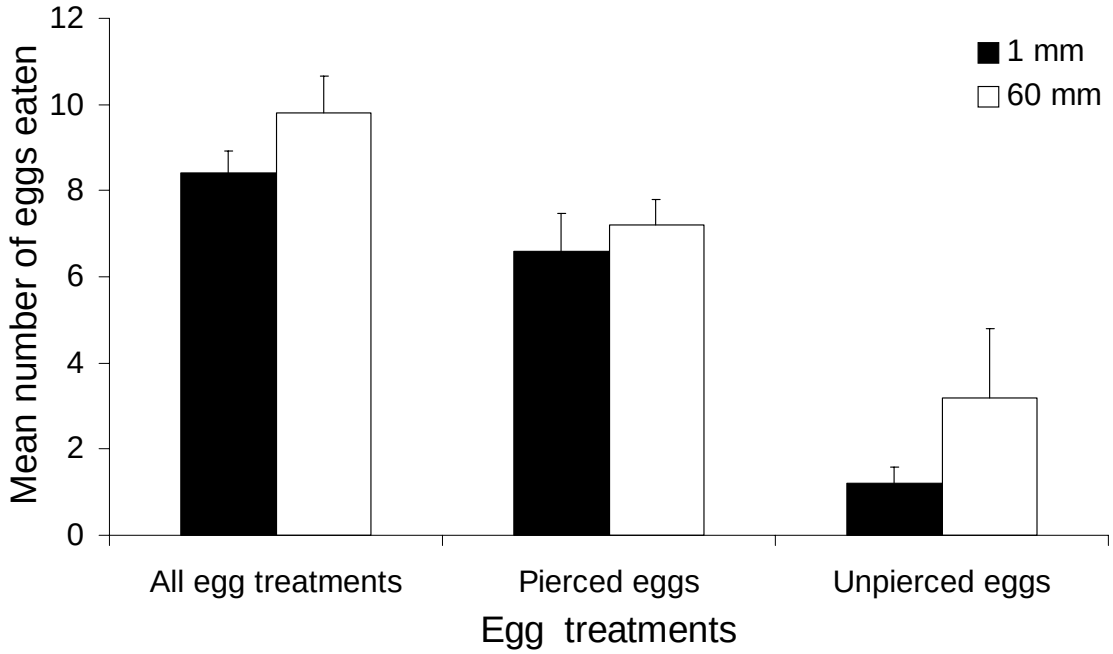

Figure 20. Mean numbers (+SE) of pierced and unpierced blowfly eggs, spaced at either 1 or 60 mm, eaten by *P. opilio*.

3.9 *P. opilio* 'preference' for blowfly eggs previously pierced by mites or controls

3.9.1 *P. opilio* 'preference' for freeze-killed blowfly eggs previously pierced by *A. baccarum* or unpierced live eggs

There was no significant ($P > 0.05$) difference between the mean number of freeze-killed eggs fed on by *A. baccarum* or unpierced live eggs, eaten by *P. opilio* (Figure 21).

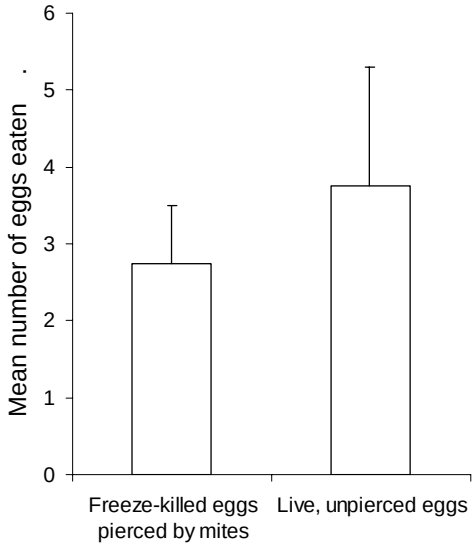

Figure 21. Mean (+SE) numbers of freeze-killed blowfly eggs pierced by *A. baccarum* , or live unpierced eggs, eaten by *P. opilio* over a 6 h period.

3.9.2 P. opilio 'preference' for live brown blowfly eggs pierced by *Balaustium* spp. and controls

In contrast to the experiment in Section 3.9.1 using *A. baccarum* to pierce eggs, *P. opilio* ate significantly more eggs pierced by *Balaustium* spp. than unpierced eggs (paired *t*-test, $t = -2.83$, 6 df, P = 0.03, Figure 22). However, the mean number of eggs eaten was very low compared with the number of hand-pierced live eggs consumed. Therefore, hand piercing and mite piercing are not equivalent in terms of the numbers of eggs eaten by *P. opilio*.

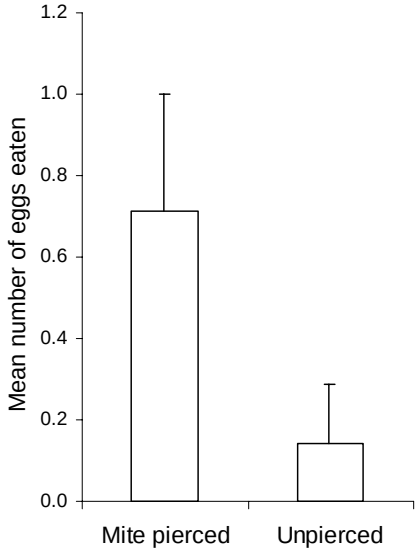

Figure 22. Mean (+SE) numbers of live blowfly eggs pierced by *Balaustium* spp. or unpierced, eaten by *P. opilio* over a 6 h period.

3.10 *P. opilio* 'preference' for *Balaustium* spp. pierced or manually-pierced brown blowfly eggs

P. opilio ate nearly six times more blowfly eggs that had been manually pierced than those pierced by *Balaustium* spp. (paired *t*-test, $t = 7.55$, 3 df, $P = 0.005$, Figure 23).

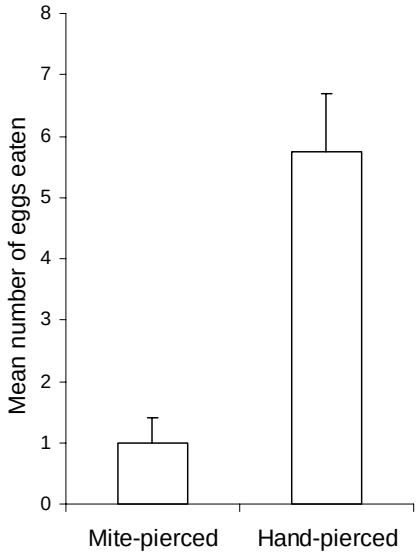

Figure 23. Mean (+SE) numbers of live brown blowfly eggs pierced by *Balaustium* spp. or hand-pierced, eaten by *P. opilio* over a 6 h period.

Chapter 4: Discussion

4.1 *P. opilio* 'preference' for pierced or unpierced, freeze-killed blowfly eggs

4.1.1 Eggs eaten

The clear 'preference' of *P. opilio* for pierced eggs indicates that a mite feeding on an egg could increase the attack rate (Hassell, Lawton *et al.* 1977) of *P. opilio* for such eggs, as the piercing and sucking method of mite feeding is similar to manual piercing. However, visual observations showed that despite the use of a minuten pin and efforts to minimise the size of the hole made, mites make a considerably smaller hole and no egg contents were seen to escape. This is probably due to the much smaller size of the mite's stylet-like mouthparts, which measured approximately 2 µm across compared to the 20 µm diameter of the minuten pin. In addition, as the mites suck out a considerable proportion of the egg contents this would reduce its internal pressure, making it less likely that egg contents would escape. Therefore, caution should be exercised in extrapolating the results from manual piercing to mite piercing.

Although the simulation of mite feeding technique was imperfect, the result is interesting because it shows that manual piercing alters the reaction of *P. opilio* to the prey. Piercing is assumed to have two effects; to kill the developing blowfly larvae, starting the process of decay, and to expose the egg contents to the atmosphere allowing oxidation to occur. With the egg chemistry altered, it is possible that the volatiles released by the pierced egg, or the altered chemicals on the egg surface make it easier for *P. opilio* to detect the egg. No published research was found that analysed the decay process or changes to volatiles from, or surface chemicals of arthropod eggs due to death or piercing. However, Jones (1956) showed that at certain stages the eggs of *Locusta migratoria* (L.) the puncturing of an egg activated the enzyme-substrate system which then sealed the puncture. While it has been known for a long time that spiders react to chemical stimuli, detailed research into olfaction and chemoreception in the Arachnida is a relatively new area (Foelix 1996). Studies on spiders and mites have shown that they have both contact chemoreception and olfactory abilities; see, for example, (Kraus 1990; de Bruyne, Dicke *et al.* 1991; Baker 1996; Searcy, Rypstra *et al.* 1999). However, equivalent detailed research on harvestmen has not been done, although, there have been few very general studies, for example, that of Phillipson

(1960). Therefore, it is not possible to speculate further on the mechanisms which result in *P. opilio* eating more pierced than unpierced eggs.

4.1.2 'Egg inspections' and 'eggs inspected'

The collection of data on inspections of eggs by *P. opilio* was initially carried out because of its use in prior studies by Berry (1997) and Navntoft (unpublished data) who video-recorded brown blowfly and Indian meal moth egg predation by soil-surface dwelling arthropods. However, it was discovered that there are a number of difficulties interpreting the results of inspections of eggs.

It is unclear what factors lead to *P. opilio* inspecting eggs. Inspection, as defined here, requires that *P. opilio* detect the egg but then 'decides' not to eat it. The reasons for that 'decision' are not clear. For example, it could be that the *P. opilio* is temporally satiated, that the egg is rejected as unsuitable food, or that *P. opilio* stops moving while over an egg entirely by chance. With limited information on the olfactory and chemoreception abilities of harvestmen and the effect on the chemical changes caused by piercing eggs, (discussed in Section 4.1 above) it is not possible to determine why *P. opilio* sometimes detects eggs, but does not eat them.

It is also unclear what constitutes inspection of prey by *P. opilio*. In this research and in the work of Berry and Navntoft discussed above, inspection was considered to have occurred when a harvestman paused for more than one second with its mouth parts directly over an egg. However, *P. opilio* individual also uses its second pair of legs for detecting prey and sensing the ground ahead, rather than for walking (Hillyard & Sankey 1989). This was observed on many occasions during experiments, when a *P. opilio,* moving slowly across the arena, touched an egg with one of the second pair of legs and then rapidly moved to the egg and ate it. It could be argued that inspection also occurred when one of the second pair of legs touched an egg. Therefore, a potentially large numbers of inspections may have gone un-recorded. Re-analysis of the data was not possible as the video image resolution was too low to consistently determine when a second leg touched an egg.

Furthermore, the number of inspections could be biased due to the higher depletion rates of the pierced eggs, increasing the ratio of unpierced : pierced eggs. This would increase the number of unpierced 'eggs inspected' and / or 'egg inspections' compared with an experiment where eggs were replaced once they were eaten.

Because of the issues outlined above, it is unclear exactly what the inspection data comprise. Therefore, they cannot give any useful understanding to the behaviour of *P. opilio*. What is clear, however, is that there are interesting behavioural questions raised, for example, why an unsatiated predator would detect prey and then not eat it. The issues surrounding prey inspection, the chemoreception abilities of harvestmen and the changes to eggs caused by piercing could be a valuable future research area.

On the basis of the above arguments it was decided to discontinue the recording of the inspection of eggs. However, as the following two experiments had been completed at the time of the above decision, these data were analysed and presented for completion.

4.2 *P. opilio* 'preference' for live or freeze-killed blowfly eggs

The highly significant 'preference' of *P. opilio* for freeze-killed eggs was unexpected. The result clearly demonstrates that the type of prey pre-treatment used can have a highly significant effect on a predator's reaction to prey. This is important because previous workers (Berry 1997) and Navntoft (unpublished data) studying soil surface predators and carrot rust fly (*Psila rosae* F.) egg predation used both live and freeze-killed, brown blowfly and Indian meal moth eggs as prey facsimiles. Differences in their results could be due to the different egg pre-treatment techniques. Other studies have also used freeze-killed prey or prey facsimiles to measure predation or parasitism rates. For example, Thomas (1988; 1991) used freeze-killed third-fourth instars of the pea aphid *Acyrthosiphon pisum* (Harris) and *Drosophila melanogaster* (Meigen) pupae to study predator predation rates out from overwintering sites. Halsall (1990) used freeze-killed aphids of a number of species to study the response of a selection of carabid beetles to a range of aphid densities in a fixed area in the laboratory. Powell (1982) used freeze-killed eggs of the pentatomid bug *Nezara viridula* (L.) as hosts for the parasitoid *Trissolcus basalis* (Wollaston). Of these three studies, only Powell compared the behaviour of the study arthropod towards live and freeze-killed prey and found no significant difference. Care should, therefore, be exercised when using freeze-killed prey, as predation or parasitism rates could be significantly different compared with those of live prey. Ideally, if, freeze-killed prey or prey facsimiles are used, predation and parasitism rates between live and freeze-killed prey should be compared.

If freezing can alter predator or parasitoid behaviour towards a prey item, it indicates that there may also be significant differences in predator or parasitoid behaviour

between prey and a prey facsimile. For example, Berry (1997) used Indian meal moth eggs as facsimiles of carrot rust fly eggs because of their similar size and the difficulty of producing carrot rust fly eggs in laboratory culture. Indian meal moth eggs are not found in agricultural fields, as this insect is a pest of stored food crops (Freeman 1976). They would, therefore, be novel food items for predators which may attack them at different rates compared with the rate of predation of carrot rust fly eggs. Ideally, predation rates of facsimiles and real prey should be compared, if, facsimiles are planned to be used.

4.2.1 Differences between live and freeze-killed eggs

The results of this experiment indicate that freezing changes the physical or chemical status of the eggs, which made them easier for *P. opilio* to detect, or more attractive as food once detected. When freeze-killed and live blowfly eggs were compared there was no visible difference between the two. No previous work has been done analysing the effects of freezing on insect eggs. This area would benefit from further research given the value of prior storage in experiments of this type.

4.2.2 Choice of prey for further experiments

With such a clear indication that freezing substantially alters *P. opilio* 'preference' it was decided to use only live eggs for the remainder of this study. Despite the problems with using prey facsimiles noted above, it was decided to continue using brown blowfly eggs. This was because the previous work by Berry (unpublished data) that suggested that mite feeding may increase the feeding rates of harvestmen, used brown blowfly eggs. Therefore, using a different prey item, that would be a frequent constituent of the diet of both mites and *P. opilio* was not adopted because little is know of these predators' prey range culturing candidate prey would probably be impossible.

4.3 The effect of egg replacement on *P. opilio* 'preference' and consumption of pierced and unpierced live blowfly eggs

The increased rates of egg consumption, both over time (Figure 14), percentage of eggs eaten and mean numbers of eggs eaten (Table 2 and Figure 15) indicates that *P. opilio* was not satiated during previous experiments, and that it could consume more than the 16 eggs available in previous experiments. The provision of additional eggs also

increased the significance of the 'preference' of *P. opilio* for pierced eggs. This indicates that the smaller number of eggs used in previous experiments did not distort the type of result, only the statistical influence of degrees of freedom.

The overall reduction in the numbers of eggs eaten as the experiment progressed is an indication that the *P. opilio* was becoming satiated and reaching its maximum consumption rate of 16.4 (SE 0.62) eggs over 12 h. Contrary to expectations there was no consistent increase in egg consumption with egg replacement. There was a significant decrease in egg consumption after egg replacement after two hours, a non-significant decrease after eggs were replaced after nine hours, and non-significant differences at the other times when eggs were replaced. The reasons for this variability are not known. The lack of a consistent increase in egg consumption after blowfly eggs were replaced does not justify further attempts at interpretation of the data.

4.4 *P. opilio* 'preference' for egg positions in four by four grid

The lack of a significant difference between the numbers of eggs eaten by *P. opilio* from the periphery and the centre of the grid indicates that there was no obvious edge effect associated with this experimental design.

The result also demonstrates that *P. opilio* walked over peripheral eggs without eating or inspecting them, a phenomenon also observed on the video recordings. This phenomenon of moving over prey without detecting it has been noted in other predator species. For example, Wratten (1976) found that the larvae of the ladybird *Adalia bipunctata* (L.) could walk over early instar lime aphids *Eucallipterus tiliae* L. as it relies on touch, rather than sight to detect prey (Hodek 1967). Prey detection and acceptance by predators and parasitoids is well studied, with a number of factors including, prey size, shape, movement, kairomones, and if the host has already been parasitised all influencing predator and parasitoid behaviour (Jervis & Copland 1996). Future research into the mechanisms of prey detection by *P. opilio* would be valuable, as discussed in Section 4.1.1.

4.5 *P. opilio* 'preference' for unpierced eggs with or without a pierced egg in close proximity

Results from previous work by Berry, N. A. (1997) suggested that increasing the aggregation of blowfly eggs increased egg consumption. Therefore, as *P. opilio* ate all the pierced eggs placed next to the unpierced ones it was expected that it would consume more of the neighbouring unpierced eggs. The lack of a significant result was, therefore, unexpected. The result also contrasted with the finding that the percentage of eggs eaten in the experiments increased from 6.3% to 21% when the spacing between the egg decreasing from 5 mm to 1 mm, an indication that increasing the aggregation of the eggs increases egg consumption by *P. opilio*. The implications of this will be discussed in the following section.

4.6 The effect of distance between blowfly eggs on consumption rate of, and 'preference' by, the predator

4.6.1 *P. opilio* 'preference' for pierced or unpierced eggs

The 'preference' for pierced compared with unpierced eggs by *P. opilio* at the 15 and 60 mm spacings reinforces the results from previous experiments. The results also demonstrate that the spacing between the eggs had no effect on the 'preference' of *P. opilio* for pierced eggs. However, in the second experiment with eggs spaced at 1 and 60 mm the lack of significant difference between the number of pierced and unpierced eggs eaten at the 60 mm spacing differed from all previous results. The reason for this anomalous result is unknown.

4.6.2 The effect of distance between blowfly eggs on their consumption rate by *P. opilio*

The lack of a significant difference in the mean number of eggs eaten at 15 and 60 mm spacings, either for pierced and unpierced treatments combined or when analysed separately, was unexpected. It is at variance with the observations of Berry (1997), and the *post hoc* analysis discussed in Section 4.5, where mean egg consumption rose when egg spacing decreased. The lack of a significant difference between the mean number of eggs eaten at 1 and 60 mm spacings was, therefore, even more unexpected. The 15 mm spacing between the eggs is at least three times the body length of the *P. opilio*

individuals used in the experiments. Therefore, *P. opilio* may not be able to detect more than one egg at a time at such spacings. However, when eggs are spaced only 1 mm apart it was expected that *P. opilio* would be able to detect more than one egg at a time as this distance was small compared to the size of *P. opilio* individuals used in the experiment.

There are, however, differences between the methods of Berry (1997) and those from the current experiments. Berry altered the number of eggs in each patch rather than the distance between them, while the current experiments kept the number of eggs constant and altered the distance between eggs. Therefore, while both experiments measured the effect of increasing densities of eggs, they are not directly comparable.

Previous studies have shown variation in the responses of other polyphagous predators to prey aggregation. For example, Bryan (1984) studied the responses of polyphagous predators to artificially created aggregations of the aphid *Sitobion avenae* (F.) in winter wheat fields. Several species of polyphagous beetles (Carabidae and Staphylinidae) aggregated in these patches while other species did not.

4.6.3 Kinesis of predators in response to prey

It appears that changing prey density has no effect on the consumption of eggs by *P. opilio,* indicating that *P. opilio* does not focus its search for prey in the immediate vicinity of previously located prey. This is unusual because, as discussed in Section 1.7, a number of studies have demonstrated that predators and parasitoids intensify their searching pattern to the immediate area where prey was last located. This involves a decrease in the speed of movement (orthokinesis) and increase in the amount of turning (klinokinesis) (Fraenkel & Gunn 1961). This behavioural change can result in an increase in the number of prey consumed or of hosts parasitised, for example, see (Murdie & Hassell 1973; Sabelis 1981; Mols 1986; Casas 1988; McEwen, Clow *et al.* 1993; El Kareim 1998). Kinesis is considered to be of such significance that it has been suggested as a means of ranking the efficacy of predators as biological control agents (Putman & Wratten 1984). Considering the importance of kinesis to many predators and parasitoids, the lack of such behaviour by *P. opilio* as demonstrated by the results of the experiments in Sections 3.7 and 3.8, therefore, appears unusual. However, Winder (1997) used simulation and analytical models to show that the intensified searching pattern of the epigeal predatory carabid beetle *Agonum dorsale* Pont. would not benefit it when looking for live aphid prey that had fallen to the ground, due to the short

residency time before the aphids climbed the crop plants. It was suggested that it would require patches of dead aphids or Collembola to provide aggregations that would result in higher prey capture by *A. dorsale*. Additionally, Mols (1993) showed that when aphids were randomly distributed, klinokinesis resulted in lower prey capture than did a random search.

Harvestmen are generalist feeders (Hillyard & Sankey 1989). Identified prey items include: other harvestmen, small snails, earthworms, millipedes, spiders, earwigs, flies, mites, Collembola, aphids, leaf-hoppers and woodlice (Bristowe 1949; Sankey 1949; Edgar 1971; Sunderland & Sutton 1980). Many of these prey items do not form intense aggregations, so therefore there may be no advantage, or even a disadvantage, for *P. opilio* to have evolved increased klinokinesis and decreased orthokinesis for finding prey. This area would benefit from further research aimed at using established techniques, particularly video, see (Wratten 1994), to study kinesis in harvestmen, to confirm these preliminary results.

4.7 *P. opilio* 'preference' for eggs previously pierced by mites / control blowfly eggs

4.7.1 *P. opilio* 'preference' for freeze-killed eggs pierced by *A. baccarum* or unpierced live, blowfly eggs

The lack of a significant difference between these egg categories was not unexpected. The difficulty in getting mites to feed on eggs, and the low numbers of mites available, meant that the pierced eggs had to be stored for up to 48 h prior to the experiment. It was suspected that being placed on moistened filter paper for this length of time may well have caused any egg contents that had been left by the mite (most mites completely drained the egg) to be absorbed by the paper.

The length of time from piercing to consumption may also have affected the results. As noted in Section 4.1.1, there is very little research on the sensory characteristics of *P. opilio* or the changes to arthropod eggs caused by piercing or mite feeding. Despite refrigeration of the eggs after piercing by *A. baccarum*, it is suspected that the decomposition process and loss of volatiles may have progressed to the point where the egg's 'attractiveness' to *P. opilio* was considerably reduced.

Live eggs were used in these experiments because previous results with unpierced freeze-killed egg indicated that prior freezing influenced egg acceptability by the predators. Therefore, it was considered that the use of live eggs would facilitate a more realistic comparison.

4.7.2 *P. opilio* 'preference' for eggs pierced by *Balaustium* spp. for unpierced live brown blowfly eggs

Results demonstrated that commensal interactions can occur between two predator species in agroecosystems and confirm the observations of Berry (1996), discussed in Section 1.6, that feeding on blowfly eggs by predatory mites in an agroecosystem appeared to be increasing the number of eggs eaten by harvestmen.

The simulation of mite feeding by piercing blowfly eggs with a minuten pin was also justified, although, the lower number of mite-pierced eggs eaten by *P. opilio* in this experiment, compared with hand-pierced eggs (Figure 9) indicated that hand-piercing and mite-piercing may be quantitatively different. This difference was assessed by directly comparing *P. opilio* 'preference' for mite- and hand-pierced eggs (Section 3.10).

4.8 *P. opilio* 'preference' for eggs pierced by *Balaustium* spp. for manually pierced brown blowfly eggs

The significantly smaller number of mite-pierced eggs consumed compared to hand-pierced eggs, means that hand piercing cannot be considered a complete substitute for mite feeding. However, as the reaction of *P. opilio* was qualitatively the same, i.e., both mite- and hand-piercing increased the number of eggs consumed by *P. opilio*, hand piercing can be used to indicate the type of effect mite piercing of eggs would have on *P. opilio* feeding behaviour. There is also potential to refine the technique by using a piercing implement with the diameter of a predatory mite's mouthparts.

While manual piercing has its limitations in simulating mite feeding, there are a number of other arthropods that feed on fly eggs in agroecosystems. For example, Carabidae have been shown to be important predators of eggs of the cabbage root fly (*Delia radicum* L.) (Finch & Elliott 1992a; Finch & Elliott 1992b; Finch 1996). Staphylinidae (Coleoptera) also predate fly eggs (Fincher 1995; Hu & Frank 1997). These beetles chew their prey rather than pierce it (Ball 1985). *P. opilio* may react differently to fly

eggs that have been fed on by predators that chew their prey compared to eggs fed on by predators that pierce eggs and suck out the contents.

It is also possible that other aspects of mite feeding, other than egg piercing, may alter *P. opilio* behaviour. For example, the mites are likely to inject extra-oral digestive enzymes the effect of which may attract *P. opilio*. These effects would be additional to those resulting from changes to the egg following damage. This could also be an interesting area of future research.

Chapter 5: Conclusion

There are a number of implications arising from this demonstration of commensalism between *P. opilio* and predatory mites. These include: the possibility of the existence of similar commensal interactions in agroecosystems and the importance of such interactions in conservation biological control (Barbosa 1998). The work also raises potential methodological problems associated with the pre-treatment of sentinel prey (i.e., introduced prey of the same species as the natural prey of a predator or parasitoid), and the reliability of prey facsimiles (i.e., introduced prey of a different species to that of the natural prey of a predator or parasitoid) (Dent & Walton 1997). This chapter will consider the more specific implications arising from this research, before looking at the broader ecological implications and suggestions for future research.

5.1 Aspects of *P. opilio* feeding behaviour

5.1.1 Lack of kineses in response to prey location by *P. opilio*

The lack of kineses shown by *P. opilio* in response to its location of prey, as discussed in Section 4.6.3, appears unusual. While there are a number of studies showing kinesis in response to prey location and the evolutionary advantages of this strategy among arthropods, for example, the work of Murdie & Hassell 1973; Sabelis 1981; Mols 1986; Casas 1988; McEwen, Clow *et al.* 1993; El Kareim 1998, there has been little research into arthropod species that do not show this kind of behaviour nor any adaptive advantages that it may offer. One example of research that does demonstrate that klinokinesis and orthokinesis may be disadvantageous for a predator is that of Winder (1997) who showed klinokinesis and orthokinesis reduced prey consumption by the carabid beetle *A. dorsale* for some prey species. Research into correlations between a prey species' aggregation level and the types of kinesis displayed by their predators or parasitoids could be a valuable area of future study.

5.1.2 Brown blowfly eggs as prey facsimiles

The commensal interaction between *P. opilio* and *Balaustium* spp. in this study involved only one type of prey - brown blowfly eggs. As discussed in Section 5.1.2, these eggs are an unlikely prey item for *P. opilio* or *Balaustium* spp. in their natural habitat. Therefore, blowfly eggs can be considered to only be prey facsimiles and the direct and immediate application of the findings of this research to agroecosystems may be

limited. However, both *P. opilio* and *Balaustium* spp. feed on a wide range of prey types (Hillyard & Sankey 1989) (Zhang, Z. Q. pers. comm.) (see Section 4.6.3 for details). Some, for example, aphids, of these are readily available to both species and can be found at high densities in agroecosystems (Wratten, Bryan *et al.* 1984; Oakley, Walters *et al.* 1998). Therefore, the commensal feeding interactions of *P. opilio* and mites may involve a number of prey species in agroecosystems, so the impact of the interaction could be wider than suggested by this study. The identification and testing of other common prey species for *P. opilio* and predatory mites could be an important area of further research.

5.1.3 Pre-treatment of sentinel prey and prey facsimiles

Sentinel prey and prey facsimiles have been used to research various aspects of arthropod biology, including mating (Suiter, Patterson *et al.* 1998), parasitism (Lawson, Nyrop *et al.* 1997; Bourchier & Smith 1998; Floate, Khan *et al.* 1999) and predation (Knight, Turner *et al.* 1997). Mills (1997) notes that while non mobile prey stages, for example, pupae, can readily be placed in the field at natural densities to monitor predation losses, it is important that the 'sentinel' prey are no more or less susceptible to predation than is the wild population. The results of this study have clearly shown that freezing blowfly eggs can significantly alter the rate of predation by *P. opilio*. However, freeze-killing is not the only technique that can alter predation rates of prey used for monitoring. Wesloh (1990) estimated that predation of the larvae of the large gypsy moth (*Lymantria dispar* L.) by ants (Hymenoptera: Formicidae) was almost doubled by tethering. This information was used to calculate a factor that could be used to correct the rates of predation of tethered larvae measured in the field. The age of the sentinel prey or facsimile, particularly arthropod eggs, can also alter results. For example, older arthropod eggs can be parasitised less and have lower parasitoid emergence rates than do younger eggs (Powell & Shepard 1982; Suiter, Patterson *et al.* 1998). Even the means of attachment of arthropod eggs to the substrate can also alter parasitism rates (Lawson, Nyrop *et al.* 1997).

Section 4.2 discussed the need for comparisons of predation or parasitism rates of freeze-killed and live prey to determine if they were equivalent. The above examples show that a much wider range of pre-treatments can significantly influence experimental results. Therefore, care is required when using sentinel prey or facsimiles to ensure that experimental methods and handling do this to a minimal extent. Comparisons of different pre-treatment and handling techniques for sentinel prey or

prey facsimiles, for example, those of Weseloh 1990, could help address these problems. However, this may not be possible in studies such as that carried out by Berry (1997) where the number of predator species and individuals in the experiments were not controlled. To compare real prey or facsimiles for all predators in such experiments would be very time consuming.

5.1.4 Time from egg piercing to exposure to *P. opilio*

In all the experiments in this study blowfly eggs were pierced by mites or manually immediately prior to the start of the experiment, with the exception of the experiment using whirligig mites (see Section 3.9.1). In a natural situation there could be a period of several hours or days between an egg being fed on by a mite and then by *P. opilio*. This time delay may alter the reaction of *P. opilio* to the eggs. It may prove valuable to study the effect on egg consumption by *P. opilio* of eggs presented at a range of intervals after piercing.

5.2 Critique of methodology

5.2.1 Benefits and disadvantages of laboratory experiments

These experiments were designed to address the central question of whether a commensal interaction exists between *P. opilio* and predatory mites, as suggested by Berry (1997) from her video monitoring of ground-dwelling arthropod predators in agroecosystems. The experiments also analysed *P. opilio* feeding behaviour to address specific interactions and behavioural questions; a controlled laboratory arena was used to the number of environmental variables that exist in the field (Wyatt 1997). However, a controlled environment can also introduce artefacts which may have altered the behaviour of *P. opilio*. For example, chalcid wasps would not make orientated flights to host olfactory stimuli in the laboratory, but would do so under natural light in a greenhouse because of the absence of polarised light in the laboratory (Kamm 1990).

Particular aspects of these laboratory experiments that may be problematic include the small size of the arena compared with the natural habitat. It is not known how far *P. opilio* can travel in search of food in the field over a 12 h period. However, it can move at considerable speed and could run from one side of the arena to the other, a distance of 320 mm, in two to four seconds. The restricted space may have impacted on the results; however, a circular arena was used in an attempt to address this as it allowed

P. opilio to walk unimpeded, following the edge of the arena allowing *P. opilio* to walk a considerable distance with minimal impediments.

The uniformity of the arena substrate was different from that of the natural habitat of *P. opilio*, which normally consists of tall grasses and other dense vegetation. However, the predator was found in experimental sites used by Berry (1997) that consisted of bare soil. These were mainly sites next to *Cupressus macrocarpa* hedges, where the lack of soil vegetation appeared to be caused by sheep resting there during the night and the plant competition effects of the hedge. It would have been possible to substitute the bare soil of the arena for grass or other vegetation; however this would have made it difficult to video-record *P. opilio* eating blowfly eggs against such a background. The alternative of having most of the arena covered with natural vegetation and the eggs placed on bare soil was considered less desirable than having a uniform arena.

The use of two individuals of *P. opilio* in experiments may have altered their behaviour compared to with the use of only one. This was done to reduce the possibility of no result, which would arise from a single *P. opilio* not eating any eggs (see Section 2.3 for details). However, during collection, *P. opilio* occurred in aggregations of up to twenty individuals. While it is not known if *P. opilio* forages singly or in a group it seems likely that individuals would meet by chance while foraging. Therefore, the use of two individuals does not appear problematic.

Other concerns were raised earlier about various aspects of the experiments; for example, the potential 'preference' for eggs on the periphery of the four-by-four grid of eggs, (see Section 2.9), however, these concerns all proved unfounded.

5.2.2 Brown blowfly eggs as a prey facsimile

Potential problems arising from the use of prey facsimiles were discussed in Section 4.2 and issues surrounding pre-treatment of both sentinel prey and prey facsimiles have been discussed in Section 5.1. These have shown that care is required to ensure that facsimiles produce the same behavioural response in the predator as does the real prey.

In light of these concerns, brown blowfly eggs were used instead of a more commonly occurring prey species of *P. opilio* and mites, because the work of Berry (1996), which was the stimulus for this study, used brown blowfly eggs. The use of another prey species would not have allowed Berry's observations to be pursued experimentally. However, as noted in Section 5.1.2, there would be considerable value in repeating the

experiments using prey species common to *P. opilio* and mites, for example, aphids, to extend the results of this work.

5.2.3 Egg storage

Due to a short hatching time and intermittent supply, live brown blowfly eggs had to be kept in a refrigerator for periods of up to four days. As discussed in Section 5.1 pre-treatment of prey can affect predators' behaviour (Mills 1997). It is unknown if storage in a refrigerator causes any changes to blowfly eggs compared with those that have been kept at ambient temperatures. No comparisons were completed on the effects of storage or egg age on the numbers eaten by *P. opilio*, which is a potential experimental gap. However, for any one replicate, eggs of the same age were always used.

5.2.4 Egg piercing by mites

There are potential shortcomings in the method used obtain mite pierced eggs. The eggs to be pierced were exposed to the mites on a glass coverslip for about 15 minutes, then transferred to the peat-filled Petri dish (see Section 2.13.5). In the field, eggs were pierced *in situ* (Berry 1997), while in the experiment described here, the mites had no contact with the experimental substrate. There may be other changes to the eggs resulting from a mite feeding, other than the piercing of the blowfly egg, that could alter *P. opilio* behaviour. For example, it is possible that mites excrete waste products on to the substrate during feeding and that *P. opilio* may be able to detect these. An alternative design would have been for the mites to feed on the eggs while in their final positions on the peat-filled Petri dish. However, this proved difficult to achieve because of the difficulty of standardising and predicting mite behaviour; therefore severe problems associated with getting mites to feed on eggs on demand.

5.2.5 Value of video recording

Wratten (1994) listed a number of advantages and disadvantages of using video techniques for studying arthropod behaviour, for example, more efficient use of the researchers time and less disturbance to the study animals. A number of these advantages were applicable to this study. For example, video recording allowed considerably more detailed data to be gathered than could otherwise have been achieved without excessive expenditure of time. It also allowed more detailed analysis to be achieved, for example, rates of egg consumption. More importantly, it allowed a much

better understanding of the behaviour of *P. opilio*, including what constituted prey inspection by *P. opilio*. Therefore, video recording was an essential part of the experimental method and was responsible for a number of key results and explanation of *P. opilio* behaviour in the present work.

The use of video techniques in laboratory studies is less problematic than in the field, as there is easy access to electrical power, protection from the weather, better security, and equipment can be left *in situ* for long periods of time (Varley, Copland *et al.* 1994). These were the main reasons why video was selected for use in this study.

5.2.6 The use of field-captured *P. opilio*

P. opilio in the United Kingdom is generally univoltine, with individuals becoming mature from mid summer onwards (Hillyard & Sankey 1989). Eggs are laid in the autumn and hatch in the following spring. There are occasional reports of a second generation on the English south coast (Hillyard & Sankey 1989). In contrast, all life stages of *P. opilio* were found all year round at the collection site in the present study (see Section 2.1 for details), except for eggs, which were not searched for.

The relatively slow growth of *P. opilio* meant that it would have taken several months to establish a laboratory colony to provide sufficient numbers of the predator for experiments. In addition, Klee (1968) found that a fixed humidity resulted in the death of the third and fourth instars, and that a daily variation in humidity was required for these immature stages of *P. opilio* to survive. It was impossible to vary the humidity in the room containing the vivarium and experimental arenas due to a lack of suitable control equipment. Therefore, to mass-rear *P. opilio* would have required additional vivaria kept in an area where humidity could be varied diurnally.

Collecting the predators from the field also had the benefit of avoiding potential changes to their behaviour that could occur in laboratory cultures (Wyatt 1997). However, it was also possible that individuals collected at different times of the year may have behaved differently (Sankey 1949).

5.3 Commensalism between arthropod predators in agroecosystems

5.3.1 Length and level of commensal interactions

Commensal interactions can be both long and short term, and occur at a range of levels, for example, individual or population (Abrams 1987; 1992; 1995) and within or between trophic levels. This study has shown a commensal interaction between *P. opilio* and *Balaustium* spp. only at the individual level over the short term. No additional prey were killed as a result of the *P. opilio* mite interaction as mite feeding alone is enough to kill the blowfly egg. This may be true for other potential prey species discussed in Section 5.1.2. Therefore, a decrease in the prey population in the short term appears unlikely, as no additional prey are killed.

For the mite-harvestmen interaction to reduce pest populations, a long-term effect would need to be demonstrated (Hodge & Wallace 1996). However, the interaction may not be commensal over the long term. Unlike the aquatic, beetle / midge / mosquito ecosystems, discussed in Section 1.6 where the species involved did not directly interact with each other (Heard 1994; Paradise & Dunson 1997), *P. opilio* feeds on mites (Sankey 1949). Because of this it is not known what impact an increase in the population of *P. opilio* would have on the mite population. One possibility is that an increased *P. opilio* population would result in more mites being eaten by *P. opilio*. In this instance the *P. opilio* / mite interaction would be contramensal (Arthur 1986; Arthur & Mitchell 1989) i.e., one species has a positive effect on a second, which then has a negative effect on the first. In contrast, in the aquatic system discussed above, an increase in the population of the first species caused a population increase in the second, without then reducing the population of the first (Hodge & Wallace 1996).

Therefore, to make predictions of the effect of the mite-harvestmen interaction at the ecosystem level the laboratory-based results from this study need to be reproduced in the field and extended to study the longer term effects of the interaction. Berry (1997) began this, but that was a very preliminary investigation.

5.3.2 The potential for other inter-predator commensal interactions in agroecosystems

While this research has demonstrated the existence of a particular commensal interaction between *P. opilio* and predatory mites, it is only one example and it may turn out to be contramensal in the long term (Section 5.3.1). For inter-predator commensalism to have a significant impact on pest populations in agroecosystems, evidence is required of interactions between other predator species. However, most inter-specific interactions in agroecosystems are 'negative', for example, competition for resources, predation, parasitism, competition between predators within a guild (Rosenheim, Wilhoit *et al.* 1993; Evans & England 1996; Lucas, Coderre *et al.* 1998), superparasitism and hyperparasitism. Also, it is only recently that researchers have started to focus on the combined effects of predators, for example, predation by a guild rather than by individual predator species. There is little work on 'positive' inter-specific interactions and none on commensalism between predators. It is, therefore, unknown how common the latter type of interaction is in agroecosystems.

However, a study by Dennis (1994), while not directly looking for commensal interactions, indicated that staphylinid and carabid beetles could be in a commensal relationship. Dennis researched the activity of staphylinid beetles, principally *Tachyporus* spp., to determine their ability to climb cereal plants to reach aphid colonies. Nine and a half percent of the total aphid population was eaten and 35% was displaced to the ground where they were at risk of predation from epigeal Carabidae. Therefore, the disturbance of aphids by *Tachyporus* spp. could increase the number of aphids consumed by carabids, without *Tachyporus* spp. suffering any loss of prey resource - a commensal relationship. It would be valuable to repeat Dennis's experiments and compare the numbers of aphids eaten by carabids foraging in cereal crops with and without *Tachyporus* spp. present, to determine if a commensal relationship does in fact exist. There are parallels here with the idea of a more removed interaction between trophic levels. Induced defences in the first trophic level (plants) can enhance herbivore movement and may make these herbivores more vulnerable to epigeal predators (Hodge, Wratten *et al.* 1999).

If a commensal interaction does exist between *Tachyporus* spp. and carabids, it would be of a different nature from that of the mite / *P. opilio* relationship. The mites killed prey items followed by *P. opilio* consuming the remains while *Tachyporus* spp. caused aphids to fall off the cereal plants onto the ground, due to either an alarm pheromone

response or physical disturbance (Quarles 1999). Carabids, lacewings and other predators alter their behaviour in response to aphid alarm pheromones (Boo, Chung *et al.* 1998; Kirkland, Evans *et al.* 1998; Quarles 1999). Therefore, the effect of *Tachyporus* spp. may be two-fold - to cause aphids to fall to the ground within reach of carabids and to increase the numbers of carabids in the area mediated via an aggregated numerical response (Barlow & Wratten 1996) due to the release of alarm pheromones from aphids.

5.4 Suggestions for future research

5.4.1 Effects of freeze-killing and piercing of eggs on the ability of *P. opilio* to detect them

Having shown that freeze-killing, manually piercing and mite feeding on blowfly eggs significantly increased consumption by *P. opilio,* the causes of this increase need to be studied. There are two aspects to this. Research into the physical and chemical changes to the prey due to freezing or manual or mite piercing, and the chemoreception abilities of *P. opilio*. For example, freezing insect tissue ruptures cell membranes (Ohyama & Asahina 1972) and electron-micrographs of blowfly eggs is certain to reveal changes due to freezing.

5.4.2 Fluid-feeding predators in agroecosystems

The importance of fluid feeders, such as spiders and mites, in pest control in agroecosystems may well be underestimated. For example, Nyffeler *et al.* (1990) reviewed the literature on spiders as predators of insect eggs, and found that spiders from the families Salticidae, Oxyopidae, Lycosidae, Clubionidae and Anyphaenidae, consumed insect eggs from five Lepidopteran families and also eggs of Coleoptera in the family Curculionidae. However, spiders are often ignored in studies predation of insect eggs and therefore their role is underestimated. Exclusion of fluid feeders is in part due to the difficulties of studying such predators; for example, they are often smaller and have nocturnal habits than other commonly-studied species such as beetles and hoverflies (Walter, Frampton *et al.* 1995). Also, dissection of mandibulate predators, which chew their prey is relatively easy and can allow ranking of predator species in relation to particular prey groups, such as aphids (Sunderland & Vickerman 1980). However, techniques such enzyme-linked immunosorbent assay which are more

costly and time-consuming are needed for fluid feeders (Sopp & Chiverton 1987). Further research into the roles of fluid feeders as predators in agroecosystems would be beneficial.

5.4.3 Kinesis reactions in predators and parasitoids

With the lack of obvious klinokinesis or orthokinesis in *P. opilio* after locating food, and indications that food intake by carabids could be lower for some food sources because of klinokinesis and orthokinesis than if they exhibited a random searching pattern (Winder, Wratten *et al.* 1997), there is a need for research into the benefits and costs of kinesis in predators and parasitoids whose prey / host species show different levels of aggregation, with an aim of showing a relationship between the extent of klinokinesis or orthokinesis displayed by the predator or parasitoid and the level of prey / host aggregation.

5.4.4 Inter-predator commensal and mutual effects

As discussed in Section 5.3.2, most inter- and intra-specific interactions studied in agroecosystems concern negative effects, either competition, amensalism or contramensalim (Hodge & Wallace 1996). Relatively few studies consider positive interactions, whether either commensalism or mutualism, between predators or parasitoids. There is a clear need for further research to establish the existence of other commensal or mutual relationships between predators and / or parasitoids, and to determine how common they are and their impact on pests in agroecosystems.

Chapter 6: References

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