From Individuals to Ecosystems

A Study of the Temporal and Spatial Variation in Ecological Network Structure

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I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

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Abstract

Ecological network theory has developed from studies of static, binary trophic relationships to the analysis of quantitative, dynamic communities consisting of multiple link-types. Particularly, work has focused on the dynamic nature of ecological networks, which maintains stability in complex communities. However, there are few *in situ* network-level studies of the determinants of temporal and spatial variation in community structure. This thesis utilises data from a 10-year study of a host-parasitoid network and a collaborative study in an applied ecological setting to identify individual level factors important to network structure. The work aims towards an empirical, predictive framework linking adaptive foraging behaviour to ecological network structure.

The results show that condition-dependent foraging behaviours structure host-parasitoid networks. The realised niches of the studied parasitoid species were generally biased towards larger host species and condition-dependent sex ratio allocation increased the likelihood that females would eclose from relatively larger hosts and males from relatively smaller hosts, which resulted in sex ratios deviating from Hamiltonian (50:50) predictions. Further, both of these aspects of behaviour are plastic, where parasitoid behaviour responded to environmental heterogeneity. Particularly, host preference behaviour conformed to an egg-/time-limitation framework, where the size dependency of the behaviour is greater when individuals have a greater likelihood of being egg-limited. Both the size-dependency and the plasticity of these behaviours differed significantly between secondary parasitoid species. This species identity effect interacted with landscape heterogeneity, which may explain some inter- and intra-specific variation in network structure. With respect to applied ecology, the results show that the benefits of natural vegetation for pest control are dependent upon the dispersal capabilities and the diet breadth of the pest and its natural enemies.

The findings are evaluated towards a predictive framework for understanding the effects of future climate change on community structure and stability. We consider this framework in terms of applied ecology, particularly pest control ecosystem services provided by natural vegetation in an agricultural environment. The synergistic nature of the multiple determinants of network structure found in this thesis suggest that future studies should focus on the whole network, which is not necessarily the sum of its parts.

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Thanks to my friends and family who managed to visit me in the beautiful corner of the world and from whom my character, ambitions and self-assurance manifest.

My dearest Louisa, although your name is not on any author list this is as much your success as it is mine.

Now that it is finally finished with; I have time to do something that I have wanted to do for a very long time...

To my foundation
and moral compass,
empathic lodestone
and sense of purpose.
So full of beauty,
within and without.
I love you truly
and without doubt
you are the strongest
person that I know.

For each reason here
and so many more,
everything you are
and that you stand for.
I ask one question,
of my hoped-for wife.
Can my profession
and one task for life
be to be your star,
forever aglow?

Louisa Rose Briggs, will you marry me?

“It always seems impossible until it is done”

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Chapter 4. Henri, D.C., Hodgson, D., Shuker, D. & van Veen, F.J.F. (**In Review**) Field evidence of the 'relativity' of condition-dependent sex allocation. *Nature*

Chapter 2. Henri, D.C., Seager, D., Weller, T. & van Veen, F.J. (2012) Potential for climate effects on the size-structure of host-parasitoid indirect interaction networks. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367, 3018-3024.

Cha[ter 1. Henri, D.C. & van Veen, F.J.F. (2011) Body size, life history and the structure of host–parasitoid networks. *Advances in Ecological Research*, 45, 136-174.

Chapter 1 Body Size, Life History and the Structure of Host-Parasitoid Networks

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1.1 Abstract

Recent studies of the allometric scaling of metabolism, resource handling and space use have provided a mechanistic understanding of how interactions within ecological networks are arranged. Especially, the ‘allometric diet breadth model’ (ADBM), which considers the association between consumer size, resource availability and handling costs, has shown that food webs are predictably shaped according to the body-size relationships of the organisms within them. However, size-based models of network structure are more applicable to predator-prey webs than to insect host-parasitoid networks because the relationship between body-size and host use appears to be less straightforward in host-parasitoid interactions. Herein, we describe the structuring of host-parasitoid networks using frameworks that are based not only upon parasitoid body-size considerations, but also upon the life-history characteristics that are commonly used to describe variation among

hymenopteran parasitoids: the degree of ovigeny, idio/koinobiosis and endo/ectoparasitism. We compare these frameworks with those suggested by the ADBM and elucidate upon why it has been unable to successfully predict host-parasitoid network structure. For instance, body-size constraints upon foraging capability are a stronger determinant of whether an interaction is possible in predator-prey webs than they are in host-parasitoid networks because the ultimate determinant of host-suitability is its phylogeny. Furthermore, the degree to which the taxonomic host range of a parasitoid is constrained by phylogeny is largely determined by parasitoid life-history, e.g. whether the larva develops as an endo- or ecto-biont. In addition, we describe how parasitoid life-history influences host-choice decisions, which are expected to be tailored towards the optimal allocation of scarce resources, through the determination of how species are limited in their reproductive success. To conclude, we describe some fruitful avenues for future research and highlight the importance of considering how temporal or spatial variation in the characteristics of parasitoids or their hosts affect how networks are structured.

1.2 An Introduction To Ecological Network Theory And Host-Parasitoid Networks

Ecological networks and their role in ecology

Ecological networks document the interactions among organisms within an ecosystem, such as predators feeding upon prey or insects pollinating plants (Woodward *et al.* 2005; Ings *et al.* 2009). Networks are generally resolved at the species level, where each species forms a node within the network and a link demarks which pairs of species have been observed (or are assumed) to be interacting (Woodward *et al.* 2005), although more recent work has emphasised the role of individual-level interactions (Woodward *et al.* 2010b; Gilljam *et al.* 2011). Although ecological networks have been perceived to be difficult to compile and analyse, the study of how species interact has taken a central role in investigating key aspects of ecological theory; such as the complexity-stability debate (the ongoing debate as to whether biodiversity promotes long-term ecological stability) (McCann 2000), and the debate as to which species should receive priority in the global conservation effort (i.e. either rare, endemic species most at risk of extinction or those that are integral to the stability of ecosystems (Ings *et al.* 2009). Furthermore, the investigation of the properties and structure of ecological networks has been shown to be a powerful tool for use in applied ecology, such as assessing the impact of biological perturbations within ecosystems (e.g. invasion of an ecosystem by an alien species or a biological control) and determining the effectiveness of conservation programmes (Memmott 2009). Because of the wide-spread importance of networks within the field of ecology, understanding the mechanisms by which interactions within networks are structured has been highlighted as a priority for future research (Ings *et al.* 2009).

Most published ecological networks belong to one of three categories, which are defined by the nature of the interactions between the individuals within the network (Ings *et al.* 2009). Most commonly studied are food-webs, which depict antagonistic interactions that transfer energy across trophic levels, focussed particularly upon predator-prey and primary consumer- basal resource relationships (Hall & Raffaelli 1993; Ings *et al.* 2009). Host-parasitoid networks also depict antagonistic interactions, but they are typically focussed on a particular guild of insect herbivores and their specialist parasitoid enemies (Hawkins 1992). Mutualistic-networks consist of beneficial interactions between species, such as plant-pollinator interactions. While much of the pioneering work on ecological networks was carried out in terrestrial host-parasitoid systems, the recent emphasis on the role of body-size in ecological network structure has resulted in the increased prominence of aquatic food webs and “traditional” predator-prey interactions; e.g. Gilljam *et al*. (2011). However, due to recent recognition of the importance and prevalence of parasitoid interactions within ecosystems (Lafferty *et al.* 2008) and the relative ease with which links in these networks can be identified and quantified (van Veen, Memmott & Godfray 2006), there has been a resurgence in the number of studies considering host-parasitoid networks (Ings *et al.* 2009).

Host-parasitoid networks

The study of host-parasitoid networks considers a specific type of trophic interaction in which the ‘prey’ resource is used as a nursery for offspring, as opposed to as an energy source for the foraging adult. In insects, parasitoidism describes a life-style in which the parasitoid oviposits in, on or near a suitable host that the hatched larvae will consume during development, which always results in host death (Quicke 1997). Although the parasitoid life-cycle has evolved in many insects groups, including the Diptera and Coleoptera, the greatest diversity of parasitoids has been described in the Hymenoptera

(Quicke 1997). Roughly half the currently described species within the order Hymenoptera are parasitoids, ~57,500 species according to Sharkey (2007), although it is predicted there are significantly more undescribed parasitoid Hymenopteran species than non-parasitoid species. Estimates suggest if all insect species were described then 10-20% of them would be parasitoid wasps, according to estimates of total Hymenopteran diversity being between 300,000 to 3 million species (Whitfield 1998; Pennacchio & Strand 2006; Sharkey 2007). As a result of the ubiquity of parasitoid wasps within ecosystems, most host-parasitoid networks - and thus the empirical evidence referenced in this review - have considered these organisms, rather than parasitoids from other insect orders.

Previously defined parasitoid networks have generally considered two fixed trophic levels, in an analogous manner to mutualistic networks, consisting of primary parasitoids (for definitions and examples of terms describing the traits of parasitoids, their hosts or host-parasitoid networks, please see Table 1) and their hosts (Memmott, Godfray & Gauld 1994; Rott & Godfray 2000; Lewis *et al.* 2002; van Nouhuys & Hanski 2002; Cagnolo, Salvo & Valladares 2011b). The hosts of the primary parasitoids considered in parasitoid network studies are generally phytophagous arthropods of a particular guild (Hawkins 1992), e.g. leaf miners (Memmott, Godfray & Gauld 1994; Rott & Godfray 2000; Lewis *et al.* 2002). Other studies have considered another, higher trophic level that comprises of the secondary parasitoids, which feed on the primary parasitoids (Müller *et al.* 1999; van Veen *et al.* 2002; Eveleigh *et al.* 2007; Bukovinszky *et al.* 2008). This secondary-parasitoid trophic-level is not always as fixed as the lower levels, and some species are facultative hyperparasitoids, switching from a primary to a secondary parasitoid life-history under conditions of high inter/intra-specific competition (Sullivan 1987; Eveleigh *et al.* 2007; Mustata & Mustata 2009). Further trophic levels of hyperparasitoids have been documented that include tertiary and quaternary parasitoids, but such instances are probably rare (Mustata & Mustata 2009). Due to the importance of plant assemblage in determining host, and therefore parasitoid, communities, host-parasitoid network studies may also include information regarding the host-plants, which make up the bottom trophic level in these networks (Tylianakis, Tscharntke & Lewis 2007; Petermann *et al.* 2010). The hosts of primary parasitoids often comprise parts of the diets of “true” predators within the same ecosystem, suggesting there is potential for indirect competitive interactions between components of host-parasitoid networks and food webs (Memmott, Martinez & Cohen 2000; van Veen *et al.* 2008). Furthermore, direct interactions between predators and parasitoids may have a significant impact on the structure of both types of network; for example, the ladybird beetle, *Harmonia axyridis*, feeds upon larvae of *Aphidius evri*, a parasitoid wasp, while they are inside their aphid hosts (Synder & Ives 2003), or the parasitoid wasp *Dinocampus coccinellae* which utilises ladybird species as hosts.

Table 1-1 Key definitions with regard to parasitoid physiology and host-parasitoid network structure.

n/a = example species not applicable because terms are concepts or actions and, as such, are not embodied by any particular species.

Term	Definition	Example species (Family)
Eclosure	The act of an adult parasitoid emerging from its pupa.	n/a
Ectoparasitoid	The larvae of the parasitoid feeds upon the host externally.	*Nasonia vitripennis* (Pteromalidae)
Egg parasitoid	A specific type of parasitoid that attacks the eggs of its hosts.	*Dicopomorpha echmepterygis* (Mymaridae)
Electivity	The degree to which a consumer shows preference in which resources it consumes.	n/a
Endoparasitoid	The larvae of the parasitoid feed upon the host from inside of it.	*Aphidius evri* (Braconidae)
Host-plant	Plant on which the hosts of the primary parasitoids can be found.	n/a
Hyperparasitoid	Any parasitoid species that feeds upon other parasitoids	Alloxyistini: hyperparasitoids of aphids (Figitidae, Charipinae)
Idiobiont	Parasitoid species life-history trait in which the host development is arrested by the act of oviposition.	"Tarantula hawk" (*Pepsis* spp.; Pompilidae)

Koinobiont	Parasitoid species life-history trait in which the host continues development after a successful oviposition event.	*Aphidius evri* (Braconidae)
Mummy	A cocoon formed by the parasitoid larva within the dried exoskeleton in which it pupates.	n/a
Mummy parasitoid	Specific type of hyperparasitoid that attacks its hosts during the mummy stage.	*Asaphes vulgaris* (idiobiont hyperparasitoid of aphids) (Pteromalidae)
Oviposition	The act in which females parasitoids lay their eggs.	n/a
Primary parasitoid	A trophic level in host-parasitoid networks; describes a parasitoid that attacks non-parasitoid hosts (such as aphids).	Aphidinae: parasitoids of aphids (Braconidae)
Pro-ovigeny	A parasitoid life-history trait where the parasitoid ecloses with its entire egg complement in a mature state; can be an adjective, i.e. more pro-ovigenic. Exists on a spectrum with the other end being represented by a synovigenic life-history.	*Copidosoma floridanum* (Pteromalidae) a pro-ovigenic parasitoid wasp.
Synovigeny	A parasitoid life-history trait where the parasitoid matures its eggs of the course of its adult life-time; see pro-ovigeny.	*Gelis agilis* (Ichneumonidae), a synovigenic parasitoid wasp

The importance of host-parasitoid networks in ecological research

Host-parasitoid interactions are prevalent within natural ecosystems, and parasitoid organisms are considered to be the most important biological control agents used in agriculture and conservation, with parasitoid wasps saving the U.S. agriculture industry, through the control of crop pests, an estimated $20 billion a year (Pennacchio & Strand 2006; Mills & Wajnberg 2008; Pennisi 2010). The prevalence and importance, as well as key differences in structure compared to food webs, of host-parasitoid networks have led to important studies across a range of key ecological issues (Lafferty *et al.* 2008; Ings *et al.* 2009). Furthermore, the inclusive study of multiple networks is important as different network types do not exist separately of one another and the structure of one network type can have important effects upon species composition and interaction strength in other network types (Ings *et al.* 2009). For example, studies of the mutualistic protection of honey-dew producing aphids by ant species have shown that defensive behaviour differentially excludes parasitoid species and significantly affects the functional composition of both primary and secondary parasitoid species communities (Mackauer & Völkl 1993; Sanders & van Veen 2010).

Incidences of interaction and resource densities are much easier to count in host-parasitoid networks than in food-webs, which means that, as opposed to binary webs that only include presence or absence data, the strength of the interactions between species can be quantified (van Veen, Morris & Godfray 2006). The quantification of interaction strengths within trophic networks has been identified as a key area of interest in ecology (Ings *et al.* 2009); quantified webs have the potential for use in the identification of key-stone species (Jordán, Liu & van Veen 2003), the assessment of indirect effects within trophic networks (van Veen, Morris & Godfray 2006; Tack, Gripenberg & Roslin 2011), and the role of host abundance and characteristics in parasitoid foraging behaviour (Cagnolo, Salvo & Valladares 2011b), as well as for practical use within applied ecology (Memmott 2009).

Host-parasitoid interactions have a long history of use in the study of behaviour as foraging and reproduction are directly linked in these networks, as opposed to predator-prey interactions where reproduction is indirectly mediated through energy transfer (Cook & Hubbard 1977; Hubbard & Cook 1978). Patch time allocation, the length of time that a forager spends utilising a particular patch of resources, controls the distribution of individuals within their habitat according to available resources, and has been studied with parasitoids as model organisms (Hubbard & Cook 1978; Wajnberg 2006). The importance of individual behaviour upon population level processes, such as the impact of patch time allocation on population distribution, has been suggested to be an important aspect in understanding the structure of trophic networks (Abrams 2010; Valdovinos *et al.* 2010), although little work has been done on foraging behaviour in a multi-species environment.

1.3 The Aims of This Review

Keeping in mind the impending focus upon studies that consider multiple network types within the same ecosystem, it is important that host-parasitoid networks are well-understood to promote collaboration and the development of better-integrated ecological network theory (Ings *et al.* 2009). Recently, studies aimed at providing a mechanistic understanding of the way in which interactions are structured within food-webs and mutualistic networks have focussed on the role of body-size as a predictor of which species pairs interact with each other (Brose *et al.* 2006; Petchey *et al.* 2008; Stang *et al.* 2009; Arim *et al.* 2010). The next section will cover, in brief, what is meant by network structure and how optimal foraging theory has been used to predict it in food-webs according to species characteristics. We will then discuss the applicability of these studies to host-parasitoid networks and suggest a general framework for understanding the mechanisms that determine ‘who eats whom’ in host-parasitoid networks, based on how parasitoid life-history characteristics, such as those defined in Table 1, constrain or facilitate parasitoid-host interactions.

1.4 The Structuring Of Trophic Networks

What is network structure and how is it determined?

Globally, not all species are capable of interacting directly as there are numerous barriers that prevent species from coming into contact with one another. These barriers, which may be spatial, temporal, morphological or a combination of both, determine a species’ fundamental niche, which, in terms of ecological networks, describes all the other species with which a species can potentially successfully interact (Shipley, Forbey & Moore 2009). Interactions between species that, because of these barriers, are unable to occur are called ‘forbidden interactions’ (Oleson *et al.* 2010). Ecological networks, however, actually depict a species' realised niche, which describes the proportion of other species a species interacts with out of all the possible species with which it can interact (Shipley, Forbey & Moore 2009). Therefore, when we attempt a mechanistic understanding of ecological network structure, we are investigating the processes that determine who interacts with whom (and who doesn't) as well as the relative strength of these interactions.

Importantly, and not surprisingly, network structures are very different from what would be produced if species interacted at random (Brose *et al.* 2006). Optimal foraging theory suggests that individuals must maximise their resource consumption, whilst at the same time minimising the cost (to fitness) associated with acquiring and consuming the resource (Hubbard & Cook 1978). Therefore, we expect individuals to consume the most 'profitable' resources in order to forage optimally and thus maximise individual fitness. Across all network types, species interactions may be ordered according to trait-pairing characteristics, which impede or facilitate interactions between individuals; through this process, the relative profitabilities of resources change according to these characteristics (Vazquez, Chacoff & Cagnolo 2009). For example, in mutualistic pollinator networks, flowers with longer corollas have stronger interactions with pollinators that have longer proboscises, as the size of the corolla imposes a minimum size threshold for any pollination interaction (Vazquez, Chacoff & Cagnolo 2009). In reference to optimal foraging theory, one expects that interactions within ecological networks are structured according to the relative profitabilities of different resources, and, as a result, because of the individual characteristics that determine resource profitability (Petchey *et al.* 2008); with the strongest interaction occurring between consumers and their most profitable resources. Furthermore, trait-pairing characteristics determine the currency by which optimality is achieved. An example of how different currencies of optimisation effect network structure can be found in host-parasitoid networks (Figure 1-1). It is thought that parasitoids forage optimally (see page 35), but traits that determine the fitness gains from parasitizing a particular host species, such as the foraging or handling efficiency of the parasitoid and the quality or riskiness of the host, determine whether the host-parasitoid interaction strengths are structured according to the relative abundance of each host species (Figure 1-1a) or according to other host characteristics (such as quality) (Figure 1-1b). The adoption of either of these two strategies can be explained by whether parasitoids are optimally allocating eggs or time (see page 44).

The most important characteristics determining a species' realised niche are those that dictate how it interacts with other species (McGill *et al.* 2006). However, the relative importance of different characteristics in determining network structure can be expected to differ among network types. Body-size is often an important trait-pairing characteristic in mutualistic networks and food webs, and determines ecological network structure directly as well as through indirect interactions with other characteristics (Woodward *et al.* 2005; Vazquez, Chacoff & Cagnolo 2009).

Body-size as a determinant of food-web structure

In food-webs, the size of an individual typically correlates closely with life-history and ecology, which affect how individuals interact. For example, larger organisms exhibit a greater scale of movement and bigger home-ranges than smaller ones (Jetz *et al.* 2004). Scale of movement can cover many orders of magnitude, according to the abiotic environment, and increases in a non-linear fashion with individual body-size (Rooney, McCann & Moore 2008). This is because the energetic cost of movement is reduced in larger organisms (Brown *et al.* 2004; Woodward *et al.* 2005). The allometric scaling of range size suggests that larger individuals forage in a more heterogeneous environment, and are more likely to interact with a wider range of species than smaller predators (Rooney, McCann & Moore 2008). In terms of network structure, this means larger predators potentially have a broader fundamental niche (Gilljam *et al.* 2011) and, due to the reduced cost of moving between resource items, are more likely to exhibit preferential prey selection, akin to the parasitoid in Figure 1-1b (Rooney, McCann & Moore 2008).

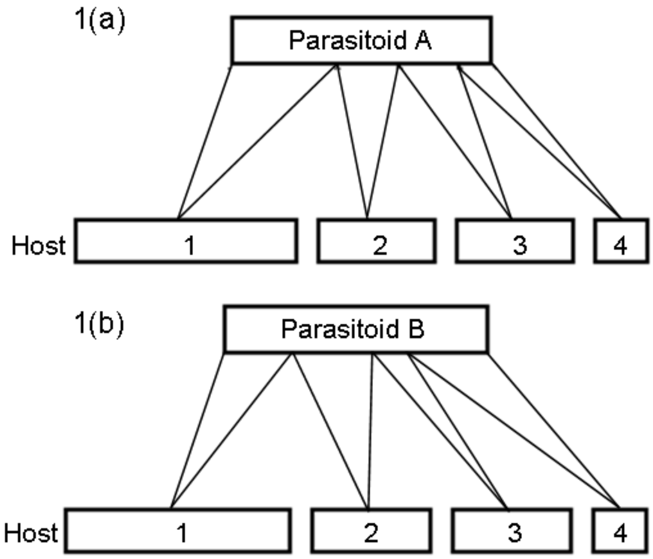

Figure 1-1: Hypothetical quantitative networks illustrating relative interaction strengths between two different parasitoid species and their hosts.

Widths of the boxes indicate abundance of the species within the ecosystem, and width of the interaction arrows at the base indicate the proportion of the parasitoid population that is derived from each respective host species; wider arrows indicate a stronger interaction between the parasitoid and that host species. (a) Parasitoid species A attacks every viable host it encounters; resultantly, the relative strengths of each host-parasitoid interaction have been determined by the relative abundances of each host species. (b) Parasitoid species B preferentially attacks hosts according to their characteristics, resulting in interaction strengths determined by these characteristics.

An important aspect of the size-structuring of food-webs is the relationship between body-size and trophic level (Gilljam *et al.* 2011; Yvon-Durocher *et al.* 2011). In many food webs energy flows from many, small organisms to fewer, large ones (Brose *et al.* 2006). Studies have suggested that the ordering of trophic links in this way can be attributed to how foraging traits co-vary with body size, whereby larger individuals have more potential pathways of energy available from which they can sustain their greater individual biomass (Woodward *et al.* 2005; Brose *et al.* 2006; Petchey *et al.* 2008; Arim *et al.* 2010). This is because, in predator-prey interactions, many so-called “forbidden interactions” are related to the mismatching of body-size as a trait-pairing characteristic (Oleson *et al.* 2010). Conversely, the strength of body-size as a constraint upon potential feeding interactions is a continuous variable dependent upon the type of interaction; for example, benthic suspension feeders often do not have diet breadths constrained by the size of the consumer, as a result, in these interactions resource size does not scale with consumer size (Riede *et al.* 2011; Yvon-Durocher *et al.* 2011). Arguments based on ‘gape limitation’ have described the manner in which body-size is related to trophic status in fish, as the diet of a fish is severely limited by the shape of its feeding apparatus; however, this limitation is reduced in larger individuals compared with smaller ones (Arim *et al.* 2010). As a result of this relaxation with increased body-size, larger predators are able to feed on a broader range of species from a wider range of habitats, simultaneously increasing the number of available energy pathways and the individual’s ‘trophic-level’ (Woodward *et al.* 2005; Brose *et al.* 2006; Arim *et al.* 2010). Petchey *et al*. (2008) and Woodward *et al*. (Woodward *et al.* 2010a), who utilised individual-based data and found an even stronger fit, successfully predicted the organisation of trophic interactions in a range of food-webs utilizing hypothesized allometric scaling of predator handling time and prey nutritional content, and optimal foraging theory. In the model, termed the allometric diet breadth model (ADBM), the size of the largest prey that could be successfully handled exhibited a steeper relationship with body size than the smallest, meaning larger predators had a wider potential diet breadth than smaller ones (Figure 1-2a). Furthermore, larger predators incurred reduced costs when preying on larger, more nutritious prey compared to smaller predators; thus, changing the relative profitabilities of different resource items for different sized consumers (Figure 1-2b). (Brose *et al.* 2006; Petchey *et al.* 2008). In all of these studies, the requirements associated with greater body-size are met by the allometric scaling of energy availability, and hence the allometric scaling of trophic level (Sole & Montoya 2001).

The structure of host-parasitoid networks

Due to the way in which parasitoids interact with their hosts, the relationship between body-size distributions and host-parasitoid network structure is less obvious than in food-webs. However, as we will argue, size-based foraging decisions can be an important structuring force in these networks but depend strongly upon species life-history. The next section will discuss how the fundamental niche of a parasitoid is determined by its evolutionary history. Then we will discuss the manner in which parasitoid traits determine realised niche.

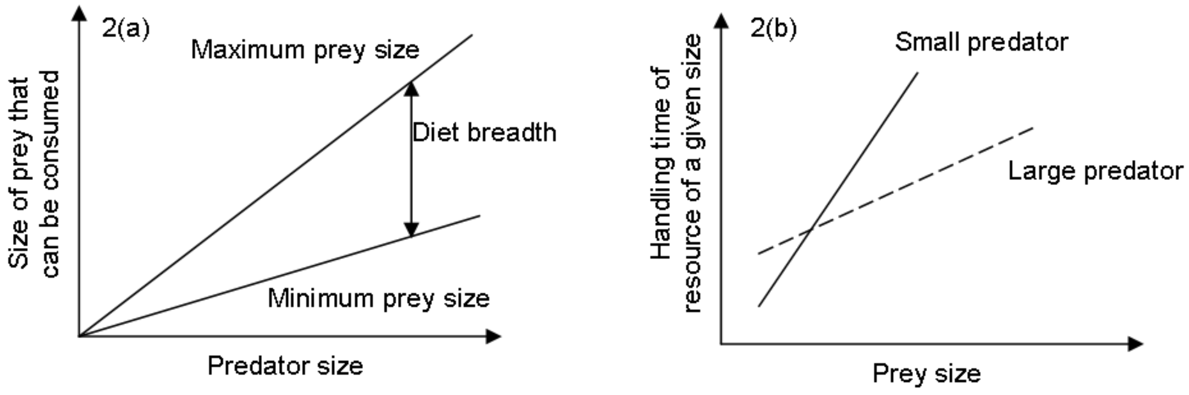

Figure 1-2 Illustrations of how body-size is thought to determine network structure in food-webs:

(a) Diet breadth, in terms of the size of available prey, increases with predator size because the size of the largest prey resource that can be handled successfully scales faster than the size of the smallest (Petchey *et al.* 2008)*. (b) The cost associated with handling resource items increases with the size of the resource item, which is proportional to its nutritional value; however, handling costs covary with consumer size in such a way that larger predators incur smaller costs from handling larger prey items than smaller predators. In a recent extension of the model, Woodward et al. (Woodward et al. 2010a) found that the accuracy with which network structure could be predicted by the ADBM increased markedly when size classes of individuals, irrespective of species identity, were used in a range of aquatic food webs, highlighting the overarching effect of size versus taxomonic identity in these systems.*

1.5 Limitations On Host Range

Fundamental niches in host-parasitoid networks

An ecologically important difference between food-webs and host-parasitoid networks concerns 'host range or diet breadth' (Memmott, Martinez & Cohen 2000; van Veen *et al.* 2008), which refers to the range of host/prey species with which each parasitoid/predator species interacts in their respective networks. For food-webs this is species consumed (Memmott, Martinez & Cohen 2000; Petchey *et al.* 2008), whereas in host-parasitoid networks it is the number of host species in which a parasitoid oviposits (van Veen *et al.* 2008). Diet breadth is determined by the range of species with which a forager can successfully interact, i.e. the fundamental niche. In parasitoids, this is species from which offspring can complete juvenile development (van Veen *et al.* 2008). Parasitoids are generally more specialist than predators, and thus have narrower diet breadths, due to the physiological constraints associated with the parasitoid life-history, such as over-coming host defences, successfully recognising viable hosts and ensuring the larvae has access to host biomass (Mackauer, Michaud & Völkl 1996; Quicke 1997; Whitfield 1998). These constraints are opposed to the idea presented in food-webs, where the diet breadths of predators are thought to scale allometrically, and as a result so does their trophic level (Brose *et al.* 2006; Petchey *et al.* 2008; Arim *et al.* 2010).

Fundamental niche constraints result in generalised differences between host-parasitoid networks and food-webs. For example, a greater reliance on fewer host species for nutrition results in high levels of trait-matching between parasitoids and their hosts (Memmott, Martinez & Cohen 2000; van Veen *et al.* 2008; Ings *et al.* 2009). Furthermore, a narrower 'diet breadth' results in many strong interactions between species, and networks that consist mostly of strongly interacting species are prone to reduced stability (van Veen *et al.* 2008; O'Gorman & Emmerson 2009). The strong interactions between the components of host-parasitoid networks have been suggested to be an important aspect of the effectiveness of parasitoid biological control programmes (Mills & Wajnberg 2008).

The role of phylogeny in host-parasitoid network structure

Due to the intimacy of the interaction between host and parasitoid, host defences and parasitoid counter-offenses are highly specialised. This may lead one to expect that diet breadth and network structure in these systems are determined by evolutionary history, with little scope for generalisation based on traits such as body size. Correspondingly, a recent study that explored the structure of a host-parasitoid network of parasitoid wasps and leaf miners revealed that the network was highly compartmentalised, with host phylogeny playing a significant role in the organisation of these compartments (Cagnolo, Salvo & Valladares 2011b). However, as we will show here, differences in certain life-history traits are linked with diet breadth and structure host-parasitoid networks in a manner analogous to variation in body-size in food webs.

1.6 Life-History and Host Range

Parasitoid species traits related to how a parasitoid forages determine which hosts can, and which cannot, be used successfully as a nursery for their offspring: i.e., they determine the parasitoid’s fundamental niche. This section will introduce some of the axes of insect parasitoid life-history that have been used to distinguish between species, and discuss how they determine a species' fundamental niche.

Egg placement

Parasitoid species are often categorised according to where they place their eggs in relation to the host during the act of oviposition. The position of the egg determines the level of the interaction between the parasitoid and the host; species with more intimate interactions with their hosts, such as endoparasitoids, will have narrower diet breadths (van Veen *et al.* 2008). Endoparasitoid larvae have to overcome specialised internal host defences, such as egg encapsulation. The development of countermeasures to these internal defences require high levels of phylogenetic specificity and dramatically reduces the number of viable host species for endoparasitoids compared with ectoparasitoids, which only have to overcome generalised external defences, such as kicking or rolling (Quicke 1997; Sullivan & Völkl 1999). We would expect, therefore, endoparasitoids to have narrower diet breadths than ectoparasitoids and promote a phylogeny based compartmentalised structure within the host-parasitoid network (Quicke 1997; Sullivan & Völkl 1999; van Veen *et al.* 2008).

Some ectoparasitoids have been suggested to be able to switch facultatively from a primary to a hyperparasitoid life-history (Sullivan & Völkl 1999). This is the only example of flexible trophic levels in host-parasitoid networks. All endo-hyperparasitoids are obligate hyperparasitoids and show very high levels of host specificity, having much narrower diets that ecto-hyperparasitoids (Sullivan & Völkl 1999).

Developmental diapause

Hosts that have been attacked by koinobionts (Table 1-1) will continue development while the parasitoid offspring develops inside them. The parasitoid offspring inside the host will generally undergo embryonic diapause, allowing the host to reach a suitable size, and hence provide a suitable level of nutrition, before entering the larval stage (Godfray 1994). Because the host is not paralysed by the act of oviposition, it is thought that, in order to protect the egg from the machinations of the host, many koinobionts are also endoparasitoids (Pennacchio & Strand 2006). As such, in order to evolve successful counter-measures against host internal defences, they suffer the constraints to diet breadth associated with endoparasitism outlined above. Idiobionts (Table 1-1) typically paralyse their hosts during oviposition and their larvae do not have to contend with host defences, and idiobionts generally exhibit an ectoparasitoid life-history (Hawkins 1994). This generalisation is not universal but, rather, the rule with some exceptions. Parasitoid wasps of the genus-group *Polysphicta* for example are koinobiont ectoparasitoids, that place their eggs in such a manner as to avoid disposition by the host (Gauld & Dubois 2006). A more detailed review of the relationship between koino/idiobiosis and diet breadth, with empirical evidence, can be found in Hawkins (1994).

According to the ‘Dichotomy hypothesis’, the long development time associated with koinobiontism further constrains parasitoid fundamental niche in regards to the developmental stage of the host that they can attack. Koinobionts must attack earlier developmental stage hosts in order to have the time required to complete development (Blackburn 1991; Godfray 1994; Hawkins 1994). Conversely, because their hosts represent all of the available nutrition for their offspring, idiobionts must attack larger late stage hosts to ensure that offspring have the energy available to complete development. This concept is one of the fundamental theories in parasitoid ecology, and the developmental stage of the host used has been hypothesized to be an important driver of life-history and morphology (Godfray 1994); this concept will be revisited when we discuss realised niches in parasitoids.

Hyperparasitoids are also either koinobionts or idiobionts. Idiobiont hyperparasitoids are constrained in that they have to attack their hosts during the mummy stage, koinobionts typically attack while the primary parasitoid's host is still alive or, rarely during the mummy stage. Very few koinobiont hyperparasitoids can utilise both host stages (Buitenhuis *et al.* 2004). These host stage constraints have for example been shown to play an important role in determining a parasitoid's diet breadth in the presence of host mutualists (Sullivan & Völkl 1999; Sanders & van Veen 2010).

1.7 Realised Niche In Parasitoids

Optimal foraging

In regards to how parasitoids maximise their reproductive output, Cook and Hubbard (1977) stated that: "*In a consideration of the strategies adopted by* *insect parasites when searching for their hosts it is realistic to assume that an underlying objective of their behaviour is to leave as many offspring as possible which survive to reproduce in the next generation. Natural selection will favour those strategies which result in a reproductively efficient distribution of the parasite's egg complement among the available host population*." (p. 115).

As the above quotation suggests, in parasitoids, foraging success is directly related to reproductive success, meaning that parasitoid foraging behaviour should be more closely related to optimal foraging theory than is evident in food-webs because of a reduced level of conflict between reproductive and feeding processes (Wajnberg 2006). Optimal foraging theory is thought to determine how fundamental niches are structured into realised niches, where interactions between consumers and their resources are strongest/most likely with the resources that best increase consumer fitness (Petchey *et al.* 2008). It is important, therefore, if this theory is to hold, that that we are able to demonstrate that parasitoids forage in an optimal manner, what the limited resources are that need to be allocated optimally, how these relate to parasitoid ecology and thereby how optimal foraging impacts upon host-parasitoid network structure.

Maximising host encounter rate

In order to produce as many offspring as possible, parasitoid foragers need to make sure that they experience the maximum number of oviposition opportunities during their life-time (Cook & Hubbard 1977; Hubbard & Cook 1978; Wajnberg 2006). For the purpose of parasitoid optimal foraging theory, hosts are typically considered to exist as a network of aggregated patches distributed in a habitat, patches of higher host density theoretically offer an increased host encounter rate, which decreases as hosts within a patch are utilized (Hubbard & Cook 1978). In order to maximise the number of hosts a parasitoid encounters, a forager should spend time within each patch in such a way that host encounter rate is the same across all available patches; this time allocation strategy is called the 'Marginal value theorem' (MVT) (Charnov 1976). As a result of this pattern foragers are expected to allocated proportionally more time to patches of higher than patches of lower host density; density dependent foraging (Cook & Hubbard 1977; Hubbard & Cook 1978). With the introduction of multiple foragers a similar pattern is expected, where individuals should distribute themselves in space according to host availability, density dependent aggregation. The 'Ideal Free Distribution' (IFD) predicts that more foragers should be located in patches of higher host density, in such a manner that all foragers within the habitat encounter hosts at the same rate (Wajnberg 2006). In terms of ecological network structure, this results in the interaction strengths between parasitoids and their hosts being determined by the relative abundance of each viable host. In reality, the relative adherence of foragers to the above predictions of parasitoid distribution are evident in different degrees in different studies; it has been suggested that differences can be explained by parasitiod ecology, host distribution and the abiotic environment (Lessells 1985; van Veen *et al.* 2002; Wajnberg 2006; Corley, Villacide & van Nouhuys 2010). In addition, and of particular importance, when foraging on a multiple host species, the quality of individual hosts is predicted to play an important role in foraging decisions.

An important mechanism that determines the distribution of foragers across patches is the patch allocation time (PAT), which describes the amount of time that a forager spends within a host patch (Wajnberg 2006); according to the MVT, PAT should be higher in patches of higher host density. PAT is currently thought to be determined by host encounter rates, where each encounter with a host increases (incremental PAT) or decreases (decremental PAT) the time spent within a patch before the forager moves to the next patch; for an ‘in depth’ review see Wajnberg (2006). Incremental PAT rules, in response to viable hosts for oviposition, result in positive density dependent foraging and parasitoid distribution (van Alphen, Bernstein & Driessen 2003); conversely, decremental PAT rules result in density independent foraging, where parasitoids do not conform to the IFD. However, the idea that we see decremental PAT rules seems to contradict the above idea that species are trying to maximise their oviposition rate. *In situ* studies have shown that parasitism rates can be positively or negatively related to, as well as be independent of, host density within a patch; a single study has reported all three types of variation can be found under the same conditions within the same host-parasitoid networks (van Veen *et al.* 2002). A series of theories have been suggested that attempt to explain how parasitoids can exhibit this range of relationships between host abundance and parasitism rate and still be foraging optimally.

In a study of the parasitoid wasp *Ibalia leucospoides*, the study population exhibited a strong adherence to the IFD, but the strength of the adherence decreased with increased distance from the experimental release point (Corley, Villacide & van Nouhuys 2010). This corroborates current theory, which suggests that when a high cost to maximum fecundity is associated with dispersal between patches, then the adherence of the population to the IFD, across its entire potential distribution, is reduced (Bernstein, Kacelnik & Krebs 1991). Conversely, if there is little fitness cost associated with moving between patches, then host density at different patches has less of an impact upon host encounter rates and there is no incentive to allocate resources according to host density, resulting in density independent parasitism and parasitoid aggregation (Völkl 1994; Wajnberg 2006). In these cases, foragers may still be optimising the number of hosts that they encounter, and host abundance may still structure realised niche for these parasitoid species, even though they do not conform to the IFD.

Similarly to stochasticity in host abundance, stochastic levels of juvenile mortality have been suggested as an alternative mechanism by which parasitoids forage optimally. If offspring mortality is unpredictable, bet-hedging strategies suggest that available host patches should be under-utilized in case a stochastic event causes high offspring mortality (Cronin 2003). Similarly, high levels of primary parasitoid offspring mortality due to hyperparasitism have been reported, and it has been hypothesized that suboptimal patch use may be a strategy of reducing offspring mortality resulting from the host density dependent aggregation of hyperparasitoids (Mackauer & Völkl 1993; van Veen *et al.* 2002). These studies suggest that some parasitoids are unwilling to attack risky hosts, implying that host quality plays a role in structuring a forager's realised niche.

Host Quality and Offspring Fitness

An alternative method of increasing individual fitness is to improve the fitness of one's offspring (Hubbard & Cook 1978). Offspring fitness is determined by host choice decisions made by the parent; therefore, we would expect that in order to maximise fitness parasitoids should preferentially attack hosts that produce the fittest offspring, while at the same time reducing the costs to future reproduction associated with oviposition; i.e. parasitoids should utilise the most profitable hosts, as suggested in predator-prey food webs (Mackauer, Michaud & Völkl 1996; Morris & Fellowes 2002; Ode, Hopper & Coll 2005; Lacoume, Bressac & Chevrier 2006; Petchey *et al.* 2008; Sampaio, Bueno & de Conti 2008; Nakamatsu, Harvey & Tanaka 2009; Dannon *et al.* 2010; Luo & Liu 2011).

In parasitoid and predator studies, body-size is often used as a proxy for fitness, because it is generally correlated with a greater potential fecundity and a better ability to realise that potential (Roitberg, Boivin & Vet 2001; Kingsolver & Huey 2008; Lykouressis *et al.* 2009; Boivin 2010). Corroboratively, body-size has been suggested to be the primary constraint of potential fecundity in insects from a range of orders of insects, suggesting a generally applicable positive relationship between size and fecundity in insects (Honěk 1993). Unlike consumers in food-webs, offspring body-size in parasitoids is determined by the amount of nutrition available from a single consumption event during the larval stage, rather than from multiple meals integrated over a far longer period of feeding events (Jervis, Ellers & Harvey 2008). Because of the limitations associated with the single consumption event, the nutritional value of the host plays a highly significant role in determining offspring characteristics, which determine fitness (Morris & Fellowes 2002; Cohen *et al.* 2005; Ode, Hopper & Coll 2005; Nakamatsu, Harvey & Tanaka 2009). Primarily, larger hosts have been shown, over a range of parasitoid and host species, to produce larger, fitter offspring; owing to a greater biomass availability (Sequeira & Mackauer 1992; Cohen *et al.* 2005; Ode, Hopper & Coll 2005; Lacoume, Bressac & Chevrier 2006; Jervis, Ellers & Harvey 2008; Sidney *et al.* 2010; Luo & Liu 2011). Empirical evidence involving parasitoid choice experiments in the laboratory have shown categorically, over a range of parasitoid and host species, that some parasitoid foragers preferentially attack certain host species over others (Morris & Fellowes 2002; Buitenhuis *et al.* 2004; Ode, Hopper & Coll 2005; Brotodjojo & Walter 2006; Sidney *et al.* 2010).

There are some problems associated with using size as a measure of host quality. In order to eclose, tissue feeding koinobiont parasitoids, such as *Hyposoter didymator*, must consume all host biomass, which imposes a maximum limit upon the size of hosts from which offspring can successfully complete development; although in the original study, host size was positively correlated with offspring fitness and survival when excluding the largest groups of available hosts (Reudler-Talsma *et al.* 2007). Similarly, survival rates of offspring developing within different species may not be directly related to host-size. For example, female *Aphidius colemani,* a wasp that parasitizes a range of aphid species, were more likely to reject available oat aphid, *Rhopalosiphum padi*, hosts because, even though the species is of an average size, successful eclosion rates were much lower in that host species compared to the others available (Ode, Hopper & Coll 2005). Furthermore, host characteristics can impose restrictions on the maximum oviposition rate of parasitoid foragers by altering handling times. For example, aggressive host defensive behaviour has been suggested to affect optimal host utilization, where, for example, the smaller host subspecies *Uroleucon jaceae* spp. *jaceae* was preferentially attacked by *Aphidius funebris* as it was less capable to defending against attacks than the larger *U. jaceae* spp. *henrichi* [Stadler, 1989 in (Mackauer & Völkl 1993)]. However, these exceptions aside, we can generally assume that host species present different opportunities for parasitoids to maximise their fitness and that size is a good proxy for host quality.

To the best of our knowledge, no studies have considered the effect of patches differentially composed of host species of different quality and PAT. An experiment testing the co-variant effects of host patch density and quality, in terms of composition of different species, in a range of parasitoids, could clearly help to characterise what determines parasitoid realised niches in host-parasitoid networks.

The Optimal Foraging Strategy

The previous sections have discussed two foraging strategies by which parasitoids can maximise individual fitness: optimising host encounter rate or optimising host quality (and by proxy offspring fitness). These two strategies are consist of multiple decisions made by parasitoid foragers as to whether to utilise an available host or to forego the available host in favour of finding one of higher quality; optimal foraging theory predicts that parasitoids will make the decision that best profits their fitness (Figure 1-3a). When foregoing an available host in favour of finding a more suitable host increases the fitness of an individual more than using the available host, we would suggest that the forager will be highly elective and exhibit the second of the two strategies. This should result in a network that is structured according to the characteristics of the available host species (Figure 1-1b), and not by the relative abundance of each host species within the ecosystem. This has considered how host characteristics change the relative profitabilities of each host (summarized in Figure 1-3b); the next section will explain how different life-history characteristics can be used to predict electivity through their relation to the limited resources that must be optimally allocated.

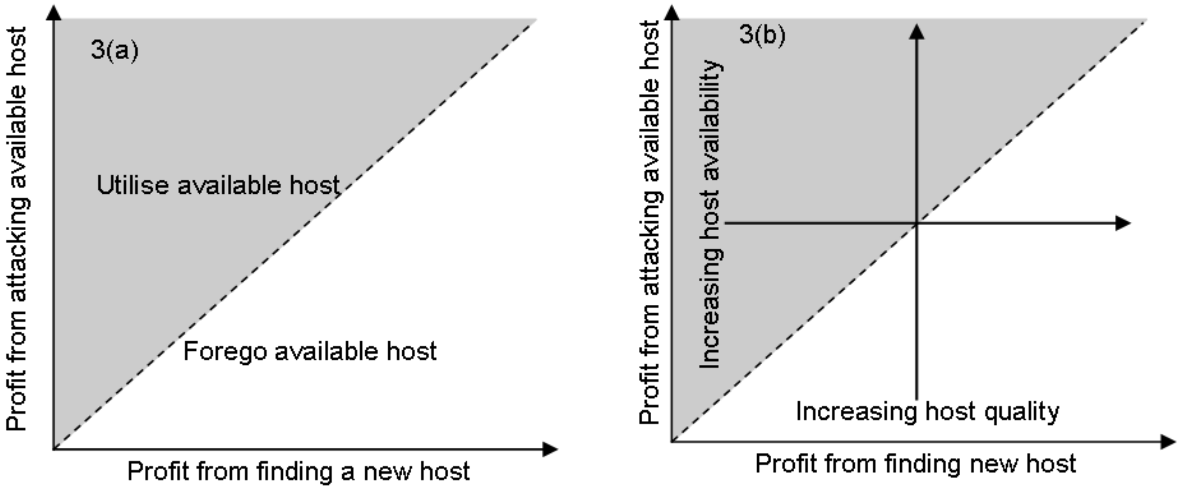

Figure 1-3 Diagrams considering the effect of the relative profit of a host, where host profitability is the benefit to individual fitness minus the costs of different foraging decisions, according to predictions made by optimal foraging theory: *(a) The effects of the costs and benefits associated with finding hosts and utilising them related to attacking or foregoing an available host. (b) The effects of host characteristics on the profitability of hosts and how this affects optimal foraging decisions. When the profit to using a host is greater than the profit associated with finding another host, optimal foraging theory predicts that the parasitoid will utilise the available host. This concept has been applied to all further profit comparison diagrams.*

1.8 Parasitoid Life-History And Host Electivity

Time and egg limitation

It has been suggested that adult parasitoids may be limited in the number of offspring they can produce by either the number of eggs available for oviposition or the number of hosts they encounter during their life-time; therefore, eggs and time can be considered currency that must be optimally allocated in order to maximise parasitoid reproductive output (Cook & Hubbard 1977; Hubbard & Cook 1978; Wajnberg 2006; Rosenheim *et al.* 2008). Ideally, a parasitoid will produce exactly the same number of eggs as the number of viable hosts it encounters, while allocating resources in such a way as to maximise its realized fecundity (Rosenheim *et al.* 2008). However, this realisation is unlikely due to the stochasticity of population dynamics, and foraging individuals most likely either encounter viable hosts without available eggs (egg limitation) or die before laying all of their mature eggs (time limitation). As has been shown above, there are two aspects of optimal foraging: investment in quantity of offspring or investment in the quality of offspring. Which of these two methods best optimises individual fitness is dependent on the relative levels of egg or time limitation that an individual experiences; as the relative costs and benefits to future reproduction associated with finding a host and utilising it can be explained by how foragers must allocate their time or their eggs in order to maximise individual fitness (Rosenheim *et al.* 2008; Rosenheim, Alon & Shinar 2010).

The cost of egg or time limitation

Egg and time limitation has played an important role in theories regarding the evolution of different life-histories in parasitoids; however, there has been some debate as to which has been the more important driving force (Jervis, Ellers & Harvey 2008; Rosenheim *et al.* 2008). As has been suggested in the Lepidoptera (Jervis, Boggs & Ferns 2007) and Coleoptera (Tatar, Carey &

Vaupel 1993), there exists in parasitoid Hymenoptera a trade off between reproduction and survival (Ellers 1996). This is described by the ovigeny index, which quantifies the relative allocation of an individual's reproductive capacity towards early or late reproduction; specifically, the proportion of an individual's life-time egg-load that is mature upon eclosure (Jervis *et al.* 2001). The allocation of resources towards early reproduction, pro-ovigeny, results in species with greater reproductive potential but a shorter life-span; conversely, synovigenic species, which mature eggs during their life-time, have fewer offspring but live longer (Blackburn 1991; Jervis *et al.* 2001; Jervis, Ellers & Harvey 2008). Previous studies have considered how egg limitation or time limitation drives the proportional allocation of resources, during development within the host, to allow species to optimally utilise host resources (Jervis, Ellers & Harvey 2008). Recently, the division between the two trains of thought has been bridged. In actuality individual parasitoids exhibit different levels of egg or time limitation over their life-time, differing according to species ecology, where they both, roughly, equally contribute to selection of optimal allocation strategies (Rosenheim *et al.* 2008). However, the relationships between life-history and resource limitation, which have already been considered in previous studies regarding evolution, have strong applications to optimal foraging and host-parasitoid network structure (Heimpel & Rosenheim 1998; Casas *et al.* 2000; Ellers, Sevenster & Driessen 2000; Jervis, Ellers & Harvey 2008; Rosenheim *et al.* 2008).

In order to reconcile the two schools of thought based on the importance of time versus egg limitation in parasitoid evolution, Rosenheim (1999b) considered the two conditions in terms of their effect on future fitness returns. This outlook is an important way of considering the effect of resource limitation on foraging strategy, as parasitoids are thought to forage in a manner where they are maximising individual fitness (Cook & Hubbard 1977; Hubbard & Cook 1978). The cost of laying an egg is two-fold: firstly, that egg cannot be used again, which only incurs a cost to future fitness if the forager does not have an egg available when a better host becomes available (egg-limitation); secondly, the time taken to lay the egg cannot be used to find and attack another host, which only incurs a cost if the forager does not have enough time to allocate all of its eggs (time-limitation). Therefore, an increased likelihood of egg-limitation means there are greater costs associated with the use of each egg, and time limitation means there are greater costs to utilising each unit of time (Figure 1-4); which will affect the profitability of hosts (Rosenheim *et al.* 2008). The rest of this review will consider how these two costs are related to the life-history of parasitoids and how egg and time limitation can be related to foraging strategy.

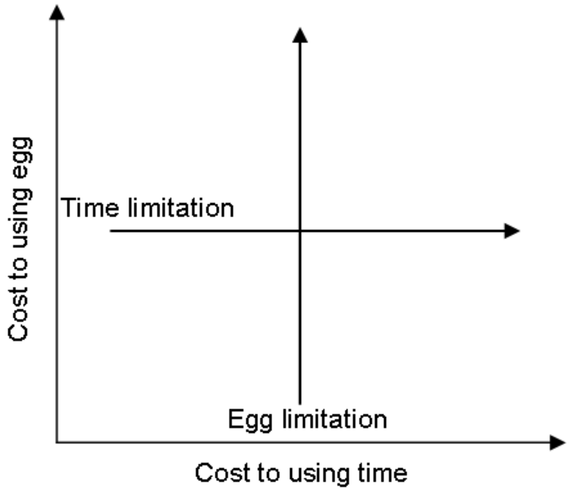

Figure 1-4 Diagram indicating how the likelihood of a forager experiencing egg or time limitation affects the cost associated with allocating an egg or a unit of time.

Where whichever of the two resources is more likely to be a limitation on reproductive success is the resource that should be allocated optimally.

Egg limitation, life-history and electivity

In egg-limited foragers, eggs are the limited resource that must be allocated optimally. Individuals that are more likely to be egg-limited during their life-time incur higher fitness costs to utilising sub-optimal hosts because the forager is more likely to encounter a better host but not have any eggs available (Minkenberg, Tatar & Rosenheim 1992; Rosenheim *et al.* 2008). By having a low likelihood of dying before allocating their entire egg complement, an egg-limited individual should maximise its individual fitness not by optimising its host encounter rate, but by foraging according to host characteristics, thus maximising offspring fitness. This means that parasitoids with a high likelihood of experiencing egg-limitation should be more likely to forego an available host if it is of low quality than those with a low probability of egg-limitation (Figure 1-5). The reduced importance of host encounter rate in egg-limited foragers is evident in the results a study of the dynamics of PAT rules in the cereal aphid parasitoid, *Aphidius rhopalosiphi*, where foragers switched from an incremental to a decremental PAT pattern as they used up their eggs (Outreman *et al.* 2005). Furthermore, an optimal foraging model suggested that parasitoids that are more likely to be egg limited best optimise their fitness by preferentially allocating their eggs to hosts of higher quality, when host quality was considered in terms of whether the host had already been parasitized or not (Outreman & Pierre 2005). Species that forage in a manner where they are unlikely to utilise a sub-optimal host in favour of finding a more suitable host are highly elective. Electivity has been related to relative egg-limitation in the synovigenic parasitoid *Aphytis melinus*, where foragers became more elective as they used up their daily egg-load (Casas *et al.* 2000); although this pattern is not applicable to all parasitoid species (Javois & Tammaru 2006).

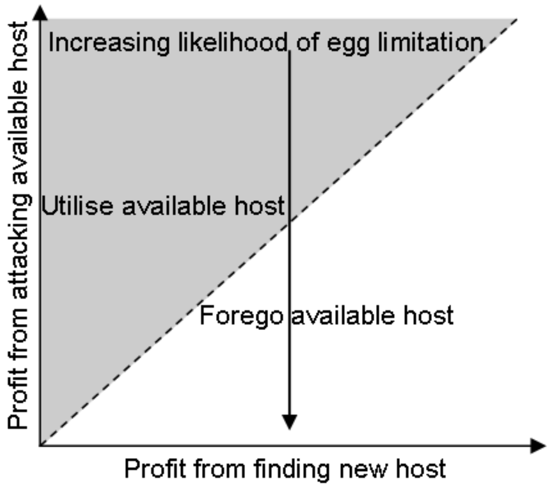

Figure 1-5 The effect of egg limitation on the cost to utilising an available host and foraging strategy.

As there is a high likelihood of egg limited species encountering a host and not having an egg available to allocate to it, there is a greater cost to optimal fitness associated with allocating each egg to a sub-optimal host. We suggest, therefore, that species with a higher likelihood of experiencing egg-limitation are more likely to forego an available host than species than are less likely to run out of eggs.

The ovigeny index is related to the importance of egg or time limitation experienced by an individual. Synovigenic species have a reduced mature egg-load compared to pro-ovigenic species and have a greater risk of experiencing egg-limitation at any given time (Casas *et al.* 2000). Conversely, pro-ovigenic species experience greatest fitness gains by maximising the number hosts in which they successfully oviposit; as they have shorter lives and are more likely to die before allocating all of their eggs (Ellers, Sevenster & Driessen 2000;

Jervis, Ellers & Harvey 2008). The effect of pro-ovigeny on foraging strategy is suggested in the results of a study of the pro-ovigenic parasitoid *Ibalia leucospoides*, where the study population exhibit strong adherence to the IFD (Corley, Villacide & van Nouhuys 2010); this corroborates the idea that species with a reduced likelihood of egg-limitation must maximise host encounter rate in order to forage optimally. We could suggest, therefore, that the ovigeny index is related to the realised niche of a parasitoid, where foragers with a high likelihood of running out of eggs before they die, i.e. synovigenic species with a index score close to zero, preferentially utilise host species of greater quality (i.e. a greater body size), resulting in networks structured by host characteristics and not abundance (Figure 1-1b). This could explain the lack of a relationship between host density and egg load in the synovigenic parasitoid, *Aphytis aonidiae*, reported in a previous study (Heimpel & Rosenheim 1998).

Blackburn (1991) reported a significant negative correlation between egg size and fecundity in parasitoids, suggesting that larger eggs incur a greater cost to potential fecundity than smaller eggs. This correlation presents a similar scenario to that suggested above, representing a trade-off between investment in offspring success and investment in the total number of offspring produced. In cases where a greater energetic cost is associated with the production of an egg, there is a greater cost to fitness associated with wasting the egg on an unsuitable host (Rosenheim *et al.* 2008). Species with large eggs are likely to be egg-limited due to the high cost of producing each egg, combined with the increased cost to potential reproduction associated with each egg, suggesting that optimal foraging strategies in these species are based on host quality and not encounter rate. Egg size in parasitoids is strongly determined by life-history: for example, embryos of ectoparasitoids do not have access to host resources during development to the larval stage and often require large, yolk-rich (anhydropic) eggs to complete this initial stage of development; conversely, endoparasitoid embryos may utilize the host haemolymph and species will most often lay small, yolk-deficient (hydropic) eggs. We suggest for endoparasitoids, which also have a more constrained fundamental niche, interactions with available hosts within the network are structured by host abundances and not relative host qualities; with the opposite being true for ectoparasitoids. The relationship between egg-size and the structure of fundamental and realised niches in parasitoids has not, to the best of our knowledge, previously been considered; a study comparing the egg sizes of different parasitoid species and how their networks are structured could help validate the above hypothesis.

Time limitation, life-history and electivity

If we consider time limitation to be the opposite of egg-limitation, we would expect parasitoids that have a greater likelihood of dying before allocating their eggs to experience a higher cost to future fitness associated with not attacking an available host; i.e. spending time not ovipositing incurs a greater cost when time is a more limited resource than eggs. This idea only holds when the lifetime foraging success is limited by searching time alone, and there is a negligible time cost associated with oviposition (Figure 1-6) (Outreman & Pierre 2005). However, where time is limited because a high cost to future reproduction is associated with using an available host and not finding it, i.e. high handling time as opposed to searching time, we expect species to exhibit high levels of electivity (Figure 1-6). This is because, in this instance, utilising high quality hosts is the best way to maximise fitness per unit of time spent. There is some empirical evidence corroborating this idea: a study of two parasitoid wasps of the genus *Aphidius* determined that the species with longer handling time constraints (*A. picipes*) was significantly less likely to attack an already parasitized host, analogous to low quality, than the species less constrained by handling time (*A. rhopalosiphi*) (van Baaren *et al.* 2004). Similarly as with egg limitation, we would expect parasitoid species that forage electively, because of handling time limitations, to structure their realised niche according to host characteristics and not encounter rate.

These ideas are supported by theories related to functional responses and density-dependent foraging. Where functional responses determine the fitness returns associated with increasing host encounter rate, which in turn determines whether parasitoid forage in a density dependent manner (Wajnberg 2006; Corley, Villacide & van Nouhuys 2010). High handling time limitations on foraging parasitoids result in a saturating response of oviposition rate to host density. With a decelerating (saturating) oviposition rate response to host availability, there is a possibility that host populations can reach a density where oviposition rate of an individual is no longer density dependent because it cannot increase further, resulting in host density independent parasitism rates (Heimpel & Casas 2008). Conversely, where parasitoids are primarily searching time limited, resulting in a directly proportional relationship between host encounter rate and life-time reproductive success, parasitoids should maximise host encounter rate and forage in a host-density dependent manner (Wajnberg

2006; Heimpel & Casas 2008); i.e. construct a realised niche according to host abundance (Figure 1-1a).

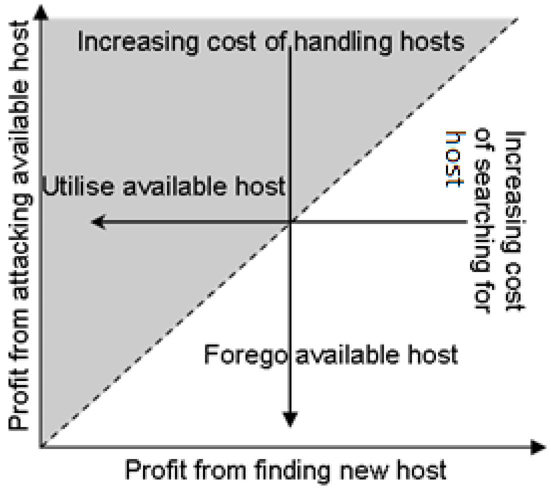

Figure 1-6 Diagram illustrating the effects of searching and handling time limitations on host profitability and parasitoid foraging strategy.

Parasitoid foragers can be limited in their reproductive success by time limitation, i.e. they will die before they deposit their eggs. This can manifest in two ways: (i) they are limited by the time required to find new hosts, which will result in a high cost to finding a new host, and thus will reduce the profit associated with foregoing an available host in search of a host of better quality; (ii) conversely, the parasitoid can be limited because there is a large handling time associated with attacking an available host, in this case the forager is limited in the number of hosts that it can attack in its life-time, analogously to egg-limited foragers, so it should maximise the quality of each host that it parasitizes.

Handling time and life-history in parasitoids

Since the allometric structuring of food-webs is determined by predator body-size altering the handling times of resources, larger predators should extract greater profits from large, more nutritious resources (in absence of social behaviour such as pack hunting) (Brose *et al.* 2006; Petchey *et al.* 2008). However, size restrictions to trophic level are not evident in host-parasitoid networks, and fundamental niche in parasitoids is determined by host phylogeny and parasitoid life-history, although there is some evidence that parasitoid body-size and host handling times are related, but this is determined by host characteristics (Henry, Ma & Roitberg 2009). For example, for parasitoids that attack sessile host stages, such as egg-parasitoids or idiobionts that parasitize cocoons or pupae, handling time costs do not scale positively with host size or potential fitness gain (Gross 1993). Conversely, some hosts are capable of aggressive defensive behaviours, such as aphids kicking or caterpillars rolling, the effectiveness of which have been suggested to be positively correlated with host body-size, suggesting that for these aggressive types of host, those individuals that provide greater offspring fitness incur greater time costs of parasitisation (Allen 1990; Gross 1993; Henry, Ma & Roitberg 2009; Firlej *et al.* 2010).

In parasitoids that parasitize aggressive host types, it is thought that larger adult parasitoids are less affected by defensive host behaviour, providing a mechanism by which host handling time correlates negatively with adult parasitoid body-size, analogously to the pattern observed in food-webs (Gross

1993; Henry, Ma & Roitberg 2009; Lykouressis *et al.* 2009). In a study of the primary parasitoid *A. colemani*, larger female parasitoids were capable of parasitizing larger hosts of the same species, while small females were limited to small and early stage hosts (Lykouressis *et al.* 2009). Differences in handling time due to parasitoid size have also been reported for host species of different size; larger parasitoid wasps of the species *Pachycrepoideus vindemiae* spent less time handling larger host species in choice tests, and as a result exhibited greater preference for the larger host species than smaller parasitoids (Morris & Fellowes 2002). Conversely, studies of the parasitoid *Mastrus ridibundus*, which attacks the sessile cocoon stage of the moth *Cydia pomonella*, did not find any correlations between adult parasitoid size and host handling time (Bezemer & Mills 2003). The results of these studies suggest, for parasitoid species that utilise mobile hosts that exhibit aggressive defensive behaviours, handling time costs associated with attacking a host are related to the sizes of both the parasitoid and the host; however, for parasitoids that attack sessile or juvenile host stages, size constraints on handling ability do not play a part in foraging decisions.

We can use parasitoid characteristics to predict relative costs associated with searching and handling times according to knowledge of how host choice is constrained by parasitoid life-history. For example, mummy hyperparasitoids are known to have much higher handling costs than koinobiont endohyperparasitoids, and should exhibit high levels of electivity (Sanders & van Veen 2010). Evidence of the effect of handling time restrictions in determining network structure is evident in a study by Bukovinszky (2008), in which an increase in the quality of aphid hosts resulted in a proportionally greater increase in the species assemblage of the highly elective mummy parasitoids, such as *Pachyneuron aphidis*, compared to the specialist koinobiont hyperparasitoids, such as *Alloxysta fuscicornis*. Similarly, idiobiont parasitoids must attack later, larger host stages, which are better able to defend themselves and incur greater costs to handling time. This suggests idiobionts that attack mobile stage hosts should be more elective than koinobiont species, which typically attack poorly defended, early stage hosts (Hawkins 1994; Henry, Ma & Roitberg 2009). Conversely, egg parasitoids have very short lives, and incur very large fitness costs to foregoing available host eggs, and we would expect these species to exhibit reduced host electivity (Boivin 2010).

While parasitoid size may have some influence on how parasitoid foragers construct individual realised niches, the effect is dependent upon how the parasitoids fundamental niche is constrained by the life-history of the parasitoid. The analysis of quantitative network data could help elucidate the relative importance of different parasitoid life-history characteristics in determining the structure of host-parasitoid networks (van Veen, Morris & Godfray 2006; Cagnolo, Salvo & Valladares 2011b; Tack, Gripenberg & Roslin 2011).

1.9 Sex Allocation and Host Quality

The sex allocation process

Most parasitoid wasps exhibit arrhenotoky, a subtype of haplodiploidy, in which female offspring develop from fertilized and males from unfertilized eggs

(Heimpel & de Boer 2008). In this manner the sex ratio of offspring can be controlled by an adult female, who can decide whether to fertilise an egg before oviposition or not (Heimpel & de Boer 2008). It has been clearly shown in laboratory experiments that the allocated sex of the offspring is influenced by host quality, where unfertilized eggs are laid in hosts of lower quality (Charnov *et al.* 1981; Morris & Fellowes 2002; Ode, Hopper & Coll 2005). This differential host utilization is based on the idea that the relationship between adult characteristics and reproductive output is stronger for females than for males; therefore, allocating females to more suitable hosts will increase individual fitness more than if a male were oviposited to the same host (Charnov *et al.* 1981; Heinz 1991; Sullivan & Völkl 1999).

Allocation strategies and parasitoid life-history

We would expect then that proportionally more female parasitoids eclose from larger, more suitable hosts than males, and there is some evidence for this in the field (Mackauer 1996; Bukovinszky *et al.* 2008). However, sexual size dimorphism has been suggested to be related to parasitoid life-history. For example, koinobiont parasitoids, which are less capable of discerning host-size for offspring use because the size of the host at time of oviposition is not the same as at the end of the embryonic diapause, will be less likely to differentially allocate offspring sex according to host size (Mackauer, Michaud & Völkl 1996). Parasitoids in which female fitness is less related to size are also predicted to exhibit reduced sexual size dimorphism; for example, species that oviposit in sessile host stages do not incur increased reproductive success from the size-based relaxation of handling-time costs (Mackauer 1996). Furthermore, the differential use of host species regarding sex ratio is related to host availability. Early in the season more female *Aphidius ervi* were reported to eclose from large hosts and more males from small hosts, but as favourable host stages became less available adults did not exhibit such strong sex allocation preferences (Sequeira & Mackauer 1992).

Sex allocation and network structure

Sex ratio allocation decisions can have strong impacts upon the structure of host parasitoid networks. Relative size differences between available hosts have been shown to be important, a female exposed to only larger hosts will produce a more male biased sex ratio than those exposed to a mixture of large and small hosts (Chow & Heinz 2005). A female-biased sex ratio is an important aspect of biological control, especially inundation biocontrol, where only females control host populations and a female biased sex ratio increases the ‘killing power’ of the parasitoid population, increasing its capacity to control the pest population (Mills & Wajnberg 2008).

Sex ratio related host choice decisions also present an important opportunity to study apparent competition mediated by a shared natural predator. If parasitoids preferentially utilize host species B for males, which represent an egg sink as they do not interact with hosts, in a patch containing species A and B, then there will be fewer eggs available for allocation towards species A. Conversely, the presence of species A will increase the female ratio of the parasitoid population, which will result in the asymmetric suppression of species B (Figure 1-7) (Heimpel, Neuhauser & Hoogendoorn 2003). Quantified web data can be used to test for any strength of indirect effects, such as sex related host choice mediated apparent competition, and determine whether these processes significantly shape host-parasitoid networks (Tack, Gripenberg & Roslin 2011). In theory this size-selective sex allocation could result in a size structured indirect interactions within networks where negative apparent competition effects are typically directed from larger hosts to smaller hosts.

1.10 Conclusions

This review has discussed the empirical evidence for a mechanistic relationship between parasitoid life-history traits and the structure of host-parasitoid networks. To conclude, we will combine the series of ideas that have been presented thus far, and construct an organised framework, based on optimal foraging theory, that will illustrate which aspects of parasitoid life-history are important in determining host-parasitoid network structure, and how these aspects interact with each other. This framework will be compared with the body-size based framework suggested by the allometric diet breadth model, which has been used so successfully to provide a mechanistic understanding of the structure of food-webs (Petchey *et al.* 2008).

The structure of ecological networks has been defined as the differences between each species' fundamental and realised niches, as well as considering how the relative interaction strengths between species pairs vary within the realised niche. Therefore, for ease of understanding, the frameworks presented here have been split into two groups: those that consider the structure of fundamental niche, which includes the determination of both diet breadth and trophic level, and those that consider the realised niche structure, which focuses upon what influences optimal foraging decisions made by consumers.

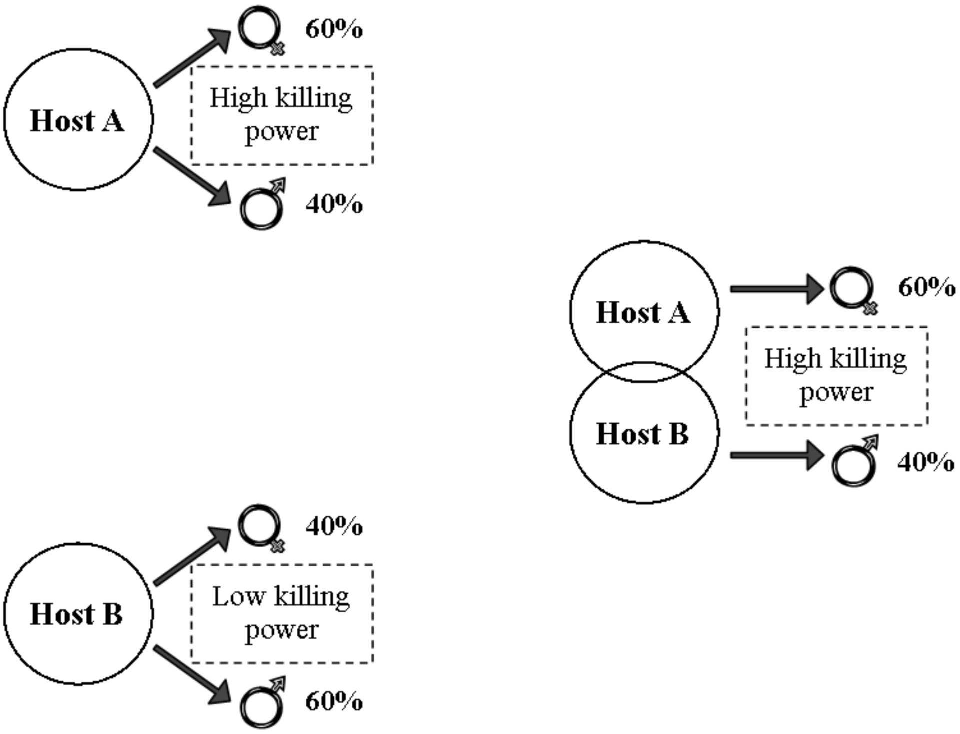

Figure 1-7 Hypothetical sex ratio allocation decisions made by female parasitoids in the presence of three separate host patches.

Foraging parasitoids are thought to allocate a larger number of fertilised (female) eggs to populations of larger hosts (Host A in this case) because the allometric scaling of fitness is stronger/steeper for female offspring than for males, i.e. larger female offspring provide a greater increase to inclusive fitness than large male offspring. This results in a female biased sex ratio for parasitoid populations reared on Host A, which, as female parasitoids (and not male ones) are responsible for the death of hosts, results in an high killing power (more eggs to allocate to available hosts) of the parasitoid population. Conversely, *Host B is a small, poor host, and parasitoid populations reared on it have a male biased sex ratio and a low killing power. Parasitoid populations reared upon both hosts have a high killing power, resulting in an increased rate of attack for Host B compared to when it exists on its own. However, for Host A experiences a reduced rate of attack compared to when it exists on its own as fewer eggs as it shares the burden of parasitism with Host B. This disproportionate effect of parasitism by a shared parasitoid is known as 'apparent competition' and may represent a significant structuring force within host-parasitoid networks.*

The determinants of fundamental niche

Predator body-size relationships have been hypothesized, and shown, to play an important role in determining fundamental niche structure (Brose *et al.* 2006; Petchey *et al.* 2008; Arim *et al.* 2010; Riede *et al.* 2011; Yvon-Durocher *et al.* 2011) (summarized in Figure 1-8). The allometric scaling relationships for consumer handling capabilities, such as 'gape-limitation' constraints, according to the ADBM (Brose *et al.* 2006; Petchey *et al.* 2008), and space use parameters, such as the scale of movement, according to Rooney (2008) and Woodward (2005), are strong determinants of diet-breadth in marine and terrestrial food-webs. These relationships occur in such a way that, in many food-webs, diet-breadth broadens with consumer size (Brose *et al.* 2006; Arim *et al.* 2010). Studies have also observed a positive relationship between consumer body-size and trophic level (Riede *et al.* 2011); this has been suggested to be because a broader diet results in a greater number of energy pathways by which an individual can sustain its biomass, which simultaneously results in the individual inhabiting a higher trophic level (Arim *et al.* 2010). Similarly, larger predators consume larger prey, which further reinforces the size structuring of fundamental niche in food-webs (Petchey *et al.* 2008; Riede *et al.* 2011).

Alternatively, fundamental niche structure in host-parasitoid networks is very strongly determined by the interaction between parasitoid life-history and host phylogeny constraints upon host suitability (summarized in Figure 1-9) (Sullivan & Völkl 1999; Cagnolo, Salvo & Valladares 2011b). In parasitoids, diet breadth is related to the intimacy of the interaction between the parasitoid and its hosts, which concerns both the length of time during which the parasitoid or its offspring are in contact with the host and the species specificity of the countermeasures required to overcome host defences. Life-history traits, such as ecto/endo-parasitism and idio/koino-biosis, determine the intimacy of interaction; traits that increase the degree of intimacy, such as endoparasitism and koinobiosis, increase the degree to which the diet breadth of a parasitoid is constrained by host phylogeny, which results in a narrower diet breadth than for ectoparasitoids or idiobionts (Godfray 1994; Hawkins 1994). Trophic levels in host-parasitoid networks are, in most cases, fixed, and there is no direct relationship between diet-breadth and trophic level as is found in food-webs (Sullivan & Völkl 1999). The cases where trophic levels are not fixed can again be related to parasitoid life-history and the intimacy of interaction. For example, ecto-hyperparasitoids, such as *Asaphes vulgaris*, by nature of their non-specific host exploitation tactics, have been shown to facultatively switch between both primary and secondary parasitoid life-histories (Sullivan 1987; Sullivan & Völkl 1999), and secondary and tertiary life-histories (Sanders & van Veen 2010).

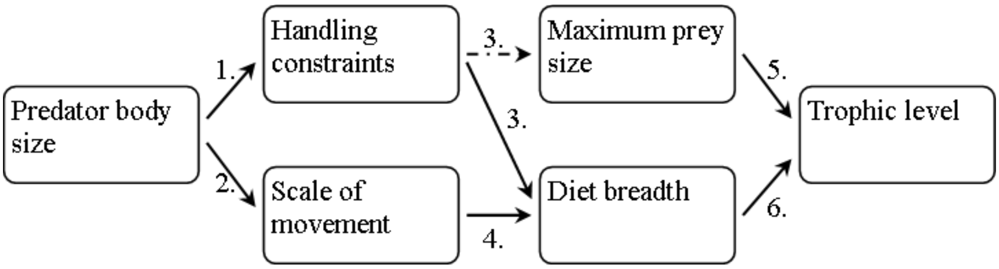

Figure 1-8 Effect of predator body-size on fundamental niche structure.

Legend *(1.) Larger predators are less physiologically constrained in the size diversity of hosts that they are capable of handling, e.g. gape limitation in fishes (Brose et al. 2006; Petchey et al. 2008; Arim et al. 2010). (2.) Larger predators forage across a greater scale of movement, which encompasses a more diverse array of habitats, than is the case for smaller predators (Jetz et al. 2004; Woodward et al. 2005; Rooney, McCann & Moore 2008). (3.) The size of the largest resource that can be handled successfully scales with predator-size faster than the smallest, resulting in a broader diet breadth (Brose et al. 2006; Petchey et al. 2008); however, this relationship is not present across all interaction types, and this model is not suitable for the description of benthic suspension feeders (Riede et al. 2011) or host-parasitoid networks (Petchey et al. 2008). (4.) Because they forage across a more heterogeneous environment, larger predators encounter, and thus are capable of interacting with, a wider range of prey species (Woodward et al. 2005; Rooney, McCann & Moore 2008). (5.) Because of the allometric scaling of trophic level, larger predators, which* *eat larger prey and are themselves only consumed by higher trophic levels, must be higher in the food web (Riede et al. 2011). (6.) A broader diet implies that larger predators consume resources from a greater number of energy pathways than smaller predators; therefore, the inherent scaling of diet-breadth with body-size results in a positive relationship between body-size and trophic level (Brose et al. 2006; Petchey et al. 2008; Arim et al. 2010).*

Despite these recurrent patterns across many systems, there is variability in the strength by which ecological networks are structured by body-size (Yvon-Durocher *et al.* 2011). This strength can be considered as the degree to which size-constraints determine forbidden interactions in a network (Vazquez, Chacoff & Cagnolo 2009; Oleson *et al.* 2010; Yvon-Durocher *et al.* 2011). For example, in benthic suspension feeders, where resource consumption barriers are typically not determined by consumer body-size characteristics, there is no relationship between the size of the resource and the size of the consumer (Vazquez, Chacoff & Cagnolo 2009; Oleson *et al.* 2010; Riede *et al.* 2011; Yvon-Durocher *et al.* 2011). This review has provided strong evidence that, similar to benthic suspension feeders, forbidden interactions in host-parasitoid networks are not predominantly determined by body-size scaling relationships: this supports the growing body of evidence that size-structuring models are best applied to predator-prey interactions (Oleson *et al.* 2010; Riede *et al.* 2011; Yvon-Durocher *et al.* 2011). This lack of size structuring in host-parasitoid networks is especially evident when considering the allometric scaling of handling constraints, where, while there is evidence for size related handling capabilities constraining or facilitating host use events (Morris & Fellowes

2002), there is no compelling evidence of complete exclusion of an interaction because of forager size. It is important to note, however, that there is a distinct correlation between body-size and trophic level in host-parasitoid networks, where the inhabitants of higher trophic levels are smaller than those of lower levels (Cohen *et al.* 2005). This is not a result of mechanistic relationships between parasitoid size, and host suitability and availability, but arises because parasitoid size is constrained by the energy available during the larval stage, i.e. from a single host, and because energy transfer between trophic levels is never 100% efficient (Cohen *et al.* 2005).

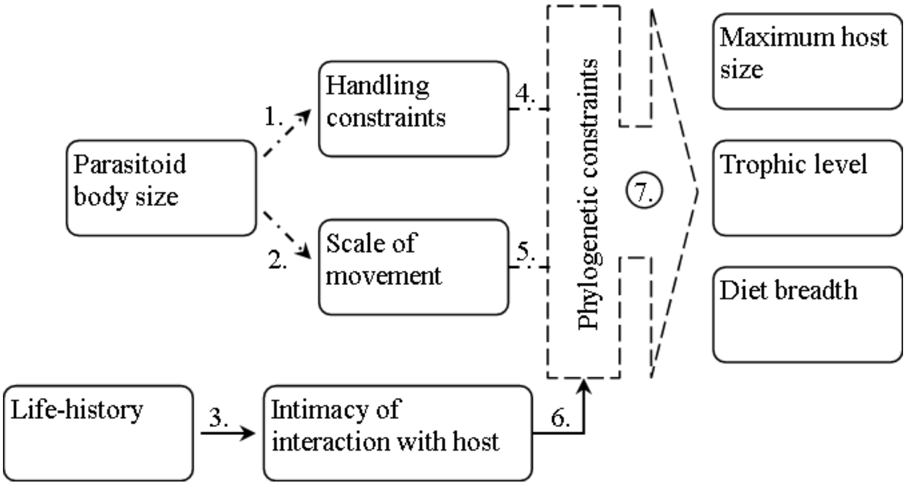

Figure 1-9 Body-size, life-history and the structure of fundamental niches in parasitoids.

Legend (1.) Similarly to predators, there is some evidence that larger parasitoids are less constrained in the range of developmental stages of the host that they can successfully attack (Lykouressis et al. 2009); however, host developmental stage is not part of fundamental niche structure, and no studies, *to the best of our knowledge, have shown a relationship between parasitoid size and host species range. (2.) It has been shown that larger parasitoids are better able to disperse through their environment, and can potentially forage across a broader range of habitats, than smaller parasitoids (Ellers, van Alphen & Sevenster 1998); in host-parasitoid networks, this relationship has only been hypothesized to have an effect on fundamental niche structure (Laliberte & Tylianakis 2010). (3.) Life-history characteristics, such as koinobiosis or endoparasitism, determine the length of time spent associated with a host and the specificity of the countermeasures to host defences. These two characteristics describe the intimacy of the interaction between a parasitoid and a host. (4. & 5.) Where handling or dispersal capabilities do in fact respond to parasitoid body-size constraints, host suitability is still strongly regulated by host-phylogeny; unlike in food-webs (Sullivan & Völkl 1999; van Veen et al. 2008; Sanders & van Veen 2010). (6.) The intimacy of the interaction between the parasitoid and its hosts determines the degree to which phylogeny constrains host viability; species with highly intimate interactions are more constrained by host phylogeny than parasitoids with less intimate interactions (Godfray 1994; Hawkins 1994). (7.) Ultimately, phylogenetic constraints determine, of all those available, which hosts are suitable for use; therefore, phylogenetic factors determine maximum host size, the trophic level of the parasitoid (and whether they can switch trophic levels), and parasitoid 'diet breadth'. It is important to note that diet breadth and maximum host size are not related to trophic level in host-parasitoid networks (Godfray 1994; Hawkins 1994; Sullivan & Völkl 1999; Sanders & van Veen 2010).*

The determinants of realised niches

Realised niches describe which resource items available to consumers are actually utilised within an ecological network: i.e., the realised niche is the culmination of all of the foraging decisions made by all of the individuals of a consumer species population (Ings *et al.* 2009). Optimal foraging theory suggests that the realised niche of a consumer is structured by the relative profitability, in terms of individual consumer fitness, associated with the consumption of resources within the consumer's fundamental niche (Petchey *et al.* 2008). Trait-pairing characteristics facilitate or hinder interactions between species within ecological networks, changing the profitability of resource items (Vazquez, Chacoff & Cagnolo 2009). Consumer and resource body-sizes have been identified as important trait-pairing characteristics in food-webs and mutualistic networks (Brose *et al.* 2006; Petchey *et al.* 2008; Rooney, McCann & Moore 2008; Stang *et al.* 2009).

In the ADBM studies, which focus on modelling predator-prey interactions, prey profitability is determined by searching time costs, handling costs (which are both functions of the sizes of both predators and their prey), and nutritional benefit (which is a function of prey size) and these costs and benefits interact in such a way that larger, more nutritious prey items are more profitable for larger predators (Petchey *et al.* 2008). As optimal foraging theories predict that consumers should preferentially consume the most profitable resources, the ADBM predicts that larger predators consume larger prey (Petchey *et al.* 2008); these patterns have been confirmed in a wide range of marine, fresh-water and terrestrial predator-prey networks (Petchey *et al.* 2008;

Riede *et al.* 2011). Although, under conditions where prey items are scarce, predators should, and have been shown to, exhibit a reduced level of size-selectivity in their prey consumption decisions (Galarowicz, Adams & Wahl 2006).

We have provided evidence that, similarly to food-webs, foraging decisions made by parasitoids are determined by costs associated with searching for and handling different host resources (Heimpel & Casas 2008). However, parasitoids may be limited in their foraging success by either the time available for finding and utilising viable hosts (time-limitation), or by the number of eggs available to allocate to the hosts that they find (egg-limitation) (Figure 1-9). This additional limitation on foraging success can change the way that host-parasitoid networks are structured when compared to food-webs as it changes the currency of optimisation: i.e. for predators optimal foraging always considers energy consumption per unit time, but for parasitoids foraging decisions can be related to the optimal allocation of time and/or eggs (Hubbard & Cook 1978; Petchey *et al.* 2008; Rosenheim *et al.* 2008). Parasitoids that are more likely to experience egg-limitation can only use a certain number of hosts irrespective of their host encounter rate. Consequently, these parasitoids maximise their individual fitness by preferentially allocating their limited eggs to the best quality hosts (Minkenberg, Tatar & Rosenheim 1992). Conversely, parasitoids that are not egg-limited should make host-choice decisions according to the relative costs associated with finding a resource and utilising it, similar to predators in food-webs (Wajnberg 2006). If foraging success is more strongly limited by the time taken to encounter a host, then parasitoids should utilise every host they encounter, provided that it is viable. Alternatively, if handling time is more costly than searching time, then fitness costs are associated with attacking a host, and parasitoids should only use hosts that satisfy a minimum quality threshold. Life-history traits determine the number of eggs a parasitoid has to allocate, the time it has to do it in, and often provide constraints upon host and space use; therefore, the likelihood of different species being egg or time limited is strongly related to parasitoid life-history (Rosenheim *et al.* 2008). Through this mechanism, life-history characteristics will change the propensity of foragers to exhibit different foraging strategies and, therefore, can be used to predict host choice-decisions made by different species (Figure 1-10)

Realised networks are constructed from the foraging decisions made by all the individuals within a species population; therefore, optimal foraging strategies play an important role in the formulation of the structure of ecological networks (Petchey *et al.* 2008). In host-parasitoid networks, the interactions strengths between the parasitoid and the available host species can either be determined by host-characteristics, such as quality, if the parasitoid exhibits a high degree of electivity (expected in handling-time- or egg-limited individuals), or by the relative abundances of each host species, in searching-time limited individuals (Figure 1-10) (Minkenberg, Tatar & Rosenheim 1992).

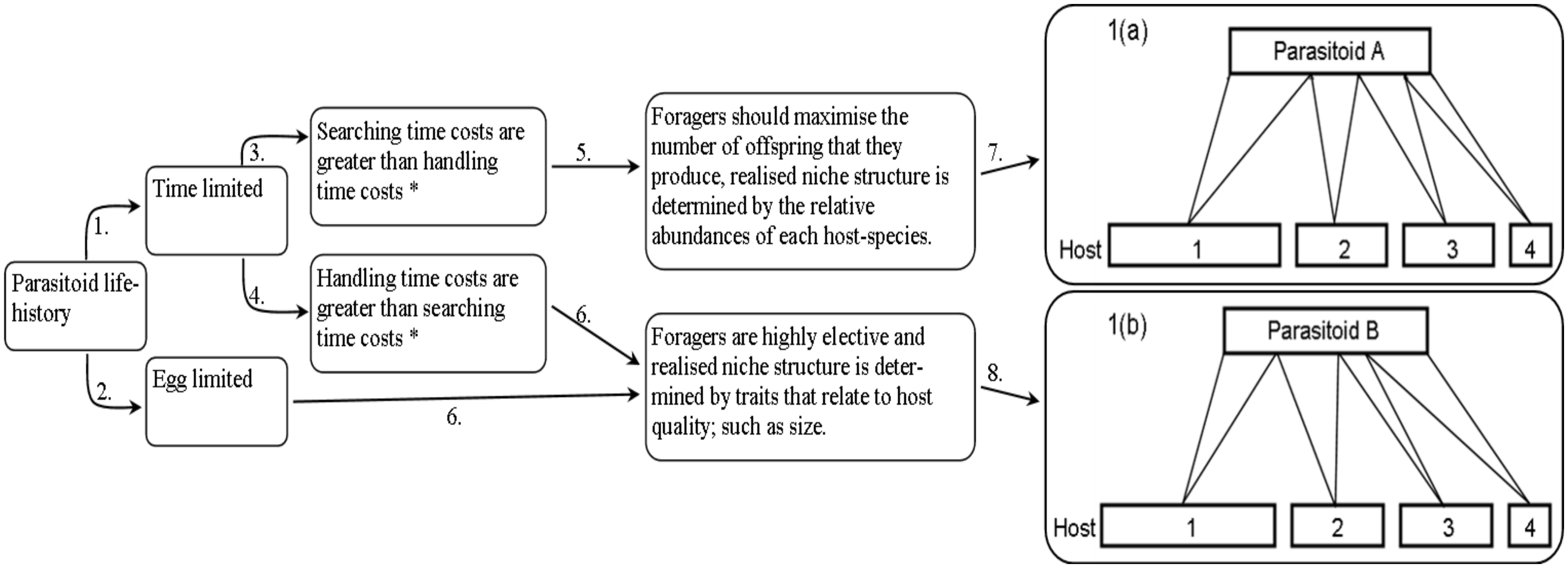

Figure 1-10 Life-history and realised niche structure in host-parasitoid networks.

Legend *(1. & 2.) Life-history traits, such as the degree of ovigeny, determine whether a parasitoid is more likely to experience egg or time limitation because these characteristics determine the availability of eggs at any given time, the life-span of the parasitoid and the rate of parasitism (Rosenheim et al. 2008). (3. & 4.) Time limited parasitoids must optimally allocate their time in order to maximise reproductive success. Parasitoids that are limited because they cannot find enough hosts to utilise all their eggs experience searching time limitation of reproductive success; while those that are limited in their parasitism rate because they cannot handle hosts fast enough, experience handling time limitation of reproductive success. The likelihood of either of these limitations occurring is determined by both parasitoid characteristics, such as wing venation, and how host choice is constrained by life-history (e.g. idiobiont hyperparasitoids must attack their hosts during the mummy stage and have long handling times) as well as by host characteristics, such as abundance (Sanders & van Veen 2010). (5.) When time costs are most incurred during the process of searching for hosts, parasitoids should utilise all viable hosts that they encounter. (6.) When the costs to the currency that must be allocated optimally, which can be time or eggs, are most incurred through utilising hosts, hosts utilised should be of optimal quality, so as to gain the greatest fitness benefits from using limited resources (Minkenberg, Tatar & Rosenheim 1992). (7. & 8.) The realised niche of a parasitoid species is constructed from multiple host-choice decisions made by each parasitoid species within an ecosystem. Each decision consists of whether to use an available host or not, and the likelihood of either decision is determined by a foragers degree of electivity. (7.)*

Foragers that are not very elective, and attack every viable host that they encounter, have a realised niche constructed according to the relative abundances of the different host species within the ecosystem. (8.) In foragers that are highly elective, the relative interaction strengths between the parasitoid and the available hosts are determined by the characteristics of the host.

Future research avenues and the effect of spatio-temporal variation in host-parasitoid networks

Analysis of host-choice decisions from quantitative host-parasitoid networks in relation to parasitoid life-history will help elucidate a mechanistic understanding of the structuring of these networks. For example, the degree of electivity exhibited by different parasitoid species could be investigated in regards to their morphology and ecology. Similarly, behavioural studies investigating the relationship between life-history and foraging strategy by looking at the state dependent behaviour of individual foragers, in terms of their host-choice decisions, could further clarify the relationship between life-history and the currency of optimisation. Linking together state-dependent foraging patterns and network structure in parasitoids would contribute to the strong shift towards individual-based foraging models (Abrams 2010).

The idea of state-dependent foraging contributes a new facet to the ideas presented in this review; namely, that the factors that determine host-parasitoid interactions are not constant through space or time (Duffy & Forde 2009; Oleson *et al.* 2010). The dynamic nature of ecological networks has been identified as being important to long-term stability of complex communities (Kondoh 2003). For example, the susceptibility of hosts to their parasitoids changes through time; strong exploitation interactions by a parasitoid wasp, *Aphidius colemani*, resulted in the evolution of a strain of peach-potato aphid, *Myzus persicae*, that was highly resistant to attack (Herzog, Muller & Vorburger 2007). It is possible, therefore, that differences in interaction strengths between parasitoids and their hosts are a reflection of the relative abilities of different host populations to resist parasitoid attack, and not preferential host-choice decisions made by the foraging parasitoids. To prove that the distribution of link strengths within host-parasitoid networks is indeed due to electivity on behalf of the forager, network analysis needs to be followed up with behavioural studies of the foraging strategies exhibited by different parasitoid species.

Foraging decisions made by parasitoids are dependent upon host-characteristics, including abundance and quality, which are temporally and spatially variable and changes to these characteristics will have impacts upon host-parasitoid network structure (Tylianakis, Tscharntke & Lewis 2007; Bukovinszky *et al.* 2008; Laliberte & Tylianakis 2010). For example, in two different studies, reductions in the quality (size) of phytophagous insect hosts, due to changes in the host-plant community, resulted in the homogenisation of host-parasitoid network structure (Bukovinszky *et al.* 2008; Laliberte & Tylianakis 2010). Similarly, as abiotic conditions, such as temperature or weather patterns, affect the foraging efficiency of ectothermic invertebrates, including searching and handling time in insect parasitoids, future climate change could have a profound impact upon host-parasitoid network structure according the frameworks presented in this review (Tylianakis, Tscharntke & Lewis 2007; Bukovinszky *et al.* 2008; Laliberte & Tylianakis 2010; Woodward *et al.* 2010a). The effect of temperature on foraging efficiency could be exploited to investigate the effect of changing the costs and benefits of host-choice decisions and whether any resulting changes in foraging pattern corroborate the predictions made by the framework above.

Studies of sex ratio allocation decisions made by parasitoids in the presence of different host-species have gone some way to investigating the relationship between optimality and foraging strategy (Sequeira & Mackauer 1992; Chow & Heinz 2005). Due to the different impacts of male and female parasitoids upon host populations, studies of the relationship between host community structure and sex ratio allocation strategies could provide some insight into the more complex, indirect relationships between species within host-parasitoid networks, such as apparent competition (Heimpel, Neuhauser & Hoogendoorn 2003; van Veen, Morris & Godfray 2006).

The ideas and frameworks presented in this review have shed some light upon the differences in the processes that structure host-parasitoid networks and food webs. We conclude that while body-size considerations may play a role in determining host-use patterns exhibited by some insect parasitoids, the relationships between parasitoid life-history and fundamental and realised niche structures are the greater structuring force in host-parasitoid networks. However, host-parasitoid networks and food webs are not so profoundly different as to exclude collaborative studies that consider interactions between the two network types within ecosystems.

1.11 Thesis Chapter Descriptions

Chapter 2 is an initial analysis of data from a 10-year study of a single host-parasitoid-secondary parasitoid community. Patterns in network structure resulting from adaptive foraging behaviour in the secondary parasitoid *Asaphes vulgaris* are identified, focusing on host preference behaviour (electivity) and condition-dependent sex ratio allocation. A framework of how these behaviours and the patterns resulting from them may shape indirect interactions between host species is suggested. The chapter analyses focus on the potential of global climate change to alter community structure and stability through its effect on foraging behaviour.

Chapter 3 builds upon the previous chapter by considering multiple parasitoid species and testing for the effect of changes in explicit environmental conditions (competition for hosts) on foraging behaviour. The chapter studies inter- and intra- species differences in network structure (e.g. link-strength) and relates these to two aspects of adaptive foraging behaviour, electivity and sex ratio allocation. The results are discussed with respect to the ability of the egg-/time-limitation framework to provide a mechanistic understanding of spatial and temporal variation in network structure.

Chapter 4 compares the ability of four parasitoid species to adapt their behaviour to environmental heterogeneity. We test a hypothesis that parasitoid sex ratio allocation behaviour should respond to changes in average host sex and attempt to maintain Hamiltonian sex ratios. The differences in behavioural plasticity between species are discussed and used to corroborate a previous hypothesis about the evolution of binary condition-dependent behaviours. The effect of environmental heterogeneity on the precision of foraging behaviour is also considered.

Chapter 5 reports on the development on a computational model analysing how multiple determinants of network structure interact: elective foraging behaviour, condition-dependent sex ratio allocation, and spatial heterogeneity in host quality. The chapter is particularly concerned with whether these multiple determinants act in an additive or syngergistic manner. The model is used to test the predictions made in Chapters 1 & 2 regarding the ability of adaptive parasitoid foraging behaviour to determine the outcome of indirect interactions between host species. The results are further considered in terms of agricultural biological control, where host species may be segregated spatially.

Chapter 6 develops the spatial and applied ecology themes of the previous chapter, testing the pest control ecosystem services provided by natural vegetation in the field. Specifically, the density/severity of multiple natural enemy, pest and pathogen are measured in the agricultural environment as a function of distance from the natural environment. The differences in distance response between species are considered with respect to species ecology. The results are used to further develop a mechanistic, predictive approach to effect conservation biological control

1.12 Acknowledgements

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Chapter 2 Potential for climate effects on the size-structure of host-parasitoid indirect interaction networks

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2.1 Chapter Concept

The previous chapter identified foraging behaviours with the potential to impact upon host-parasitoid network structure. This chapter focuses upon identifying patterns in host-parasitoid interactions at the community level and considers temporal variation in network structure.

2.2 Abstract

Communities of insect herbivores are thought to be structured mainly by indirect processes mediated by shared natural enemies, such as apparent competition. In host-parasitoid interaction networks, overlap in natural enemy communities between any pair of host species depends on the realised niches of parasitoids, which ultimately depend on the foraging decisions of individuals. Optimal foraging theory predicts that egg-limited parasitoid females should reject small hosts in favour of future opportunities to oviposit in larger hosts, while time-limited parasitoids are expected to optimise oviposition rate regardless of host size. The degree to which parasitoids are time- or egg-limited depends in part on weather conditions, as this determines the proportion of an individual's lifespan that is available to foraging. Using a 10-year time series of monthly quantitative host-parasitoid webs, we present evidence for host-size based electivity and sex allocation in the common secondary parasitoid *Asaphes vulgaris.* We argue that this electivity leads to body-size dependent asymmetry in apparent competition among hosts and we discuss how changing weather patterns, as a result of climate change, may impact foraging behaviour and thereby the size-structure and dynamics of host-parasitoid indirect interaction networks.

2.3 Introduction

Previous studies of the effects of climate change have generally focused on the responses of species in isolation in spite of the fact that interactions between species are a significant component of the response of communities to climate change (Woodward *et al.* 2010a). For instance, among three *Drosophila* fly species, simulated temperature changes resulted in the extinction of the least adapted species through direct competition for resources; however, the presence of a single, shared, generalist natural enemy (the parasitoid wasp, *Leptopilina boulardi*), ameliorated competitive pressure allowing the three fly species to coexist (Davis *et al.* 1998). The indirect effects of climate change will not only alter species physiology, but the way species interact; for example, climatic warming may generally increase disease burden among marine and terrestrial organisms (Harvell *et al.* 2002), with consequences for community structure and dynamics. A general way in which climate change may affect ecological communities indirectly is through changes in the way networks are structured by species body-sizes, which in turn affects interactions among species (Brose *et al.* 2012). Herein, we focus on body-size dependent indirect interactions in insect host-parasitoid networks.

While direct interactions such as predation have a clear impact upon population dynamics, their consequences may further affect other members of a community. These complex further effects are known as indirect interactions: the impact of one organism/species on another mediated through the actions of a third. Natural enemy mediated indirect interactions are thought to be a particularly important structuring force in herbivorous insect communities due to the typically low level of interspecies competition for resources in these systems and the strongly linked population dynamics between the herbivores and their parasitoid natural enemies (Morris, Lewis & Godfray 2005). There is a particular need to consider climate change impacts on insect host-parasitoid communities, both because of their economic importance in agriculture and their prevalence within natural ecosystems (van Veen, Memmott & Godfray 2006; Hance *et al.* 2007). For example, estimates suggest that impacts on the functionality of parasitoids as control agents of crop pests could cost the United States' agricultural industry up to $20 billion annually in crop damage (Pennisi 2010).

One type of indirect interaction that has been hypothesized as being a particularly important structuring force in host-parasitoid networks (HPNs) is apparent competition (Morris, Lewis & Godfray 2005). This process is defined as a negative indirect effect between two species that share a natural enemy, and is so named because, like resource competition, can lead to competitive exclusion (Holt 1977). Indirect interactions may be density- (effects are driven by changes in abundance of the third party) or trait-mediated (effects are driven by changes in the morphology or behaviour of the third party) (Morris, Lewis & Godfray 2004; van Veen, Memmott & Godfray 2006). Apparent competition can lead to the exclusion of a species where one host species is affected by parasitism disproportionately more than the other species. This ‘parasitism asymmetry’ can result from the foraging decisions of a natural enemy; for instance, preference for one host over another by a parasitoid may result in the preferred host experiencing higher levels of mortality than the non-preferred host (Holt 1977). Conversely, if the parasitoid exhibits no preference between hosts, the hosts may experience apparent mutualism; whereby, for both host species, the presence of the other dilutes parasitism induced mortality, at least in the short term (Holt 1977; Abrams 2010; Vollhardt *et al.* 2010).

The species in a host-parasitoid network that can engage in apparent competition is determined by the host ranges of the concurrent parasitoids, as this determines whether host species can share natural enemy populations. Within these limitations, however, the strength and degree of asymmetry of indirect interactions between two species will strongly depend on whether parasitoids attack the different hosts indiscriminately or exhibit a degree of preference. A likely important host trait in this context is body size. In solitary parasitoids, where only one individual develops on each host, there is a strong correlation between host body size and offspring fitness (Morris & Fellowes 2002; Cohen *et al.* 2005; Nakamatsu, Harvey & Tanaka 2009). Further, it has been shown in a field experiment that populations of a host species that grow to a larger body size than nearby conspecific populations suffer higher parasitism rates from generalist parasitoids (Bukovinszky *et al.* 2008). If parasitoids do account for host body size when foraging, we would expect the realised niche of a parasitoid population to depend on the body size distribution of the available host species, with larger host species being over-represented within the realised niche relative to their abundance.

Another potentially important aspect of host body-size effects on parasitoid mediated apparent competition is parasitoid sex allocation. Parasitoid sex-ratio is an important component of host-parasitoid population dynamics, as only female offspring go on to induce host mortality in the next generation (Hassell, Waage & May 1983). Parasitoid wasps, like all Hymenoptera, have a haplo-diploid sex determination system whereby males develop from unfertilised eggs and females from fertilised eggs. At each oviposition event a female parasitoid can elect to lay a fertilised or an unfertilised egg. Because the effect of body size on fitness is typically greater for females, solitary parasitoids are more likely to lay fertilised eggs in larger hosts (Charnov *et al.* 1981; Bukovinszky *et al.* 2008). Sex ratio allocation behaviour could therefore mediate asymmetric apparent competition when the smaller host species receives mostly male and the larger mostly female parasitoid eggs. In this case, the larger host would be the main source of the population of female parasitoids attacking the small host, while the presence of the smaller host would either have no effect on the larger host, or even have a positive indirect effect through a dilution of parasitism (Henri & van Veen 2011).

Elective foraging behaviours, such as those described above, can determine the distribution of interaction strengths in host-parasitoid networks. In predator-prey food webs, the size-structured distribution of weak and strong links between species is known to be an important aspect of ecosystem stability (Brose, Williams & Martinez 2006). However, the understanding of the role of size-structuring in predator-prey interactions is much more expansive than that of host-parasitoid networks and there are fundamental differences between these systems (Ings *et al.* 2009). For example, the relationship between trophic level and body-size in host-parasitoid networks is inverse to that of predator-prey networks (Brose, Williams & Martinez 2006). Further, unlike in predator-prey systems, handling time and capture rate are largely independent of body size in host-parasitoid interactions (Henri & van Veen 2011). The two types of foraging electivity described above may however still drive a size-structured distribution of the weak and strong links that drive direct and indirect interactions within host parasitoid networks. Therefore, it is likely that the various degrees of foraging electivity exhibited by parasitoids are an important component of network structure and stability (Morris, Müller & Godfray 2001; van Veen, Memmott & Godfray 2006).

The degree of electivity exhibited by parasitoids depends on whether individuals are time-or egg-limited. Egg-limited parasitoids run out of eggs while still having hosts available to attack, while time-limited parasitoids die while still having eggs to allocate to hosts (Rosenheim *et al.* 2008; Rosenheim, Alon & Shinar 2010; Henri & van Veen 2011). Egg-limited parasitoids should exhibit strong preferences for higher quality hosts as they experience a greater reduction in future fitness gains through the use of every egg than time-limited parasitoids. Parasitoids that are time-limited due to shorter life-spans or short, environmentally determined, foraging windows incur low costs to future fitness when attacking suboptimal hosts and are less likely to forage electively because these individuals are expected to optimise oviposition rate, not offspring fitness (Henri & van Veen 2011).

While the effects of climate change on parasitoid physiology are relatively well documented, there have been few considerations of how parasitoid behaviour will be altered (Hoover & Newman 2004; Colinet, Boivin & Hance 2007; Boivin 2010; Corley, Villacide & van Nouhuys 2010; Johnson *et al.* 2011). Weather conditions can have strong effects on parasitoid life-span and foraging windows, thereby influencing the degree to which individuals are egg-or time-limited (Rosenheim *et al.* 2008; Boivin 2010). We predict that climate change will lead to a shift towards time-limitation through constraining foraging windows, as a result of increased precipitation (Fink & Völkl 1995), and reduced life-spans as a result of increased temperature (Hance *et al.* 2007). Such a shift should lead to less elective foraging and a breakdown of the size structure of host-parasitoid indirect interaction networks (Henri & van Veen 2011). Importantly, for the ordinarily, highly egg-limited secondary parasitoids that are the focus of this study, a reduction in foraging electivity may result in a loss of the size-structured distribution of parasitism asymmetry that drives the indirect interactions that are considered important drivers of the dynamics of these systems.

In order to assess whether these considerations have a significant effect, patterns of parasitoid preference must be ascertained at the network level (Morris, Lewis & Godfray 2004; van Veen, Morris & Godfray 2006; Tack, Gripenberg & Roslin 2011). Here, we use a 10-year time series consisting of monthly host abundances and parasitism rates by a single parasitoid species to demonstrate that parasitoid electivity does indeed play a role in structuring the host-parasitoid interaction network. We show that large hosts are significantly over-represented within the realised niche of the parasitoid at any point in time and that there is a strong female-biased sex allocation in larger hosts. Furthermore, we show that the degree of parasitoid is not constant, indicating an environmental impact on community structure and dynamics mediated by effects on parasitoid foraging behaviour.

2.4 Methods

Study species and sample collection

We focused on the wasp *Asaphes vulgaris* (Hymenoptera: Pteromalidae). *A. vulgaris* is a solitary (only one larva can develop per host individual) secondary parasitoid, i.e. the hosts of *A. vulgaris* are primary parasitoids that themselves parasitise sap-feeding aphids. The larvae of these primary parasitoids develop inside a living, growing aphid until the aphid reaches either its penultimate or final (adult) instar. At this stage the primary parasitoid larvae kills its aphid-host and spins its cocoon inside the host's exoskeleton, resulting in what is known as a 'mummy'. *A. vulgaris* oviposits in these aphid mummies, placing its egg on the primary parasitoid (pre-) pupa. It is a common and abundant species, known to attack a wide range of primary parasitoid species through a wide range of aphid hosts that span a wide range of body sizes (Müller *et al.* 1999). As such, it is particularly likely to mediate indirect population interactions among its hosts species and has the opportunity to forage selectively (Rand, van Veen & Tscharntke 2012).

The data used to determine host preference and sex ratio allocation choices made by secondary parasitoid wasps came from a long-term study of an aphid parasitoid food web (Müller *et al.* 1999; van Veen *et al.* 2008). Briefly, surveys were conducted between April and October, from 1994 through to 2003, within a single, mesohydric meadow (approx. 18 000m^2 in size) in Silwood Park, Berkshire, UK. Each month, densities of the mummies of each aphid species were estimated. Samples of 400 mummies of each aphid species (if present) were taken to the lab to rear out primary and secondary parasitoids, in order to obtain data on host-parasitoid associations.

Host-quality metrics

Preliminary laboratory experiments with fresh *Aphidius ervi* (primary parasitoid) via *Acyrthosiphon pisum* (aphid) mummies (N= 30) showed that an approximation of mummy volume (calculated as mummy length x width x width) produced a strong linear relationship with mummy mass (corr. coef. = 0.90).

Mummy length and width were measured, using a Leica M165C microscope and its associated image analysis software 'Leica Application Suite V3' from the all of the samples of *A. vulgaris* mummies collected in the field between 1994 and 1999 and measurement followed simple guidelines using easily identified anatomical structures. The measurements were used to calculate mean mummy sizes for each aphid species, irrespective of the primary parasitoid species.

Different aphid species are abundant at different times of the year and it is likely that host choice occurs according to the relative sizes of the hosts available at any given time, rather than their absolute sizes (Chow & Heinz 2005). Therefore, in order to compare the sizes of host species present during different months, a host-quality metric called size difference was calculated:

Equation 2-1: Size Difference = Sspecies - Smonth

Where $S_{species}$ was the mean size of the mummies of the focal aphid species, and S_{month} was the mean of the mummy sizes of all the aphid species present in the field during a given month. Size difference was calculated for each aphid species for every month that it was present in the ecosystem; thus, allowing a comparative metric of host-species quality across time.

Statistical analysis of host-preference

We quantified the preference for each host species in each month using the Strauss Linear Index (SLI), which is defined as:

Equation 2-2: SLI= Proportion in diet (PoD) – Proportion in environment (PoE)

Where, for each month within the experimental period, PoD was the density of *A. vulgaris* wasps emerging from the mummies of an aphid species as a proportion of total *A. vulgaris* density; and PoE was the mummy density of the aphid species as proportion of total mummy density (i.e. the sum of the mummy densities of every aphid species that can potentially be attacked) (Lechowicz 1982). The SLI has a value of 0 for a species when its proportion in the diet matches its proportion in the environment. Values greater than 0 indicate over-representation in the diet (i.e. preference) and values below 0 indicate under-representation. SLI values were calculated for each host species during each month it was present in the field along with at least one other potential host. Only aphid species that appeared in the *A. vulgaris* host-range at least once were considered in the calculation of SLI values. Further, values were not calculated for a few very rare aphid species for which no reliable size data could be collected.

Linear Mixed Effect Modelling analysis was used to test the dependent variable 'monthly Strauss Linear Index' for each aphid species and the dependent variable 'size of aphid mummies relative to other available aphid species', while 'year' and 'month' were included as nested random variables.

Statistical analysis of sex ratio allocation

The number of male and female *A. vulgaris* that eclosed from each host species were scored for each month. A binomial GLM was used to test for the dependent variable parasitoid sex ratio' reared from the mummies of different aphid species and the fixed effect ' monthly aphid mummy average volume' aphid species'. A quasibinomial distribution was used to account for overdispersion.

Measures of changing electivity through the year

In order to test for an effect of environmental conditions on foraging electivity, we calculated the absolute deviance from random foraging exhibited by *A. vulgaris* during each month as the sum of the absolute SLI values of all aphid species present in the sample. This was the only measure of deviance that was not inherently associated with the number of aphid species present during each month. We performed GLM analysis with sum deviance as the dependent variable, and the following explanatory variables: season of the year (Spring: April and May; Summer: June, July and August; Autumn: September and October), a metric of monthly competition for hosts (taken as total mummy density divided by the estimated total density for *A. vulgaris* wasps for each month), and size range (the difference in volume between the smallest and the largest aphid species present during the month).

Statistics

All Generalised Linear Mixed Effect Models were performed using R statistical software for Windows (version 3.0.1). All statistical tests of significance were performed via model simplification using Maximum Likelihood approximation where appropriate.

2.5 Results

Electivity

Our LME analysis indicated a significant positive relationship ($X^2_1 = 15.547$, $P < 0.001$) between the relative mummy size of an aphid species and its corresponding SLI value for that month (Figure 2-1).

Sex ratio allocation

The sex ratio of *A. vulgaris* wasps eclosing from the mummies of an aphid species during a given month was significantly associated with the corresponding size difference value for that aphid species ($F_{(1,118)} = 89.772$, $P < 0.001$*), where relatively smaller species hosted more male secondary parasitoids (Figure 2-2).

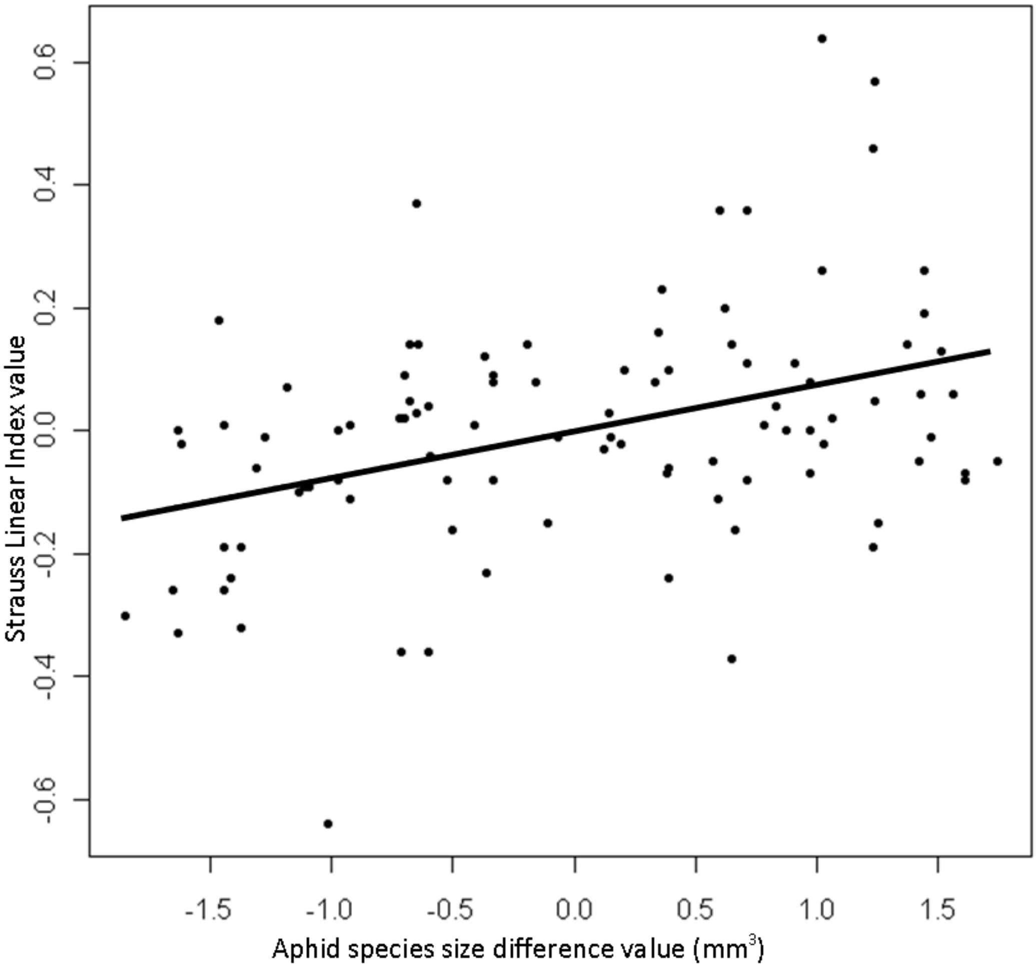

Figure 2-1 *Asaphes vulgaris* preferences for mummies of each aphid species during each month (N=101) with respect to its size relative to the mummies of other aphid species present during that month.

Preference is indicated by the Strauss Linear Index value (SLI) obtained for the aphid species during a single month, and relative size is indicated by the corresponding size difference value. The line is a fit of a linear mixed effect model illustrating the positive relationship between size difference and SLI, while accounting for variation between different months and years across the 10 year study period.

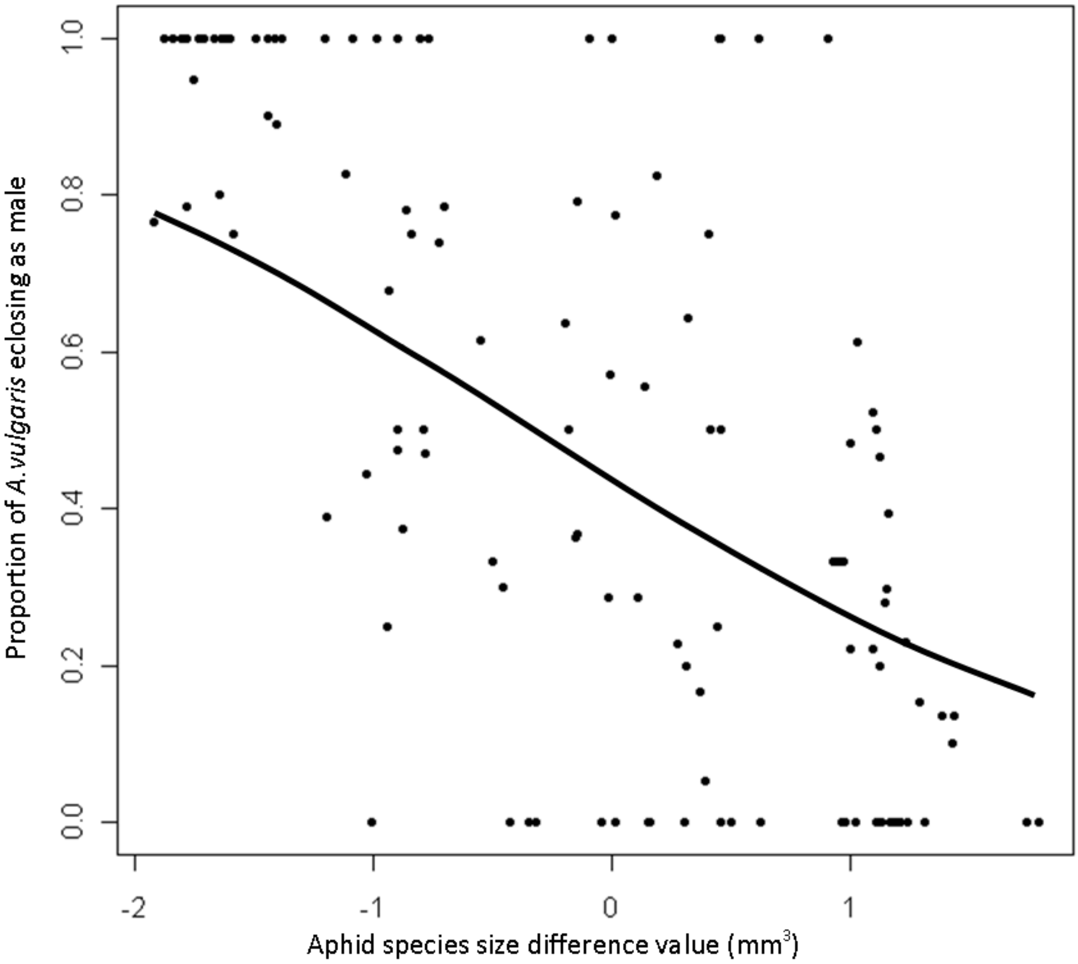

Figure 2-2 Sex ratio of the *Asaphes vulgaris* offspring that eclosed from the mummies of different aphid species during each month (N=102) against the corresponding size difference value for that aphid species during that month.

The plotted line describes a quasibinomial GLM testing for the association between the above variables, note the slightly sigmoid shape.

Seasonal change in electivity

As a measure of changing electivity across time, we calculated the variable ‘sum deviance’ (the sum of the absolute difference from 0 found for the SLI of every aphid species present during a month). According to our GLM analysis, there was no significant effect of the factors that would be expected to alter electivity, nor the interactions between them: host availability per competitor ($F_{(1,27)}$= 1.016, *P*= 0.322; Figure 2-3A), the size range of available aphid mummies ($F_{(1,27)}$= 0.277, *P*= 0.604; Figure 2-3B), and season ($F_{(2,27)}$= 0.936, *P*= 0.405; Figure 3C).

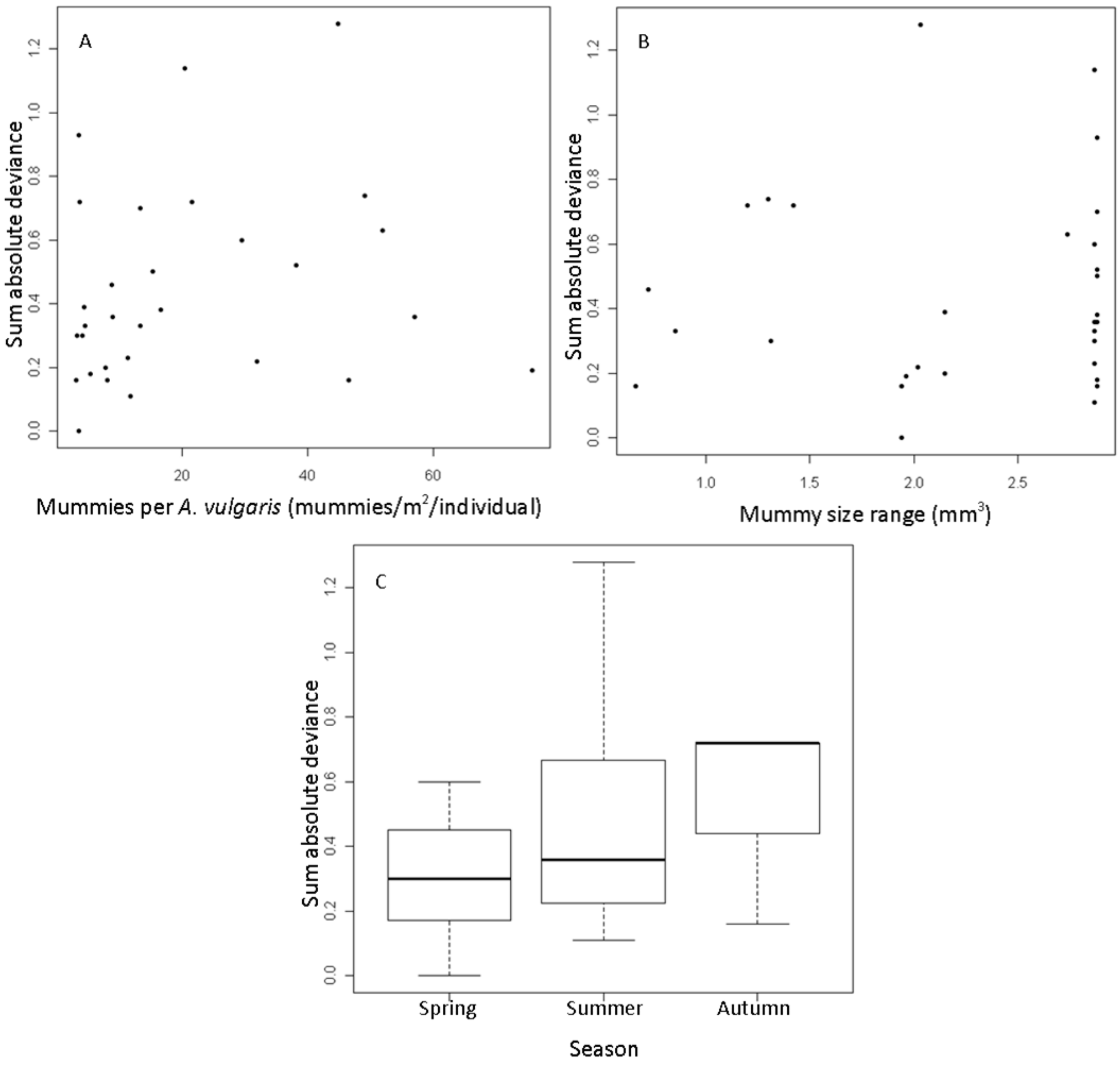

Figure 2-3 Graphs depicting monthly sum deviance in each month (N=31) for *Asaphes vulgaris* against various biotic and abiotic factors that affect egg and time limitation.

*Sum deviance was measured as the difference in host use patterns during a given month from that expected by random foraging, where the larger the value the more elective the foraging pattern: (A)***.** *The degree of electivity exhibited by foraging* A. vulgaris *at various levels of competition for host mummies. Competition is described by the sum of the densities of all of the hosts available during a given month divided by the estimated density of* A. vulgaris *during the month. (B) The degree of electivity exhibited by foraging* A. vulgaris *during months of differing host quality. The x axis describes the difference in volume between the largest and the smallest aphid species present during a given month.(C) Foraging electivity during different seasons of the year.Values for monthly deviance were grouped into seasons Spring: April and May; Summer: June, July and August; Autumn: September and October.*

2.6 Discussion

We predicted that the realised niche of a parasitoid at any point in time would not simply reflect the relative densities of the host species within its fundamental niche, but would be biased towards larger host species. Our analysis provided strong support that this is indeed the case for *A. vulgaris* (Figure 2-1). We made a further prediction that parasitoids would show a sex allocation bias placing more females in hosts that were relatively larger. Our analysis of *A. vulgaris* sex ratio across its host range (Figure 2-2) does indeed show that this species predominately lays female eggs in the largest hosts while the smallest hosts predominantly produce male parasitoids. The numerical contribution to the female parasitoid population *per host killed* therefore increases with host size, as predicted.

Both these apparent host-size effects on parasitoid foraging behaviour have implications for natural enemy mediated indirect interactions among the hosts in the community. First, as our results show, the primary parasitoids of larger aphid species suffer higher mortality rates due to parasitism, presumably due to secondary parasitoid preference for higher quality hosts. This could lead to the negative effects of apparent competition to be biased towards larger host species. This could however be countered by the sex-ratio effect. Because it is only female adult parasitoids that ultimately cause host mortality, small hosts that produce mostly male parasitoids contribute little to the effective parasitoid population and therefore have reduced potential to indirectly affect mortality of the larger hosts (Hassell, Waage & May 1983; Henri & van Veen 2011). In fact, in the short term, they may even have a positive dilution effect. In return, the majority of parasitoid-induced mortality of the smaller hosts is likely to be caused by females derived from larger hosts, leading us to predict asymmetric, negative indirect effects of larger hosts on smaller hosts. Therefore, both these effects lead us to suspect that the size-structure of the host community could significantly affect the distribution of indirect interaction strengths and thereby community dynamics. At this stage it is difficult to predict what the outcome of these combined effects is for size-structured indirect interactions and to answer that question will require a dynamic modelling approach and experimental manipulation (Tack, Gripenberg & Roslin 2011).

For the effects of climate change in this context, we predicted that environmental conditions would affect the degree of electivity shown by *A. vulgaris*. Abiotic factors such as temperature (Colinet, Boivin & Hance 2007; Boivin 2010), precipitation (Fink & Völkl 1995; Johnson *et al.* 2011), and atmospheric CO_2 concentration (Hoover & Newman 2004) have been shown to alter parasitoid life-span, egg-load and foraging efficiency. Weather conditions can affect the cost of each oviposition event with regards to future reproductive success and, therefore, whether parasitoid females would be predicted to optimise oviposition rate (low electivity) or offspring quality (high electivity) (Henri & van Veen 2011). While our data indicates that the absolute degree of electivity exhibited by foraging *A. vulgaris* varied considerably across the time-frame of this study, we could not find any definitive effects of the biotic and abiotic factors that have been predicted to drive host-choice behaviour: such as competition, the variety in size of available hosts, and the season of the year. We expect that the temporal resolution of our analysis was too crude to pick up the variation in environmental effects and that experimentation is required to test hypotheses on climate effects on parasitoid electivity.

However, importantly for the theme of this special issue, our results suggest that the degree of electivity exhibited by foraging secondary parasitoids is not constant and cannot be explained merely by the variation in host quality at any given time, which suggests a possible effect of the external environment on parasitoid foraging behaviour. Due to the evidence for a size-structured distribution of parasitism asymmetry driven by the foraging behaviour of secondary parasitoid wasps, we can suggest that climate change scenarios, particularly those that hinder foraging success, either by reducing foraging time (increased precipitation or shorter life-span at higher temperatures) or by reducing host availability (e.g. drought), may result in an increase of non-elective foraging behaviour (Rosenheim *et al.* 2008; Rosenheim, Alon & Shinar 2010; Henri & van Veen 2011). The loss of electivity by foraging secondary parasitoids could reduce the asymmetry of parasitism mortality between primary parasitoids, with knock on effects on their aphid hosts. This would most likely alter the distribution of strong and weak links within host-parasitoid networks, with a shift to greater evenness of link strength. Interestingly, studies in this issue on both theoretical predator-prey systems (Lurgi, López & Montoya 2012) and empirical litter feeding arthropod communities (Ott, Rall & Brose 2012) predict changes in diet breadth as a result changes in foraging behaviour in response to climate change, indicating the potential generality of these effects. While our predictions are based on weather variability, de Sassi et al (2012) demonstrate that changes in mean temperature and nitrogen deposition can also lead to changes in electivity. Both these factors affect host density which should lead to a higher host encounter rate for parasitoids, making it more likely that they will be egg-limited and therefore more elective. Indeed, de Sassi et al (de Sassi, Staniczenko & Tylianakis 2012) found stronger bias towards high quality hosts under these conditions. The implications of these various effects for network dynamics are difficult to predict at this stage, especially as this also has to take into account the process of sex-ratio allocation demonstrated here, and there is an urgent need to study these effects in multi-species host-parasitoid models.

A major strength of our study is that it uses a comprehensive data set of a large natural community that was sampled quantitatively every month that insects were present for ten years. Field data of this quality is very rare and, in the context of parasitoid foraging behaviour in the field, so far non-existent. An important limitation, however, that we infer parasitoid preference from the frequency of emerging offspring. An alternative explanation for our observation that *A. vulgaris* emerges more often than expected from larger hosts is that larval survival increases with host size. This could lead to the same pattern even if host size played no role in the oviposition and foraging decisions of parasitoid females. We think it is unlikely that this is the case and behavioural studies of host acceptance rates in other parasitoid species have shown that these depend on the relative quality of the available host species (Morris & Fellowes 2002; Ode, Hopper & Coll 2005). Similar observational studies of secondary parasitoid foraging behaviour and larval survival will allow us to distinguish between these mechanisms in our study system. It is also worth noting that we assumed a purely density-dependent host-choice null model which would be violated if not all hosts are consumed with exactly the same functional response (Kalinkat *et al.* 2011). While this is likely to be an issue for predator-prey systems, it should be remembered that host-parasitoid interactions do not follow the same allometric relationships between body-size, handling time and capture rate that can be used to define alternative null models for predator-prey interactions. Further studies elucidating the role of allometry in parasitoid foraging decisions are required before we can apply non-linear null-models to host-parasitoid networks.

The direct effects of climate on parasitoid physiology are well studied (van Veen, Memmott & Godfray 2006; Boivin 2010), but little attention has been paid to the effect of abiotic conditions on parasitoid foraging behaviour and the implications for community level interactions (Woodward *et al.* 2010a). Building on the work of Rosenheim (Rosenheim *et al.* 2008; Rosenheim, Alon & Shinar 2010), we have previously developed a frame work linking the life-history characteristics of parasitoids to optimal foraging behaviour based on the concepts of reproductive success being limited by either egg- or time-limitation (Henri & van Veen 2011). The analyses presented here suggest that the size structure of host communities, and the effect that this has on indirect interactions between species, may form an important further element in our mechanistic understanding of these complex systems and our ability to predict how they will be affected by climate change

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equally shared the sample measurements. DCH performed the analyses and wrote the transcript. FJFvV owns the samples and provided guidance for the manuscript contents and direction.

Chapter 3 Egg-/time- limitation and condition-dependent foraging behaviour: Mechanisms driving the dynamic nature of ecological networks

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3.1 Chapter Concept

Chapter 2 provided initial evidence that foraging behaviour shapes host-parasitoid network structure and that this structure exhibits temporal variability. This chapter expands upon this by testing the niche construction of multiple parasitoid species and tests explicit hypotheses outlined in Chapter 1.

3.2 Abstract

Recent studies highlight the importance of foraging behaviour in ecological network structure and stability. Optimal foraging behaviours respond to environmental conditions and species ecology, but there are few community-level studies with sufficient resolution to study differences in foraging behaviour between species and across time. Herein, we analyse a 10-year long, aphid-parasitoid-secondary parasitoid network and show that short-term changes in the foraging environment, namely competition for hosts, induce changes in foraging behaviour evident at the community level. Further, we show that a range of parasitoid species exhibit condition-dependent foraging behaviours, where species have different priorities when structuring their realised niche. The results corroborate a previous hypothesis that foraging behaviour should be plastic and respond to the primary limiter of foraging success. Expanding the determinants of inter- and intra-species differences in behaviour will provide a mechanistic understanding of the dynamic aspects of ecological networks, such as link rewiring, which are important to long-term community stability.

3.3 Introduction

Ecological network studies have provided important insights on both network-level processes, such as the complexity-stability debate, and individual-level processes, such as optimal foraging behaviour (Ings *et al.* 2009). The advent of quantitative networks, which consider the relative strengths of interactions within a network, has improved our understanding of how individual behaviour is linked with ecological network structure (Brose *et al.* 2006; Ings *et al.* 2009), especially for systems including herbivorous arthropods (Morris, Lewis & Godfray 2005; van Veen, Morris & Godfray 2006). Foraging behaviour determines the strengths of trophic interactions temporally and spatially, which in turn determine community structure and long-term system stability (Petchey *et al.* 2008; O'Gorman & Emmerson 2009; Abrams 2010; Valdovinos *et al.* 2010). This is especially true in host-parasitoid networks where foraging success is directly related to reproductive success (Morris, Lewis & Godfray 2005; van Veen, Morris & Godfray 2006; Bukovinszky *et al.* 2008). Insect parasitoids lay offspring in/on a ‘host’ (mostly other arthropods), which provides the sole source of biomass for the offspring’s development to sexual maturity. Furthermore, female parasitoid wasps may determine offspring sex when laying an egg in/on a host (Heimpel & de Boer 2008). Therefore in most host-parasitoid networks, foraging behaviour directly determines both host-mortality rates and the parasitoid population’s growth-rate and sex ratio. There are two aspects of foraging behaviour considered to be particularly important at the network-level:

1. The term host preference regards the relative allocation of limited resources across all available hosts. Parasitoids may either optimise the ‘number’ of offspring they produce or offspring ‘quality’(Charnov 1976). Offspring quality is related to host size, as larger hosts produce larger offspring that have greater reproductive success, and so optimal foraging theory predicts that the realised niche of a parasitoid species should be biased towards larger hosts (Roitberg, Boivin & Vet 2001; Cohen *et al.* 2005); a prediction that has been corroborated in previous studies (Bukovinszky *et al.* 2008; de Sassi, Staniczenko & Tylianakis 2012; Henri *et al.* 2012). This aspect of foraging behaviour has important community level implications because it directly determines the link-strength of individual host-parasitoid interactions, where the distribution of

strong and weak links is an important determinant of community stability (Ings *et al.* 2009). Further, if the realised niche of a parasitoid species is biased towards particular host species at any given time it can alter the structure and composition of the host community (Holt 1977; Rand & Tscharntke 2007; Prado & Frank 2014).

2. Sex ratio allocation behaviour impacts upon community dynamics because only female adult parasitoids lay eggs; female biased sex ratios are particularly favourable to biological control programs (Hassell, Waage & May 1983; Chow & Heinz 2005; Henri & van Veen 2011; Reigada, Araujo & de Aguiar 2012). Adult parasitoid size is a stronger determinant of reproductive success for females than males, as egg load, longevity and foraging range are all correlated with body size (Charnov *et al.* 1981; Heinz 1991). Charnov (1981) hypothesised that parasitoid wasps should preferentially allocate daughters to relatively larger hosts and sons to relatively smaller hosts, as has been observed in a number of species (Heinz 1991; Morris & Fellowes 2002; Chow & Heinz 2005; West, Shuker & Sheldon 2005; Bukovinszky *et al.* 2008; Mody, Spoerndli & Dorn 2012). However, this phenomenon is not evident in every parasitoid wasp species and is weakened under conditions that promote male–male sexual competition or diminish the relationship between host size and offspring fitness and, therefore, sex ratio allocation behaviour is linked to species physiology. Hosts of different sizes are predicted to interact indirectly by altering the local sex ratio of a shared parasitoid or parasitoids (Henri *et al.* 2012; Mody, Spoerndli & Dorn 2012).

Species physiology and phylogeny are associated with optimal foraging behaviour (Rohr *et al.* 2010). For parasitoids, there are multiple theories relating physiology to life-history characteristics such as life-span (Price 1973), egg-load (Rosenheim *et al.* 2008) and development time (Askew & Shaw 1986). Further, environmental conditions can alter parasitoid life-history characteristics as well as the relative quality and availability of host species, all of which link back to foraging behaviour (Bukovinszky *et al.* 2008; Boivin 2010; de Sassi, Staniczenko & Tylianakis 2012). The optimal behaviour at any given time can be related to whether reproductive success is limited by not having enough time to lay all ones eggs (time limitation), which is predicted to induce weak size-dependent foraging behaviour, or by there being too many hosts to allocate eggs to all of them (egg limitation), which is predicted to induce strong size-dependent foraging behaviour (Rosenheim 1999a; Henri & van Veen 2011). The inherent likelihood that an individual will be egg- or time- limited at any given time is related to its ecology, primarily its initial egg-load, egg production capability and its life-span (Jervis, Ellers & Harvey 2008; Rosenheim, Alon & Shinar 2010). Furthermore, environmental conditions that reduce the number of hosts a parasitoid can oviposit in (e.g. high competition or unfavourable weather) increase time-limitation and therefore the cost to investing in offspring quality (Visser, van Alphen & Nell 1990; Rosenheim 1999a).

Adherence to either an egg- or time- limited foraging strategy may alter the structure of the host-parasitoid networks, where increasing egg-limitation is predicted to result in increasingly uneven link-strength distribution among available host species; reviewed in Henri & van Veen (2011). Further, inter- and intra- species differences in foraging behaviour are hypothesised to account for some of the dynamic properties of ecological networks (Kaiser-Bunbury *et al.* 2010; Poisot, Stouffer & Gravel 2014). Recent advances in network studies have concluded that these dynamic properties are important to community stability, particularly the ability of each species to restructure its realised niche in response to changes in the foraging environment, known as link-rewiring (Kondoh 2003; Kaiser-Bunbury *et al.* 2010; Poisot, Stouffer & Gravel 2014). While foraging behaviour provides a mechanistic basis for link-rewiring, network-level studies of the determinants of foraging behaviour (i.e. physiology and the foraging environment) are limited. Herein, we study the host preference and sex ratio allocation behaviour of four species of Hymenopteran secondary parasitoid using a 10-year study of an aphid-parasitoid-secondary parasitoid community in an English meadow. We test two particular hypotheses: (i) that foraging behaviour relates to species ecology and (ii) that environmental conditions (competition for hosts) alter optimal behaviour according to the egg-/time- limitation hypothesis.

3.4 Methods

Study species

Alloxysta victrix (Westwood) [Charipidae, Alloxystinae]: A koinobiont, or ‘true’, endo-secondary parasitoid. *A. victrix* attacks a parasitoid larva while its aphid host is still alive and waits until the aphid has been consumed by the primary parasitoid before consuming the parasitoid larvae in turn. *A. victrix* is known to have a particularly broad host range for an Alloxystine secondary parasitoid, thus is an ideal candidate for comparison with the generalist idiobionts, and has been identified as a key-stone species for studies of host-parasitoid dynamics (van Veen, Belshaw & Godfray 2003).

Asaphes vulgaris (Walker) [Pteromalidae, Asaphinae] & *Coruna clavata* (Walker) [Pteromalidae, Pteromalinae]: Both species are idiobiont, or ‘mummy’, ecto-secondary parasitoids, meaning they attack primary parasitoid larvae after it has killed its host and consumed it for the most part (which results in the creation of a mummy). *A. vulgaris* foraging behaviour is well studied, previous work has shown it exhibits size-dependent preference behaviour and sex ratio allocation (Henri *et al.* 2012). Conversely, the foraging behaviour and life-history characteristics of *C. clavata* are relatively unknown.

Dendrocerus carpenteri (Curtis) [Megaspilidae, Megaspilinae]: Is also an idiobiont ecto-secondary parasitoid but belongs to a different taxonomic family to the other ‘mummy’ secondary parasitoids. The preferential foraging behaviour of this species has been well studied, and previous studies have shown that when confronted by hosts of different quality (different age, but same aphid species) *D. carpenteri* exhibits quality dependent preference attack rates and sex allocation (Sullivan & Völkl 1999).

Host samples

The data used to measure the foraging behaviour of secondary parasitoid wasps came from a long-term study of an aphid-parasitoid-secondary parasitoid network (Müller *et al.* 1999; van Veen *et al.* 2008). Briefly, surveys were conducted between April and October, from 1994 through to 2003, within a single meadow (approx. 18 000m^2 in size) in Silwood Park, Berkshire, UK. Each month, densities of the mummies of each aphid species were estimated. Samples of 400 mummies of each aphid species (if present) were taken to the laboratory to rear out primary and secondary parasitoids, in order to obtain data on host–parasitoid associations. In the laboratory we measured the size of these mummies and sexed the wasps eclosing from them. Parasitoid densities were estimated by multiplying the proportion of sample mummies eclosing as a parasitoid species by the density of mummies of that aphid species.

Host size & competition

The method by which host size has been measured is described elsewhere (Henri *et al.* 2012). Briefly, a 'Leica M165C' microscope and its associated image analysis software 'Leica Application Suite v. 3' was used to measure the length and width of ~3800 aphid mummies. Mummy volume (length x width x width) provides a strong linear relationship with fresh mummy weight (correlation coefficient = 0.9), which we consider to be a good measure of host biomass and quality. It has been shown that the relative sizes of available hosts, and not their absolute values, are important for preferential foraging behaviour; therefore, size difference was calculated as the difference between the average mummy size of an aphid species and the average size of all mummies sampled that month. Values for host competition (as a proxy for competition) were calculated as total viable mummy density for all primary host species divided by total secondary parasitoid density for each secondary parasitoid species in each month.

Measuring foraging behaviour

Host preference metrics

The various possible metrics for preferential foraging behaviour have been reviewed in Lechowicz (1982). For this study we utilised the Modified Foraging Ratio (Q) because its non-linear nature allows for meaningful comparisons between time points when host densities vary. Q values were calculated for each aphid species in each month they were present for each of the four secondary parasitoid species with the following equation:

Equation 3-1: $Q_{ij} = \frac{r_{ij}(1-p_{ij})}{p_{ij}(1-r_{ij})}$

Where r_{ij} was the proportion of all individuals of secondary parasitoid species i that eclosed from the aphid species j; and p_{ij} was the proportion of all mummies available that were aphid species j. Lechowicz (1982) recommends utilising log(Q) values, which give a range from ∞ to -∞, where negative values indicate avoidance of a host species and positive value indicate preference. A log(Q) value of zero indicates that the host species was utilised as would be expected by its relative density. A Generalised Linear Mixed-Effect Model tested the relationship between the dependent variable ‘log(Q)’ and the fixed effects ‘secondary parasitoid species’ and ‘relative host size’; ‘month’, ‘year’ and ‘primary host species’ were included as random effects. The primary host species was considered to be the species of aphid of the mummy the parasitoid eclosed from.

Sex ratio allocation

For this study we wanted to test the sex ratio of offspring allocated to each host species according to the relative size of that host in that month. A GLMM with binomial error structure was used to test the dependent variable ‘sex ratio’ and the fixed effects ‘relative host size’, ‘secondary parasitoid species’ and ‘competition for hosts’; ‘month’, ‘year’ and ‘primary host species’ were included as random variables.

Statistics

Statistical analyses were performed using R version 3.03. Model simplification using Maximum Likelihood approximation was used to test for the significance of the fixed effects.

3.5 Results

Host preference

Our linear mixed effect analysis indicated a significant positive relationship between the relative size of a primary host species and its logQ value for that month; however, this relationship differed significantly between the four secondary parasitoid species ($X^2_3 = 43.67$, $P < 0.001$; Figure 3-1). Furthermore, across all four secondary parasitoid species, the strength of the effect of host size on logQ was greater in months were there was reduced competition for hosts ($X^2_1 = 22.16$, $P < 0.001$; Figure3-1).

Condition dependent sex ratio allocation

The sex ratio of wasp offspring within each primary host species was significantly associated with the relative size of that host species during each month, where sex ratios were male biased in small hosts and female biased in large hosts; this relationship varied significantly between the four secondary parasitoid species ($X^2_1 = 12.27$, $P < 0.01$; Figure 3-2). Condition dependent sex ratio allocation behaviour was not associated with competition for hosts ($X^2_1 = 6.21$, $P = 0.15$).

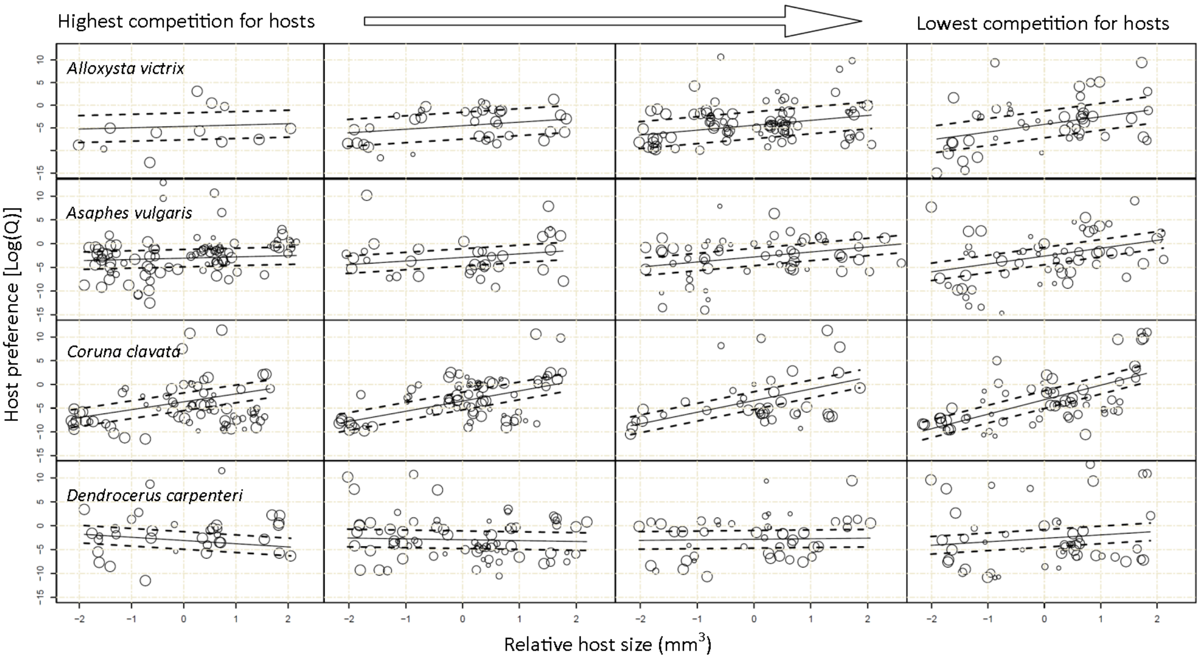

Figure 3-1 Illustration of the relationship between the Modified Foraging Ratio values for each host aphid species in each month (N= 880) against the average relative size of the species’ mummies.

Plots are separated vertically according to the species of secondary parasitoid. Plots are separated horizontally according to quartiles of host availability; with the 1st quartile (fewest hosts per parasitoid) representing the highest competition for hosts. Lines represent estimates and +/- 95% confidence intervals from a GLMM fit. Point sizes are weighted by log(host density).

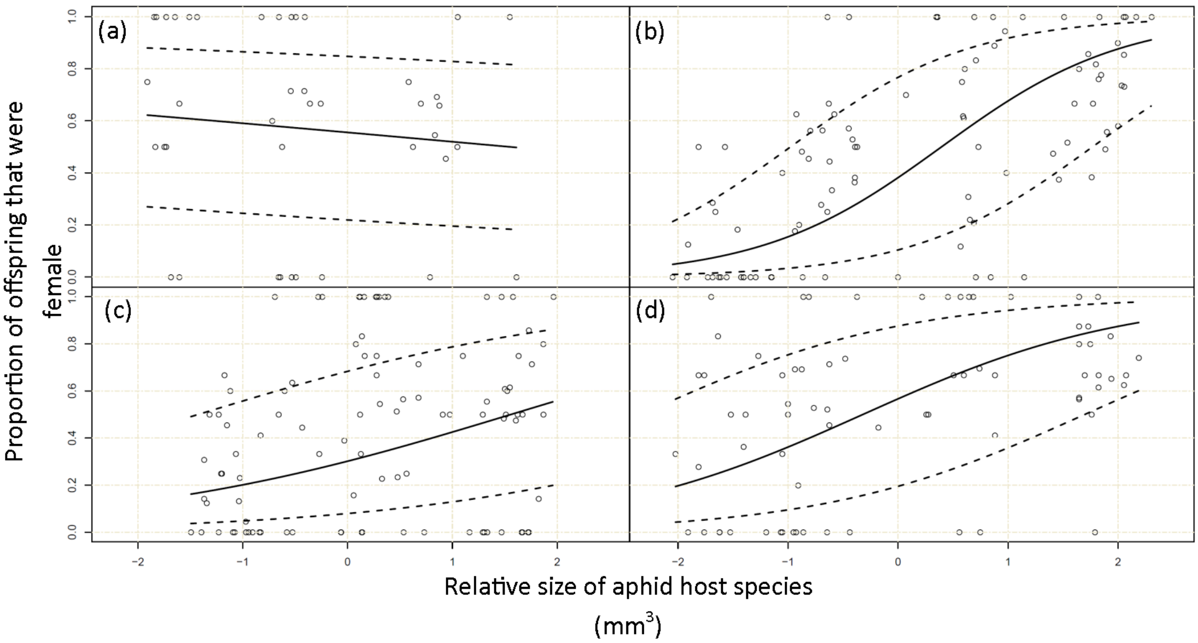

Figure 3-2 Illustration of the relationship between the parasitoid offspring sex ratio from each host aphid species in each month against the average relative size of the species' mummies (N=304).

Plots are separated by secondary parasitoid species: (a) Alloxysta victrix*, (b)* Asaphes vulgaris*, (c)* Coruna clavata*, and (d)* Dendrocerus carpenteri*. Lines represent estimates and +/- 95% confidence intervals from a GLMM fit*

3.6 Discussion

We predicted that parasitoids would exhibit significant condition-dependent foraging behaviour dependent upon host size. Correspondingly, most secondary parasitoid species exhibited preference for, and female biased offspring sex ratios in, larger primary (aphid) host species (Figure 3-1 & Figure 3-2). We further predicted that dependency of foraging behaviour on relative host size would differ according to parasitoid ecology and the foraging environment. Our analysis provided strong evidence that different secondary parasitoid species exhibit different condition-dependent foraging behaviours and that there was weaker size-dependent host preference behaviour in months with greater competition for hosts.

It is worth noting that the strength of the effect of host-size on one aspect of behaviour was not a predictor of the strength of the effect of host-size on the second aspect when comparing the different parasitoid species (Table 3-1). This suggests that the determinants of optimal foraging strategy, the characteristics that determine the relative costs/benefits to behaving in a condition dependent manner, are not the same for these two aspects of host size dependent behaviour. Further, competition for hosts significantly altered the host preference aspect of behaviour but not the sex allocation aspect. Suggesting that the egg-/time- limitation framework may not apply to sex ratio allocation behaviour in the manner predicted previously (Henri & van Veen 2011). The details of the various determinants of the two aspects of foraging behaviour are discussed hereafter.

Table 3-1 The strength of the effect of host size on parasitoid foraging behaviour, taken as the slope of the relationship between the behavioural metric and host size as estimated by the generalised mixed effect models.

Rank 1 indicates the species with the most strongly size-dependent behaviour 4 is the weakest for each aspect of foraging behaviour.

	Host preference		**Sex ratio allocation**	
Species	**Slope**	**Rank**	**Slope**	**Rank**
A.victrix	0.935708	2	-0.14404	4
A.vulgaris	0.905978	3	1.2203	1
C.clavata	2.301798	1	0.53883	3
D.carpenteri	-0.03251	4	0.83506	2

Environmental conditions and foraging behaviour

The egg/time limitation hypothesis suggests that parasitoid foraging behaviour can be altered by environmental conditions that affect the primary limiter of reproductive success (Henri & van Veen 2011). We considered the number of mummies available per parasitoid for each species as a proxy for competition for hosts, predicting that increasing competition for hosts would result in the adoption of weaker host-size dependent foraging behaviour during that month (Rosenheim 1999a; Henri & van Veen 2011). Our results show that across all four species the effect of host-size on host-preference behaviour decreased as competition for hosts increased (Figure 3-1), which supports the hypothesis that foraging behaviour becomes less condition-dependent as host availability decreases as predicted by the egg-/time-limitation hypothesis (Rosenheim 1999a; Henri & van Veen 2011). However, there was no effect of competition on the relationship between sex ratio allocation and relative host size. This leads to the hypothesis that egg/time limitation does not alter the cost/benefits to preferentially allocating daughters to larger hosts and sons to smaller hosts, which is primarily determined by the strength of the relationship between host size and gender dependent offspring fitness (West, Shuker & Sheldon 2005).

Dynamic ecological networks

Previous studies have shown that environmental conditions can alter condition parasitoid foraging behaviour (de Sassi, Staniczenko & Tylianakis 2012), and our results build on this to show that these changes in behaviour manifest as temporal fluctuations in the structure of an *in situ* host-parasitoid community. Particularly, our results suggest that conditions that increase competition for hosts will increase link-density and -evenness in the network as foragers exhibit less condition-dependent behaviours and behave in a more density dependent, or ‘random’, fashion. These changes in network structure may promote host coexistence, as strong condition-dependent behaviour can result in the local extinction of the preferred host (Holt 1977; Prado & Frank 2014). Our results support the validity of the egg-/time-limitation framework as a mechanistic understanding of the dynamic nature of host-parasitoid networks and the causes of temporal and spatial differences in community metrics such as link density and interaction evenness. This is particularly important given recent advances in ecological network theory that have concluded that temporal changes in interaction metrics are integral to community stability (Kaiser-Bunbury *et al.* 2010; Poisot, Stouffer & Gravel 2014).

Parasitoid ecology and foraging behaviour

The idiobiont parasitoids *Dendrocerus carpenteri* and *Asaphes vulgaris* both exhibited weaker condition-dependent host preference behaviour than *Alloxysta* *victrix*, as host size had a smaller effect on host preference in these two species (Figure 3-1). This pattern is converse to that expected by the ‘dichotomous hypothesis’, where koinobiont parasitoids are more likely to exhibit r-selected characteristics, particularly a reduced investment in each individual offspring, compared to idiobionts (Godfray 1994; Jervis & Ferns 2011). This hypothesis is based on the idea that koinobionts allow their hosts to continue development following oviposition and thus suffer increased juvenile mortality relative to adult mortality, in a manner analogous to the processes that promote semelparity, when compared to idiobionts (Stearns 1993; Mackauer, Michaud & Völkl 1996; Jervis & Ferns 2011). The observed differences in preferential foraging behaviour may possibly be explained by differences in relative egg-/time-limitation, but there is insufficient data of secondary parasitoid egg loads, longevity and realised foraging success due to the significant effect of primary host species on these characteristics (Sullivan & Völkl 1999).

Alloxysta victrix, did exhibit the weakest condition-dependent sex allocation behaviour as host size had the smallest effect on sex ratio of the four studied secondary parasitoid species (Figure 3-2Figure 1-1). The order of strength of the effect of host size on sex ratio allocation corroborates analyses made in Chapter 4, in which we concluded species with a stronger relationship between host size and offspring size exhibit more extreme condition dependent behaviour (West, Shuker & Sheldon 2005). This conclusion fits with general theory on foraging behaviour, where condition-dependent binary behaviour should be less precise when the relationship between the condition and the fitness pay-off is weakened (Plantegenest *et al.* 2004; Burton-Chellew *et al.*

2008; Lewis *et al.* 2010). In this regard, it has been suggested that koinobionts exhibit weak host-size dependent sex ratio allocation because host-size at time of oviposition is not necessarily linked to biomass available for offspring development (West, Shuker & Sheldon 2005).

Study limitations

A major strength of our study is that it uses a comprehensive data set of a large natural community that was sampled quantitatively every month that insects were present for ten years. While there are many community level studies of host-parasitoid networks, very few have the resolution required to study foraging behaviour in a similar manner to this study. However, we have inferred parasitoid preference and sex ratio allocation from the frequency of emerging offspring. An alternative explanation for our observations is that parasitoid offspring in general or just female offspring exhibit a positive relationship between host size and larval survival. This could lead to the same pattern even if host size played no role in the oviposition and foraging decisions of parasitoid females. We think it is unlikely that this is the case and behavioural studies of host acceptance and sex ratio allocation of some of the study species in isolation have shown significant host-size dependent responses (Sullivan 1987).

3.7 Conclusions

While there are multiple theories regarding inter- and intra- specific differences in foraging patterns there are limited long-term, field studies exploring the determinants of foraging behaviour. This report uses a uniquely detailed 10 year-long quantitative data set to show that parasitoid species with different life-histories exhibit different responses to host-size when foraging. We suggest that the cost/benefit approach highlighted in West & Sheldon (2002) is preferable to a single dichotomy hypothesis (i.e. koino/idio-biont dichotomy) for relating life-history to behaviour, with multiple distinctions interacting to produce idiosyncratic relationships that follow optimal foraging theory. Of particular importance, we found that short-term fluctuations in the strength of preferential foraging behaviour are visible at the network level, and that changes in foraging behaviour adhere to the predictions made in the egg-/time- limitation framework (Henri & van Veen 2011). Future studies of network structure and stability may wish to consider the effects of environmentally induced fluctuations in foraging behaviour and their effect on the strength of interspecies interactions.

3.8 Acknowledgements

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Chapter 4 Field evidence of the ‘relativity’ of condition-dependent sex allocation

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4.1 Chapter Concept

The previous chapters were concerned with how network level dynamics may be determined by adaptive foraging behaviour. This chapter utilises network-level data to study the determinants and evolution of flexible foraging behaviour. A specific hypothesis regarding ability of foragers to adapt their behaviour to a variable environment is tested and compared for multiple secondary parasitoid species.

4.2 Abstract

A long-standing hypothesis in evolutionary biology is that organisms should invest equally in male and female offspring, due to frequency-dependent sex-specific fitness (Fisher 1930), leading to the observed preponderance, in nature, of population sex-ratios of approximately 1:1. However, the Trivers-Willard hypothesis states that when offspring condition affects the fitness of one sex more than another, parents should make condition-dependent sex-ratio allocation decisions (Trivers & Willard 1973). Reconciling these hypotheses is the prediction that the threshold condition at which investment switches from

one offspring sex to the other should be related to the population median condition, such that the population sex-ratio remains at 1:1 (Charnov 1979; Bull 1981). Solitary parasitoid wasps are ideal study organisms to test these hypotheses because offspring body size (i.e. condition) is largely determined by the size of their host individual, and body size affects female fitness more than that of males (Charnov *et al.* 1981). Moreover, female parasitoids can control the sex of the offspring they lay in each host (Heimpel & de Boer 2008). Here, we show, using extensive monthly sampling of host communities over a 10-year period, that in two of four species of parasitoid tested, variation in switching point over time was correlated with variation in median host size, as predicted. This is the first time that this hypothesis, that the threshold of sex-ratio allocation should follow the population median condition, has been tested in wild populations. Further we show that deviation from Fisherian sex-ratios can be explained by strong condition-dependent offspring fitness.

4.3 Hypotheses

The Trivers-Willard hypothesis is based on two observations among red deer, *Cervus elaphus*: (i) offspring size correlates with maternal condition; and (ii) male fitness is determined by body-size more than female fitness. The hypothesis predicts that individuals should favourably produce sons under conditions favouring increased offspring size, such as good maternal condition or high resource availability, thereby maximising inclusive fitness (Trivers & Willard 1973). A similar, reversed, argument applies for scenarios where female fitness is determined by body-size more than male fitness (as in parasitoids, see below). In fact, Trivers-Willard-like condition-dependent sex allocation has been found in many species (West, Shuker & Sheldon 2005). Optimality models suggest condition-dependent behaviour should be a step-function (Figure 4-1); i.e. for values of offspring condition above the ‘switching point’ all offspring should be one gender and vice versa (Bull 1981). For population sex-ratios to remain Fisherian, the switching point should be the median value of offspring condition so gender is allocated relative to that of other offspring (Bull 1981; Charnov *et al.* 1981; Schwanz, Janzen & Proulx 2010). When average offspring condition varies temporally, the optimal switching point tracks with the median value (Figure 4-1). The reality of this prediction requires that (i) individuals are capable of accurately assessing the average offspring condition in the community and (ii) that individual behaviour is plastic (West & Sheldon 2002; Lewis *et al.* 2010). Previous studies have shown that some parasitoids gather information on relative host-quality from sequential oviposition experiences and adapt their foraging behaviour accordingly (Morris & Fellowes 2002; Lentz-Ronning & Kester 2013).

Many threshold traits, including sex ratio allocation, exhibit a less definite relationship with the environment than that predicted by optimal foraging theory (Charnov *et al.* 1981; West & Sheldon 2002; Plantegenest *et al.* 2004; West, Shuker & Sheldon 2005). With respect to size-dependent sex ratio allocation, this manifests as a gradual relationship between host size and offspring sex at the population level, not a step-function. A prevalent explanation for this gradual relationship is variation in the switching points of individual members of a population (Hazel, Smock & Lively 2004). Similarly, Charnov (1981) suggested that a gradual response would be evident at the individual level to account for individual error in the correct assessment of average ‘host size’. Assuming switching points are plastic in this system, the ‘individual variation’ hypothesis predicts that variance in host-size is negatively correlated with the slope of condition dependent sex allocation behaviour. Where switching point variation between individuals increases with variance in available host sizes at any given time and results in a shallower slope of the relationship between host size and offspring sex (Charnov *et al.* 1981; Hazel, Smock & Lively 2004; Lewis *et al.* 2010).

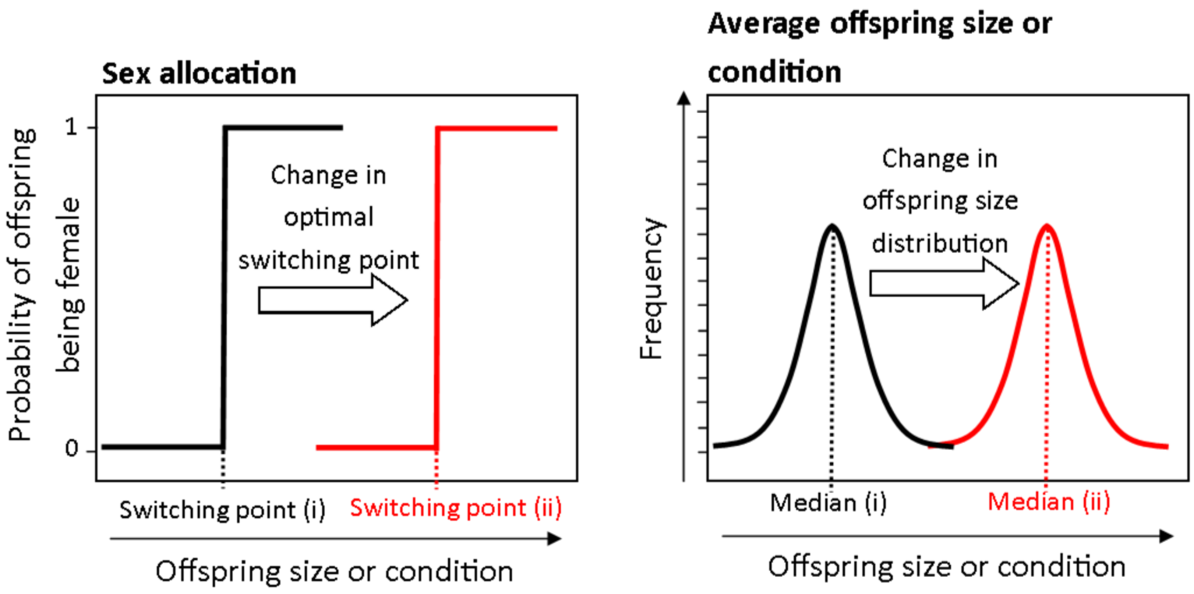

Figure 4-1 Changes in the optimal switching point of condition-dependent sex-ratio allocation according to changes in the frequency distribution of the determining factor of offspring fitness, as predicted by Charnov (1981).

Insect parasitoids lay offspring in/on a 'host' (mostly other arthropods), which provides the sole source of biomass for the offspring's development to sexual maturity. In solitary parasitoids, only one offspring will be produced per host.

The size of adult solitary parasitoids is proportional to the size of the host on which it developed and we have previously shown that parasitism in wild populations is biased towards larger hosts (Cohen *et al.* 2005; Henri *et al.* 2012). Adult parasitoid size is a stronger determinant of reproductive success for females, as egg load, longevity and foraging range are all correlated with body size (Charnov *et al.* 1981; Heinz 1991). Due to this gender bias in size-dependent offspring fitness, Charnov (1981) hypothesised that parasitoid wasps should preferentially allocate daughters to relatively larger hosts and sons to relatively smaller hosts, as has been observed in a number of species (Heinz 1991; Morris & Fellowes 2002; Chow & Heinz 2005; West, Shuker & Sheldon 2005; Bukovinszky *et al.* 2008; Mody, Spoerndli & Dorn 2012). However, this phenomenon is not evident in every parasitoid wasp species and is weakened under conditions that promote female choosiness or male–male sexual competition (Heinz 1991; Featherston, Jones & Elgar 2013; Macedo *et al.* 2013).

4.4 Methods

So far, it has not been possible to test the hypothesis that the switching point of sex-ratio allocation should coincide with median host size *in situ*. Further, the effect of intergenerational environmental variance on the precision of condition dependent sex ratio behaviour has only been modelled computationally (Lewis *et al.* 2010). Here we evaluate the realities of these hypotheses using a unique data set collected from an aphid-parasitoid-hyperparasitoid community in an English meadow. Over a ten year period, every month that insects were present, samples were taken of parasitized aphids (which act as hosts for hyperparasitoids) from all the species present and (hyper-)parasitoids were reared out and preserved, along with the host remains; methods described in detail in Müller *et al.* (1999) and Henri *et al.* (2012). Mummy length and width were measured, using a Leica M165C microscope and its associated image analysis software ‘Leica Application Suite V3’. We studied four species of hyperparasitoid wasp: *Asaphes vulgaris* (Walker), *Alloxysta victrix* (Westwood), *Coruna clavata* (Walker) and *Dendrocerous carpenteri* (Curtis). All four species are common and abundant in the UK. The body size of the primary host species attack by these species varied by a factor ~27 (0.38-10.34 mm^3). For each hyperparasitoid species we determined the sex and the host size for each individual (for a total of 3543 individual host-parasitoid pairs). As densities of different host species vary over time, so does the median host size of the community. Statistical analyses were performed using R version 3.03. Model simplification using Maximum Likelihood approximation was used to test for the significance of the fixed effects.

4.5 The Plasticity of Switching Point

To test the hypothesis that switching point follows median offspring condition, for each of the hyperparasitoid species in each monthly sample (1 month= 1-2 generations), we determined the median primary host size, the sex-ratio switching point and the slope of the relationship between offspring sex and host size, via logistic regression of hyperparasitoid sex against host size (accounting for host species identity). To account for temporal structuring of parasitoid sex-ratios, we included year and month as random variables in all of our analyses (Sequeira & Mackauer 1993). LMER models with 'switching point' as the dependent variable and 'median host size' as the independent variable, with year and month as separate random variables, found significant positive correlations between the switching point and median host size for two of the hyperparasitoid species (Figure 4-2; *Asaphes vulgaris**, X^2_1= 6.71, P= 0.001;

Alloxysta victrix, X^2_1= 1.92, P= 0.166; *Coruna clavata**, X^2_1= 10.67, P= 0.001; *Dendrocerous carpenteri*, X^2_1= 1.94, P= 0.163). Therefore, for two species (*A. vulgaris* and *C. clavata*) we can reject the null hypothesis that switching point is a constant.

To test whether variation in host size distribution resulted in deviation from a predicted 1:1 population sex-ratio, due to imperfect matching of switching point with median host size, we tested the correlation against the null model that y=x. Only one of the species with plastic switching points corroborated the prediction that the relationship between switching point and median host size should be 1:1 (Figure 3c; *Coruna clavata*, X^2_1= 1.01, P= 0.315). While *C. clavata* exhibited 'perfect' adjustment, the switching point was always slighter higher than the median host size, which can account for increased male mortality in smaller hosts, resulting in a ~1:1 sex-ratio at maturity (Charnov *et al.* 1981). For the other species that exhibited significant switching point adjustment, *A. vulgaris*, the correlation was significantly shallower than 1:1 (Figure 4-3a; *Asaphes vulgaris*, X^2_1= 11.6, P= 0.001). Switching point in *D. carpenteri* was not plastic, we suggest the non-significant relationship between switching point and median host size was not a false negative as the relationship was significantly different from 1:1 (Figure 4-3b; *Dendrocerous carpenteri*, X^2_1= 8.74, P= 0.003). We then predict that *A. vulgaris* and *D. carpenteri* should then be associated with non-Fisherian sex-ratios.

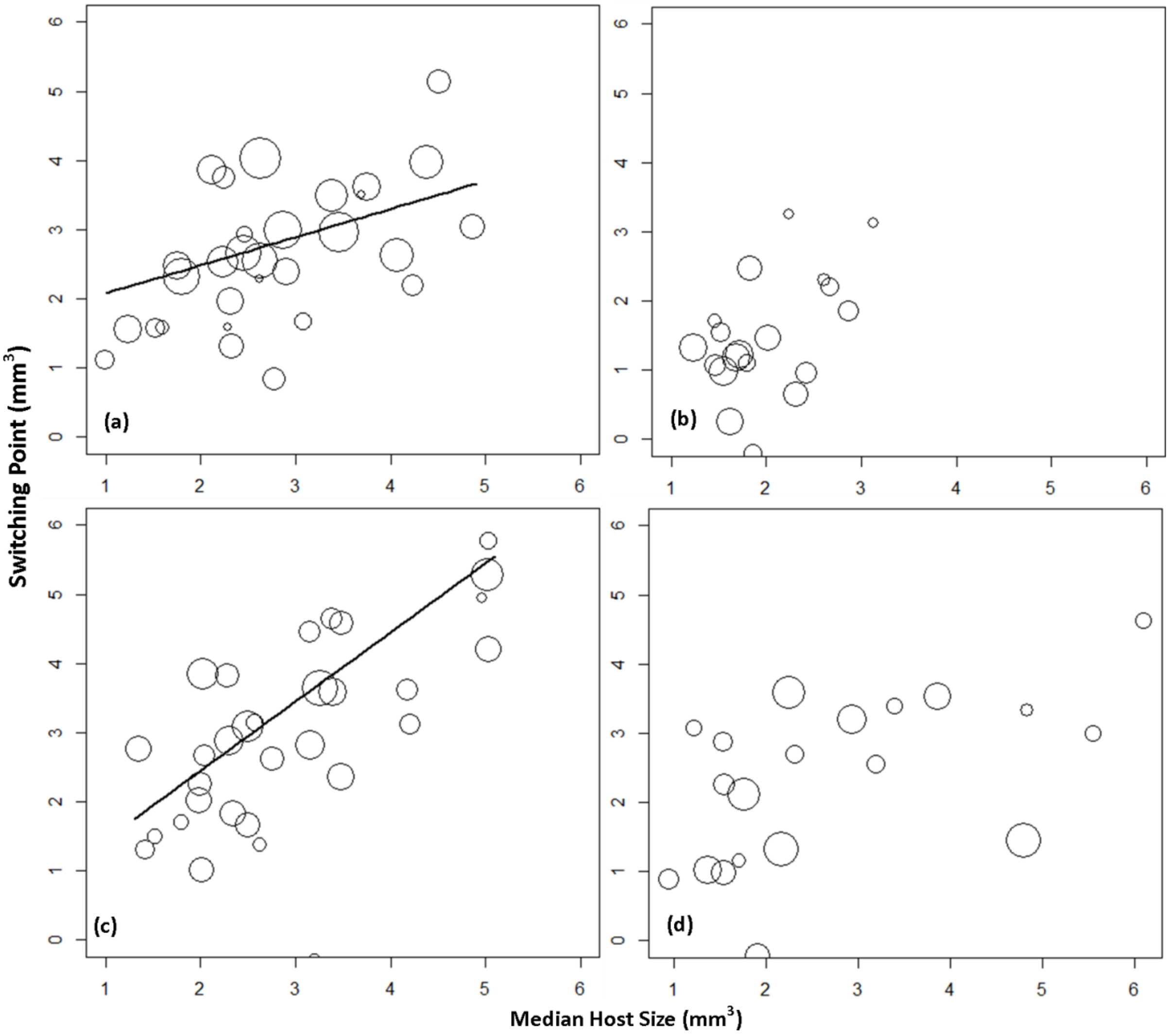

Figure 4-2 The relationship between the switching point of size-dependent sex allocation and the median host size during each month for four parasitoid species.

(a) Asaphes vulgaris (N=34), *(b)* Alloxysta victrix (N=20), *(c)* Coruna clavata (N=35) *and (d)* Dendrocerous carpenter (N=25). *Points are weighted by the number of samples collected that month.*

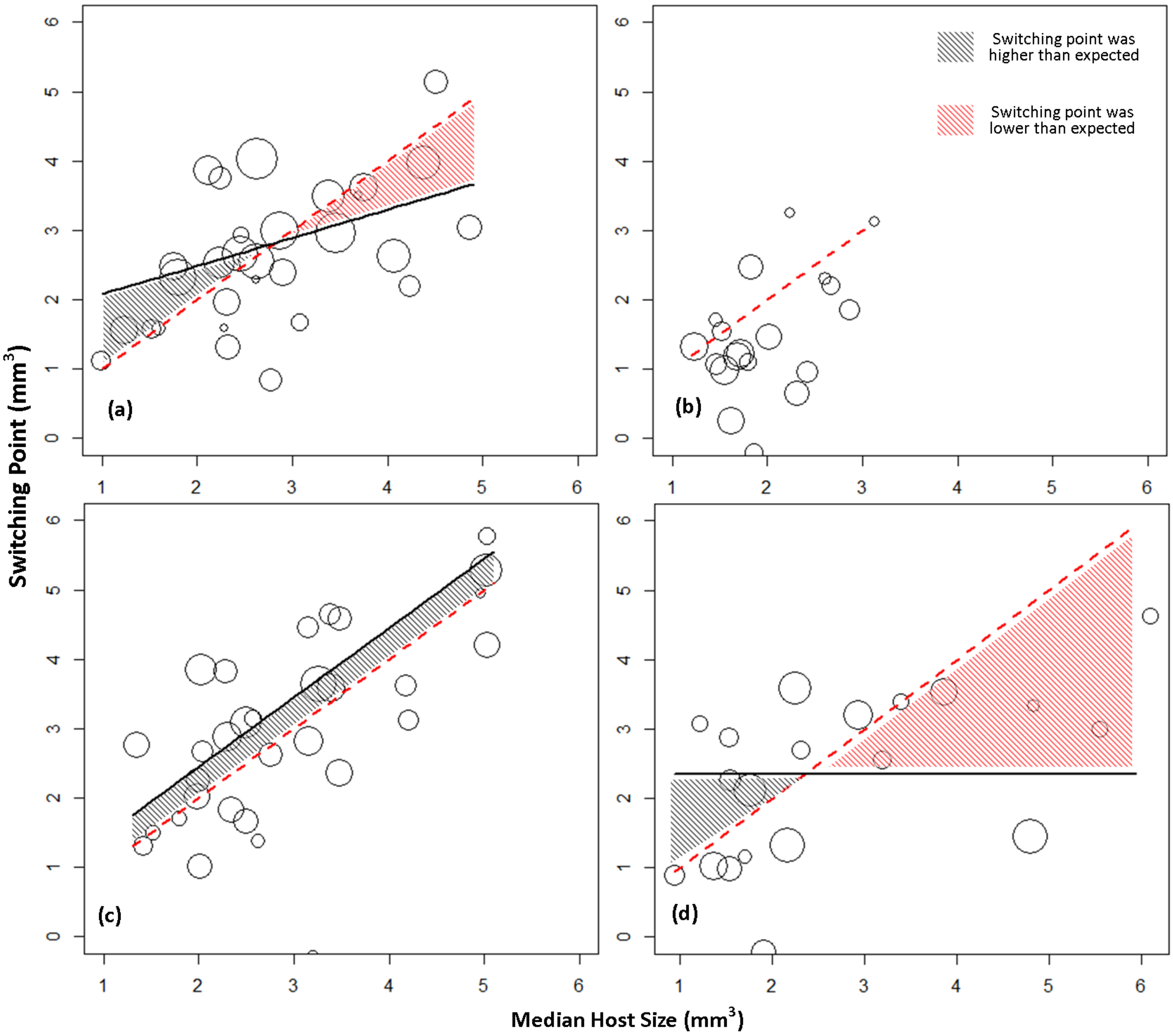

Figure 4-3 A comparison of 'perfect' adjustment of switching point (red dotted line) to the observed relationships (solid black line) between switching point and median host size for four parasitoid species.

(a) Asaphes vulgaris (N=34)*, (b)* Alloxysta victrix (N=20), *(c)* Coruna clavata (N=35) *and (d)* Dendrocerous carpenter (N=25)*. Points are weighted by the number of samples collected that month.*

4.6 Population Sex Ratios

As switching point is a derived variable, we also directly analysed the relationship between sex-ratio and median host size. We performed generalised linear mixed effect models, with a poisson error structure, with 'offspring sex ratio' as the dependent variable and 'median host size' as the independent variable; including 'year' and 'month' as separate random effects. Our analyses show that species with a relationship between median size and switching point that was not 1:1 exhibited significant sex-ratio variation (Figure 4-4a,b; *Asaphes vulgaris*, $X^2_1= 24.9$, $P< 0.001$; *Dendrocerous carpenteri*, $X^2_1= 7.35$, $P= 0.007$); exhibiting more male-biased sex-ratios in months with small median host size and more female biased sex-ratios when median host size was large. The idea that Hamiltonian predictions may not apply to parasitoid species is corroborated by other studies showing that local sex-ratios can be a function of resource quality (Green 1982; Chow & Heinz 2005; Mody, Spoerndli & Dorn 2012). Whereas, *C. clavata*, which had ‘perfect’ switching point adjustment, also had consistent population sex-ratios irrespective of host size, consistent with Fisherian sex-ratio theory (Figure 4c; *Coruna clavata*, $X^2_1= 3.55$, $P= 0.060$). While insignificant, *Alloxysta victrix* exhibited a ~1:1 relationship between switching point and median host size (Figure 4-3d; $X^2_1= 1.92$, $P= 0.166$) and consistently female biased population sex-ratios (Figure 4-4d), which are congruent with the notion that *A. victrix* has an inconsistent relationship between host and offspring size on account of being a koinobiont (West & Sheldon 2002; West, Shuker & Sheldon 2005). The hosts of koinobiont partasitoids continue development before the parasitoid larvae accumulate biomass for pupation, which means host-size at time of oviposition may not directly predict offspring fitness.

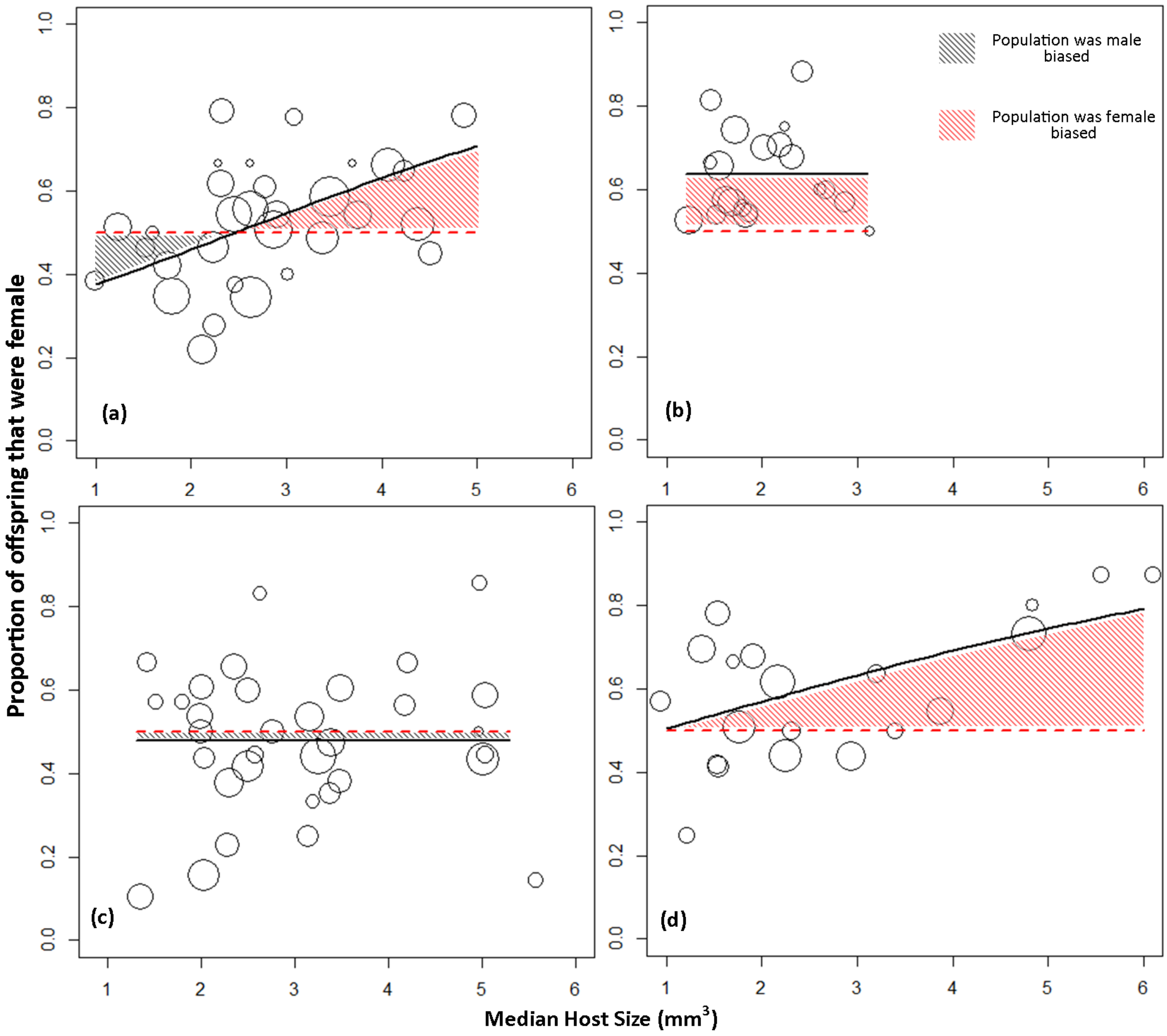

Figure 4-4 The proportion of all offspring eclosing each month that were female against the median host size for that month. The red dotted line represents Fisherian sex-ratios while the black line is a graphical illustration of the model best fit.

(a) Asaphes vulgaris (N=34)*, (b)* Alloxysta victrix (N=20)*, (c)* Coruna clavata (N=35) *and (d)* Dendrocerous carpenter (N=25).*Points are weighted by the number of samples collected that month.*

These results corroborate the general hypothesis that species will evolve more extraordinary sex-ratios when there is a strong benefit to doing so (Wild & West 2007). In this case, we suggest that the condition-dependent sex allocation behaviour is more pronounced in species that exhibit a stronger relationship between host size and size at adulthood, which suggests greater inclusive fitness pay-offs to foraging in a size-dependent manner (Table 4-1); Spearman's Rank correlation= 1, P= 0.05). A more negative slope value indicates more extreme condition-dependent sex-ratio allocation behaviour (Lewis *et al.* 2010). It is worth noting that both *A. victrix* and *D. carpenteri* had female biased populations, which is consistent with the Local Mate Competition (LMC) hypothesis (Hamilton 1967); however, inbreeding, and thus an LMC effect, is likely to be minimal due to the solitary nature of the four study species (van dem Assem, Gijswijt & Nubel 1980; Hardy 1994).

Table 4-1 The slopes of the relationships between adult size and host size compared to the slopes of the relationship between average host-size and the sex-ratio of the population for the four focal parasitoid species.

Parasitoid species	**Slope of the regression between log10(parasitoid size) and log10(host size)** [1]	**Median slope of the relationship between offspring sex and host size**
Asaphes vulgaris	0.76	-0.99
Dendrocerous carpenteri	0.57	-0.92
Coruna clavata	0.46	-0.90
Alloxysta victrix	0.45	-0.81

1. Data are taken from the appendices in Cohen et al. (2005).

4.7 Variability and the Precision of Behaviour

We evaluated the relationship between intergenerational variance in host sizes and the precision of condition dependent sex ratio allocation with a general linear model analysis of monthly coefficient of variation in host size against the log(slope) of sex allocation behaviour (offspring sex vs host size) for each of our four parasitoid species. We found no relationship between environmental variability and the step-like nature of sex ratio allocation behaviour for any of the parasitoid species studied (*Asaphes vulgaris*, $F_{31,32}$=0.61, P= 0.441; *Alloxysta victrix*, $F_{14,15}$= 0.10, P= 0.762; *Coruna clavata*, $F_{28,29}$= 0.90, P= 0.351; *Dendrocerous carpenteri*, $F_{19,20}$= 0.25, P= 0.623). These results particularly suggest that differences in the switching points of individuals, whether they result from genetics or individual error, within a population do not explain the gradual relationship between host size and offspring sex. The rejection of the notion that there is high individual variation in switching point is corroborated by recent modelling analysis using artificial neural networks, which determined that theoretically there is significant natural selective pressure on individuals to correctly assess the switching point (Lewis *et al.* 2010).

It is important to separate this from previous conclusions on the nature of unpredictability and slope of threshold behaviours (West & Sheldon 2002; West, Shuker & Sheldon 2005). An alternative hypothesis explaining the gradual nature of condition dependent threshold behaviours is that a step-like response may not be optimal where the relationship between a behaviour and fitness is unpredictable (Plantegenest *et al.* 2004). With regards to condition dependent sex-ratio allocation, species with a more uncertain relationship between host size and offspring fitness will exhibit less precise sex ratio allocation behaviour because there is weaker selection pressure on the evolution of precise behaviour (West, Shuker & Sheldon 2005; Lewis *et al.* 2010) (Table 4-1); for example, across the idio/koino-biont dichotomy (Mackauer, Michaud & Völkl 1996; West & Sheldon 2002). Our measure of environmental heterogeneity, the coefficient of variation of host size, does not measure any fundamental changes in the relationship between host size and offspring fitness nor does it measure the effect of environmental heterogeneity at the evolutionary scale, so our results do not alter the validity of previous studies. However, our study clearly shows that while different species have evolved different threshold strategies, there is a distinct evolutionary pressure towards the exhibition of the optimal switching point for all individuals in the population for any given foraging environment (Lewis *et al.* 2010). Future studies should compare the precision of condition dependent threshold behaviours among allopatric populations of species with respect to local levels of environmental heterogeneity.

4.8 Conclusions

From an evolutionary perspective, an expanded analysis of the relationship between host size and offspring size and the degree to which a species' sex allocation behaviour is size-dependent would allow us to quantify the costs/benefits associated with the evolution towards, so called, 'extraordinary' sex-ratios. Further, we could expand upon the long-debated relationship between life-history traits (such as the idio/koino-biont dichotomy) and the evolution of foraging behaviour (West & Sheldon 2002; West, Shuker & Sheldon 2005; Henri & van Veen 2011). This study provides evidence of community level adjustments of parasitoid population sex-ratios, which significantly impact upon host-parasitoid dynamics (Hassell, Waage & May 1983; Reigada, Araujo & de Aguiar 2012). Future studies could consider the ecosystem level impacts of this behaviour and its applications; for example, the manipulation of the sex-ratios of biocontrol agents in the field.

4.9 Acknowledgments

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FJFvV performed all initial field work. DCH collated and measured the samples. DCH, DS & FJFvV proposed the topic and line of study. DCH & DH collaboratively performed the statistical analyses. All authors discussed the results and commented on the manuscript.

Chapter 5 Natural enemy behaviour drives indirect 'apparent' interactions between noncompeting hosts that determine community structure and stability

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5.1 Chapter Concept

The previous chapters studied network level patterns in host-parasitoid dynamics that may have resulted from parasitoid foraging behaviour, but were unable to resolve how multiple aspects of foraging behaviour interact when determining community structure. This chapter details a computational model studying the effects of multiple parasitoid foraging behaviours on the outcome of indirect interactions between non-competing hosts. The chapter expands upon the temporal focus of the previous chapters by including a consideration of spatial variation in network structure.

5.2 Abstract

Communities of herbivorous arthropods are thought to be particularly structured by indirect processes, as in these systems herbivores are more specialist than their natural enemies. While many factors are known to alter the outcome of these indirect processes, it is not known whether these factors interact in an additive or synergistic manner. This report details a model of a community where multiple hosts do not compete for resources but may interact through their effects on the foraging behaviour of a shared parasitoid. Utilising this model we test whether two aspects of foraging behaviour (host preference and sex ratio allocation) and landscape structure determine community composition in a synergistic or additive manner. Instead of cancelling each other, as would be expected in an additive framework, the counteracting aspects of foraging behaviour resulted in highly oscillatory dynamics that promoted host co-existence. Our results further suggest that host species may indirectly interact by altering the adaptive foraging behaviours of a shared natural enemy, and that the outcome of the interaction is dependent upon the behavioural plasticity of the parasitoid. Spatial segregation of small and large host species generally benefitted the small host as parasitoid dispersal into the small host environment was limited. With respect to applied ecology, in highly disturbed agricultural systems alternative host species in the natural environment will only benefit the control of a focal pest if they increase the initial ratio of parasitoids to hosts after a disturbance event.

5.3 Introduction

Indirect processes, such as apparent competition and apparent mutualism, have been empirically shown to have a structural role in the composition and stability of natural systems (Ives & Cardinale 2004; Morris, Lewis & Godfray 2005; Bukovinszky *et al.* 2008; DeCesare *et al.* 2010; Sanders, Sutter & van Veen 2013). Particularly, top-down indirect processes are thought to be major structural determinants of herbivorous insect communities, which comprise the majority of the world's agricultural pest systems (Hairston, Smith & Slobodkin 1960; Morris, Lewis & Godfray 2004; Morris, Lewis & Godfray 2005; van Veen, Memmott & Godfray 2006). Species traits, such as foraging behaviour, are being increasingly considered for the structural role they play in indirect interactions (Ohgushi, Schmitz & Holt 2012). This is unsurprising as foraging behaviour has been a recognised determinant of ecosystem stability and dynamics for some time (Ings *et al.* 2009). This study outlines a model that illustrates how species which do not directly compete for resources may interact by altering the foraging behaviour of a shared natural enemy.

Parasitoids are organisms that develop on or within another organism, their host, they utilise host biomass as an energy source for development to adulthood; by the time the parasitoid reaches the adult (reproductive) stage the host will have died. Host-parasitoid interactions have long been used to study foraging behaviour as, in these networks, foraging and reproduction are directly linked because foraging success determines host mortality and parasitoid reproductive output (Cook & Hubbard 1977; Hubbard & Cook 1978). This is as opposed to predator-prey interactions where reproductive success is indirectly mediated through energy transfer (Henri & van Veen 2011). Due to their easily quantifiable nature, host-parasitoid networks have been successfully utilised to study indirect interactions (van Veen, Morris & Godfray 2006; Tack, Gripenberg & Roslin 2011). Herbivorous insects rarely compete directly for resources, due to high trophic specialisation, but concurrent herbivores may interact through their effects on shared natural enemies (Holt 1977; Cronin 2003; Morris, Lewis & Godfray 2005; van Veen, Morris & Godfray 2006). Parasitoids are known to have strong top-down impacts on herbivorous insect populations in natural ecosystems and in agricultural environments, where they provide important biological pest control services (Chaplin-Kramer *et al.* 2011). In agroecosystems, non-pest herbivore species may interfere with or benefit the effective control of pest species through apparent competitive or mutualistic effects (Winqvist 2011).

The outcome of any top-down indirect interaction is dependent upon the relative effects of the shared natural enemy on the different host/prey populations, where each species considered may be affected positively or negatively by the presence of the other (Holt 1977). Foraging behaviour is known to determine the link-strength of species interactions, and thus may determine the outcome of indirect processes (Rooney, McCann & Moore 2008; Ings *et al.* 2009). Two parasitoid foraging behaviours in particular are strongly linked to host-parasitoid interaction strengths and may structure indirect processes: elective host preference and sex ratio allocation (see Henri and van Veen, 2011). Some parasitoids exhibit stronger links with relatively larger host species, and vice versa, as a result of elective foraging behaviour (Chapters 2 & 3). Further, as host mortality rate is determined by the number of adult female parasitoids (males are incapable of parasitism), parasitoid sex ratios strongly influence host-parasitoid dynamics (Hassell, Waage & May 1983; Reigada, Araujo & de Aguiar 2012; Kraft & Van Nouhuys 2013). Parasitoid populations exhibit strong sex ratio adjustment in response to available host quality (Charnov *et al.* 1981), such that the presence of higher quality hosts increases parasitoid female bias, as was evident in previous studies and other studies (Henri *et al.* 2012; Mody, Spoerndli & Dorn 2012). Alternative host presence may alter parasitoid sex ratios at the patch level altering relative parasitism levels for both hosts (Henri *et al.* 2012). Because of the inherent size-dependency of many foraging behaviours, the outcome of behaviourally mediated interactions can be predicted by the relative sizes of available hosts (Heimpel, Neuhauser & Hoogendoorn 2003). While both sex-ratio allocation and host preference behaviour have been shown to impact upon host-parasitoid dynamics, they do not occur in isolation, to the best of our knowledge no studies have considered how systems are affected when these behaviours occur simultaneously (Tylianakis & Binzer 2013). While the presence of a smaller alternative host will negatively affect the larger host via host preference behaviour, we may expect the large host species to benefit from an egg dilution effect and a decrease in the female bias of the shared parasitoid population (Heimpel, Neuhauser & Hoogendoorn 2003; Henri *et al.* 2012; Prado & Frank 2014). An additive framework may expect the different aspects of foraging behaviour to counteract each other when occurring concurrently.

Foraging behaviours such as host preference and sex allocation are highly plastic and respond to changes in external conditions including host availability and quality (Henri & van Veen 2011; Tylianakis & Binzer 2013; Roitberg & Gillespie 2014). The presence of multiple host species allows foraging parasitoids that learn with sequential oviposition experiences to ascertain the relative quality of available hosts (Morris & Fellowes 2002). Therefore, size-dependent foraging behaviours, such as sex ratio allocation and elective behaviour, are most strongly exhibited when the foraging parasitoid has experience attacking hosts of different size (Charnov *et al.* 1981; Chow & Heinz 2005; Brotodjojo & Walter 2006; Prado & Frank 2014). The effect of plasticity in size-dependent foraging behaviours on network level processes such as indirect interactions have not been modelled before but we would expect increased behavioural plasticity to result in more extreme indirect interaction outcomes.

Spatially explicit models provide stability in host-parasitoid systems by allowing hosts to disperse and escape from natural enemies (Nicholson & Bailey 1935). For many parasitoids hosts are distributed as discrete patches within the foraging environment. The degree of fragmentation and connectivity between these patches has been shown to significantly impact upon the population dynamics of parasitoids (Tscharntke *et al.* 2005; van Nouhuys 2005). Further the ability of shared natural enemies to disperse between different prey/host species can decouple particular links and alter the relative importance of different determinants of interaction outcome, such as multiple aspects of foraging behaviour (DeCesare *et al.* 2010). Particularly, in agricultural landscapes host plants are separated into distinct patches, each with their associated herbivore complexes. As indirect interactions are more likely to be evident when natural enemies may easily disperse between patches (Morris, Lewis & Godfray 2005; Macfadyen & Muller 2013), we can expect different host-parasitoid dynamics when host species occupy the same ‘patch’ to when host species are segregated spatially. To this end, we propose a spatially explicit host-parasitoid model in which we can define where different host species may colonise. We consider two distinct landscapes: one where both hosts may colonise all patches, and another that is analogous to an agricultural environment where a central herbivore is surrounded by a spatially-segregated alternative host species.

Herein, we use parameters for preferential foraging behaviour extracted from a 10-year-long quantitative analysis of an aphid-parasitoid field community, to create a size structured mathematical model of a two-host-single-parasitoid system composed of spatially distinct metacommunities.

We utilise this model to study:

The implications of the concurrent expression of host preference and sex ratio allocation behaviours for host parasitoid dynamics

How host quality may structure community composition through top-down, trait mediated indirect interactions

The importance of landscape structure as a determinant of indirect interaction mechanics

Throughout the report we relate our results to applied ecology, particularly biological control efforts.

5.4 Methods

Study Species

Foraging parameters for this model were taken from a 10-year field study of a tritrophic aphid-parasitoid system, in which parasitoid foraging decisions were quantitatively recorded on a bi-weekly basis (see Henri et al., 2012). The focal species for this study is the idiobiont hyperparasitoid wasp, *Asaphes vulgaris* (Walker) (Hymenoptera: Pteromalidae). *Asaphes vulgaris* is a solitary (only one larva can develop per host individual) secondary parasitoid, i.e. the hosts of *A. vulgaris* are the primary parasitoids of sap-feeding aphids. We focused on this species because it has a documented history of size-dependent foraging behaviour and has already been shown to be a key component of indirect interactions in the field (Bukovinszky *et al.* 2008; Rand, van Veen & Tscharntke 2012). It was also the most abundant species within the field study samples, which ensures our parameters are as accurate as possible.

For this study, we have focused on *A. vulgaris* behaviour with respect to two primary hosts, the aphid species *Microlophium carnosum* and *Capitophorus carduinis*. Both of these species belong to the family Aphididae and are common in the UK. They are often present at the same time of the year at various relative densities. Within our study network, *C. carduinis* was one of the smallest primary host species within the system (average volume ~1.5mm^3) and *M. carnosum* was the largest (~4.15mm^3)(Henri *et al.* 2012).

It is important to note that while the foraging parameters for this model have been developed using specific host species in mind, the model parameters describe dynamics that can be applied to a wide range of host-parasitoid communities. Our model parameters were chosen because they represent the best available dataset of field observations with which to parameterise the model. Many primary and secondary parasitoid species exhibit similar dynamics and host-size dependent foraging behaviours to those portrayed herein; although the size-dependency of the behaviour varies (Chapters 3 & 4). Our model accounts for inter-species differences as we compare simulations with weak and strong size-dependent behaviours as well as altering the behavioural plasticity of the parasitoid.

Model framework

We developed a model of the metapopulation dynamics of two host species that share a parasitoid. The model explores the roles of size-dependent foraging behaviours (host preference and sex ratio allocation) on metapopulation structure and stability. This report is particularly concerned with the potential for host species to indirectly interact through changes in the foraging behaviour of a shared parasitoid. The model is deterministic, however, when testing we ran multiple simulations to ensure data convergence.

Four phases: pre- and post-dispersal for the hosts and the parasitoid

The overall habitat is modelled by a 40x40 grid of patches in which host resources are limited by a carrying capacity. Hosts and parasitoids may disperse between patches, and it is generally assumed that females mate on their natal patch. The foraging strategy adopted by female parasitoids occurs at two moments: (i) the pre-dispersal period, where the decision to leave a patch is based on the density of female competitors and the host abundance at the current patch, and (ii) the post-dispersal period, where size-dependent foraging behaviours are determined by the composition of small and large hosts within the current patch. Part of each host generation that survives parasitism disperses to adjacent patches. The new parasitoid generation disperses according to its responsiveness to patch conditions, and this response will determine the number of dispersers.

Figure 5-1 shows a brief conceptual diagram of the model dynamics. We divide the host–parasitoid metapopulation dynamics into two phases: (1) interaction within a patch, and (2) the dispersal of a fraction of emerging adult hosts and female parasitoids. Table 5-1 provides the parameters utilised for important growth rates and dispersal distances. The model structure and certain parameters have been adapted from Reigada *et al.* (2012).

Table 5-1 Values and descriptions of any initial fixed model terms

Symbol	Term	Value
Λ	Intrinsic host growth rate (small & large)	1.5
K	Carrying capacity (small & large)	1600
B	Strength of host preference behaviour	0 - 1
sSize	Size of small host	1.5mm3
lSize	Size of large host	4mm3
P0	Initial parasitoid population	50
H0	Initial host population	1600

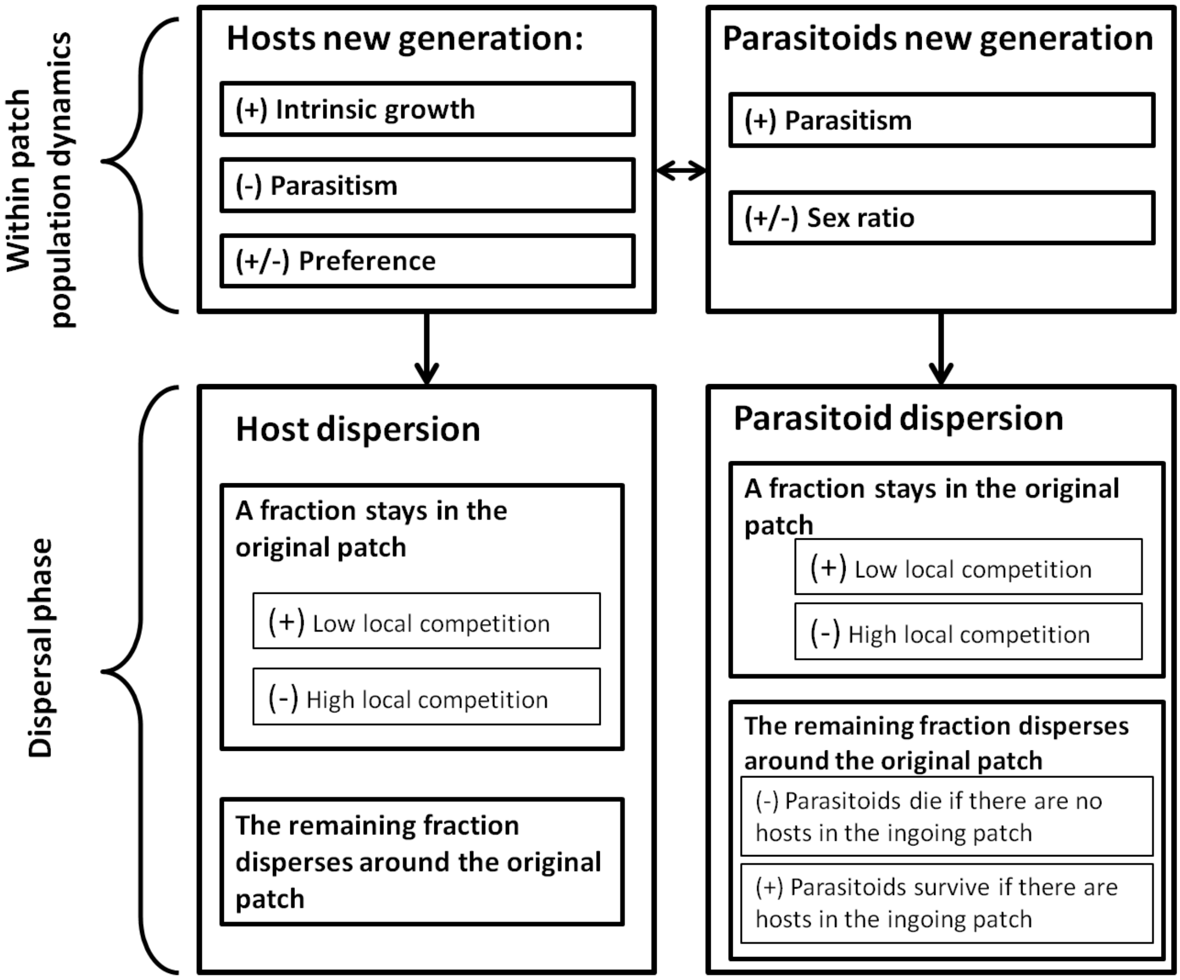

Figure 5-1 Graphic illustration of the different functions comprising the pre- and post-dispersal phases for the hosts and the parasitoid.

1. Within patch dynamics

This section describes the part of each time step in which each host species produces offspring, which are attacked by the adult female parasitoids born the previous generation that are that patch. In this model, both hosts had the same growth rate and life-history parameters (Table 5-1), as life-history characteristics are known to alter the outcome of top-down indirect interactions (Holt 1977), and so any differences in population dynamics between hosts were due to parasitism. Let $HS_{i,t}$, $HL_{i,t}$ and $F_{i,t}$ represent the populations of small hosts, large hosts and female parasitoids on patch *i* at time *t*, respectively. We focus on female parasitoids because of their direct effect on host population dynamics. Each time step describes a generation, and we assume parasitoids and hosts have synchronous generation lengths. The equations describing the in-patch interactions are given below, small letters have been used to illustrate that the values are not final patch population totals. We switch back to capital letters after parasitoid dispersal in phase 2.

Equations:

In this study, we have taken *M. carnosum* to be the large host and *C. carduinis* to be the small host.

Large Host Growth

$$\boldsymbol{hL_{i,t+1}} = yL - pL$$

The next generation of large hosts is equal to the number of offspring produced (***yL***) minus those killed by parasitism (***pL***), where

$$\boldsymbol{yL} = HL_{i,t}\left(\frac{\lambda k}{HL_{i,t}(\lambda - 1) + k}\right)$$

Small Host Growth

$$\boldsymbol{hS_{i,t+1}} = yS - pS\left(yS_{i,t}, F_{i,t}\right)$$

The next generation of small hosts is equal to the number of offspring produced (***yS***) minus those killed by parasitism (***pS***), where

$$\boldsymbol{yS} = HS_{i,t}\left(\frac{\lambda k}{HS_{i,t}(\lambda - 1) + k}\right)$$

In order to solely test the effects of size-dependent foraging behaviour both host species were given the same intrinsic growth rate (***λ***) and carrying capacity (***k***) (Table 5-1).

Parasitism of the small host

$$\boldsymbol{pS}\left(\boldsymbol{yS_{i,t}F_{i,t}}\right) = \begin{cases} vS\left(yS_{i,t}, yL_{i,t}, F_{i,t}\right), & vS\left(yS_{i,t}, yL_{i,t}, F_{i,t}\right) < yS \\ yS, & vS\left(yS_{i,t}, yL_{i,t}, F_{i,t}\right) \geq yS \end{cases}$$

The number of small host offspring parasitised (***pS***) is given by a function (***vS***), which accounts for the patch densities of small host offspring (***yS***), the number of large host offspring (***yL***) & and the number of female parasitoids (***F***). If the value of ***vS*** is greater than the number of small offspring available then all small offspring are parasitized and the remaining parasitoid eggs are allocated to large hosts or wasted (***pS*** = ***yS***).

$$\boldsymbol{vS}\left(\boldsymbol{yS_{i,t}}, \boldsymbol{yL_{i,t}}, \boldsymbol{F_{i,t}}\right) = e\left(F_{i,t}, yS_{i,t}, yL_{i,t}\right) * u\left(\beta, yS_{i,t}, yL_{i,t}\right)$$

The function (***vS***) gives the number of small host offspring parasitised and is dependent upon the total number of host offspring (small & large) that could be parasitised this generation (***e***) multiplied by the proportion of those offspring that are small (***u***)

$$\boldsymbol{e}\left(\boldsymbol{F_{i,t}}, \boldsymbol{yS_{i,t}}, \boldsymbol{yL_{i,t}}\right) = \begin{cases} E\left(F_{i,t}, yS_{i,t}, yL_{i,t}\right), & E\left(F_{i,t}, yS_{i,t}, yL_{i,t}\right) < yS_{i,t} + yL_{i,t} \\ yS_{i,t} + yL_{i,t}, & E\left(F_{i,t}, yS_{i,t}, yL_{i,t}\right) \geq yS_{i,t} + yL_{i,t} \end{cases}$$

The total number of offspring that are parasitized (***e***) cannot be greater than the total number of offspring in that patch at that time (***yS*** + ***yL***).

$$\boldsymbol{E}\left(\boldsymbol{F_{i,t}}, \boldsymbol{yS_{i,t}}, \boldsymbol{yL_{i,t}}\right) = F_{i,t} * Umax(yS_{i,t}, yL_{i,t})$$

The maximum number of offspring that **can be** attacked is the number of parasitoids (***F***) multiplied by the average number of hosts attacked by each parasitoid (***Umax***), which is given by the functional response of the parasitoid to host density.

The functional response

Rather than vary or choose an arbitrary functional response we decided to derive a ‘realistic’ functional response from the same parasitoid species as the other foraging parameters were derived, *A. vulgaris*.

$$\boldsymbol{Umax}(yS_{i,t}, yL_{i,t}) = \begin{cases} -0.004\left(yS_{i,t} + yL_{i,t}\right)^3 + 0.0174\left(yS_{i,t} + yL_{i,t}\right)^2 + 0.0348\left(yS_{i,t} + yL_{i,t}\right), & yS_{i,t} + yL_{i,t} < 23 \\ 5, & yS_{i,t} + yL_{i,t} \geq 23 \end{cases}$$

Umax is the functional response curve for *A. vulgaris* in the field, the function is a line of best fit for the number of offspring per adult parasitoid against the number of hosts available that month. The maximum average parasitism rate is 5 hosts per parasitoid, which is achieved when there are at least 23 hosts within the patch (Figure 5-2). A third order function was used as it provided the closest fit to the data, suggesting a type III functional response for the parasitoid in the field. It is worth mentioning that the average foraging success per host is lower than previous estimates of *A. vulgaris* reproductive potential, we suggest that dissection data does not account for competition, parasitoid mortality and other hindrances to realised foraging success (Sullivan & Völkl 1999).

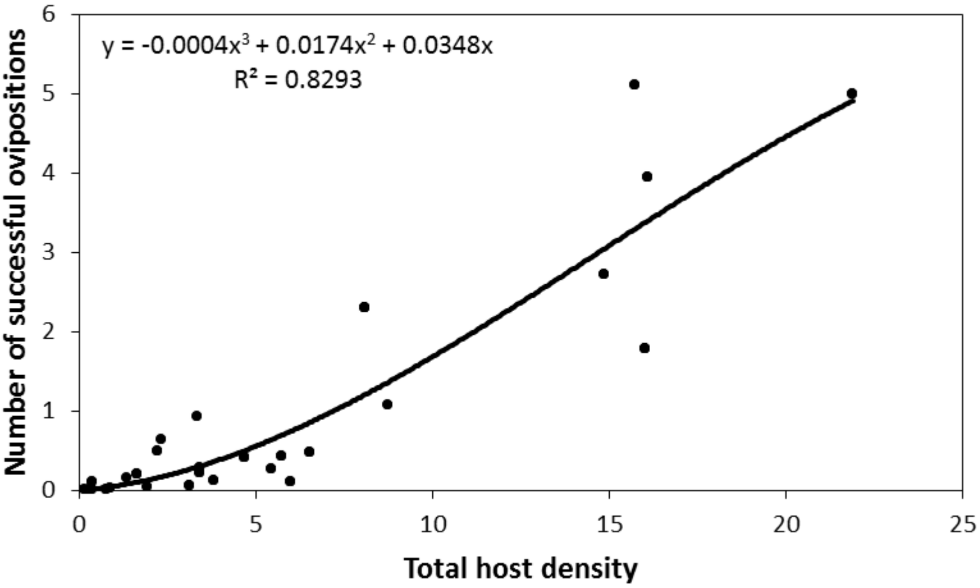

Figure 5-2 The estimated monthly density of all host species against per parasitoid foraging success in each month for the study parasitoid species. *Parasitoid foraging success (Umax) was density dependent following the function displayed in this figure, where 'x' was patch host density; at densities greater than 23 a Umax of 5 was assumed. A third order interaction provided the best fit of the data according to* R^2 *values.*

Host preference behaviour (u)

Preference is defined as when relative host attack rates are not exactly equal to relative host density (Figure 5-3A).

$$\boldsymbol{u(\beta, yS_{i,t}, yL_{i,t})} = \begin{cases} 0, u(\beta, yS_{i,t}, yL_{i,t}) < 0 \\ u(\beta, yS_{i,t}, yL_{i,t}), 0 < U(\beta, yS_{i,t}, yL_{i,t}) < 1 \\ 1, u(\beta, yS_{i,t}, yL_{i,t}) \geq 1 \end{cases}$$

The proportion of all parasitized host offspring that are small (***u***) is a function of the relative densities of small (***yS***) and large (***yL***) host offspring and parasitoid foraging behaviour (***β***), it cannot be less than 0 or greater than 1.

$$\boldsymbol{u}(\boldsymbol{\beta}, \boldsymbol{yS_{i,t}}, \boldsymbol{yL_{i,t}}) = \omega + \beta(U - \omega)$$

The proportion of parasitized hosts that are small (***u***) is a function of the proportion of available hosts that are small (***ω***), a function of preferential egg allocation (***U***), and an operator that changes the strength of preferential behaviour (***β***).

$$\boldsymbol{\omega} = \frac{yS_{i,t}}{yS_{i,t} + yL_{i,t}}$$

$\boldsymbol{\omega}$ is, therefore, the proportion of available hosts that are small for a given generation & patch

$$\boldsymbol{U} = (0.004216 + (0.126838\omega) + (0.322336\omega^2) + (0.544478\omega^3))$$

The function described by ***U*** is a best fit of the relative density of the small host against its relative attack rate by *A. vulgaris*. The function was obtained by plotting $\boldsymbol{\omega}$ for *C. carduinis* against the proportion of all parasitoids that hatched from *C. carduinis* during months when only *C. carduinis* and *M. carnosum* were available. Preference was non-linear, being most evident when equal numbers of each host were present in the environment (see Kalinkat *et al.* 2011)). As predicted by optimal foraging theory, the small host *C. carduinis* was used less than would be expected by its relative density (Henri *et al.* 2012). The operator **β** allows the strength of the preference behaviour to be altered (Figure 5-3A).

$$\boldsymbol{pL} = \begin{cases} e - pS, & (e - pS) < yL \\ yL, & (e - pS) \geq yL \end{cases}$$

The number of large offspring parasitized (***pL***) is equal to the maximum number of offpring (***e***) that can be parasitized by female parasitoids minus the number of small offspring that have been parasitized (***pS***). This value cannot be greater than the number of large offspring present in the patch.

Parasitoid growth

Parasitoid growth is equal to the number of host offspring that are parasitized in each generation (***pS*** + ***pL***). However, only female parasitoids (***F***) contribute to the maximum number of hosts parasitized at any given time (***e***). Many parasitoid species exhibit sex ratios that are a function of average available host-size, such that they are male biased when hosts are small and *vice versa* (Chapters 2, 3 & 4, Henri et al., 2012, Mody et al., 2012).

$$\boldsymbol{f}_{\boldsymbol{i},\boldsymbol{t}+\mathbf{1}} = \left(pL_{i,t} + pS\left(yS_{i,t}, yL_{i,t}F_{i,t}\right)\right) * \quad s(\boldsymbol{\beta}, \boldsymbol{Size})$$

The number of female parasitoid offspring (***f***) is the total number of hosts successfully parasitized (***pS*** + ***pL***) times the proportion of those hosts allocated daughters (***s***).

$$\boldsymbol{s}(\boldsymbol{\beta}, \boldsymbol{Size}) = 0.5 + \boldsymbol{\beta}((\frac{1}{1 + \left(\frac{1}{Exp\left(3.1565 + (-1.1945 * \boldsymbol{Size})\right)}\right)}) - 0.5)$$

The proportion of parasitoid offspring that are female in each generation is a function of the strength of size dependent behaviour (***β***) and average host size (***Size***). The equation for the relationship between average host size and parasitoid sex ratios has been taken from the same long-term data-set as the foraging preference data for the parasitoid *A. vulgaris* (Henri *et al.* 2012) (Figure 5-3B).

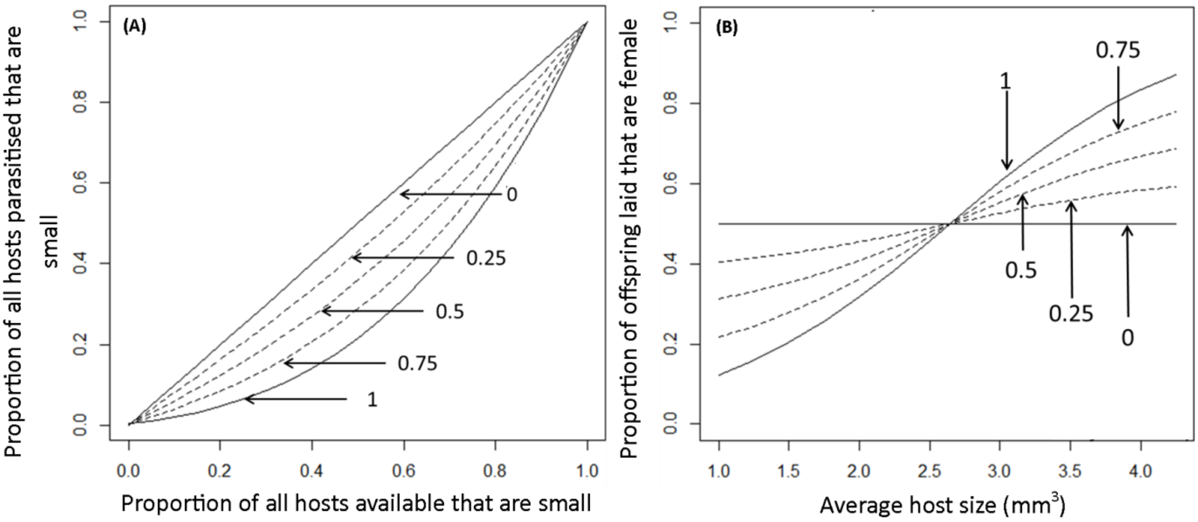

Figure 5-3 Visualisations of the functions representing parasitoid foraging behaviour.

*Lines represent functions under different values of the operator **β**, which alters the strength of size dependent foraging behaviour. A **β** value of zero corresponds to foraging behaviour that is independent of host size, and a value of 1 indicates the most extreme size dependent behaviour, which was obtained from actual values for A. vulgaris (see Henri et al., 2012). The figure on the right is elective host preference and the figure on the left is for sex allocation behaviour.*

$$\boldsymbol{Size} = (\omega * sSize) + ((1 - \omega) * lSize)$$

Average host size (***Size***) is a weighted average of the proportion of small and large host offspring in the environment multiplied by their respective average volumes (C. carduinis volume = ***sSize***; M. carnosum volume = ***lSize***).

2. Between patch dynamics

The between patch dynamics have been described in Reigada *et al.* (2012). Briefly, the model landscape was made up of a 40x40 grid, each cell represented a patch, the within patch dynamics have been described above. The outcome of the within patch dynamics determined the size of each population that may disperse for both host species and the parasitoid. The grid had reflective boundaries and dispersal of the subpopulations factored in distance effects. The dispersal of both host species was defined by the same parameters and the density of one host species had no effect on the other, this was to illustrate that the two host species considered do not compete for resources. The number of hosts of each species dispersing from a patch increased as patch density reached carrying capacity. Hosts dispersed to neighbouring patches within their dispersal distance and the number of settling hosts was inversely related to the distance of the patch from the natal patch. To avoid directional preferences, whenever, more than one patch was available for a given distance they were populated randomly.

The parasitoid dispersal phase occurred after those of the two host species. Parasitoid dispersal was dependent upon two functions:

(i) Host density affected parasitoid dispersal in two ways. Firstly, if there were no hosts in the natal patch then all parasitoids were forced to disperse to patches with hosts. Secondly, parasitoid dispersal rates decreased with increasing density of all hosts (i.e. density of both host species).

(ii) The presence of conspecifics also altered parasitoid dispersal rates such that increased female parasitoid density promoted parasitoid dispersal from that patch.

Similarly to hosts, the number of dispersing parasitoids was inversely proportional to dispersal distance and dispersal to different patches the same distance away was random. Parasitoids had reduced dispersal capabilities compared to their hosts. These dispersal characteristics of parasitoids and hosts have been observed in the field and is generally important for the persistence of all species in the simulated ecosystem as it allows hosts refuge from top-down mortality (Thies, Roschewitz & Tscharntke 2005; Tscharntke *et al.* 2005).

Studying parasitoid behaviour

In our initial simulations, we tested for the separate and synergistic effects of adaptive predatory behaviour on the population dynamics of concurrent host species. We compared the means and standard errors of average number of hosts per patch during time-steps 100-150, while altering the strength of preferential attack rates and sex allocation behaviours. Simulations were run for every combination of $\boldsymbol{\beta}$ for each behaviour. Hosts were capable of co-inhabiting every patch. Simulations started with both hosts at carrying capacity in the same patch, and 50 parasitoids were introduced after three time steps.

Indirect interaction metrics and the different types of simulation

In order to quantify top-down effects of indirect interactions, we recorded average patch density of a single host alone and compared it to when a second host was present. In our results positive values mean that alternative host presence was beneficial for the focal host and vice versa. Our results concentrate on the relative roles of foraging behaviour and landscape structure in metacommunity dynamics.

Measuring indirect effects

Indirect interactions were considered at two temporal scales. Short term dynamics consider the model during the colonisation of the grid from the initial seeding patch. These types of dynamics are important in many systems where populations are present seasonally, such as aphid systems (Müller *et al.* 1999). Short term metrics were presented as the peak of average patch host density (across all 160 patches); after which there was a sharp population crash of the hosts and parasitoid, representing the start of traditional Nicholson-Bailey dynamics (Nicholson & Bailey 1935). We would consider this to be a model of the potential of a shared natural enemy to stop its hosts from reaching high densities, which are generally damaging to host plants. Long term dynamics were primarily concerned with populations at dynamic equilibrium, which the system was assumed to have reached after 100 time steps (1000 time-steps were modelled but population trends remained consistent). Equilibrium density was the mean of average patch density within the landscape during time-steps 100-150. We also measured variance in patch density at equilibrium, which was standard error of average patch density during time-steps 100-150. Figure 5-4 provides an illustration of the various measures of host density.

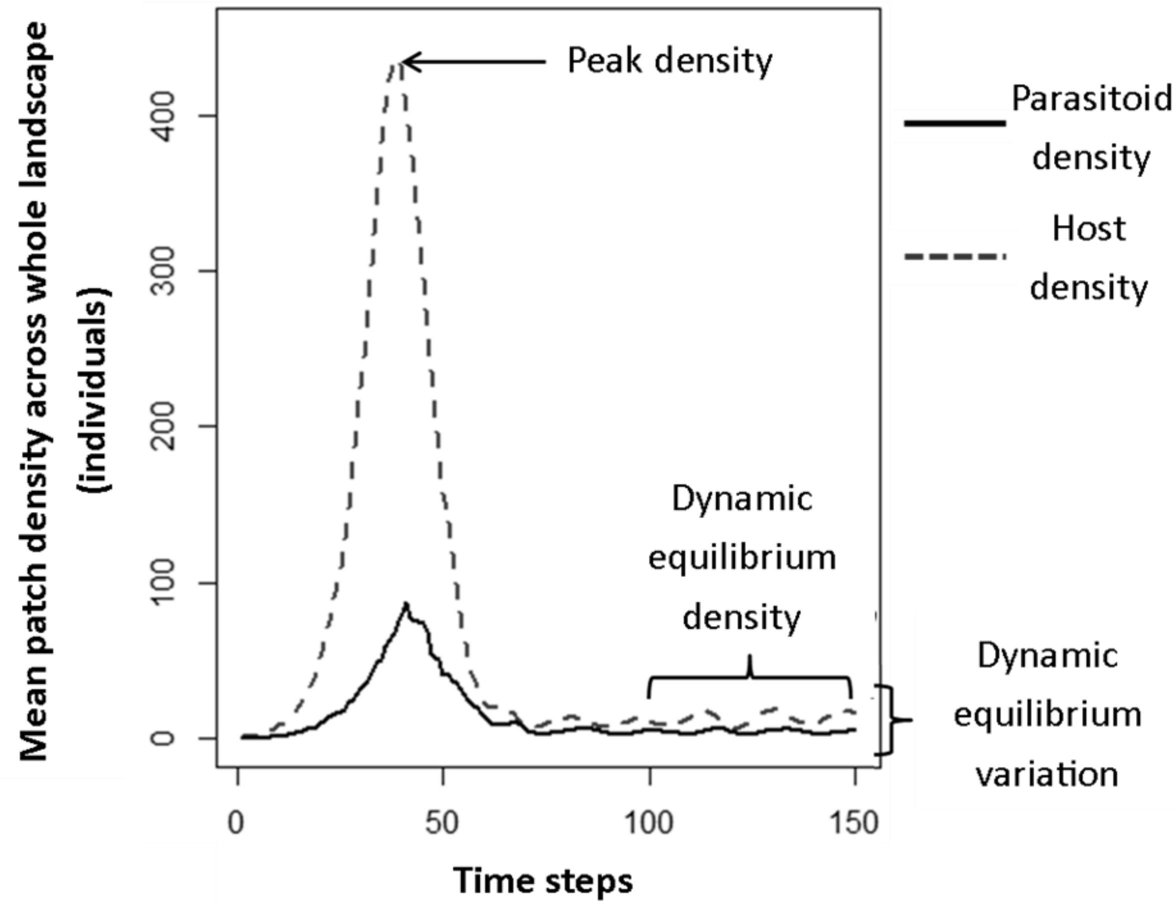

Figure 5-4 Visualisations of the aspects of host population dynamics that were considered in this report.

Namely, peak host density, mean host density and variation in host density. Graphs depict host (dotted lines) and parasitoid (solid lines) densities for each time step of a single model simulation.

Different models of parasitoid behaviour

With regard to the importance of behaviour in population dynamics, we performed three different types of model simulation covering 5 behavioural scenarios.

Scenario (**i**): *Random foraging* was modelled with a shared parasitoid that exhibited no preference behaviour and alternative host presence did not affect foraging behaviour. In these cases, the operator modifying the strength of parasitoid foraging behaviour $\boldsymbol{\beta}$ was equal to zero. Therefore relative parasitisation rates of each host were exactly equal to their relative avilability.

Scenario (**ii**): *Size-dependent foraging behaviour that was not plastic* was modelled with a shared parasitoid exhibited size-dependent foraging behaviour, the strength of which was unaffected by the presence of an alternative host. In these cases, the operator modifying the strength of parasitoid foraging behaviour $\boldsymbol{\beta}$ was equal to 0.25 with one host and with two present in the landscape. Therefore, parasitism preference was slightly skewed towards larger hosts and offspring were slightly female biased when average host size was large.

Scenarios (**iii**), (**iv**) & (**v**): *Plastic size-dependent foraging behaviour* was modelled with a shared parasitoid that exhibited size-dependent behaviour that was either weakly, moderately or strongly plastic. In these cases, the operator modifying the strength of parasitoid foraging behaviour $\boldsymbol{\beta}$ was equal to 0.25 with one host and when two hosts were present $\boldsymbol{\beta}$ was 0.5 for a weakly (**iii**), 0.75 for a moderately (**iv**) and 1 for a highly (**v**) plastic parasitoid. Therefore, when one host was available parasitism preference was slightly skewed towards larger hosts and offspring were slightly female biased when average host size was large, but the strength of the effect of size on parasitoid foraging behaviour was stronger when an alternative host was present.

Spatial segregation

Herbivorous insects are often highly host-plant specific and in agricultural setting it is unlikely that different host plants occupy the same patch. We could think of an agricultural environment being surrounded by natural environment, with each environment sustaining different herbivore species, and interactions between the two occurring through the movement of higher tropic levels such as parasitoids and predators (Chaplin-Kramer et al. 2011). Therefore, it is likely that in an agricultural setting hosts are spatially segregated, this is important as the ability of parasitoids to disperse between available hosts is integral in determining the outcome of indirect interactions. We simulated a scenario in which the central 20x20 patches (the 'agricultural environment') of the grid may only be colonised by one host and the rest of the patches (the 'natural environment') were only suitable for the other host; however, parasitoids could move and successfully colonise any patch with hosts present. We consider this scenario to be analogous to many agroecosystems where the natural and managed environments interact.

To the best of our knowledge, no previous studies have modelled these kind of dynamics. With regards to the effects of spatial segregation we considered three scenarios: (i) different host species may occur the same patch; (ii) smaller hosts may only occupy the central 20x20 patches and larger hosts must occupy the peripheral patches; (iii) larger hosts may only occupy the central 20x20 patches and smaller hosts must occupy the peripheral patches. In all scenarios parasitoids may disperse between all patches.

We ran each spatial scenario for each of the five behavioural scenarios outlined above. When hosts were able to cohabit the same patch, both hosts were initially seeded at carrying capacity and 50 parasitoids were seeded in the initial patch three time-steps later. When hosts were segregated, 300 host individuals were seeded at each of the four corner patches where their respective environments met, and 5 parasitoids were seeded at these patches three time-steps later.

5.5 Results

Behaviour and population dynamics

In our initial simulations we tested for separate and synergistic effects of size-dependent parasitoid foraging behaviour on the average patch densities of concurrent host species between time-steps 100-150, where dynamic equilibrium was evident. Strong preference behaviour resulted in the local extinction of the preferred (large) host, but did not affect mean small host patch density. More extreme size-dependent sex-ratio allocation increased the mean patch densities of both hosts, which promoted large host persistence when subject to high foraging preference (Figure 5-5A&B). Variation in mean host patch was similarly affected by size-dependent foraging behaviour (Figure 5-5C&D), where average patch host densities were most oscillatory when the parasitoid exhibited extreme preference and sex ratio adjustment.

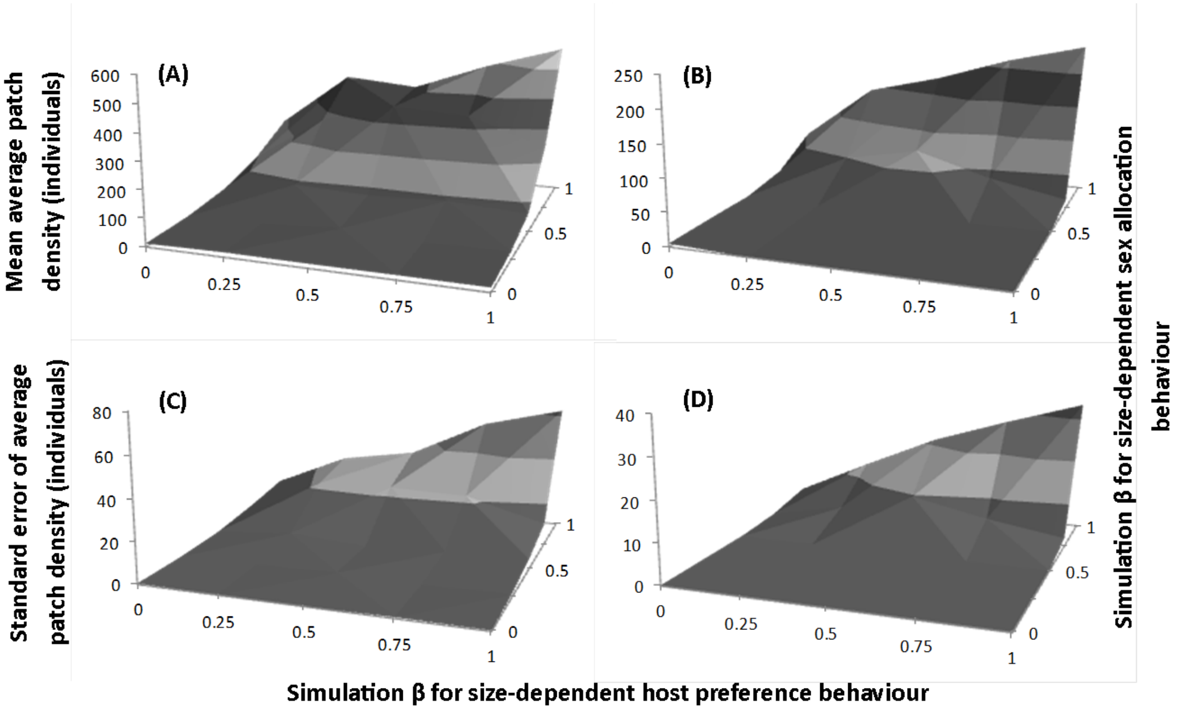

Figure 5-5 Results from our initial study of the effects of both foraging behaviours on host parasitoid dynamics.

The strength of each behaviour is given by the value for ***β*** *in each simulation. A & B depict the mean of average patch density during time-steps 100-150 for small and large hosts respectively. C & D depict the standard error of average patch density during time-steps 100-150 for small and large hosts respectively. The different shaded bands make the 3d planes easier to interpret.*

Indirect interactions

We compared peak and dynamic equilibrium mean patch host densities of each host alone compared to their respective densities when both species were present in the landscape; such that positive values indicate positive indirect interactions and negative values negative interactions. We considered five major scenarios for adaptive foraging behaviour of the shared parasitoid:

scenario (i), the shared parasitoid exhibited non-preferential foraging behaviour (***β***= 0) with one and two hosts present; scenario (ii), the shared parasitoid exhibited weak size-dependent behaviour (***β***= 0.25) in the presence of one host and two hosts; scenarios (iii), (iv) & (v) correspond to simulations which the parasitoid exhibited weak size dependent behaviour when one host was available and stronger size-dependent behaviour when two hosts were available (***β***= 0.5, 0.75 and 1 for scenarios iii, iv & v, respectively). Our results deal with these scenarios when both hosts may colonise all patches (Figure 5-6) and when each host is spatially segregated (Figure 5-7 &

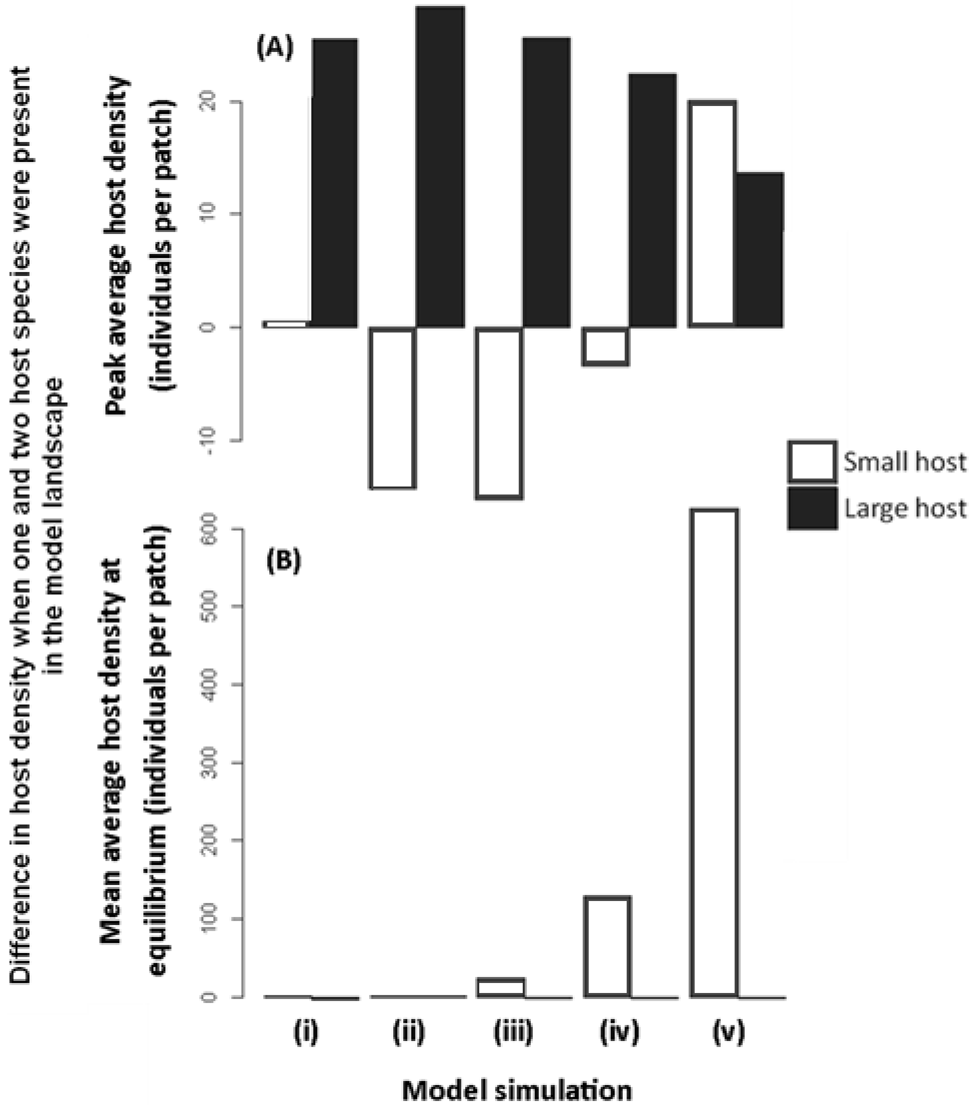

Figure 5-8).

Parasitoid exhibited random foraging

In simulations where the parasitoid exhibited random foraging behaviour (scenario **i**) apparent mutualism (+/+ interaction) was evident between host species in peak average host density and classic apparent competition (-/-) was evident at dynamic equilibrium across all spatial scenarios.

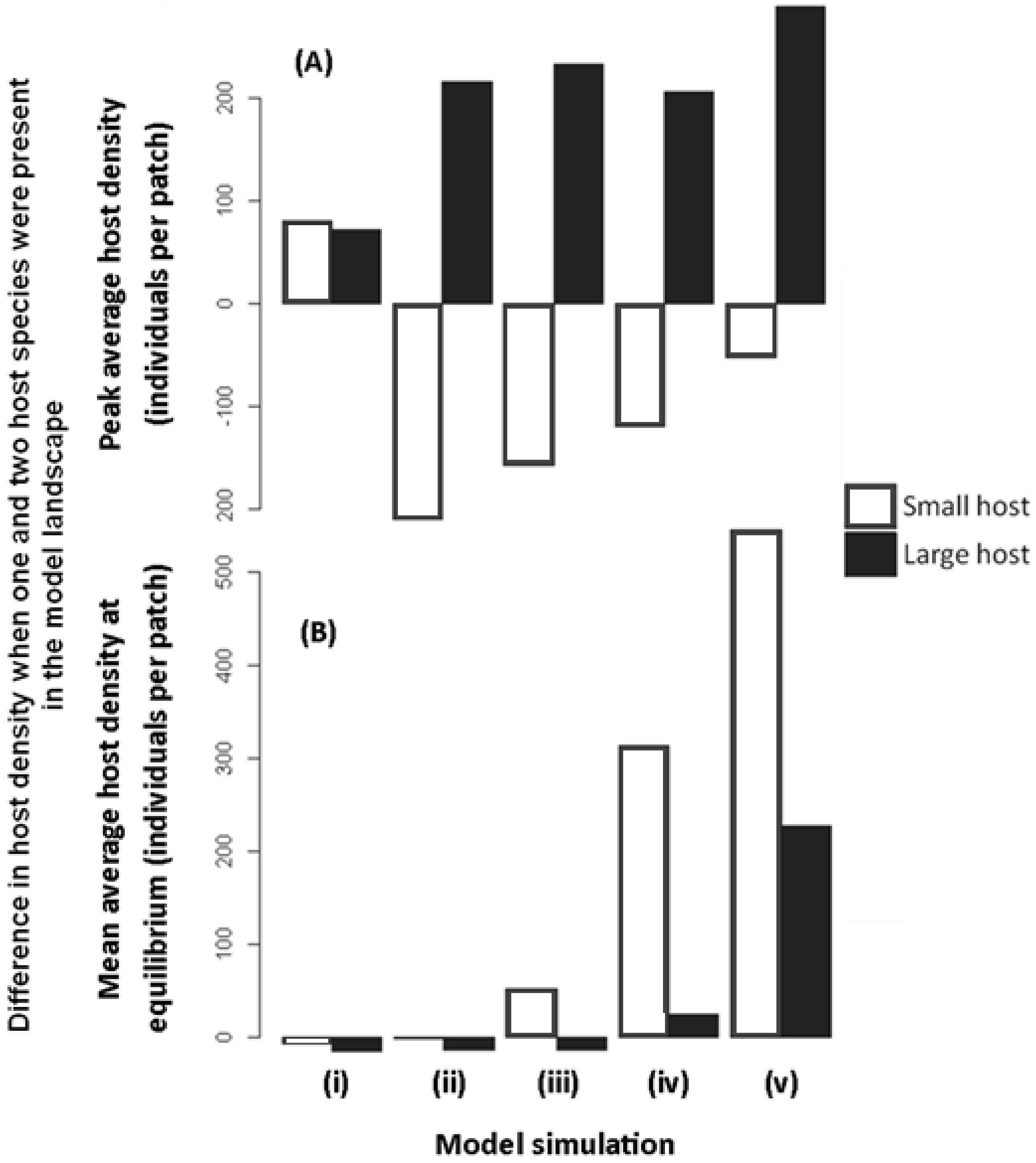

Figure 5-6 The effect of alternative host presence on peak (A) and equilibrium mean (B) average patch density when host may occupy the same patch.

*Results are of difference in focal density as a result of alternative host presence, positive values indicate positive effects for the focal host and vice versa. (i) Parasitoid foraging behaviour was irrespective of host size (**β**=0) with one and two hosts; (ii) Parasitoid foraging behaviour was weakly host size dependent (**β**=0.25) but not plastic; Parasitoid foraging behaviour was weakly* *host size dependent (**β**=0.25) with one host and (iii) weakly plastic (**β**=0.5), (iv) moderately plastic (**β**=0.75) or (v) strongly plastic (**β**=1).*

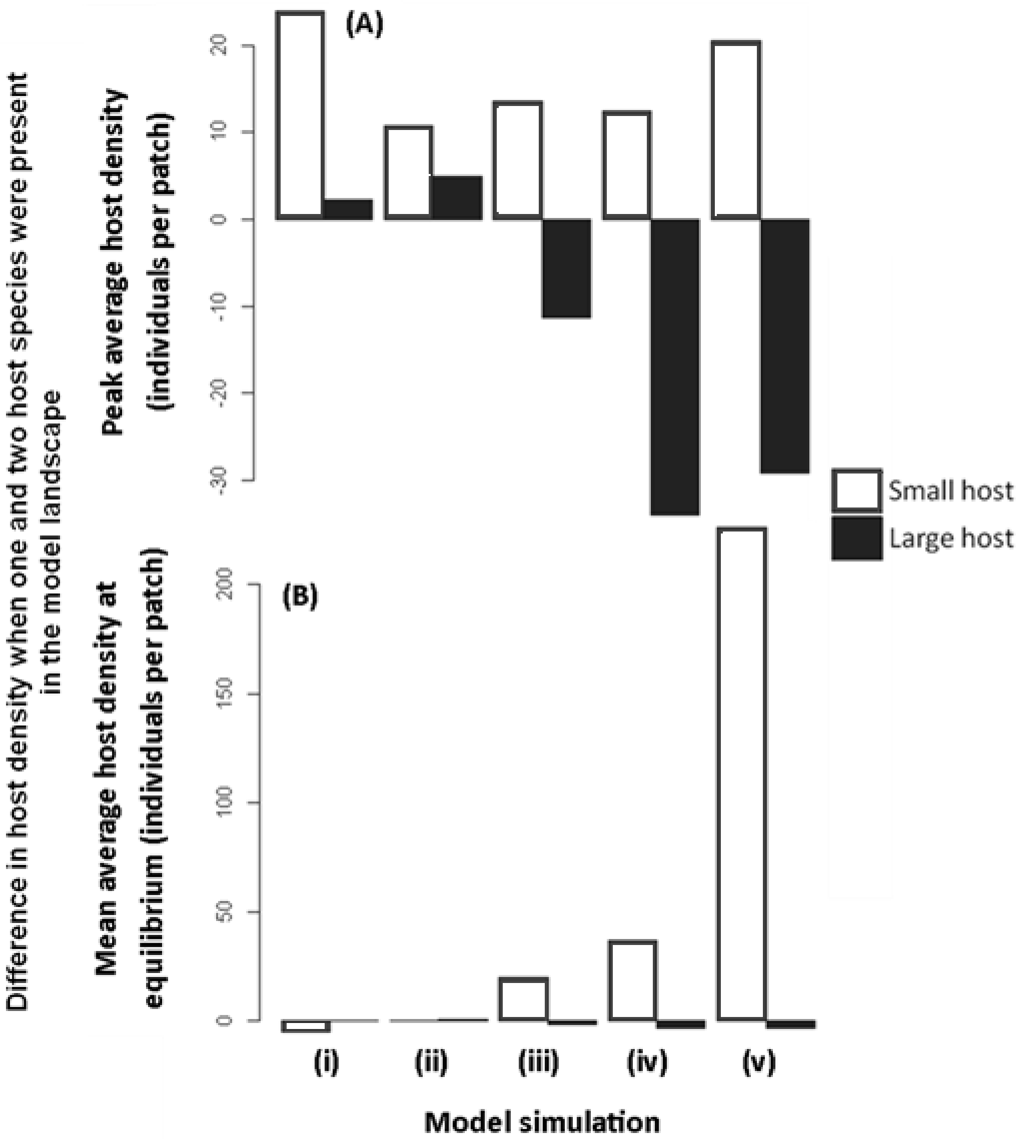

Figure 5-7 The effect of alternative host presence on peak (A) and equilibrium mean (B) average patch density when small hosts must occupy the central 20x20 patches and large hosts must occupy the peripheral patches.

*Results are of difference in focal host density as a result of alternative host presence, positive values indicate positive effects for the focal host and vice versa. (i) Parasitoid foraging behaviour was irrespective of host size (**β**=0) with* *one and two hosts; (ii) Parasitoid foraging behaviour was weakly host size dependent (**β**=0.25) but not plastic; Parasitoid foraging behaviour was weakly host size dependent (**β**=0.25) with one host and (iii) weakly plastic (**β**=0.5), (iv) moderately plastic (**β**=0.75) or (v) strongly plastic (**β**=1).*

Parasitoid exhibited size-dependent foraging

When both host species were able to colonise every patch we found apparent competition (+/-) where peak average patch density of the larger host was greater in the presence of the smaller host species; however, this effect was not linearly related to the degree of behavioural plasticity (Figure 5-6A, scenarios ii-v). The outcome of the indirect interaction between the two hosts at dynamic equilibrium was dependent upon the plasticity of parasitoid foraging behaviour, ranging from classic apparent competition (-/-), when behaviour was not plastic (ii), to apparent mutualism (+/+) when behaviour was highly plastic (v) (Figure 5-6B). When the hosts were spatially segregated the central host always benefitted from the presence of a peripheral host with respect to peak average host density (Figure 5-7A & 8A). However, apparent competition (+/-) was evident where equilibrium average density of the small host was always greater in the presence of the larger host, this effect increased with increasing behavioural plasticity (Figure 5-7B & 8B).

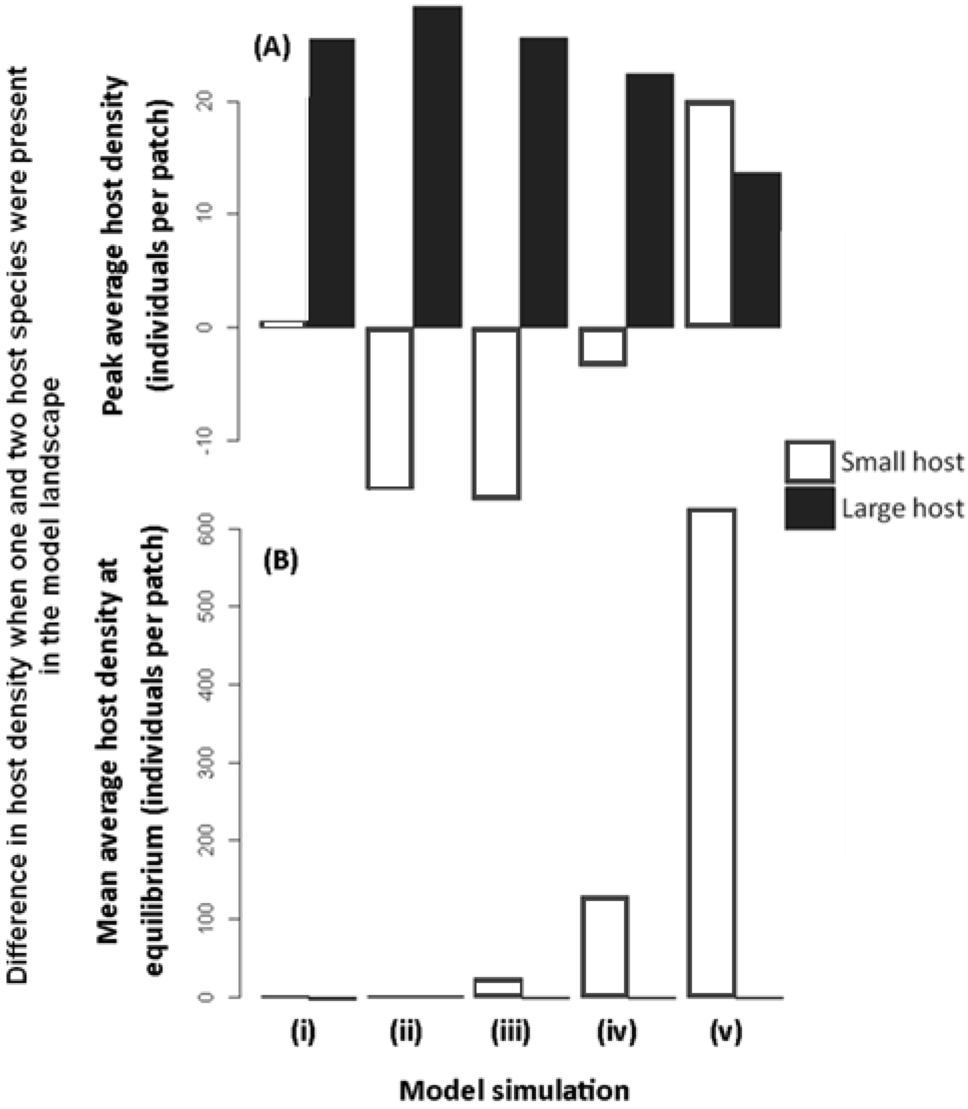

Figure 5-8 The effect of alternative host presence on peak (A) and equilibrium mean (B) average patch density when large hosts must occupy the central 20x20 patches and small hosts must occupy the peripheral patches.

*Results are of difference in focal host density as a result of alternative host presence, positive values indicate positive effects for the focal host and vice versa. (i) Parasitoid foraging behaviour was irrespective of host size (***β***=0) with one and two hosts; (ii) Parasitoid foraging behaviour was weakly host size dependent (***β***=0.25) but not plastic; Parasitoid foraging behaviour was weakly* *host size dependent (**β**=0.25) with one host and (iii) weakly plastic (**β**=0.5), (iv) moderately plastic (**β**=0.75) or (v) strongly plastic (**β**=1).*

5.6 Discussion

Parasitoid behaviour and community dynamics

This model was developed to study the synergistic effects of two size-dependent foraging behaviours that strongly influence host-parasitoid community dynamics: host preference (Ives & Cardinale 2004; Rooney, McCann & Moore 2008; Ings *et al.* 2009) and sex allocation (Heimpel, Neuhauser & Hoogendoorn 2003; Reigada, Araujo & de Aguiar 2012; Wogin *et al.* 2013). While the effect of these behaviours on host-parasitoid dynamics have been studied in isolation, their concurrent effects have not been modelled. We found that increasingly extreme size-dependent preference behaviour resulted in a greater likelihood of the preferred host going extinct, but the small (avoided) host was minimally affected. This effect of uneven host-parasitoid link-strength has been shown in a previous laboratory study and predicted in previous theoretical reports (Holt 1977; Prado & Frank 2014). Both large and small hosts exhibited greatest equilibrium densities when the shared parasitoid exhibited extreme preference behaviour and sex-ratio adjustment, the combination of the two behaviours stopped the large (preferred) host from becoming extinct. This result is similar to that in Heimpel *et al*. (2003), in which apparent mutualism was found between preferred and non-preferred hosts when the shared parasitoid exhibited strong preference and had low success survival rates in the non-preferred host.

In this study increased community stability (i.e. the co-existence of both hosts) resulted from greater temporal variation in host density. Previous models have shown that parasitoid sex-ratio adjustment causes higher variation in host density (Wogin *et al.* 2013), as was found herein, and that sex ratio adjustment with regards to patch quality may help to stabilise host-parasitoid communities (Reigada, Araujo & de Aguiar 2012). Host co-existence was promoted by increasingly male biased parasitoid populations as large host density declined reducing extinction risk in both hosts; this pattern was most extreme when the parasitoid exhibited high host preference. It is likely that the non-linearity of preference behaviour was an important aspect of this stability, such that preference was much weaker when there were relatively fewer preferred hosts in a patch, and should be an important consideration for studies of these types of behaviours (Kalinkat *et al.* 2011). We suggest that the outcome of multiple aspects of foraging behaviour act synergistically and do not fit the predictions of an additive model of network structure (Henri *et al.* 2012).

The plasticity of size-dependent foraging behaviour

Herein, we considered indirect processes between two herbivore species mediated through changes to the foraging behaviour of a shared natural enemy. The particular focus of this report was based on an observed phenomenon where size-dependent foraging behaviour is often more extreme in the presence of an alternative host of different quality, as opposed to a single host alone (Charnov *et al.* 1981; Chow & Heinz 2005; Prado & Frank 2014). We can expect community responses to differ radically as the dependence of foraging behaviour on host size and the plasticity of these behaviours is not equal for across parasitoid species (Chapter 4) (West & Sheldon 2002; Henri & van Veen 2011) and is altered by local environmental conditions (Chapter 3) (de Sassi, Staniczenko & Tylianakis 2012; Tylianakis & Binzer 2013; Roitberg & Gillespie 2014) (such as competition for hosts or climate). It would be expected then the outcome of indirect processes in the field will differ between communities, based on the range of behaviours exhibited by natural enemies. Corroboratively, our results show that the outcome of indirect interactions is dependent upon the strength of size dependent behaviour and the degree to which this behaviour is altered by changes in average host size.

Short- vs long-term indirect processes

Our results have been considered in terms of short-term effects (prior to model equilibrium) and long term effects (dynamic equilibrium density). Short-term effects describe the introduction of the parasitoid as its population increased to catch up with the already established host population. This is similar to the seasonality of host-parasitoid dynamics, where hosts establish early in the season and parasitoids develop after (Müller *et al.* 1999). Short-term dynamics are likely to be particularly important in highly stochastic environments, such as intensely managed agricultural systems (Tscharntke *et al.* 2005). In our study, when the shared parasitoid exhibited random foraging behaviour, alternative host presence reduced parasitism pressure for both host species during the initial colonisation of the landscape (peak density). Apparent mutualism has been found in previous field and computational studies where parasitoids were easily egg limited, which resulted in a dilution of top-down pressure for concurrent hosts (Evans 2008; Abrams 2010; Valdovinos *et al.* 2010). It is likely that if we had increased parasitoid egg-load, or foraging efficiency, to a high enough degree then apparent competition would have been evident (Heimpel, Neuhauser & Hoogendoorn 2003; Wogin *et al.* 2013). However, when the shared parasitoid exhibited size-dependent foraging behaviours, the preferred (larger) host benefitted from an egg dilution effect while the smaller host suffered from the increased number of female parasitoids. These dynamics were predicted in a Henri & van Veen (2011).

Long-term dynamics are more important in systems that reach equilibrium, and have been the general focus of previous models of the subject (Heimpel, Neuhauser & Hoogendoorn 2003). When the system reached dynamic equilibrium and the shared parasitoid exhibited random foraging behaviour, the presence of an equally suitable alternative host induced apparent competitive effects (-/-) like those originally predicted in Holt (Holt 1977). In our simulations, apparent competition was most strongly evident when the two hosts were equally suitable for the shared natural enemy (scenario i), as has been predicted in prior theories on the role of apparent competition in the extinction of endangered species (DeCesare *et al.* 2010). Apparent competition can only occur when parasitism pressure is aggregative, i.e. parasitoids exhibit density or patch quality dependent foraging behaviours, such that the increased density of parasitoids results in greater parasitism of both hosts (Holt 1977; Wajnberg 2006). In our model, density dependent aggregative foraging was a result of the type III functional response of the shared natural enemy, which provides a non-linear relationship between host density and parasitoid foraging success (Kalinkat *et al.* 2011).

We suggest that the outcome of indirect effects in multiple host, shared natural enemy communities is determined not only by parasitoid foraging efficiency and egg load but also the degree of disturbance and the age of the system (Holt 1977; Morris, Lewis & Godfray 2005). Apparent mutualism has previously been identified as a short-term process while apparent competition is consistent with multi-generational dynamics (Evans 2008; Abrams 2010; Valdovinos *et al.* 2010). We suggest that species interactions during the two stages (colonisation following disturbance and at established equilibrium) are governed by different processes. Indirect interactions during colonisation are determined by factors that affect parasitoid growth rate and foraging interference, such as egg load, host suitability and dispersal ability, as well as initial relative densities of hosts and parasitoids (Heimpel, Neuhauser & Hoogendoorn 2003; Evans 2008). Post colonisation dynamics are determined by the equilibrium densities of parasitoids and hosts, which includes the relative effects of top-down pressure on concurrent hosts (Holt 1977).

Spatial segregation and indirect interactions

Landscape complexity and barriers to dispersal are important aspects of community dynamics, especially in agricultural systems (Macfadyen & Muller 2013), so we considered two types of scenario: one in which both hosts may colonise the same patch, and another in which one host colonises the centre of the landscape and the other host colonises the perpheral patches. The second of these is a more relevant scenario in agriculture as herbivorous insects are highly host-plant specific, and are likely to segregated spatially by the distribution of their host plants (van Veen, Memmott & Godfray 2006; Elias, Fontaine & van Veen 2013). In general, the spatial segregation of host species favoured the smaller host as fewer females were produced in their patches and dispersal into the small host environment was limited. Our results suggest that alternative, peripheral hosts may benefit biological control programs if they are smaller (or less suitable) than the target host (

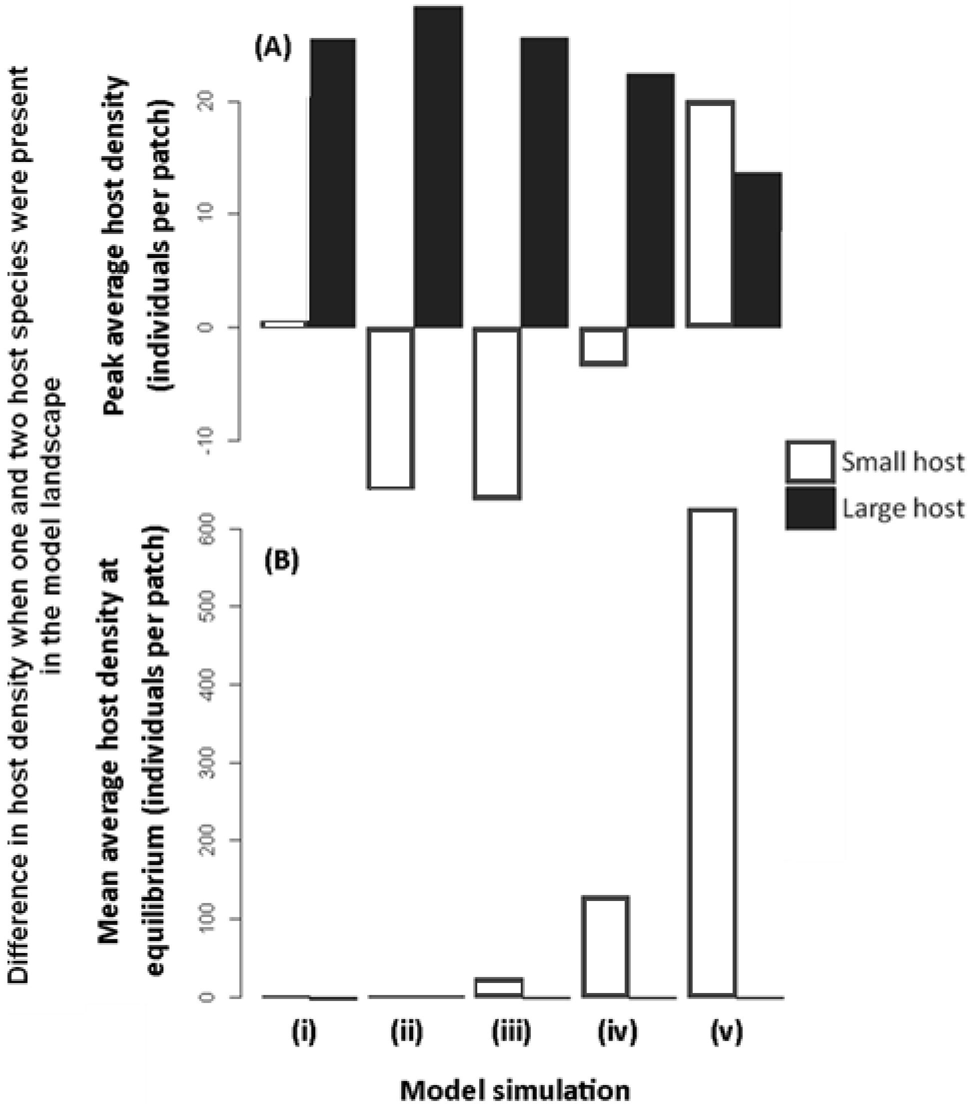

Figure 5-8B), but will reduce the number of female parasitoids within the patch if they are larger (Figure 5-7B). These patterns were only true in systems that were allowed to reach equilibrium, and the effects were especially strong when alternative host presence promoted extreme size dependent foraging behaviour. In initial dynamics, the central host generally benefitted from the presence of the peripheral host, irrespective of host quality and enemy behaviour, this is likely to have resulted from a decrease in the number of parasitoids relative to the number of hosts during seeding. While some studies have shown that landscape biodiversity benefits primary parasitism in biocontrol schemes, there are studies in which the opposite effect has been found (Chaplin-Kramer *et al.* 2011). None of these studies consider the effect of alternative host quality on parasitoid dynamics and behaviour and the effect this may have on target pest control.

5.7 Conclusions

Many studies have shown that individual adaptive foraging strategies significantly impact upon community level dynamics (Ings *et al.* 2009). This study provides initial evidence that concurrent adaptive behaviours act synergistically in structuring community level processes and not additively. We have shown that adaptive behaviours can result in highly oscillatory dynamics that, while chaotic, reduce the likelihood of host extinction.

We found that positive indirect interactions (apparent mutualism) are more evident during the initial colonisation of the system by a shared natural enemy as a result of interference (Evans 2008), while negative interactions (apparent competition) occur once the system has reached equilibrium. We have identified that short term dynamics (i.e. those occurring during colonisation) are driven by processes that affect the growth rate of the shared natural enemy and its dispersal capabilities, such as sex ratio allocation and habitat fragmentation respectively. While long-term dynamics (i.e. those occurring at system equilibrium) are determined by the relative effect of top-down pressure on concurrent hosts. Because of this relatively larger hosts generally benefit from alternative host presence during short term dynamics (Heimpel, Neuhauser & Hoogendoorn 2003; Henri & van Veen 2011; Henri *et al.* 2012), but not during long term dynamics.

With respect to considerations of applied ecology we suggest that in highly disturbed agricultural systems alternative hosts are unlikely to benefit the control of a focal pest unless they increase the initial ratio of parasitoids to hosts after a disturbance event. However, the presence of a relatively smaller alternative host may actually increase the number of female parasitoids and help suppress a large pest species. Future studies would benefit from including stochastic parasitoid mortality in the central patches to quantify the importance of alternative hosts and refuges in agroecosystems (Tscharntke *et al.* 2005).

5.8 Acknowledgements

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Chapter 6 Natural vegetation benefits synergistic control of the three main insect and pathogen pests of fruit crop in Southern Africa

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6.1 Chapter Concept

The previous chapters have explored inter- and intra-species differences in host-parasitoid dynamics. This chapter expands upon this framework by studying the effects of landscape structure and heterogeneity in an applied ecology setting. The chapter considers multiple pest and natural enemy species in an attempt to disentangle the concurrent network determinants of species identity and habitat heterogeneity.

6.2 Abstract

1 Most studies of the potential for ‘natural habitat’ to improve agricultural productivity have been conducted in predominantly transformed, temperate regions. This bias may underestimate the importance of agroecosystem services in biodiverse developing countries.

2 Natural vegetation may promote the density and/or diversity of natural enemies of crop pests, but the strength of the effect varies, and few studies directly measure the concurrent impacts on pest density. Considering multiple pest species within the same agroecosystem may help explain why some pests are more affected than others by distance to natural vegetation. Here, we investigated multiple pest species (leaf-galling midges, three species of Tephritid fruit fly and pathogenic fungi *Fusarium spp.*) and their enemies in cultivated mango *Mangifera indica*, in North-Eastern South Africa.

3 The density of generalist Tephritid fruit flies increased with distance to natural vegetation, and predation rate of pupae sharply decreased from ~50% at the edge to 0% 250m into the field. Density of the specialist, gall-forming fly was unrelated to natural vegetation but parasitism rates by a specialist parasitoid increased with proximity to natural vegetation. Incidence of the fungal pathogen disease increased with distance from natural vegetation, possibly due to decreased predation of commensal mites.

4 The strength of the relationship between natural vegetation and biological control varied across pest species and the type of natural enemy studied. However, we found strong distance effects in all studied species,

suggesting the benefits of natural vegetation depend on each species' ability to disperse into the agricultural environment.

5 *Syntheses and applications.* Our results suggest that natural vegetation is a net source of natural enemies in a region of South Africa that still contains much of its natural biodiversity. Pro-biodiversity land-use practices in this region may improve the effectiveness of biological control, but must ensure that natural enemies can effectively disperse from the non-managed to the managed environments. Future reports would benefit from considering species taxonomy and life-history for a predictive approach to agroecology and pest management. Studying the effects of provision of patches of natural habitat for natural enemies within plantations may also contribute to guidelines for sustainable management.

6.3 Introduction

Native predators and parasitoids can contribute significantly to the control of agricultural insect pest populations, a process known as 'conservation biological control' (Thies *et al.* 2011). The presence and state of local natural habitat could be particularly important in supporting this ecosystem service, because species at higher trophic levels are generally more sensitive to land use intensity and habitat fragmentation than the insect pests they attack (Chaplin-Kramer *et al.* 2011). This idea is supported by a recent meta-analysis which found an effect of proximate natural/semi-natural vegetation on the intensity of pest suppression by native predators and parasitoids (i.e., natural enemies), in 45 out of 72 studies (Veres *et al.* 2013). However, natural enemy effectiveness can be unrelated to, or even negatively affected by, proximate natural habitat (Macfadyen *et al.* 2009; Chaplin-Kramer *et al.* 2011; Macfadyen *et al.* 2011; Thies *et al.* 2011; Sohrabi *et al.* 2012; Lohaus, Vidal & Thies 2013; Shackelford *et al.* 2013). This is because natural enemy effectiveness is influenced by a number of factors, including the taxonomies of the pest and the natural enemy, and the geographic location and crop type of the agroecosystem.

To date, most studies relating land-use to pest suppression have been conducted in more developed, temperate regions, with a particular bias towards studies in Europe & North America (Shackelford *et al.* 2013; Veres *et al.* 2013). For example, of the studies included in a recent review of crop pests and natural enemies, 91% were conducted in Europe or North America, but only 4% were conducted in less developed, tropical regions (Chaplin-Kramer *et al.* 2011). Ultimately, to be able to make generalisations about the relationship between habitat management and biological control efficiency, detailed quantitative analyses of real systems, from a variety of habitats and geographic locations are required (Thies *et al.* 2011; Lohaus, Vidal & Thies 2013).

Our study system, in Hoedspruit, (NE) South Africa, is situated within the tropical, biologically diverse Kruger to Canyons Biosphere, ~55% of which is intact vegetation, unimpacted by human development (Mucina & Rutherford 2006; Coetzer *et al.* 2013). Our target crop, mango *Mangifera indica* (Anacardiaceae) is economically important in the region, and the dominant tropical fruit produced globally (FAO 2003). Previous analyses of our study system found that productivity (kg of mangos per tree) was greatest for smaller fields, declining with distance from natural vegetation (Carvalheiro *et al.* 2010).

While part of this pattern was associated with declines in pollinator diversity and density, productivity was lower than would have been predicted by pollinator declines alone; therefore, there may have been additional effects mediated by pest density that were not tested. In addition to the need for studies in more geographically diverse locations, there is also a need for studies that identify the effect of proximate natural vegetation on populations of different pest species within the same ecosystem (Chaplin-Kramer *et al.* 2011; Veres *et al.* 2013).

Natural vegetation may benefit pest control via two possible mechanisms: increasing natural enemy abundance or increasing natural enemy diversity. The positive impact of arthropod biodiversity on pest control is reviewed in Tscharntke *et al.* (2005). Natural enemy biodiversity and density are negatively correlated with farming intensity (high intensity = commercial farming vs. low intensity = subsistence farming), but are positively correlated with the proximity and size of patches of local, natural, non-managed vegetation (Attwood *et al.* 2008; Chaplin-Kramer *et al.* 2011; Shackelford *et al.* 2013; Veres *et al.* 2013). Natural vegetation may benefit natural enemy communities by increasing local habitat heterogeneity (generally correlated with species diversity) or by acting as a population reservoir that increases local density and resistance to environmental stochasticity (Corbett & Rosenheim 1996; Macfadyen *et al.* 2011). Landscape complexity may also benefit natural enemies by providing food sources (e.g. pollen, nectar, & protein and lipids from other insects) or by providing shade and shelter (Heimpel & Jervis 2005; Bianchi & Wäckers 2008; Vollhardt *et al.* 2010; Zumoffen, Salto & Salvo 2012).

Population reservoirs of predators and parasitoids in natural vegetation are only effective if individuals may practically disperse from the vegetation to the target pests (Hossain *et al.* 2002). Similarly, vegetation that provides shelter or nutrition is only beneficial to pest control if it is close enough to target pest populations (Vollhardt *et al.* 2010). This gives rise to the prediction that the benefits of proximate natural vegetation dissipate with distance within agroecosystems; i.e., with increasing distance into the agricultural fields, natural enemy density and diversity should decrease, resulting in reduced pest control. This effect could have contributed to the productivity declines found in Carvalheiro *et al.* (2010).

Predictive theories may relate biological control to the life-history characteristics of pest and enemy species. For example, the effect of natural habitat on pest control may be related to the trophic generalism of the most effective natural enemies. Biological control by specialist natural enemies, such as parasitoids, may be weakened by landscape complexity because of increased intraguild predation or hyperparasitism rates in structurally diverse environments (Gagic *et al.* 2011; Gagic *et al.* 2012; Rand, van Veen & Tscharntke 2012; Reigada *et al.* 2012). Conversely, control by generalist predators is often most effective when natural enemy diversity is highest (Martin *et al.* 2013). The life-history of a pest species may relate to that of its most effective control agent; e.g. the control of highly cryptic pest species is more likely to be dependent upon a single specialist natural enemy than multiple generalist predators (Memmott, Martinez & Cohen 2000). Finally, the effect of natural vegetation on pest control is related to the ability of species of natural enemies to persist in the natural environment (Corbett & Rosenheim 1996). It follows then that natural vegetation may be more beneficial to native than to non-native species of native natural enemy, and especially those with high trophic or habitat specificities.

Here, we consider the effect of proximity to natural vegetation on the conservation biological control of two types of Dipteran pest and a fungus on cultivated mangos near Hoedspruit, South Africa. We consider a suite of closely-related Tephritid fruit flies *Ceratitis spp.*, the invasive Mango leaf-gall-forming fly *Procontarinia matteiana* and a pathogenic fungus *Fusarium spp.*, which causes the malformation of mango flowers. We test a series of hypotheses using these three pest types, which exhibit vastly different life-histories and whose control depends upon different groups of natural enemies. Specifically, we ask (i) does the density of these pests/pathogens increase with distance from natural vegetation? And (ii) For the insect pests, does this correspond to a decline in predation/parasitism rates with distance from natural vegetation? We carried out these investigations using surveys of pest density and parasitism, and experiments to assess predation rates, with respect to distance from natural vegetation.

6.4 Methods

Field site

Africa accounts for 9% of global mango production (FAO 2003). Fruit plantations are important employers in Limpopo Province (one of the poorer South African provinces) and provide a major source of foreign investment for

South Africa as a whole (DAFF 2012). We carried out pest, pathogen and natural enemy surveys on four spatially distinct belt transects (each covering ~70x350m and spaced ~140-700m apart) within a large fruit plantation (March-May, 2013). Surveys were performed at a range of distances from the natural vegetation within these transects by walking in a straight line parallel to the border for 20m (see methods for clarification).

We used plantation bordering large areas of natural vegetation that are occasionally grazed by cattle. The vegetation type in this area falls within the savanna biome of South Africa, and is classified as “Granite Lowveld” (Mucina & Rutherford 2006). It is dominated by large *Acacia (Senegalia) nigrescens* (Fabaceae) and *Sclerocarya birrea* (Marula, Anacardiaceae), whilst the smaller-trees/shrubs include members of the Combretaceae (e.g. *Combretum apiculatum* and *Terminalia prunioides),* various species of *Grewia,* as well as *Dichrostachys cinerea.* The grass sward is dominated by the grasses *Pogonarthria squarrosa, Panicum maximum,* and *Aristida congesta* interspersed with various small shrubs and herbaceous species.

The plantations are split into blocks of mango trees (~70x150m) within a grid of non-native *Casuarina sp* trees acting as wind breaks. The natural vegetation is separated from the plantation by narrow paths and the windbreak; so that the nearest mango trees are ~20m from the natural vegetation edge. Within the mango plantations, the herbaceous cover is dominated by non-native agricultural weeds (e.g., *Tridax procumbens* and *Bidens pilosa*).

Study species and their surveillance

1. Tephritid fruit flies (Ceratitis spp.)

The plantation was infested by three closely-related Tephritid flies of the genus *Ceratitis*: the Marula (a.k.a. Mango) fruit fly *C. cosyra* (Walker); the Mediterranean fruit fly *C. capitata* (Wiedemann); and the Natal fruit fly *C. rosa* (Karsch). Tephritid fruit flies are considered to be the most economically important insect pest of mango crops worldwide (Chin *et al.* 2010). Adult females lay egg clutches under the fruit's skin and the resulting larvae eat the flesh causing decay. The larvae pupate outside the fruit in the soil below. Most currently-recognised parasitoid species attack the fruit flies during the larval stages, while pupae are sessile and vulnerable to predation by generalist predators (Chin *et al.* 2010). All three focal *Ceratitis* species are polyphagous, with a host-list compiled by De Meyer *et al.* (2002) comprising over 180, 40 and 100 species of wild and cultivated plants in the Afrotropical region oviposited on by *C. capitata, C. cosyra and C. rosa*, respectively. Therefore, we can reasonably suggest that natural vegetation can be a source of these pests and their natural enemies. Given the close phylogenetic relationship of the three *Ceratitis* species, we expect they are likely to share natural enemies (Cagnolo, Salvo & Valladares 2011a).

Ceratitis spp. density surveys were performed across a ~2km^2 section of a large fruit estate, near Hoedspruit, South Africa, by the plantation employees across four mango seasons (December-April, 2009-2013). Sensus™ traps using Capilure™ (River Bioscience Ltd, Port Elizabeth, SA) were placed within 51 of the total 160 mango tree blocks in our study area. Using a Generalised Linear Mixed Effect Model with a Poisson error structure we tested the dependent variable 'fly count' for each of the studied *Ceratitis* species against the fixed effects 'distance from the focal edge of the plantation' and 'month of the sample collection'; with 'year', 'the full date' and 'mango cultivar' as random effects.

We also reared fruit fly clutches from mangos (n=62) collected in the plantation. We performed a binomial GLMM analysis testing the dependent variable 'proportion of pupae pupated' against the fixed effect 'distance of the host mango from the natural vegetation'; with the 'date of collection' and 'mango colour (green or red)' as random factors. Distances were calculated using handheld GPS (eTrex10®, Garmin, Southampton, UK). We considered the ripeness of the mango as a fixed effect in our analyses, interpreted as the primary colour of the mango, as previous studies have shown this affects parasitism rates (Eben *et al.* 2000).

Finally, we placed cohorts of eight fly pupae (n=48) at 300, 150 and 10 meters into the natural vegetation, and 250, 150 and 10 meters into the plantation, from the border of the natural and managed environments; cohort experiments were performed for three parallel transacts and repeated three times in each transect. For each cohort we recorded the proportion of pupae that survived for two days, and photographed any predation events occurring in our presence. Binomial GLMM analyses were used to test the dependent variable 'pupal mortality rate' against the fixed effect 'distance of the sample from the border', including date and transect number as random effects. Ant species were identified by Caswell Munyai (University of Venda).

2. Mango leaf gall midge (Procontarinia matteiana)

Procontarinia matteiana (Kieffer and Cecconi), commonly known as the mango leaf gall midge, is thought to have originated in India. *Procontarinia matteiana* lays its eggs on young mango leaves, which hatch into larvae that bore into the leaf tissue. Larval action causes the formation of leaf-galls, in which the larvae pupate emerging as adults (Mahmood ur Rehman, Mahmood & Razaq 2013). As the gall fly has a highly cryptic life-history, we would expect its control to be reliant on a specialist natural enemy (Memmott, Martinez & Cohen 2000) and it appears that *P. matteiana* is primarily controlled through the actions of a single parasitoid, *Chrysonotomyia pulcherrima* (Kerrich) (Waite 2002). In the absence of the specialist parasitoid, high gall midge densities can cause substantial reductions in mango crop (Augustyn *et al.* 2013). There is no documented evidence of *C. pulcherrima* persisting on native vegetation in the South African bushveld, and no records of native natural enemies attacking the gall midge, so it is unlikely proximate natural vegetation benefits the control of *P. matteiana*. However, natural vegetation may provide direct benefits to the parasitic *C. pulcherrima* population, such as shelter and floral nectar, which could benefit suppression of gall midges near these natural resources (Bianchi & Wäckers 2008; Vollhardt *et al.* 2010; Zumoffen, Salto & Salvo 2012).

We collected mango leaves at 0, 10, 50, 100 & 200 meters from the edge of the plantation that bordered the natural vegetation. Two sets of collections were performed in two parallel transects in each of the Kent and Tommy Atkins cultivars. At each distance, we surveyed two leaves below head-height and two leaves above. Each leaf was then frozen for 24hrs before data collection. The number of galls on each leaf was recorded, after which five randomly chosen galls of between 4-10 weeks old were dissected. Open galls were examined and the contents were classified as either: *C. pulcherrima*, *P. matteiana*, or Unidentifiable. To assess gall numbers and parasitism rates as a function of distance from the plantation edge, we used two GLMM analyses (binomial error) one testing the dependent variable 'average gall count per leaf' the other the dependent variable 'parasitism rate' and the fixed effects in both models were 'sample distance from the natural environment' and 'tree cultivar (TA/K), with the 'date of leaf harvest' and 'leaf height (high/low)' included as random effects.

3. Pathogenic mango malformation fungus (Fusarium spp.)

Mango malformation disease (MMD) is caused by a number of fungi in the Genus *Fusarium*. It is of growing concern because it has now been described in most mango growing countries and infection is irreversible (Kumar, Singh & Beniwal 1993). The disease causes malformed inflorescences, which do not bear fruit, and yield losses of up to 86% have been recorded. Spread from tree-to-tree is slow, taking years and relying on aerial dissemination of fungal conidia (Kumar, Singh & Beniwal 1993). The severity of the disease on infected trees correlates with density Eriophyid mite density; particularly of the mango bud mite, *Aceria mangiferae*. The bud mites increase the spread of the pathogen from bud-to-bud and increase disease severity by opening multiple infection points via their feeding actions (Gamliel-Atinsky *et al.* 2010).

We studied five transects from the edge near the natural vegetation and 300m into the crop. Each transect was in a different block of crop. Within each transect, eight mango trees were selected at different distances from the edge. For each tree the total number of inflorescences and the number of malformed inflorescences were counted. Only inflorescences that displayed the typical cauliflower appearance of advanced malformation caused by *Fusarium* spp were scored as malformed. We performed a GLMM analysis (binomial error) testing the dependent variable 'proportion of inflorescences malformed per tree' against the fixed effect of 'log distance of the tree from natural vegetation', including 'transect number' as a random effect.

Statistics

All Generalised Linear Mixed Effect Models were performed using R statistical software for Windows (version 3.0.1) and we performed R^2 analysis to provide goodness-of-fit values of the data to each model (Nakagawa & Schielzeth 2013). Test of statistical significance were performed via model simplification using Maximum Likelihood approximation. Marginal R^2 values indicate fit for fixed effects alone and conditional values indicate fit for fixed and random model effects.

6.5 Results

i) Does the density of pests/pathogens increase with distance from ‘natural vegetation’?

Tephritid fruit flies

Multi-year fly trapping data suggest that adult fly densities increased with distance from natural vegetation for all three species of fruit fly: *C. cosyra* (X^2_1 =120.27, $P < 0.001$); *C. capitata* ($X^2_1 = 6.88$, $P < 0.01$); and *C. rosa* ($X^2_1 = 456.39$, $P <0.001$) (Figure 6-1a,b&c). Similarly, fly densities exhibited consistent, significant differences between months, peaking in March, the penultimate month of the growing season: *C. cosyra* (X^2_1 =56.37, $P < 0.001$); *C. capitata* ($X^2_5 = 41.00$, $P < 0.001$); and *C. rosa* ($X^2_5 = 59.19$, $P <0.001$)(Figure 6-1b,d&f). The R^2 values for the full models for each species were high when including the random effects: *C. cosyra* (R^2 Marginal = 0.25; R^2 Conditional = 0.71); *C. capitata* (R^2 Marginal = 0.61; R^2 Conditional = 0.84); and *C. rosa* (R^2 Marginal = 0.40; R^2 Conditional = 0.88).

Mango leaf gall midge

Mango leaf gall midge-gall counts per tree were not significantly related to distance to natural vegetation ($X^2_1 = 1.37$, $P = 0.242$; Figure 6-2a). However, there were significantly more galls on Tommy Atkins than Kent trees ($X^2_1 = 45.87$, $P < 0.001$; R^2 marginal = 0.34; R^2 conditional = 0.97; Figure 6-2b).

Pathogenic fungi (Fusarium spp.)

The proportion of inflorescences that were malformed was significantly greater on trees further from natural vegetation ($X^2_1 = 70.94$, $P < 0.001$; R^2 marginal = 0.12; R^2 conditional = 0.14; Figure 6-3).

ii) Does predation/parasitism of the dipteran pests decline with distance from 'natural vegetation'?

Tephritid fruit flies

Parasitism rates of fly larvae decreased in green (unripe)but increased marginally in orange (ripe) mangos, with distance from the natural vegetation (interaction term; X^2_1=8.72 $P < 0.01$; R^2: marginal= 0.10, conditional= 0.25; Figure 6-4).

Survival rates of fly pupae were lowest 300m into the natural environment and highest 200m into the crop (X^2_1=33.16, $P<0.001$; R^2: marginal= 0.36, conditional= 0.52; Figure 6-5). Our observations suggest that the majority of pupal predation was performed by ants. In particular, *Pheidole cf megacephala* (big-headed ant), was seen to attack pupae on multiple occasions.

Mango leaf-gall midge

Rates of gall parasitism were significantly lower in transects further from natural vegetation (X^2_1 = 4.79, P <0.001; R^2 Marginal = 0.03, R^2 Conditional = 0.19; Figure 6-6).

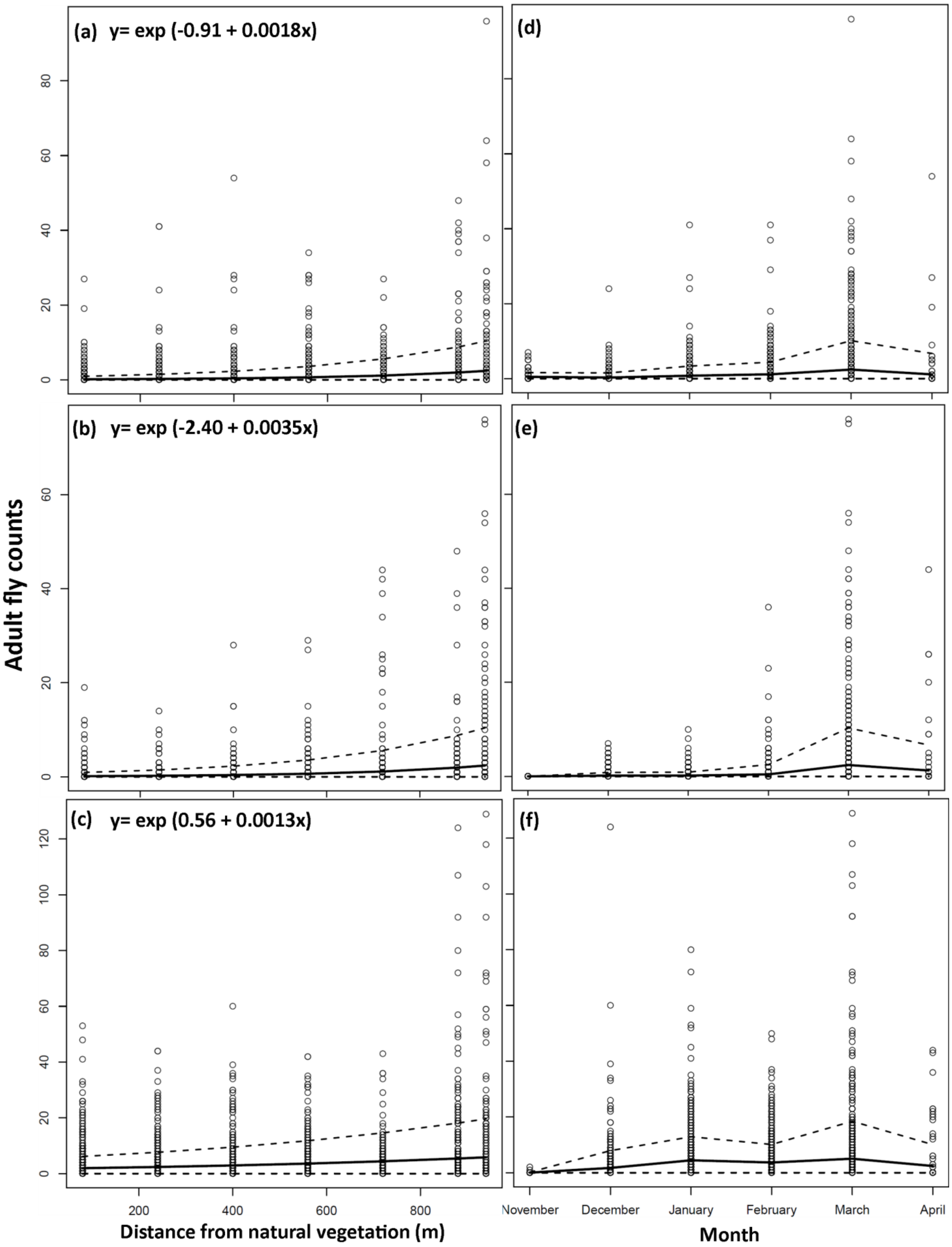

Figure 6-1 Counts of adult *Ceratitis spp.* flies caught in Census™ traps against distance from the natural/agriculture environment border (N=3212 sampling events per species).

[(a)-C. cosyra; (b)-C. capitata; and (c)-C. rosa] and against month [(d)-C. cosyra; (e)-C. capitata; and (f)-C. rosa]. Lines illustrate median values +/- 1s.d. Equations are poisson glm fits of median values.

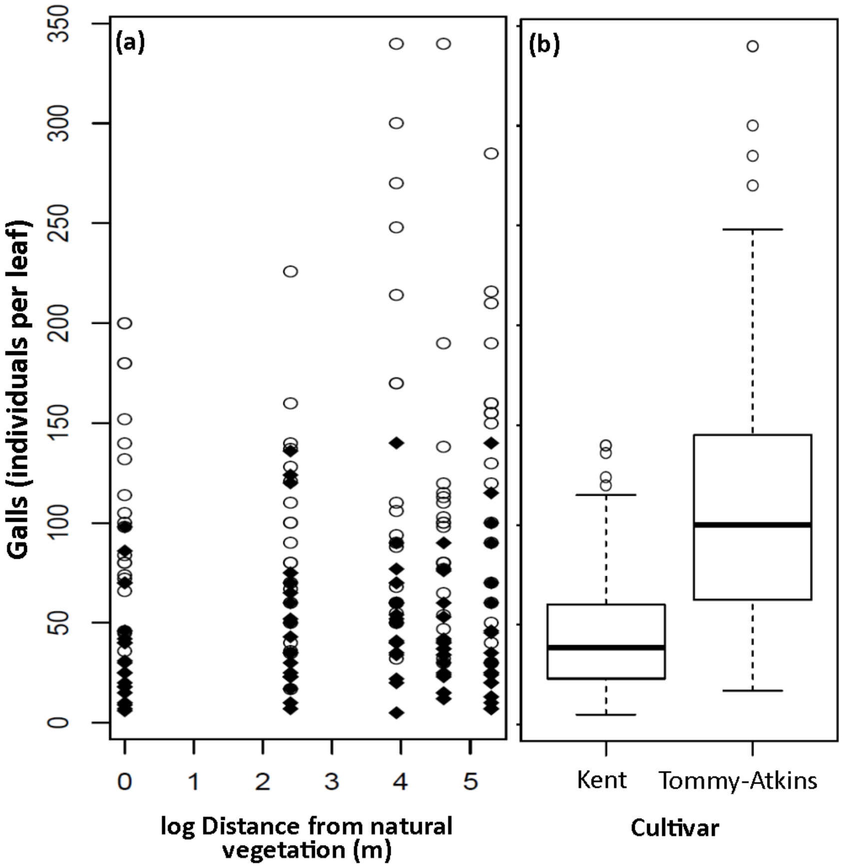

Figure 6-2 (a) Mean leaf gall counts per tree against the log(distance) of the tree from the natural/agriculture environment border (N=199). Filled diamonds indicate Kent cultivar data, open circles indicate TA data and filled circles indicate points relevant to both cultivars; (b) Mean leaf gall counts per tree for each cultivar studied.

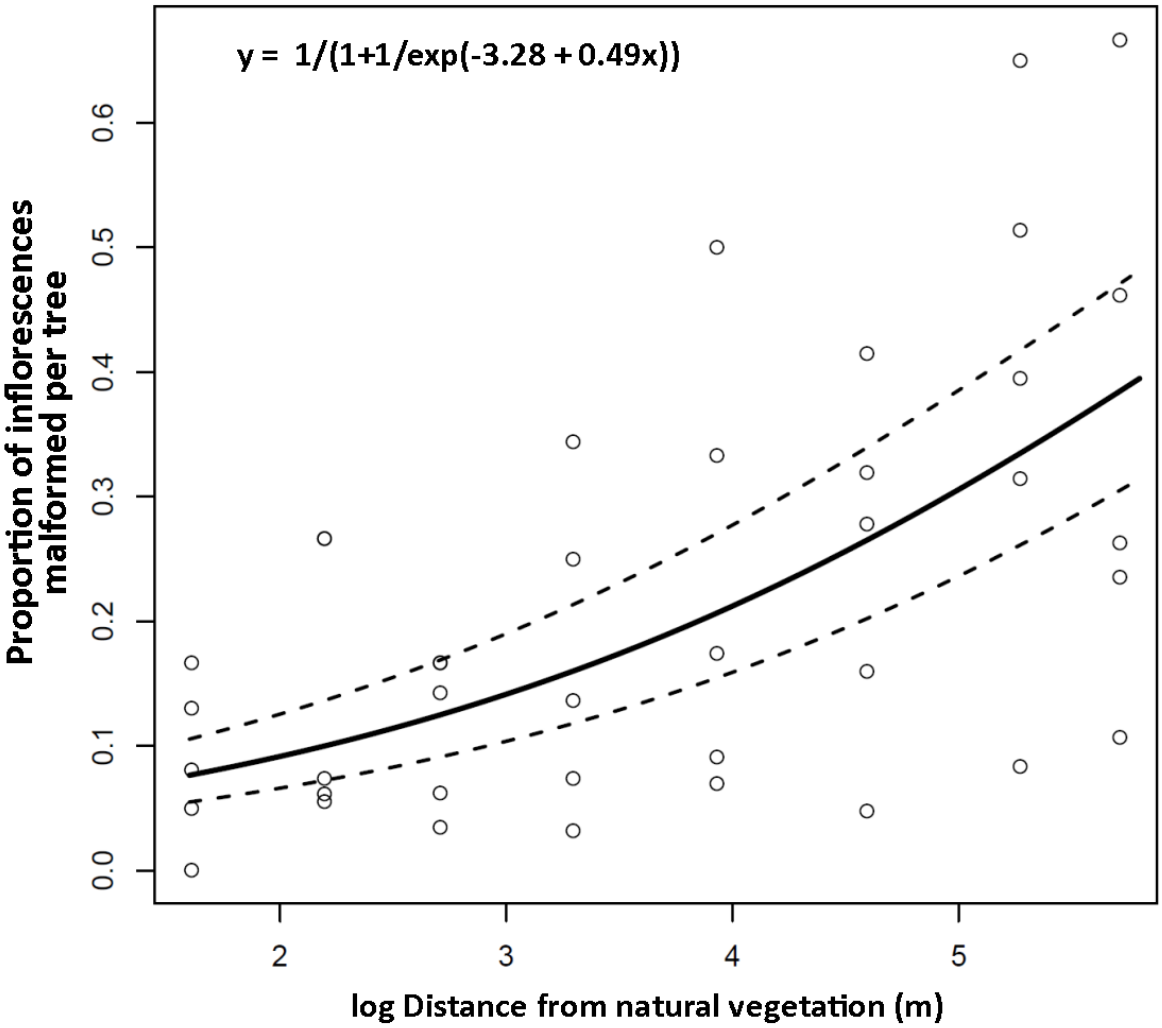

Figure 6-3 The proportion of inflorescences per tree that exhibited pathogenic flower malformation against the log(distance) of the tree from the natural/agriculture environment border (N=40). Lines and equations illustrate model best fit +/- 1s.e.

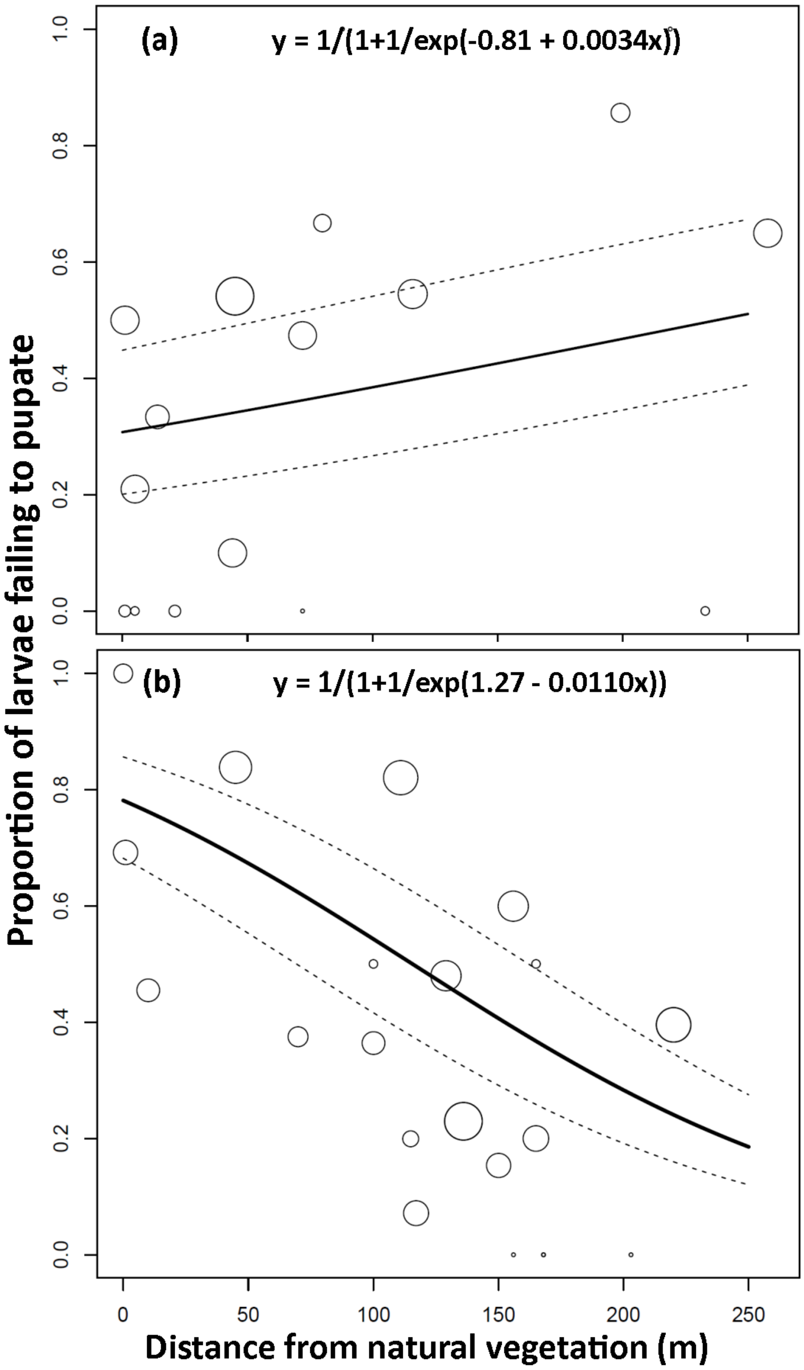

Figure 6-4 Percentage of reared *Ceratitis* pupae that died before eclosing against the distance of the host mango (N=51) from the natural/agriculture environment border.

For ripe (a) and unripe mangos (b). Lines and equations illustrate model best fit +/- 1s.e. Point size is weighted by log(sample size).

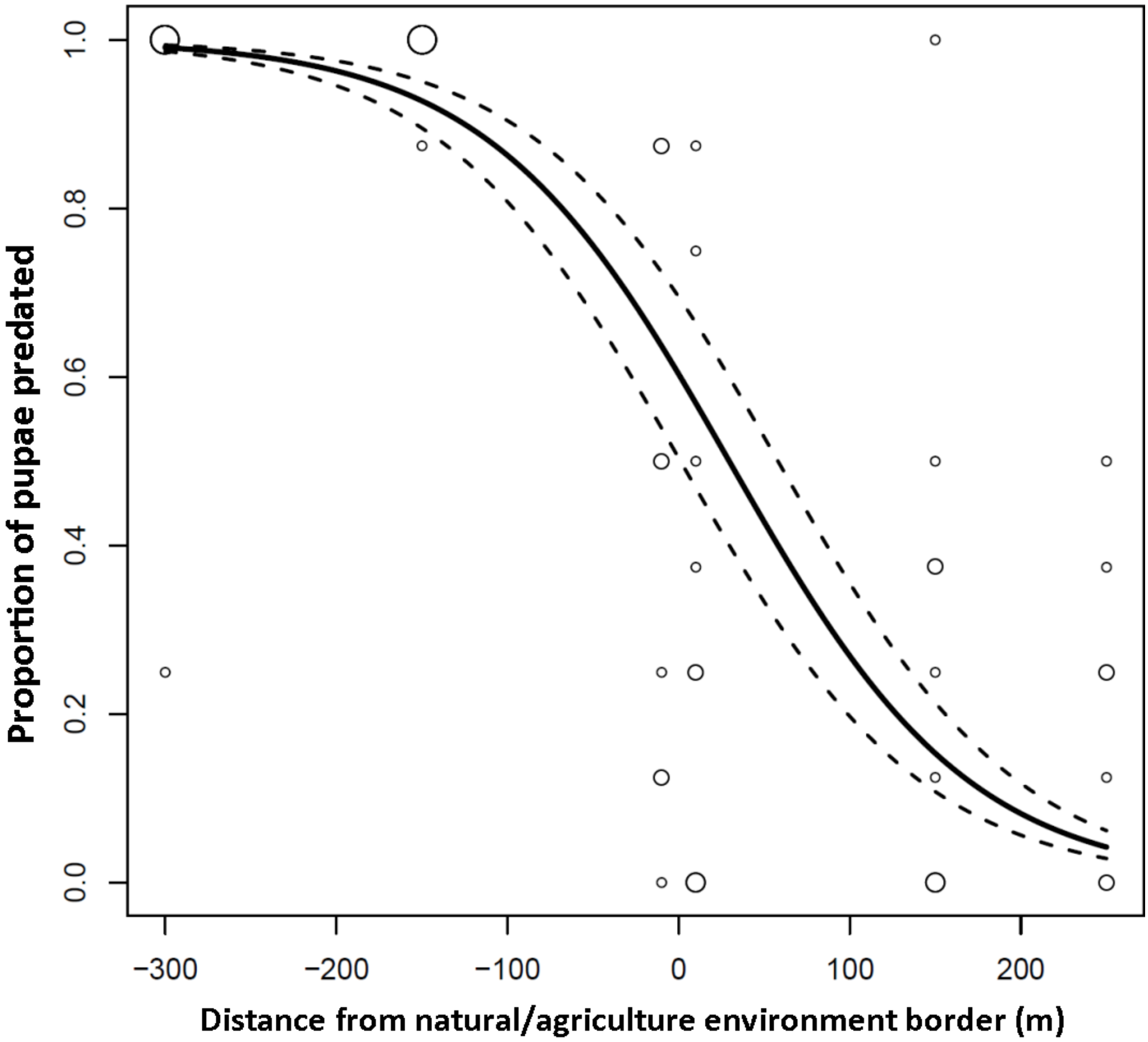

Figure 6-5 The proportion of *Ceratitis* pupae predated upon in 48hrs against the distance from the natural/agriculture environment border (N=49 sample pots). *Negative distances represent distance into natural vegetation and positive ones indicate distance into the plantation. Lines illustrate model best fit +/- 1s.e. Point size is weighted by the number of data points at that value.*

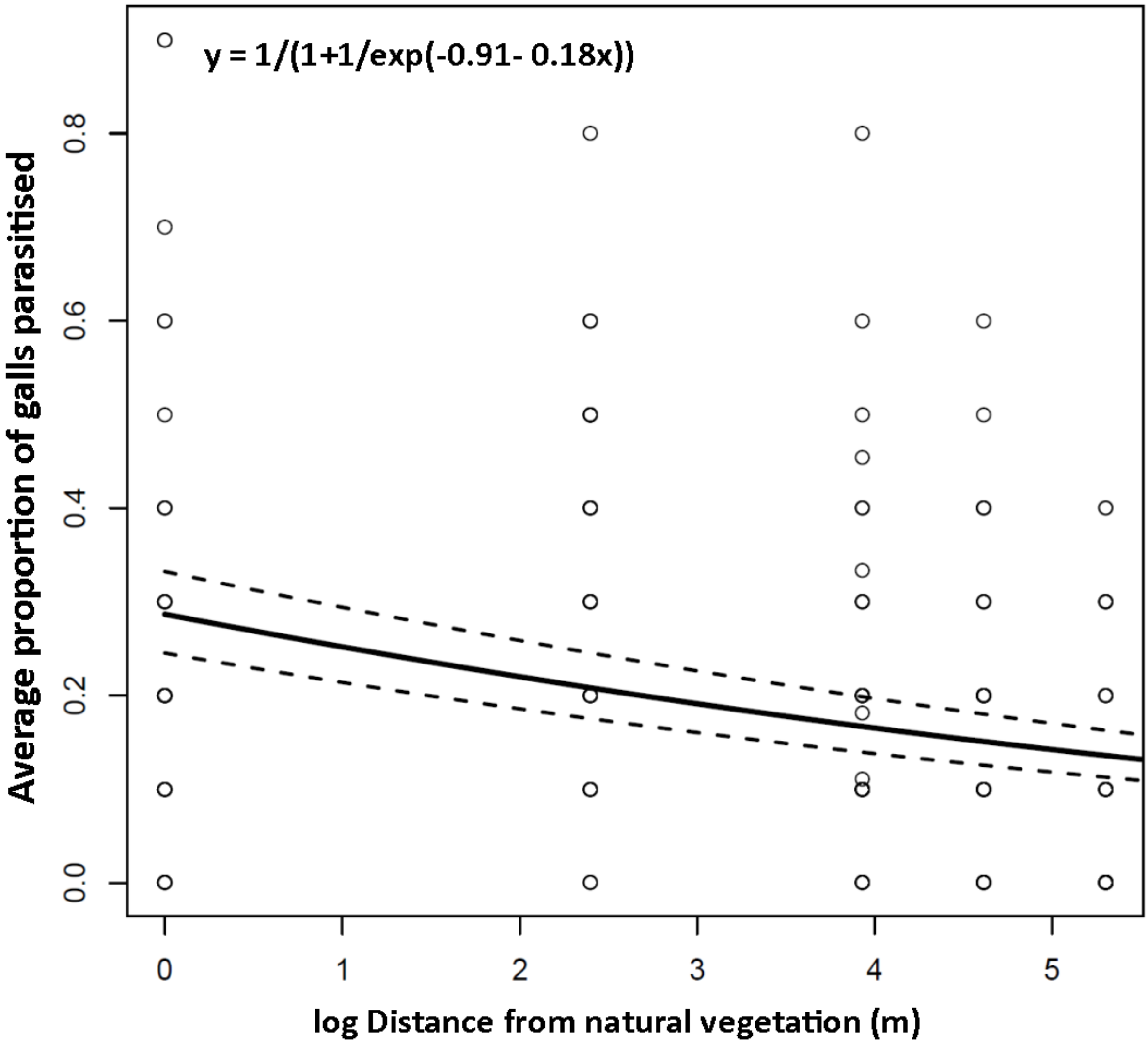

Figure 6-6 The proportion of galls per tree that were parasitised against the log(distance) of the tree from the natural/agriculture environment border (N=100).

Lines and equations illustrate model best fit +/- 1s.e.

6.6 Discussion

Effects of distance from natural vegetation on pest/pathogen density and predation/parasitism rates

In our study, pest and pathogen densities were generally lowest, and biological control action was greatest, closest to natural vegetation. Our results suggest that natural vegetation provides a positive pest control service that was significantly reduced by ~200m from the edge of plantations (average pest mortality was between 25% and 80% lower compared to the edge). These findings are consistent with previous studies showing that natural vegetation is only important within the effective movement range of natural enemies (Hossain *et al.* 2002; Bianchi & Wäckers 2008). Re-establishment of natural enemies after disturbance events, which are common in agricultural ecosystems, depends upon both proximity of source population and species life-history (Hossain *et al.* 2002). These results support our hypothesis that natural vegetation provides significant benefits for crop productivity through both pest control and pollination services, which decline significantly with distance from the natural environment (Carvalheiro *et al.* 2010).

Previous work has shown that proximate natural vegetation can be an important reservoir for natural enemy species and aid in their re-establishment after disturbance events (Corbett & Rosenheim 1996). Re-establishment of natural enemy species is thought to be important for agricultural environments, as higher trophic levels are proportionately more affected by disturbances (such as pesticides) and intensive land-use than the target pests (Chaplin-Kramer *et al.* 2011; Herbst *et al.* 2013). Natural vegetation can also increase the diversity of natural enemies in proximate agricultural environments, which has been shown to be correlated with improved pest control (Martin *et al.* 2013). Non-crop vegetation may benefit pest control in agri-environments by improving the foraging environment for individual natural enemies. Shade, shelter, pollen and nectar have all been identified as potential boons that increase individual longevity and foraging efficiency; reviewed in Heimpel and Jervis (2005).

The benefits of natural vegetation to biological control and the differences between species

Our results suggest that natural vegetation promotes the control of three very different types of pest/pathogen by benefitting local populations of natural enemies. However, as has been found in meta-analyses, the strength of the effect of natural vegetation proximity on pest density and/or damage varies (Chaplin-Kramer *et al.* 2011). Here, we examine the relationship between natural vegetation and pest control with respect to the life-histories of the pest and its control agent, focusing on diet breadth.

1. Natural vegetation and the control of generalist pests

We studied three closely related species of polyphagous Tephritid fruit flies *Ceratitis spp.*, for which natural vegetation could be a significant reservoir. The density of these generalist Tephritid fruit flies increased with distance to natural vegetation, suggesting that natural vegetation is a net source of natural enemies, and/or that the mango crop is more of a source of *Ceratitis* flies than natural vegetation. We found that predation and parasitism rates of juvenile fruit flies declined with distance from natural vegetation, suggesting that the natural environment is more important as a refuge for natural enemies, than for *Ceratitis*, in this study system. These results support the previous hypothesis that the presence of natural vegetation is more beneficial for higher trophic levels than lower ones (Chaplin-Kramer *et al.* 2011).

There was also some evidence that the positive effect of natural vegetation on higher trophic levels can disrupt biological control by increasing the density and/or diversity of species that feed on the biological control agents. Previous studies have shown that biological control by specialist natural enemies, such as parasitoids, can be reduced in systems with greater biodiversity (Gagic *et al.* 2011; Gagic *et al.* 2012), because of an increase in intraguild predation (Reigada *et al.* 2012) or a lack of functional redundancy among parasitoids (Gagic *et al.* 2012). We found that among fruits preferred by parasitoids (ripe mangos), *Ceratitis* larvae mortality increased with distance from natural vegetation (Fig 1). The reduced mortality closer to the natural environment may have arisen through greater hyperparasitism rates or intraguild predation, because hyperparasitoids exhibit greater responses to landscape composition than primary parasitoid species (Gagic *et al.* 2012; Rand, van Veen & Tscharntke 2012). Nevertheless, the size of the positive effect of natural vegetation proximity on larval mortality in unripe fruits was much stronger than the negative effect in ripe fruits (Figure 6-4), so we suggest that overall natural vegetation benefitted the control of fruit fly larvae.

The 'Species Identity Effect' states that increased biodiversity increases the likelihood of highly effective species being present in sufficient numbers to be a significant biological control agent (Tscharntke *et al.* 2005). Predation of

Ceratitis fly pupae was declined from ~100% within the natural vegetation furthest from the agricultural environment to ~50% at the border, and further declined to ~0% by 250m into the crop field (Figure 6-5). We observed predation of *Ceratitis* pupae by ants on multiple occasions; the most commonly observed ant predator being *Pheidole cf megacephala*. While many studies suggest that specialist natural enemies make the most effective biocontrol agents (Diehl *et al.* 2013), there are multiple reports of significant control by generalist predators (Symondson, Sunderland & Greenstone 2002). Further, the aggregative response of generalist natural enemies may explain the positive effect of natural vegetation on pest control programs (Martin *et al.* 2013). As *Ceratitis* spp. pupae survival rates were significantly lower closest to the edge of the plantation and *Pheidole cf megacephala* is known to exhibit highly localised foraging behaviour (~5m from nest) (Caswell Munyai, personal communication, August 2013), here, natural vegetation was an important source of generalist predators.

The identification of a generalist predator capable of inducing high mortality in fruit fly species, in *Pheidole cf megacephala* (big-headed ant), may be important for the future of organic mango farming, as it is possible that *P. cf megacephala* will attack pupae of *Bactrocera invadens*, a fruitfly that is a relatively new arrival to the area and that is currently of great concern to farmers. *Pheidole cf megacephala* was not observed in the plantation, suggesting a management practice is preventing its establishment. Identification of this practice would help enable this species to be an effective biological control agent. We would advise some caution as *P. megacephala* is on the 100 World’s Worst Invasive Species list (GISD 2005); this species is native to Africa and may be indigenous to our study area, and this needs to be established.

2. Natural vegetation and the control of specialist pests

Previous meta-analyses have found the positive benefits of natural vegetation to be much weaker for specialist natural enemies (like parasitoids) compared to generalist natural enemies (Shackelford *et al.* 2013). Part of this effect is probably because specialist natural enemies are less likely to have population reservoirs in the natural environment, especially if the preferred prey/host is a specialist feeder itself (Shackelford *et al.* 2013). The mango leaf gall midge *Procontarinia matteiana* and its parasitoid *Chrysonotomyia pulcherrima* are not native to South Africa and, while limited, research does not suggest that either have persistent populations in the natural environment. Parasitism rates of the specialist mango leaf gall midge, by its similarly specialist parasitoid, were significantly higher closer to natural vegetation (Figure 6-6). However, we did not find a concurrent, significant effect on gall density (Figure 6-2). The increased parasitism rates closer to natural vegetation may have resulted from direct provisioning effects of the natural environment; for example, previous studies suggest that flower diversity and density provide nectar and pollen for local parasitoids, increasing their longevity and parasitism rates (Heimpel & Jervis 2005).

The species-specific pathogenic fungus responsible for mango malformation disease (MMD), *Fusarium spp* also showed an effect of distance to natural vegetation (Figure 6-3.), despite the previous studies suggesting that the fungus, and hence the disease, spreads within plantations and nurseries, making it unlikely to be affected by the presence of natural vegetation (Kumar, Singh & Beniwal 1993). Severity of MMD has previously been shown to correlate with the density of eriophyid mites, such as the mango bud mite *Aceria mangiferae* (Gamliel-Atinsky *et al.* 2010). The increase in disease severity may have been caused by a decline in the control of these mites away from natural vegetation. To the best of our knowledge there are no studies assessing the potential for natural vegetation to act as a reservoir for eriophyid mites. *Aceria mangiferae* and eriophyid mites in general are known to be predated upon by a wide range of generalist predators, including other eriophyid mites, stigmaeid mites and generalist arthropod predators (Lindquist, Sabelis & Bruin 1996). Future studies should test the hypothesis that the densities of these natural enemies are positively related to proximity to natural vegetation and that this corresponds to a decline in *A. mangiferae* density. Mango malformation disease is a growing concern globally, having spread to most mango growing countries (Chakrabarti 2011), and was a topic of concern during personal communication with local farmers. Indeed, on average, over a third of inflorescences (maximum ~60%) were infected at ~250m into the agricultural environment. Our results suggest that biological control may comprise an important aspect of the management of this threat.

Our results lend support to the hypothesis that the trophic breadth of the pest and the major control agent are important aspects of the relationship between biological control and natural vegetation (Shackelford *et al.* 2013). The natural environment can support natural enemies either because they have a broad diet breadth (e.g. mite predators and the big-headed ant) and/or because their favoured prey species is polyphagous and persists in the natural environment (e.g. Tephritid fruit flies), thus, either or both the natural enemy and the pest are generalist. Specialist species with specialist enemies (e.g. the mango leaf gall midge and its parasitoid) are less likely to benefit from proximate natural vegetation.

Limitations and future studies

In the case of Tephritid fruitfly population density, our data cover multiple months with various pest control practices. Particularly, in the months January to March the study area was sprayed aerially with the spinosad-based GF-120 insecticide (Dow Agro-Sciences LLC, Indianapolis, U.S.A.), with sprays occurring once a month. The chemical has been shown to cause mortality on a wide range of pest and beneficial species, including parasitoid wasps of multiple Genera (Wang *et al.,* 2005). In our fruit fly Census data we have accounted any potential effects on fly density by including date of trap monitoring as a random effect; ensuring that variability resulting from insecticide use are not misinterpreted as distance or Month effects. With regards to distance effects there is no reason to believe that aerial spraying is more/less effective or concentrated according to distance from natural vegetation. But we would recommend that future studies may account for this by performing surveys across multiple farm holds that use a variety of pest control methods and including this as a model term.

We measured natural enemy densities indirectly by surveying parasitism and predation rates, without directly identifying all of the natural enemies responsible. Because of this limitation we were not able to obtain actual natural enemy density or species diversity data, only their effects on pest density. We assumed that the inability of fly pupae to mature was due to mortality from parasitoids or pathogens, very few parasitoids were reared within short time-frame of our study. Because of this we were unable to do a full survey of parasitoids of Tephritid flies at our study site, but previous studies have suggested that increased parasitism rates are unlikely to result from greater parasitoid biodiversity as there is low functional redundancy within this group (Chaplin-Kramer *et al.* 2011; Shackelford *et al.* 2013). Biodiversity surveys of adult parasitoids in this system would elucidate whether greater Tephritid control was the result of greater parasitoid biodiversity or the increased density of a single species. In general, an expansion of our knowledge of the biodiversity of the agricultural and natural environments would be useful for guiding management practices that prioritise the use of biological over chemical control. Despite the limitations outlined above, the net effect of natural vegetation in providing a support service to farmers in reducing pest density was apparent in this study.

6.7 Conclusions

Our results emphasise that landscape management can influence a wide range of agricultural pest species through beneficial effects on native natural enemies. In conjunction with a previous study of our system, our results suggest that pest control and pollination services provided by proximate natural vegetation can have a significant impact on plantation productivity (Carvalheiro *et al.* 2010), even in the form of small planted patches (Carvalheiro *et al.* 2012). While the strength of the effect of natural vegetation varied between pest and enemy species, the decline in benefit with distance from the edge was consistent. We conclude that effective conservation biological control programs should consider species dispersal capabilities and the spatial scale of landscape structure (Tscharntke *et al.* 2005). Finally, our study highlights the importance of considering species life-history, particularly diet-breadth, towards the development of predictive studies of landscape-use, biodiversity and ecosystem services.

6.8 Acknowledgements

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Chapter 7 Conclusions

The studies that make up this thesis are some of the first to analyse the role of foraging behaviour in structuring community dynamics using data from a long-term, quantitative host-parasitoid network. The thesis focused on comparing multiple species within the same community using a high temporal resolution in an effort to study the important life-history traits and environmental conditions that determine inter- and intra-specific differences in foraging behaviour. Our results have helped to develop a mechanistic understanding of the dynamic nature of ecological networks, which contributes to both ecological network theory and applied ecology.

7.1 Condition-dependent foraging behaviour

It was found that two aspects of secondary parasitoid foraging behaviour, host preference and sex ratio allocation, exhibited strong responses to host size, where parasitoid species preferentially allocated eggs and daughters to relatively larger hosts. These foraging behaviours induced distinct patterns at the network level, which corroborates previous models and laboratory studies showing that parasitoid foraging behaviour can determine community structure and stability (Heimpel, Neuhauser & Hoogendoorn 2003; Abrams 2010; Valdovinos *et al.* 2010; Reigada, Araujo & de Aguiar 2012; Prado & Frank 2014). Particularly, as was evident in Chapter 5, these aspects of foraging behaviour impact on host communities by determining the outcome of indirect 'apparent' interactions between host species (Holt 1977; Heimpel, Neuhauser & Hoogendoorn 2003).

Chapters 2 and 3 illustrated that strong host-preference behaviour was associated with an uneven distribution of link-strengths between a parasitoid and its hosts at the network- level. Uneven link-strength has important implications to host community composition, where the preferred host can become locally extinct in the presence of an alternative (non-preferred) host, even when the preferred host and parasitoid can co-exist in isolation (Holt 1977; Heimpel, Neuhauser & Hoogendoorn 2003; Prado & Frank 2014). In two secondary parasitoid species (*Asaphes vulgaris* and *Dendrocerus carpenteri*), host-size dependent sex ratio allocation resulted in absolute changes in local parasitoid sex ratios, where sex ratios were female biased when median available host-size was relatively larger and male biased when average host-size was relatively smaller (Chapter 4); it was predicted that this pattern would benefit relatively larger host species at the expense of concurrent smaller hosts (+/- apparent competition) (Henri *et al.* 2012). Somewhat corroboratively, in Chapter 5, we showed that condition-dependent sex-ratio allocation behaviour promoted host coexistence by creating highly oscillatory community dynamics, where the strength of top-down control was strong when there were many hosts and weak when there were fewer hosts. This shift in host-parasitoid dynamics stopped the preferred host from becoming extinct. This propensity of condition-dependent sex ratio allocation behaviour to increase the amplitude of oscillations in host-parasitoid dynamics has been shown previously (Reigada, Araujo & de Aguiar 2012; Wogin *et al.* 2013), but this study was the first to show it in the context of multiple host species. Chapter 5 further confirmed that multiple determinants of community structure act in a synergistic manner, as opposed to additively (Tylianakis & Binzer 2013), where the outcome of each model simulation was dependent upon the size-dependency of both aspects of foraging behaviour and the spatial structure of the community.

7.2 Understanding differences in foraging behaviour

The first chapter outlined a framework explaining inter- and intra-species differences in parasitoid foraging behaviour (Henri & van Veen 2011). The framework was based upon the assumption that optimal foraging behaviour is determined by the primary factor limiting foraging success; in this case, time or eggs (Heimpel & Rosenheim 1998; Rosenheim 1999b; Rosenheim 1999a). Egg-limited parasitoid will not be able to parasitise all available hosts before running out of eggs, which was predicted to induce strong condition-dependent foraging behaviour. Time-limited parasitoids will die before allocating all of their eggs, which was predicted to induce weak condition-dependent foraging behaviour. The likelihood of an individual being egg- or time-limited at any given time is related to the species' ecology and the foraging environment (Rosenheim *et al.* 2008; Rosenheim, Alon & Shinar 2010; Jervis & Ferns 2011).

The results in Chapter 3 corroborate the predictions of the egg-/time-limitation framework as all secondary parasitoid species exhibited weaker condition-dependent host preference behaviour in months where there was greater competition for hosts where competition for hosts is predicted to increase the likelihood an individual is time-limited (Rosenheim 1999a; Wajnberg 2006). Further, Chapters 3 and 4 show the host-size dependency of parasitoid foraging behaviour varied between species, which lead to the conclusion that different species have different priorities when structuring their realised niche, as predicted by the framework. However, we had insufficient data of parasitoid life-histories (particularly egg-load and life-span) to identify traits important to the evolution of host preference behaviour. We attribute this lack of knowledge to the significant variation in these characteristics depending upon natal host species and environmental conditions (Sullivan & Völkl 1999; Boivin 2010).

We did identify that the evolution of condition-dependent sex-allocation behaviour does not correspond to the predictions of the egg-/time-limitation framework (Chapters 3 & 4). In Chapter 4, we found that species with a stronger correlation between host size and offspring size, values from Cohen et al., (2005), exhibited sex ratios that were more likely to deviate from Hamiltonian (50:50) predictions. This substantiates a previous hypothesis on the evolution of condition-dependent binary behaviours, such as sex determination, that the relationship between the expression of the behaviour and the determining condition will be stronger when there is a stronger relationship between inclusive fitness and the condition (West & Sheldon 2002; Plantegenest *et al.* 2004).

7.3 Dynamic networks and foraging behaviour

Ecological network theory has developed from studies of static, binary trophic relationships to the study of quantitative, dynamic communities consisting of multiple different link types: trophic, parasitic and mutualistic. Particularly, there has been a recent focus on the importance of the dynamic nature of ecological networks where processes like link-turnover, link-rewiring and spatial heterogeneity maintain long-term stability in complex communities (McCann 2000; Kondoh 2003; Kaiser-Bunbury *et al.* 2010; Poisot, Stouffer & Gravel 2014). Computational models and laboratory studies have shown two traits of parasitoids that may contribute to the dynamic nature of host-parasitoid communities: first, parasitoid behaviour determines host-parasitoid dynamics (Hubbard & Cook 1978; Godfray 1994; Heimpel, Neuhauser & Hoogendoorn 2003; Heimpel & Casas 2008; Prado & Frank 2014); and secondly, that individual behaviour adapts to changes in the foraging environment (Morris & Fellowes 2002; Bukovinszky *et al.* 2008; Abrams 2010; de Sassi, Staniczenko & Tylianakis 2012; Lentz-Ronning & Kester 2013). However, few studies consider the role of temporal differences in foraging behaviour and network stability by analysing network-level data.

We found that parasitoid foraging behaviour responds to changes in the foraging environment, which significantly alters realised niche construction and, therefore, community structure (Chapters 3 & 4). Firstly, the strength of condition-dependent behaviour was related to the degree of competition for hosts, where parasitoids exhibited weak condition-dependent host preference when there was high competition for hosts (Chapter 3). This may promote multiple host coexistence by reducing pressure on preferred host species when there is a high likelihood of them becoming locally extinct (see non-linear preference Kalinkat et al., 2011 and Chapter 5). And secondly, the monthly switching-point of host-size dependent sex ratio allocation tracked with median host-size, as predicted in Charnov et al., (1981), suggesting that parasitoid behaviour at any given time is dependent upon host community composition and that learning behaviours have important community level implications. The degree of a species' ability to adapt its foraging behaviour to changes in the foraging environment is likely to be related to its ecology, as foraging behaviour was not equally plastic in all species (Chapter 4). We showed that the plasticity of foraging behaviour, particularly the differences in plasticity between species, can structure host-parasitoid networks by determining the outcome of indirect interactions between multiple hosts (Chapter 5).

We suggest that the egg-/time-limitation framework proposed in Chapter 1 (Henri & van Veen 2011) and supported in Chapter 3, may form the basis of a mechanistic understanding of the dynamic nature of ecological networks by explaining inter- and intra-species differences in foraging behaviour. This could be particularly important in understanding how networks may be affected by global climate change (Ings *et al.* 2009; Woodward *et al.* 2010a; de Sassi, Staniczenko & Tylianakis 2012; Poisot, Stouffer & Gravel 2014).

7.4 Landscapes, network structure and biological control

In the penultimate chapters of this thesis we attempted to expand our mechanistic understanding of inter- and intra- species differences in network structure to applied ecology, particularly conservation biological control. Previous meta-analyses have found significant variability in the efficacy of conservation biological control with respect to agricultural intensification (Chaplin-Kramer *et al.* 2011; Thies *et al.* 2011; Shackelford *et al.* 2013; Veres *et al.* 2013). A prominent hypothesis suggests that these differences are the result of differences in the response of pest and enemy species to the availability of proximate natural vegetation (Tscharntke *et al.* 2005). Corroboratively, Chapters 5 & 6 found that in cases where landscape structure was related to species dispersal, it significantly altered community dynamics and this effect varied according to species ecology.

Our results corroborated a previous hypothesis that landscape structure may alter the relative importance of different determinants of network structure (DeCesare *et al.* 2010). In Chapter 5, the spatial segregation of small and large host species benefitted the relatively smaller host species as parasitoid dispersal into its environment was limited, this effect was directly proportional to the strength of condition-dependent foraging behaviour exhibited by the shared parasitoid. Future uses of the model should include stochastic variation in host and parasitoid mortality, to test the importance of alternative hosts as reservoirs for natural enemies in highly disturbed agricultural environments.

In Chapter 6, we found significant declines in natural enemy action within the agricultural environment as a function of distance from natural vegetation, which generally corresponded to an increase in pest/pathogen density/severity. However, the strength of the effect of natural vegetation and the decline with distance into the agricultural environment varied according to both pest and natural enemy life-history, particularly diet breadth and dispersal capabilities. In our study highly generalist natural enemies with low dispersal rates, such as *Pheidole cf megacephala* (big-headed ant), exhibited the most extreme distance response to natural vegetation, while density of the specialist parasitoid *Chrysonotomyia pulcherrima* was weakly associated with distance from natural vegetation. Our results further corroborate previous hypotheses that landscape complexity benefits higher trophic levels more than lower trophic levels, as pest density never benefitted from proximate natural vegetation (Herbst *et al.* 2013). Correspondingly, among parasitoids of the mango fruit flies, we found some evidence that proximate natural vegetation may result in an increase in hyperparasitism or intra-guild predation (Sidney *et al.* 2010; Gagic *et al.* 2011; Rand, van Veen & Tscharntke 2012).

Our results highlight the importance of species identity in the effective application of biological control. While previous meta-analyses and reviews have concluded that species traits such as diet generalism and dispersal capabilities are important determinants of the effect of agricultural intensification on conservation biological control, to the best of our knowledge Chapter 6 is the first study to explicitly consider distance effects in multiple pest and natural enemy species simultaneously and compare the response strengths (Tscharntke *et al.* 2005; Rand & Tscharntke 2007; Shackelford *et al.* 2013). These considerations are particularly important in relatively untransformed regions with high biodiversity, where natural enemy reservoirs may have a particularly strong impact on local biodiversity (Tscharntke *et al.* 2005).

7.5 Final thoughts and future studies

These results highlight the importance of individual foraging behaviour as a determinant of network structure, as well as the ability of ecological network studies to provide insight into the determinants and evolution of foraging behaviour (Ings *et al.* 2009; Woodward *et al.* 2010a; Woodward *et al.* 2010b; Sohrabi *et al.* 2012). Future studies could significantly contribute to our understanding of network dynamics by considering multiple species within the same study system in multiple geographic locations and across multiple time points. These studies could help identify mechanistic processes that determine network structure and how they contribute to long-term system dynamics and stability.

We suggest four particular areas of study that can explain differences in community response across space and time: species life-history and ecology (particularly diet breadth), resource quality and availability, landscape structure and spatial scale, and environmental conditions. Understanding how these different areas contribute and interact will help develop a predictive approach to problems associated with global climate change, agricultural intensity and ecological sensitivity (van Veen, Morris & Godfray 2006; Ings *et al.* 2009; Woodward *et al.* 2010a; Shackelford *et al.* 2013; Tylianakis & Binzer 2013). Finally, we propose that we need improved knowledge of inter-species relationships centred around agricultural environments in less transformed countries, which maintain much of their natural biodiversity. Understanding these relationships will allow effective landscape management and biological control, which is essential for the development of high-nature-value agriculture and the species conservation in these regions (Memmott 2009).

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