

Parasitoid foraging behaviour in a competitive environment

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ACADEMIC DISSERTATION

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“I cannot persuade myself that a beneficent and omnipotent God would have designedly created parasitic wasps with the express intention of their feeding within the living bodies of Caterpillars.”

— Charles R. Darwin

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CHAPTER I

Effects of intraspecific competition and host-parasitoid developmental timing on foraging behaviour of a parasitoid wasp

CHAPTER II

Effectiveness of deterrent marking by a parasitoid wasp: Behavioral and genetic approaches

CHAPTER III

The puzzle of sub-maximal resource use by a parasitoid wasp

CHAPTER IV

Spatial genetic structure of a parasitoid wasp in a fragmented habitat

The thesis is based on the following articles, which are referred to in the text by their Roman numerals:

- I **Couchoux C.** and van Nouhuys S. 2013. Effects of intraspecific competition and host-parasitoid developmental timing on foraging behaviour of a parasitoid wasp. – *Journal of Insect Behavior*. DOI 10.1007/s10905-013-9420-6
- II **Couchoux C.**, Seppä P. and van Nouhuys S. Effectiveness of deterrent marking by a parasitoid wasp: Behavioral and genetic approaches. – *Manuscript*.
- III Montovan K. J., **Couchoux C.**, Jones L. E., Reeve H. K. and van Nouhuys S. The puzzle of sub-maximal resource use by a parasitoid wasp. – *Manuscript*.
- IV **Couchoux C.**, Seppä P. and van Nouhuys S. Spatial genetic structure of a parasitoid wasp in a fragmented habitat. – *Manuscript*.

Table of contributions

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ABSTRACT

In my thesis I investigated the foraging behaviour of the wasp *Hyposoter horticola*, an egg-larval parasitoid of the Glanville fritillary butterfly *Melitaea cinxia*, in the Åland islands in Finland. The particularity of this system is that the wasp is resource limited and faces strong intraspecific competition.

I first focused on behaviour at an individual scale. In a series of experiments I tested how *H. horticola*'s host searching behaviour was affected by developmental timing of both the parasitoid and the host, and direct intraspecific competition among foraging females. I found that the wasps visit host egg clusters before the hosts are susceptible to parasitism, presumably to cope with the limited time availability of the hosts. As the unparasitized hosts matured their value increased, competition became more frequent, and the wasps foraged more actively. Competition can also affect the parasitoid at earlier stages in its life. As larvae inside the hosts, the immature *H. horticola* suffered from competition due to superparasitism. Combining behavioural experiments in the laboratory and genetic analyses of sibship, I found that adult *H. horticola* deposit a chemical marking after oviposition that deters conspecifics from parasitizing a previously exploited host cluster. This protects parasitized host clusters from further exploitation. I found that the effectiveness of the deterrent persisted under natural conditions, where individual host egg clusters were each primarily parasitized by a single female *H. horticola*. Even when several females parasitized a cluster, the great majority of the offspring were full-siblings and the parasitism rate did not increase above the average 1/3 observed throughout the population. Considering that *H. horticola* is resource limited and faces intraspecific competition when foraging for hosts, it is surprising that only they parasitize a fraction of the hosts in each host egg cluster. After testing several physiological and evolutionary hypotheses for what might lead to this sub-maximal rate of host exploitation, I concluded that optimal foraging with avoidance of superparasitism was the most plausible explanation, as long as the search time between host clusters was low.

Then, I worked at a larger scale than individual behaviour. In the Åland islands, the butterfly host lives as a classic metapopulation with a high extinction rate of local populations. Due to strong competition, almost all the *M. cinxia* egg clusters in the population are found and parasitized by *H. horticola*. This suggests that the wasps must be good dispersers, which could influence the spatial genetic structure of the parasitoid population. I used DNA microsatellite markers and analysed *H. horticola* individuals sampled from over the entire population. My results indicate that, contrary to theory that higher trophic level species are more affected by habitat fragmentation than the species upon which they depend, the *H. horticola* population was less strongly genetically structured than the metapopulation of its butterfly host. It seems that *H. horticola*'s dispersal ability allows it to compensate for the fragmented distribution of its host and not suffer from the metapopulation dynamics of the host local populations.

Overall, the results of my thesis show that interactions between *H. horticola* and its host *M. cinxia* are strongly affected by competition among the adult female wasps. Intraspecific competition has an important role from an evolutionary perspective. *Hyposoter horticola*'s deterrent marking behaviour has evolved in response to competition and the risk of superparasitism faced by immature offspring. Avoidance of superparasitism to limit competition is also the fundamental mechanism that controls *H. horticola*'s optimal foraging strategy. And intraspecific competition modifies individual female host searching behaviour, increasing their foraging activity.

Interactions within a multitrophic system are complex and predictions concerning host-parasitoid interactions are difficult to generalise. However, as in this system, competition is factor that should receive more attention in empirical and theoretical studies of host-parasitoid interactions.

SUMMARY

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1. Introduction

Factors affecting parasitoid foraging behaviour

Parasitoids are insects that lay their eggs in or on other arthropods, and whose larvae develop by feeding on host tissue, eventually resulting in the hosts' death (Godfray 1994). Parasitoids demonstrate well the link between foraging behaviour (adult females searching for hosts) and fitness because each egg laid in a host represents a fitness increase for the parasitoid (until Lack's clutch size is reached (Lack 1947)). Therefore, they are often used to test predictions of optimal foraging theory (Hubbard & Cook 1978; Stephens & Krebs 1986; Wajnberg *et al.* 2006). But host-parasitoid interactions are complex and a number of parameters must be taken into account to determine the optimal foraging strategy (Mills & Wajnberg 2008; Corley *et al.* 2010). Factors influencing parasitoid foraging behaviour include individual physiological state, host quality, and competition with conspecifics. The effects of those factors interact with each other, increasing the complexity of optimal foraging strategies.

The physiological state of a parasitoid, especially egg load, can affect its host-searching behaviour (Heimpel *et al.* 1998; Babendreier & Hoffmeister 2002; Burger *et al.* 2004). Parasitoid egg production strategies such as resource allocation, total number of eggs produced, number that are mature at a time, presence of a pre-reproductive adult stage, and capacity to reabsorb eggs vary greatly among parasitoid species and depend on a number of life-history traits such as body size, longevity, egg size, clutch size, and host use type (whether or not the host continues to develop after being parasitized) (Jervis *et al.* 2001; Jervis *et al.* 2008).

A second factor that may influence parasitoid foraging behaviour is host patch quality. Host patch area, number of hosts, and proportion of healthy hosts have been shown to affect parasitoid foraging strategies (studies reviewed in Wajnberg 2006). Hosts are vulnerable to parasitism for a limited time only so host quality, in terms of susceptibility to parasitism, varies over time. The hosts are of highest quality, most valuable, when they are susceptible to parasitism. However, even a resource that is not ready to be used still may have value as it can provide information, such as the location of a potential host, to be used later by the foraging individual (Collett 2008).

In addition to the physiological state of the wasp and host quality, competition for hosts can affect parasitoid foraging behaviour. Since the distribution of hosts is usually aggregative (Godfray 1994; Wajnberg 2006), foraging adult females may face intraspecific direct competition for hosts (Godfray 1994; Goubault *et al.* 2005; Hardy *et al.* 2013). Mathematical models predict that intraspecific direct competition can affect the strategies of wasps foraging for hosts (Hassell & Varley 1969; van Alphen 1988) and studies have shown that presence of competitors can lead to behavioural modifications (Field & Calbert 1998, 1999; Hardy *et al.* 2013).

Post-oviposition marking

Competition can also affect parasitoids at earlier stages in their life. As larvae inside or on the host, the immature parasitoids can suffer from competition for space or food (Brodeur & Boivin 2004) due to superparasitism (van Alphen & Visser 1990). Indeed, in some solitary parasitoid species, a parasitoid larva (Harvey *et al.* 2009) or mother (Collier *et al.* 2007) kills competitors because only one individual can complete development inside a

host (Harvey & Strand 2002). Superparasitism is costly in terms of time and fitness for solitary parasitoids. Thus, most species attempt to avoid it (Prokopy 1981), though not all are able (van Alphen & Visser 1990; Cronin & Strong 1993).

In order to reduce direct competition among offspring, a number of parasitoid species indicate that a host has already been parasitized by depositing chemical signals after oviposition that influence the behaviour of subsequent conspecifics visiting the host; typically by deterring them from laying eggs in previously exploited resource patches, thus reducing the risk of superparasitism (van Lenteren 1981; Hoffmeister & Roitberg 1997; Nufio & Papaj 2001; Stelinski *et al.* 2007).

Restrained parasitism

Sub-maximal use of a resource can allow exploiter-resource interactions in systems such as herbivore-plant, predator-prey or parasitoid-host to persist over time (Maiorana 1976; Strevens & Bonsall 2011). Possible mechanisms restricting the ability of a parasitoid to exploit a host are numerous and varied. Constraints limiting resource use can be biological, physiological, or physical. For example phenological asynchrony between a parasitoid and its host (Godfray 1994; van Nouhuys & Lei 2004), immune defence of the host against the parasitoid (Lavine & Strand 2002), or spatial refuge allowing the host to escape or hide (Holt 2002).

Alternatively, a parasitoid might parasitize only a fraction of the available hosts as an evolved behaviour. Classical ecological or evolutionary explanations include: 1) Prudent predation (Wilson 1978), in which restrained harvesting strategies increase resource availability for future generations. 2) Bet-hedging (Hopper & Rosenheim 2003), by which a wasp might reduce the risk of offspring mortality by spreading its eggs over multiple locations. 3) Cooperative benefits: the gregarious host caterpillars depend on group cooperation for foraging, development, and nest building. If parasitism decreases individual host performance, then the whole group will suffer when too many caterpillars are parasitized. 4) Optimal foraging (Stephens & Krebs 1986), in which individuals maximize

fitness by optimizing the balance between time spent at a given resource patch, and time spent searching for or traveling to a new resource patch (Charnov 1976). Over time the wasp experiences decreasing parasitism efficiency at a host egg cluster and eventually it may be beneficial for the wasp to find another host cluster.

Effect of fragmented distribution of hosts on parasitoids

Spatial structure of a landscape is an important component of population dynamics (Hassell 2000) and coevolutionary processes (Thompson 2005; Urban *et al.* 2008) for closely interacting species. In insect multitrophic systems of plants, herbivores and parasitoids, resources are often distributed heterogeneously in the landscape. Habitat fragmentation has been shown to greatly influence the distribution and dynamics of herbivores and their parasitoids, and to differ among species at different trophic levels (Holt 2002; van Nouhuys 2005). In theory, higher trophic level species, such as predators and parasitoids, are more sensitive to habitat fragmentation than their herbivore preys or host species because resource distribution becomes increasingly fragmented for the species at higher levels (Holt *et al.* 1999; Holt 2002). Some studies (Johannesen & Seitz 2003; Kankare *et al.* 2005; Anton *et al.* 2007) support this hypothesis but others find that high trophic level species are not more negatively affected by habitat fragmentation than species upon which they depend (Nyabuga *et al.* 2012).

Third trophic level species, such as parasitoids, may be less mobile than their hosts, which would make them more negatively affected by habitat fragmentation (Roland 1993; Kruess & Tschardt 1994; Komonen *et al.* 2000). Indeed, a review of movement and population dynamics of hosts and their parasitoids in heterogeneous landscapes by Cronin and Reeve (2005) showed that most parasitoids disperse less than their hosts. Differences in dispersal abilities between parasitoids and their hosts are though to contribute to the persistence of some host-parasitoid interactions. When hosts are more dispersive than their parasitoids, a fraction of them continuously escapes parasitism by

colonizing new habitat patches, allowing the metapopulation to persist (Amarasekare 2000; Hassell 2000; Urban *et al.* 2008). However, if parasitoids are mobile, they can be relatively unhindered by the discontinuous distribution of their hosts (Murdoch *et al.* 1996; Weisser 2000; Esch *et al.* 2005) and show only weak spatial genetic structure.

My dissertation investigates the foraging behaviour of the wasp *Hyposoter horticola*, an egg-larval parasitoid of the Glanville fritillary butterfly *Melitaea cinxia*, in the Åland islands in Finland and, combining behavioural experiments, genetic analyses and modelling, tries to answer the following questions:

How is *H. horticola*'s foraging behaviour affected by developmental timing of both the parasitoid and the host, and direct intraspecific competition among adult females? (I)

Does *H. horticola*'s post-oviposition marking effectively deter conspecific wasps from ovipositing? How many mothers have progeny in a single host egg cluster? Is the fraction of eggs parasitized in one host cluster affected by the number of wasps by which it is parasitized? (II)

Which mechanism constrains *H. horticola* to parasitize only one third of the available hosts? (III)

What is the spatial genetic structure of *H. horticola* in the Åland islands? How is it related to the fragmented distribution of the host and the dispersal abilities of the parasitoid? (IV)

2. Material and Methods

Study species

The solitary wasp *Hyposoter horticola* (Gravenhorst) (Ichneumonidae: Campopleginae) is an egg-larval endoparasitoid, specialist of the Glanville fritillary butterfly *Melitaea cinxia* (Lepidoptera: Nymphalidae) (van Nouhuys & Ehrnsten 2004; Shaw *et al.* 2009). *Melitaea cinxia* lives as a metapopulation in the Åland islands, a Finnish archipelago situated in the Baltic Sea between Sweden and mainland Finland (Hanski 2011). The metapopulation persists in stochastic balance between extinctions and colonisations, with the butterfly

occupying around 500 of the 4000 patches of suitable habitat in any given year (Figure 1) (Hanski 2011).

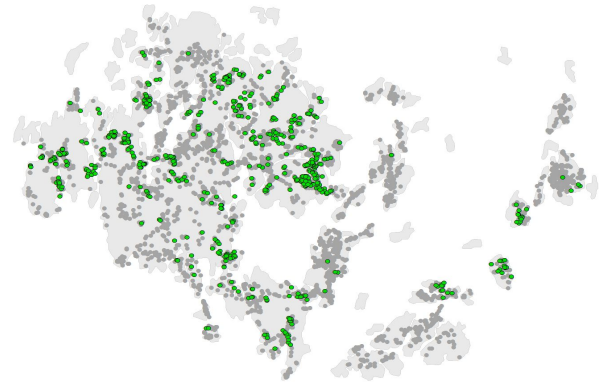


Figure 1. *Melitaea cinxia* metapopulation in the Åland islands. Grey dots represent the ~4400 suitable habitat patches. Green dots represent the 645 patches occupied by the butterfly in 2009.

The butterflies lay clusters of 100-200 eggs on the underside of leaves of their host plants, *Veronica spicata* and *Plantago lanceolata* (Plantaginaceae) (Kuussaari *et al.* 2004). Female *H. horticola* are attracted to *M. cinxia* eggs and plants upon which egg clusters have been laid (Castelo *et al.* 2010). They forage for these host egg clusters to parasitize in June-July (Photo 1) (van Nouhuys & Ehrnsten 2004). As the parasitized caterpillar develops, the *H. horticola* larva remains inside its host through winter diapause. In the spring the larva consumes the caterpillar and pupates inside it, just before the host itself would have pupated (van Nouhuys & Punju 2010).



Photo 1. Female *H. horticola* parasitizing a *M. cinxia* egg cluster. © C. Couchoux.

The particularity of this host-parasitoid system is that the host is only susceptible to parasitism for a very short time, when the caterpillars are close to hatching from the eggs (van Nouhuys & Ehrnsten 2004). To overcome the limited time availability of the host, the female parasitoids learn the location of potential hosts and visit them for up to two weeks before they are susceptible to parasitism (van Nouhuys & Kaartinen 2008). During the visits to the host clusters, the wasps probe the eggs with their ovipositor, pushing on the eggs, presumably to assess if the host has yet become suitable for parasitism. Monitoring potential hosts before they are susceptible to parasitism increases the time available for foraging, but, because the location of a host egg cluster is known by several wasps, it also intensifies competition among foraging females (van Nouhuys & Ehrnsten 2004; van Nouhuys & Kaartinen 2008).

Behavioural experiments and dissections

Behavioural experiments have been carried out to study how the foraging behaviour of *H. horticola* was affected by different parameters: wasp maturity (I), host susceptibility (I), intraspecific competition among foraging females (I), previous parasitism and/or marking of the host egg cluster (II), presence of *H. horticola* in the host population (III), presence of a hyperparasitoid of *H. horticola* in the population (III). The experiments were conducted either in a 26 by 32 by 3 m outdoor cage (Photo 2) that simulates a host habitat patch (I) or in the laboratory in a 40 by 40 by 50 cm mesh cage (I, II, III).

During all the behavioural experiments the foraging behaviour of any wasp visiting a host egg cluster was observed and recorded. The principal behaviours analysed, in terms of presence and duration, were the following: probing/parasitizing the host eggs, marking the host cluster, standing on the plant, and interacting with conspecifics. The wasps released in the outdoor cage were marked so they could be individually identified (Photo 3).

In addition to the behavioural experiments, parasitoid ovaries and oviducts were dissected to assess the egg load of females at different

ages (I), and caterpillars (from host clusters parasitized during a laboratory experiment or naturally parasitized in the field) were dissected to determine if they were parasitized by *H. horticola* and calculate the parasitism rate in each host cluster (II, III).



Photo 2. Outdoor cage simulating a habitat patch. Outside (a) and inside (b) views. © C. Couchoux.



Photo 3. Female *H. horticola* 'yellow-blue' individually marked to be released in the outdoor cage. © C. Couchoux.

Genetic analyses

Thirteen new polymorphic microsatellite markers were developed for *H. horticola* and used to study different topics. Genotype data from 407 females collected all over the population were analysed. The spatial genetic structure of *H. horticola* in the Åland islands was explored using Bayesian clustering, analysis of molecular variance and isolation by distance (IV). Using the same dataset, maternity assignment was performed to identify full-siblings among parasitoid offspring across the landscape. The geographic distance between the offspring was used to calculate the minimum foraging range of the mothers (IV). Maternity assignment was also performed on all parasitoid offspring from each of ten naturally parasitized host egg clusters to determine the number of females that had parasitized a single cluster. This allowed to assess the effectiveness of post-oviposition marking under natural conditions (II).

3. Results and Discussion

Foraging behaviour varies with wasp maturity, host susceptibility and intraspecific competition (I)

Under laboratory conditions, *H. horticola* females lived for about six weeks. Upon emergence the adults contained no mature eggs. They were therefore classified as extremely synovigenic (Jervis *et al.* 2001), as most long-lived species are (Quicke 1997). The number of mature eggs increased through their life, at a high rate during the first ten days and then more slowly. During the pre-reproductive adult stage, the wasps were limited in the number of eggs they could lay (as in Ellers *et al.* 2000). It is possible that *H. horticola* foraged little for hosts during this time, waiting until they have accumulated a threshold number of mature eggs in their ovaries before actively foraging for hosts.

A particularity of *H. horticola* is that females not only forage for actual resources, (hosts susceptible to parasitism) but also for potential resources that are not yet ready to be exploited (hosts before they are susceptible to

parasitism). Previous studies have shown that this is not simply a foraging error but that they gain useful information from these visits (van Nouhuys & Ehrnsten 2004; van Nouhuys & Kaartinen 2008). Attending to potential resources has been shown in insects (Brown 1981; Collett 2008), but rarely in parasitoid wasps (Rosenheim 1987). Thus the wasps visited young host egg clusters, before the hosts were susceptible to parasitism. But as the host eggs matured, the wasps modified their behaviour, foraging more actively, presumably because as the hosts became closer to being susceptible to parasitism their value increased. These results are in agreement with a number of studies, reviewed in Wajnberg (2006), that showed that, as predicted by the marginal value theorem (Charnov 1976), the time parasitoids spend foraging in a patch increases with patch quality.

In the Åland islands, four parasitoid species attack the butterfly *M. cinxia* (Lei *et al.* 1997; van Nouhuys & Hanski 2005), but *H. horticola* is the only one that forages for eggs. Therefore adult females do not suffer from interspecific exploitation competition since they parasitize the hosts at the earliest stage. However, because the wasps visit the same host egg clusters repeatedly, *H. horticola* suffer from intraspecific direct competition when several foraging females attempt to parasitize the same host cluster. Competition varied according to host age; it became more frequent as the hosts became more valuable, and was maximal when the hosts were susceptible to parasitism.

In presence of conspecifics, the adult female wasps modified their behaviour, foraging more actively. They visited the plant for longer and probed the host eggs more often and for longer (Figure 2). Indeed, intraspecific direct competition is known to affect parasitoid foraging behaviour (Field & Calbert 1998; Hardy *et al.* 2013) and, when the foraging wasps interfere, it has been shown that time spent in the patch increases with competition (Visser *et al.* 1990; Haccou *et al.* 2003; Wajnberg *et al.* 2004; Goubault *et al.* 2005; Hardy *et al.* 2013).

Spending more time foraging at a cluster when there is competition, especially at a high value patch (hosts susceptible to parasitism), can be interpreted as playing a war of attrition

(Maynard Smith 1974), and perhaps guarding the host cluster. The hosts are only susceptible for a short time (van Nouhuys & Ehrnsten 2004; IV) but, because there is intraspecific competition, another female might visit a parasitized cluster while the hosts are still susceptible to parasitism. Therefore females might protect the host clusters they parasitize to avoid superparasitism or host overexploitation, which was investigated in chapter II.

Post-oviposition marking deters subsequent wasps from laying eggs in a previously parasitized host egg cluster (II)

A way to protect offspring from competition is to deter conspecifics from ovipositing in previously parasitized hosts. Post-oviposition marking of hosts to indicate that a host has already been exploited is widespread in Hymenoptera (Nufio & Papaj 2001). Behavioural experiments showed that female *H. horticola* exhibit a marking behaviour, strongly associated to oviposition; they only marked a host cluster if they had parasitized the eggs. Previous egg laying in the host cluster

(presence of parasitoid eggs) did not affect the wasps' foraging behaviour. However, the mark was effective in reducing the propensity of subsequent wasps to parasitize the host egg cluster (Figure 3). This has been observed in other Hymenoptera species as well (Chow & Mackauer 1999; Agboka *et al.* 2002; Stelinski *et al.* 2007), suggesting that marking, rather than oviposition, induces the deterring effect.

Genetic analyses assessing how many females laid eggs in host clusters parasitized in the field showed that, under natural conditions, a host egg cluster was primarily parasitized by one female *H. horticola*. Also, even when several females parasitized a host egg cluster, the great majority (74%) of the offspring were full-siblings.

Parasitism rate, as the number of eggs parasitized in one host cluster, did not increase when more than one wasp parasitized the cluster. Therefore parasitism by several individuals did not lead to resource overexploitation. Explanations for this sub-maximal use of resource were considered in chapter III.

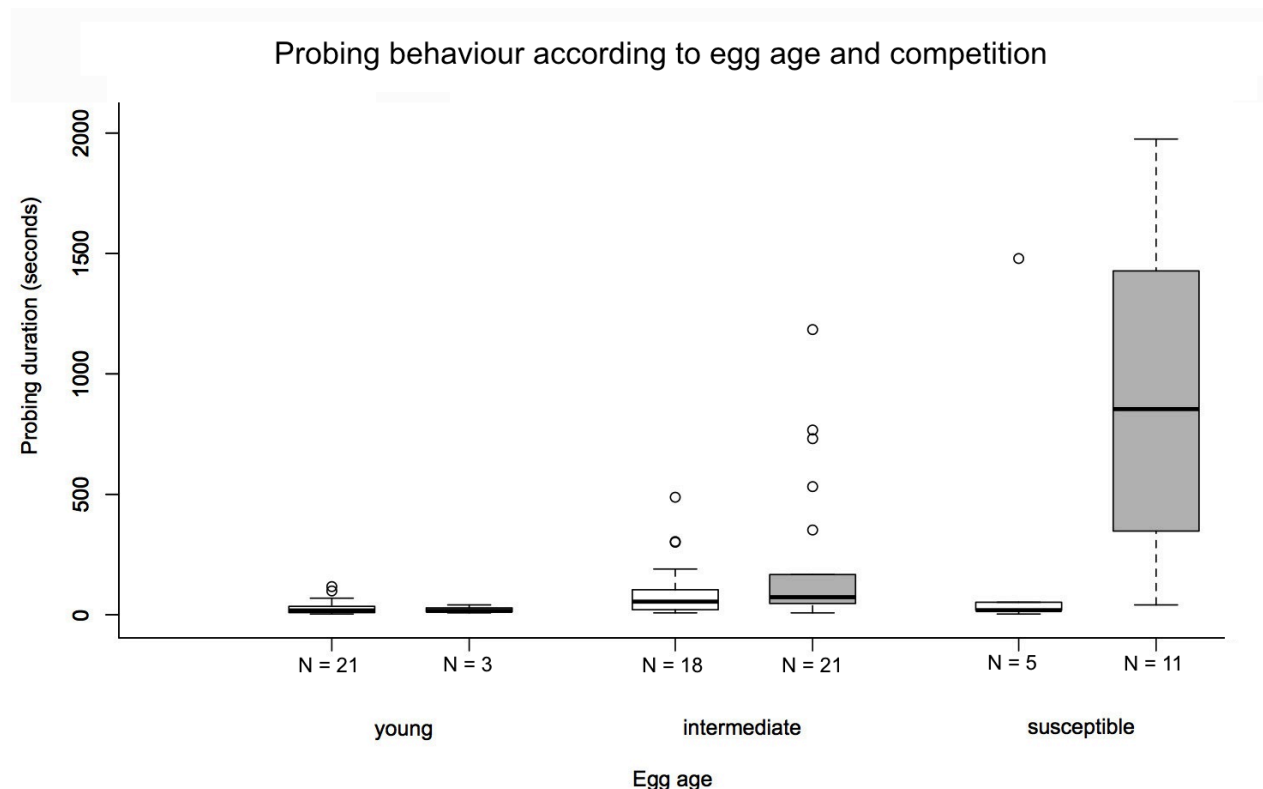


Figure 2. Duration of the probing of young, intermediate and susceptible eggs, in the absence of competition (open bars) and in presence of competition (grey bars)

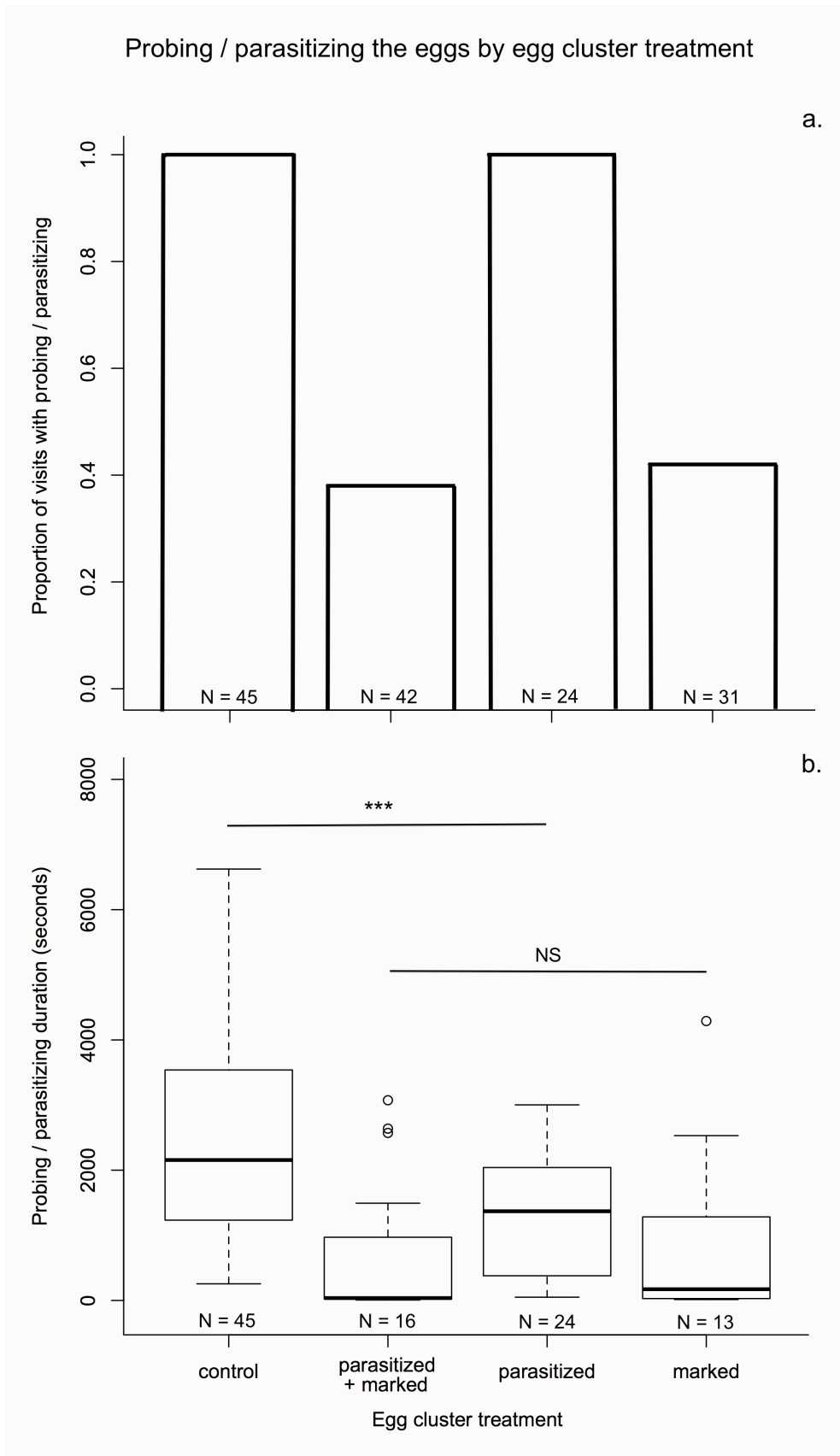


Figure 3. Proportion of visits in which the wasps probed the eggs (a) and duration of the probing (b) for control, parasitized + marked, parasitized, and marked host egg clusters. *** indicates a significant difference ($p < 0.001$) and NS indicates no significant difference.

Parasitism rate is controlled by optimal foraging with avoidance of superparasitism (III)

In the Åland islands practically all *M. cinxia* egg clusters are parasitized by *H. horticola*, but only a fraction (on average 1/3) of the eggs in each host cluster is used (van Nouhuys & Hanski 2002; van Nouhuys & Ehrnsten 2004). Considering the limited availability of the host and the intraspecific competition among foraging females, such a low parasitism rate is surprising. In a series of experiments, physical and physiological constraints such as wasp egg limitation (I), host egg cluster architecture, and immune host defence, were each rejected as explanations for the sub-maximal use of the host exhibited by the wasp. This is not surprising; *H. horticola* is well adapted to *M. cinxia*, as it is its only known host species in this population.

Behavioural restraints such as prudent predation and bet-hedging were considered, but since in Åland the *H. horticola* population is large and reasonably well mixed across the landscape (Kankare *et al.* 2005; IV), they are not plausible explanations. A third potential behavioural constraint, due to the effects of parasitism on cooperative benefits in a host group, was also tested. The parasitoid stays inside the host caterpillar as a larva for almost a year and then consumes the host rapidly just before it would have pupated. Given the long residence time of the parasitoid in the host, it is not surprising that experiments showed no cost of parasitism for individuals, and no effect of the fraction of hosts parasitized in a group on the development of the caterpillars or wasps.

Hyposoter horticola is a solitary species; only one individual can develop within each host. Superparasitism is therefore costly, in terms of waste of time and eggs. Results showed that females are able to avoid superparasitism with a 75% accuracy. Optimal foraging with avoidance of superparasitism was the most plausible explanation for the observed sub-maximal rate of host exploitation. Foraging efficiency at a host cluster decreases because of avoidance of superparasitism. The more time a wasp spends at a host egg cluster, the fewer unparasitized hosts it finds. Therefore it becomes increasingly beneficial in terms of

fitness to leave the host cluster to find another one. The model predicted sub-maximal parasitism close to the observed 1/3 when the searching time to find another susceptible host cluster is short, *i.e.* when the probability of successfully parasitizing another cluster is high.

Spatial genetic structure: *H. horticola* is less affected by habitat fragmentation than its host (IV)

The host butterfly metapopulation is influenced by habitat fragmentation and shows spatial genetic structure at the scale of habitat patches (Orsini *et al.* 2008; Hanski 2011). Bayesian clustering showed that the *H. horticola* population in Åland is geographically genetically structured, with genetic clusters larger than individual networks of habitat patches (Figure 4). Apart from a couple of anomalies, the genetic clustering is unusually precise and makes intuitive sense in terms of spatial distribution. Delimitation of the clusters is consistent with the distances *H. horticola* can travel. For example, the isolated islands in the East constitute a separate genetic cluster.

In addition to the genetic clusters identified with Bayesian clustering, *H. horticola* population was hierarchically structured at two lower levels, following the habitat structure of its host *M. cinxia*: habitat patches and patch networks. The negative inbreeding value within habitat patches, although not statistically significant, suggested outbreeding that could be due to mating between individuals from different genetic sources (habitat patches). This is consistent with the results on female dispersal that showed that half of the wasps forage further than one habitat patch. Therefore, in contrast to the butterflies that mate mostly in their natal patch (Hanski *et al.* 1994; Kuussaari *et al.* 1996), the breeding population for the parasitoid is probably defined at the level of patch networks rather than habitat patches.

The *H. horticola* population in Åland seems to be less strongly genetically structured than the metapopulation of its butterfly host, *M. cinxia* (Orsini *et al.* 2008). This is rather expected considering that, where a host lives as a metapopulation, as does *M. cinxia* (Hanski 2011), the wasp must be able to disperse among

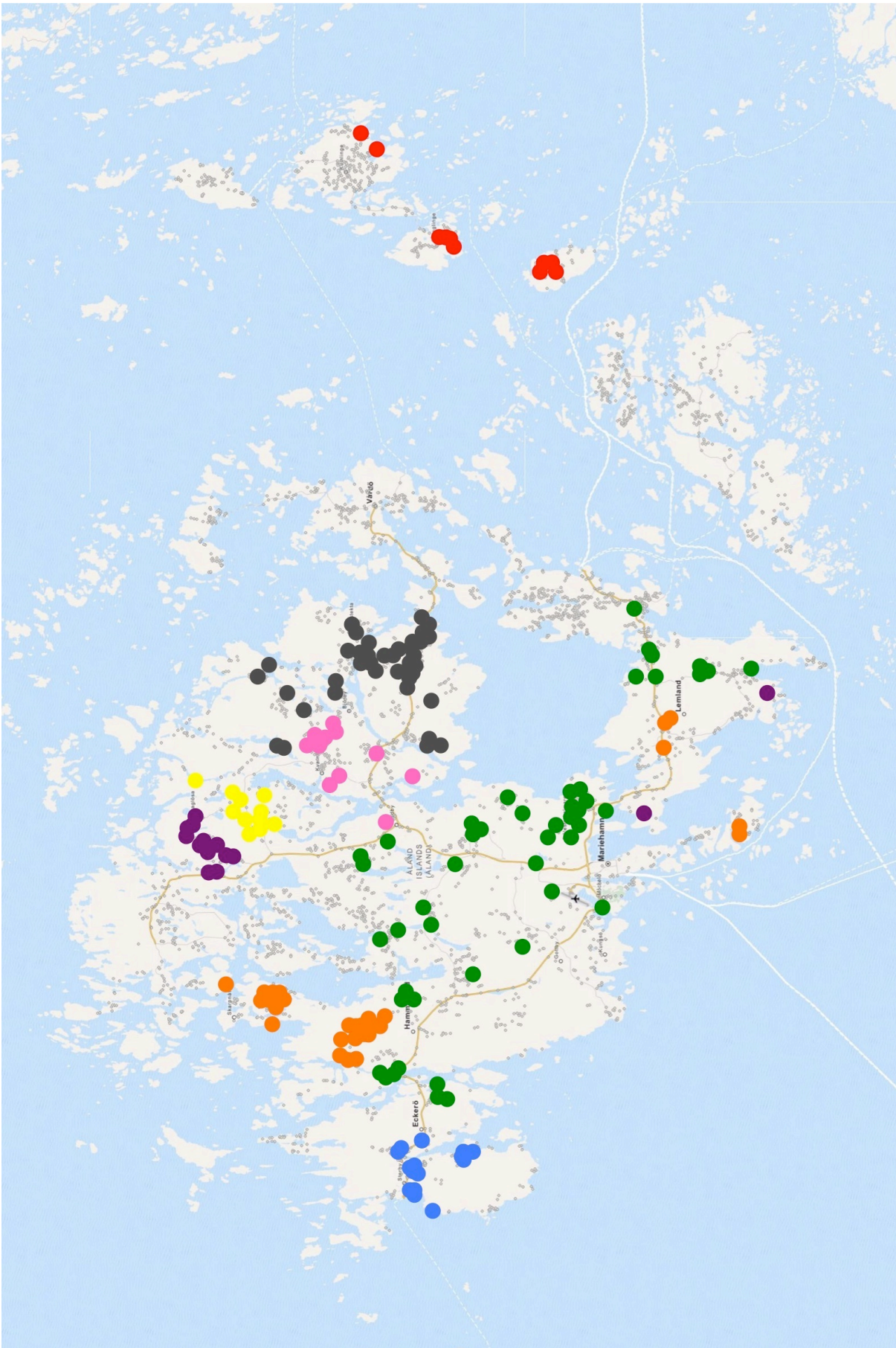


Figure 4 . Map representing the eight genetic clusters detected by the spatial clustering of groups analysis in the *H. horticola* population in the Åland islands. Coloured circles represent habitat patches from which samples are coming. Different colours indicate genetically significantly distinct clusters.

unstable local host populations to persist. Also, the wasp is uniformly widespread across the whole host population (van Nouhuys & Hanski 2002).

Estimation of female dispersal range, by identifying full-siblings among parasitoid offspring using maternity assignment, showed that the majority of females moved only little (less than 1 km) but that half of them moved across patches and could travel up to 7.5 km. This result is consistent with a previous study using survey data that showed that *H. horticola* colonized new host populations up to several kilometres away, but could not colonise patches 8.5 km away from existing populations (van Nouhuys & Hanski 2002). The host butterfly disperses an average of 500 m and up to 3 km (Hanski *et al.* 1994; Kuussaari *et al.* 1996). Therefore, individual *H. horticola* move at a larger scale than the host, dispersing at least twice as far. The mobility of *H. horticola* allows it to be present in all the local host populations irrespectively of their spatial isolation, including newly colonized host populations. Thus, the wasp does not seem to suffer from the metapopulation dynamics of the host populations (van Nouhuys & Hanski 2002; van Nouhuys & Ehrnsten 2004).

Dispersal is an important factor when considering multitrophic systems in a spatial context. Higher trophic level species, such as parasitoids, experience a more fragmented foraging habitat than do the species upon which they depend. However, this can be compensated for by greater dispersal ability, as it has also been shown in other studies (Esch *et al.* 2005; Elzinga *et al.* 2007; Nyabuga *et al.* 2012).

4. Conclusions

This study of *H. horticola* showed that parasitoid host-searching behaviour is complex; multiple factors such as forager's physiological state, resource value and intraspecific competition, as well as their interactions, should be integrated into conceptual and theoretical models of parasitoid foraging strategy (I).

Competition has a particularly important role in parasitoid foraging behaviour. It can affect parasitoids when they are adults foraging

for hosts, but also when they are immature and still inside the hosts. To avoid superparasitism and protect offspring from competition, some solitary parasitoids, such as *H. horticola*, have evolved a post-oviposition marking behaviour that deters subsequent wasps from parasitizing a host egg cluster that has been previously exploited. In chapter II, use of both manipulative laboratory behavioural experiments and genetic analyses of samples from the field has shown that the deterrent effect of the marking detected under controlled conditions functions in a complex natural environment as well. Results in chapter II also revealed that parasitism rate does not increase above 1/3 when several individuals parasitize the same host cluster.

As discussed in chapter III, there are many potential explanations for the evolution and maintenance of sub-maximal resource use as observed for *H. horticola*. Experiments and existing data showed that simple physiological or biological, and group selection hypotheses are not applicable. The most plausible explanation is that *H. horticola* practices sub-maximal parasitism and deterrent marking as a way to forage optimally for hosts. However, the plausibility of this hypothesis is dependent on the expectation that the wasp will relatively quickly find another suitable host egg cluster in a setting that is known to be strongly competitive. Female reproductive success is the topic of an upcoming article. Assessing competition among foraging females and the number of hosts a female can expect to parasitize under natural conditions will allow to estimate the searching time, and therefore test how realistic the model is.

Study of the spatial genetic structure of *H. horticola* in chapter IV showed that dispersal is an important factor when considering multitrophic systems in a spatial context. Thanks to its dispersal ability, *H. horticola* is relatively unhindered by the fragmented distribution of its host *M. cinxia*. Since the host cannot escape parasitism by colonising unoccupied local populations, the wasp appears to have an undeniable advantage in the antagonistic interaction with its host.

Overall, the results of my thesis show that interactions between *H. horticola* and its host

M. cinxia are strongly affected by competition among the adult female wasps. Intraspecific competition has an important role from an evolutionary perspective. *Hyposoter horticola*'s deterrent marking behaviour has evolved in response to competition and the risk of superparasitism faced by immature offspring. Avoidance of superparasitism to limit competition is also the fundamental mechanism that controls *H. horticola*'s optimal foraging strategy. And intraspecific competition modifies individual female host searching behaviour, increasing their foraging activity.

Interactions within a multitrophic system are complex and predictions concerning host-parasitoid interactions are difficult to generalise. However, as in this system, competition is factor that should receive more attention in empirical and theoretical studies of host-parasitoid interactions.

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