Chapter 5
Genetics of the Behavioral Ecology of Egg Parasitoids

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Contents

5.1 Introduction

The release of insect parasitoids for biological control programs of phytophagous pests has regularly increased over the last decades all over the world to protect crops in open fields (e.g., cereals), greenhouses (e.g., vegetables) and even in forestry (Boller et al. 2006). Important successes were obtained in different

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agro-ecosystems, and egg parasitoids (also called "oophagous") are most probably the most important amongst the different parasitoids species used as biocontrol agents, leading sometimes to spectacular pest control efficacy (Wajnberg and Hassan 1994). Egg parasitoids, and especially those belonging to the Trichogrammatidae, the Scelionidae and the Mymaridae families, present interesting features that elect them as real good candidates to control several pests attacking a variety of crops. They are usually easy and cheap to rear in the laboratory and in large-scale mass-rearing facilities, since they can be produced on factitious hosts that are easier to handle than the natural hosts. Since they are attacking the egg stage, they are also preventing hatching of the larvae which are the damaging stages for the crop to be protected (Wajnberg and Hassan 1994). These are most likely the main reasons why egg parasitoid species are the most intensively produced animals for biological control programs worldwide (Wajnberg and Hassan 1994).

However, biological control programs with insect parasitoids and especially with egg parasitoids, even if sometimes they lead to spectacular pest control efficacy, still need to be improved, at least for reducing the cost and/or increasing the success of several pest control programs or sometimes just to enable the biological control on new-coming pests that was not initially feasible. For this, several authors over the last 15–20 years progressively proposed to develop a more scientifically-based, formal approach of biological control that is then not only based on an usual trial-and-error method (e.g., Waage 1990, Wajnberg 2004, Roitberg 2007, Wajnberg et al. 2008). The general idea is to use the concept and development of behavioral ecology, a growing scientific discipline that aims at understanding the behavior animals should adopt in different environmental situations to maximize their long-term offspring production (their so-called fitness) (Stephens and Krebs 1986, Godfray 1994). Any optimal behavioral strategy leading parasitoid females to maximize the total number of progeny produced will directly maximize the number of hosts attacked and killed, and will thus maximize the pest control efficacy when parasitoids are released in biological control programs (Mills and Wajnberg 2008).

As pointed out by Wajnberg (2004), considering optimal a behavioral strategy that maximizes long-term offspring production supposes that the corresponding behaviors have been settled progressively by natural selection, and thus that there is/was, in the parasitoid populations, genetic variability upon which natural selection could act. Without such genetic variability, transmissible over generations, no adaptation and evolution toward optimal behavioral strategies would be possible.

The aim of this chapter is thus to discuss the genetics of behavioral ecology of insect parasitoids, and especially egg parasitoids. After presenting the general concepts of behavioral ecology of insect parasitoids, I will give a rapid summary of the main methods that are available to quantify the genetic variation in quantitative behavioral traits in parasitoid populations. I will then present an exhaustive list of what has been done already on the quantification of the genetic variability in behavioral traits in insect parasitoids. Finally, I will discuss on what is the necessary knowledge that is currently missing in this field of research leading to the proposal of several future research directions that should hopefully be developed in the near future.

5.2 Different Behavioral Ecology Approaches on Insect Parasitoids

As briefly mentioned above, the aim of behavioral ecology is to study and to understand the behavior of animals within an ecological and evolutionary framework. The general idea is thus to understand the roles of animals' behavioral decisions in enabling them to adapt to their biotic and abiotic environment (Krebs and Davies 1997). There are several ways in which behaviors can be studied according to such a framework. Among others, looking for the so-called ultimate causation tries to identify the function of the behaviors studied to see how they can contribute to both animal survival and the number of offspring produced. Usually, optimization theory by means of theoretical models is used for this. On the other hand, the aim of the so-called proximate approach is to accurately identify the behavioral mechanisms animals are adopting to give rise to the observed behaviors. Obviously, studies of function and mechanisms must go hand to hand (Krebs and Davies 1997).

During the last 15 years or so, such a scientific approach was developed on a large variety of different animals, but a recent broad survey of the literature (i.e., more than a 1000 papers) published during a five-years period in the two main scientific international journals "Behavioral Ecology" and "Behavioral Ecology and Sociobiology" showed that only 1.7% of them were dealing with parasitoids. The remaining papers were on (1) birds: 31.8%, (2) insects, mites, etc. (except parasitoids): 25.6%, (3) fishes, reptiles, etc.: 19.3%, (4) mammals: 17.8%, (5) shellfishes, etc.: 3.1%, (6) miscellaneous: 0.7%. There is, thus, a huge gap on insect parasitoids to be exploited, which is rather surprising. Parasitoids share several ecological and biological features that are of utmost importance to understand how animal behavioral decision can be shaped by natural selection (see below). Besides, studies on these animals can be directly translated in terms of field application for biological control purposes (Godfray 1994, Wajnberg et al. 2008).

In this section, I am providing some details of the different specific behavioral features of insect parasitoids that are within a behavioral ecology framework. All parasitoid species are concerned but, for egg parasitoids, important results were recently published on Scelionidae and Trichogrammatidae.

5.2.1 Optimal Residence Time on Host Patches

Hosts of most parasitoid species are distributed in the environment in patches that are distant from each other. For egg parasitoids, this is for example the case for egg masses of the European corn borer *Ostrinia nubilalis* (Hübner) or the Southern Green Stinkbug *Nezara viridula* (L.). Furthermore, parasitoids are usually drastically short-lived animals and are thus usually so-called time-limited in the sense that they usually die before they can deposit all of their eggs (Driessen and Hemerik 1992, Seventer et al. 1998, Rosenheim 1999). Hence, parasitoids should likely maximize their offspring production per time unit, and have thus been likely selected to optimize their time allocation on every patch of hosts they visit (Wajnberg 2006). Actually, understanding how female parasitoids are managing the time they are allocating to different patches of their hosts has arguably been the most studied problem of behavioral ecology over the past few decades (van Alphen et al. 2003, Wajnberg 2006, van Alphen and Bernstein 2008).

There is now an important body of theoretical models enabling to know what should be the optimal time females should remain on each host patch under different environmental conditions. An important number of experimental work demonstrated that female parasitoids usually behave according to the corresponding theoretical predictions (see Wajnberg 2006 for a recent review). There are also now powerful statistical methods to identify from experimental data the mechanistic proximate behavioral patch-leaving decision rules females are using to reach such theoretical predictions (van Alphen et al. 2003, Wajnberg 2006). Some specific statistical methods have also been used to compare patch-leaving decision mechanisms adopted by different species of Trichogrammatidae taking into account their phylogenetic relationships through a so-called comparative analysis (Wajnberg et al. 2003, see Harvey and Pagel 1991 and Martins 1996 for details on the statistical methods used). It is clear that such a comparative approach should lead to a better description of egg parasitoid species as potential biocontrol agents, and should optimize the choice of the proper species to control a given pest, on a given crop and in a given environment.

Finally, the time parasitoid females allocate to host patches they exploit should be directly linked to their dispersion ability (i.e., the longer the time invested on each visited patch, the lower the dispersion). Therefore, an accurate understanding of the decision-making processes involved in patch-time allocation in female parasitoids should provide relevant information on spatial population dynamics, which would be especially useful for their release for biological control purposes.

5.2.2 Optimal Clutch Size

A parasitoid female encountering a host to attack has to decide how many eggs she should lay in it. Such behavioral decision is known to depend mainly on the size of the host (Vinson 1976, 1985, Waage 1986), and this is especially true for semi-gregarious species, including most egg parasitoids that attack eggs of different host species which display egg size variability (Waage and Ng 1984, Schmidt 1994). Sometimes, hosts to be attacked have been already parasitized, and the decision of the wasp female to lay additional eggs is called "superparasitism". In self-superparasitism, female attacks a host she already attacked before, while in conspecific-superparasitism, female attacks a host that has been previously attacked by a conspecific (Waage 1986, van Dijken and Waage 1987).

Several theoretical models have been developed over the years to understand what should be the optimal number of progeny females should deposit in each attacked host (Godfray 1994). Some models suggest that females have been selected to lay a clutch size that maximizes the total number of adult progeny emerging from the hosts attacked (e.g., Lack 1947), some others are assuming that this is rather the rate, per time unit, at which progeny are produced that matter (e.g., Charnov and Skinner 1984, 1985, Parker and Courtney 1984). The predictions of these models were verified on different parasitoid species (see Godfray 1994). Interestingly, these different models are also able to explain how many eggs parasitoid females should lay in a situation of superparasitism and, here again, a number of studies demonstrated that the fundamental assumptions of such theoretical approaches are well supported by experimental data.

In most cases, offspring fitness declines with increasing clutch size (Godfray 1994). This is especially true with superparasitism, leading both to progeny with lower fecundity, longevity, host searching rate, etc. (Chacko 1969, Waage 1986), and to the emergence of a population with a male-biased sex ratio (see below) (Waage 1986). This can be a real problem for designing an efficient biological control program with egg parasitoids, especially at a large-scale mass production step (Wajnberg et al. 1989). Thus, an accurate understanding of the behavioral proximate mechanisms used by parasitoid females to adjust the number of progeny laid in each host should provide us with some means to improve the quality of mass-produced parasitoids used in biological control programs.

5.2.3 Optimal Sex Ratio

Another important feature of insect parasitoids that has been intensively studied both theoretically and experimentally within a behavioral ecology framework concerns sex allocation (Godfray 1994, Ode and Hunter 2002). There are three main reasons for that. The first one is that sex allocation in most parasitoid species is usually extremely labile and is often directly linked to fitness (Ode and Hardy 2008). Moreover, since only female parasitoids are attacking hosts, releasing a wasp population with female-biased sex ratio has been assumed repeatedly to produce better pest control efficacy (e.g., Waage 1982, Heimpel and Lundgren 2000), and the study of sex allocation strategy in parasitic wasps can thus produce results that can be directly used to improve pest control strategies though biological control programs (Hardy and Ode 2007). Finally, insect parasitoids appear to be an excellent model for studying sex allocation since most species are arrhenotokous (i.e., haplodiploid), meaning that mated females can lay either unfertilized haploid males or fertilized diploid females. Hence, mated females are – at least theoretically – able to accurately control the proportion of sons and daughters in their progeny, and have been most likely selected to use such sex determination system to optimize their offspring production (Charnov 1982, Cook 1993).

Several well-known theoretical models are predicting what should be the optimal proportion of sons and daughters animals should produce to maximize their fitness. The conceptual and historical foundation of sex ratio theory is represented by the model of Fisher (1930) explaining that animal should invest equally in sons and daughters if individuals are finding mates randomly (i.e., panmixis). When sons and daughters are equally costly to produce and the sex ratio in a population is unbiased, each son will on average mate with one female and a mother will indeed realize equal fitness gains from investing in a son or in a daughter.

For most insect parasitoids, however, mating is not occurring randomly. As we have seen above, females are attacking hosts that are usually aggregated into patches, and their progeny are usually mating together before dispersing to forage for oviposition opportunities. Since only a limited number of so-called "foundress" females are contributing to offspring in a patch, mating between progeny are then among relatives, and the optimal sex ratio should be female-biased and should depend on the number of foundresses attacking the host patches (Ode and Hardy 2008). This is the Local Mate Competition theory (Hamilton 1967, Taylor and Bulmer 1980) and the predictions have been observed in several parasitoid species, including egg parasitoids (Godfray 1994).

Different proximate mechanistic rules have been identified leading parasitoid females to adjust their sex ratio according to the number of foundresses on host patches. Females were shown to respond to the frequency of physical contacts with other females (Wylie 1976) or to the perception of the chemical traces they left on host patches (Viktorov and Kochetova 1973). Females were also shown to use the frequency of encounters with already attacked hosts on the patch as a cue to the number of competing females (Wylie 1973). However, the most efficient and simple mechanism was originally observed by Waage and Lane (1984) and consists for the females in laying their son and daughter eggs in a particular order, usually with males first (Wajnberg 1993, Colazza and Wajnberg 1998, Bayram et al. 2004). The efficiency of such mechanism was quantified with a simulation model by Wajnberg (1994).

Finally, it has to be noted that parasitoid females are not only responding to the number of other conspecifics on patches of their hosts to adjust their own sex ratio, as host quality (e.g., size) was also shown to be a determinant factor (Charnov et al. 1981, Werren 1984). Parasitoid sex ratio can also be influenced by so-called sex ratio distorters (see Chapter 6, Werren 1997, Stouthamer et al. 2002, Ode and Hardy 2008), with the most well-known being the symbiotic bacteria *Wolbachia* that are especially common in egg parasitoids of the genus *Trichogramma* (Stouthamer et al. 1990, see Chapter 6). Theoretical models leading to understand accurately the evolutionary meaning of such particular sex determination system are still drastically needed.

5.2.4 Optimal Marking Strategy

In order to be able to optimize the number of eggs laid in each host encountered and attacked (see Section 5.2.2) and what sex those eggs should be (see Section 5.2.3), parasitoid females should be able to assess, in most cases, whether hosts have been already previously attacked either by themselves or by conspecifics. In most species, such ability is usually mediated through the use of marking pheromones that are chemical substances deposited by egg-laying females and that serve as messages conveying information (Roitberg and Mangel 1988). From an ecological point of view, such marking pheromones are usually complex signals that (1) can be used by the marking females to recognize where are the hosts they already attacked, (2) can be used to prevent females to attack hosts already parasitized, or (3) are used at the population level to spread more efficiently parasitoid offspring across all available hosts (Roitberg and Mangel 1988).

Marking pheromones can also have negative effects when they are used as kairomones by hyperparasitoids to locate and attack parasitoid offspring. Moreover, marking takes time and is necessarily associated with metabolic costs for producing the marking compounds (Godfray 1994). Finally, after being deposited, signal efficiency might suffer a decay with time though, e.g., evaporation (Hoffmeister and Roitberg 1998). There is thus a benefit/cost issue in such marking behavior and a growing body of theory is progressively developed to understand under what circumstance a marking behavior can evolve (Roitberg and Mangel 1988). Briefly, the general theory suggests that the production and use of signals can only evolve when there is a net benefit to the sender (Krebs and Dawkins 1984, Harper 1991). More accurately, under strong resource competition for limited resources, an increase in signal intensity and duration is expected if the animals issuing the signals obtain a disproportionate part of the resources (Hoffmeister and Roitberg 1998).

Understanding optimal marking strategies in insect parasitoids, and especially in egg parasitoids, is important if we want to use these insects in biological control programs more efficiently. However, although the theory is becoming progressively more accurate, there is currently a clear lack of experimental data to understand the associated evolutionary meaning and what can be the corresponding applications in terms of biological control (Roitberg 2007).

5.2.5 Optimal Diet Choice

As we have seen above, females of several parasitoid species are encountering and attacking different host instars or species showing different biological and/or ecological features. Especially egg parasitoids, that are mostly polyphages, can attack host eggs from different species, differing in e.g., size and/or shape, etc. Furthermore, in this respect, and as discussed before (see section 5.2.2), parasitoid females are sometimes encountering either unparasitized or already attacked hosts. In all these situations, the environment offers to the wasp females a set of different resource items (i.e., hosts) which might vary both in profitability (i.e., number of progeny that can be produced divided by handling time) and abundance and there is a growing theory, so-called optimal diet selection models, that predicts what resource type a foraging animal should accept in order to maximize its rate of progeny production (Stephens and Krebs 1986, Godfray 1994, Sih and Christensen 2001). Briefly, resource items (i.e., hosts) vary both in the number of progeny a female can produce attacking them, and in handling time (i.e., the time needed in host handling and parasitization). In this case, the theory predicts that a foraging female should accept and thus attack a host type if the progeny she will produce is worth the handling time invested (Charnov 1976, Houston and McNamara

1999, Hamelin et al. 2007). In other words, if the different host types are ranked according to their profitability, it can be shown that the foraging animal will maximize its rate of progeny production if it accepts all hosts with profitability above a given threshold and reject all hosts beneath this cutoff (Krebs and Davies 1987, Godfray 1994). The threshold level is known to depend on the number and quality of the hosts available in the environment. In rich environments with many good-quality hosts, females should optimally accept a narrow range of hosts, but should attack progressively poorer hosts if good-quality hosts are becoming less frequent.

Although the corresponding theory is still under development, there is clearly a lack of experimental data for parasitoids, and especially for egg parasitoids, trying to test the predictions of host acceptance models within the theory of optimal diet selection. What seems to be currently well established however is that hosts of better quality are usually those that are more readily accepted for oviposition, but this has been mainly demonstrated on *Drosophila* Fallén parasitoids (e.g., van Alphen and Vet 1986, Driessen et al. 1991) or on aphid parasitoids (e.g., Liu et al. 1984, Liu 1985). Trichogrammatidae egg parasitoids usually prefer young hosts, which yield higher survival and reproductive success (see Strand 1986 for a review). On these parasitoids, this problem was also approached by the accurate quantification of host handling time and the corresponding variation (e.g., Wajnberg 1989).

Like for the other behavioral decisions previously discussed, understanding why and how a host should be accepted for oviposition by a parasitoid female appears to be important for optimizing both the mass-rearing system used to produce the parasitoids and their efficiency when they are released for biological control programs.

5.3 Main Methods Available for Quantifying the Genetic Variation in Behavioral Traits

We have seen that a behavioral ecology approach on insect parasitoids can provide a list of important behaviors of parasitoid females that are most likely determining their efficiency to control pests when they are produced and released in the field for biological control programs. Quantifying the genetic variation in these behavioral traits in different parasitoid species and populations regularly appears to be an important task for different reasons. Briefly, and among others, it has been regularly admitted that an accurate quantification of the intra-population genetic variation in biological attributes of insect parasitoids, and especially egg parasitoids, can lead (1) to better estimate the ability of biocontrol agents to evolve in response to the environmental characteristics of the system used in their rearing and production (Mackauer 1976, Boller 1979), (2) to better estimate the parasitoid survival potential after field release (Hopper et al. 1993), and (3) to start a breeding selection program in order to improve the efficacy of the released animals to control the target pests (Hoy 1976, Mackauer 1976, Wajnberg 1991, 2004).

There are several review articles and book chapters presenting the main experimental and statistical methods that can be used to estimate the intra-population level of genetic variation in quantitative biological traits in animals, and particularly insects (e.g., Boller 1979, Collins 1984, Joslyn 1984, Falconer 1989, Roush 1990, Hopper et al. 1993, Margolies and Cox 1993, Wajnberg 2004, Beukeboom and Zwaan 2005). Here, I will give just a brief overview of there different methods and invite the reader to look at these review articles to understand more in details how these methods can be implemented.

5.3.1 Basic Concepts

Phenotypic variation among individuals is a common feature of all biological studies (Lewis et al. 1990), especially for behavioral traits (Roitberg 1990), and such variation is known to be the result of interactions between the genotype of each animal and the environment it lives in (Collins 1984). All methods available to quantify the genetic variation in any biological trait aim at estimating the effect of these two sources of variation, genetic and environment, and to see whether the genetic part is significantly contributing to the total phenotypic variation observed (Falconer 1989).

Variations among individuals in a population are quantified with variances and, using both standardized experimental methods and statistical models, the total phenotypic variance can be divided into the variance due to the environment and the variance due to genotypes. In turn, the genotypic variance can further be divided into (1) the variance due to additive genetic effects (i.e., the genetic variance associated with the additive effect of each allele involved in the phenotypic trait studied), (2) the variance due to dominance effect between alleles, and (3) the variance due to interaction between the loci involved in the trait under consideration (see, e.g., Falconer 1989 for a detailed description of this). Of the three types of genetic variance, the variance due to additive genetic effects is considered to be the most important since selection – natural or artificial – will essentially act on it. Hence, the methods available to quantify the genetic variation of phenotypic traits are built to estimate this particular type of variance, either directly or indirectly.

5.3.2 Parent–Offspring Regression

One of the first methods that have been proposed is based on the fact that, if a phenotypic trait is genetically determined, then offspring should resemble their parents. Then, the idea is to quantify the trait in a set of parents (mothers, fathers or both) and also on their progenies. A regression analysis is then performed with the offspring's values on the Y-axis and the parents' values on the X-axis and the slope of the regression is statistically tested. Since most of the behavioral traits discussed in the previous sections of this chapter are females' attributes, and more generally since only females are useful in most cases to control target pests in biological control programs, parent-offspring regressions are in most of the cases mother-daughter regressions. On Trichogrammatidae egg parasitoids, this method has been used successfully, for example, by Wajnberg (1989, 1993) and Bruins et al. (1994).

5.3.3 *Sib Analysis*

Another method consists of mating a number of males with a number of females. Each male has to mate with more than one female, but each female is mated with only one male. The trait is analyzed at the offspring generation, and an analysis of variance is then used to quantify the variation between males (i.e., fathers), females (i.e., mothers) and within the progeny of each female. In turn, the estimated parameters of the analysis of variance are used to test the significance of the genetic variation in the population studied for the quantified trait. As far as I know, this method was never used to quantify the genetic variation in biological traits of parasitic wasps.

5.3.4 *Family Analysis*

The most used method in the literature is the so-called isofemale strains method, also called isofemale lines or family analysis (Parsons 1980, Hoffmann and Parsons 1988). In this case, several families are founded, each from a single mated female taken at random in the population, and the trait is quantified in several offspring in each family at the F1 generation. Then, a simple one-way analysis of variance is used to test for a significant difference among average values of the different families compared. Such a significant difference will indeed indicate a significant genetic variation in the trait studied in the population. On Trichogrammatidae, this method was successfully used by Wajnberg (1994), Bruins et al. (1994) and Wajnberg and Colazza (1998), among others, and on Scelionidae by Wajnberg et al. (1999, 2004).

5.3.5 *Breeding Selection*

A modification in the average value of a quantitative trait through several generations of breeding selection proves that the phenotypic variation observed in this trait in a population is under significant genetic control (Roush 1990). This is the reason why a few number of studies used breeding selection as a mean to demonstrate significant genetic variation in biological attributes of parasitic wasps. In this case, the basic method is to quantify the trait under study on several individuals at a given generation and the individuals that are used to found the next generation are chosen according to they own phenotype. On egg parasitoids, this method was successfully used on Trichogrammatidae by Urquijo (1950), Ashley et al. (1974), Schmidt (1991) and Fleury et al. (1993). Since most, if not all, behavioral traits listed in previous sections of this chapter are most likely implicated in the efficacy of insect parasitoids to control pests in biological control programs, a significant change in the average value of such traits through breeding selection not only proves that traits have a significant genetic variation in the population studied, but also represents the starting point for improving the pest control efficacy of a biocontrol agent.

5.3.6 Common Features and Generalization

All methods briefly described previously can be used to estimate the so-called heritability of the traits studied, which can be defined as the ratio of the additive genetic variance to the total phenotypic variance (Hoffmann and Parsons 1988, Falconer 1989). Such a genetic parameter can be used to estimate the expected response to selection in the course of several breeding generations (Falconer 1989).

Also, with appropriate experimental set-ups, these different methods can sometimes be combined together. For example, a mother-daughter regression analysis can be planed over two successive generations, with several offspring measured for each mother. Then, at the F1 generation, the daughters are treated like different isofemale lines that are compared by means of a family analysis. On Trichogrammatidae egg parasitoids, such a combination of methods was successfully used by Chassain and Boulétreau (1991), Mimouni (1991), Fleury et al. (1993), Bruins et al. (1994) and Pompanon et al. (1994).

Finally, since behaviors are usually biological traits that can be difficult to measure and analyze (Martin and Bateson 1994), there is sometimes the need for the quantification of single behaviors, each with several values. In this case, all methods earlier described can be generalized using multidimensional statistical methods. For example, canonical correlation analysis can be used to perform a multidimensional parent-offspring regression, as this was done on egg parasitoids by Wajnberg (1993), or a discriminant analysis can be used to compare different isofemale lines in a multidimensional family analysis.

5.4 What Has Been Done and What Remains to Be Done?

Following Wajnberg (2004), an exhaustive survey was done over the main scientific database to find all references describing intra-population genetic variation in biological traits of egg parasitoids. Only 20 references were found, covering 11 species (since *Trichogramma brassicae* Bezdenko and *Trichogramma maidis* Pintureau and Voegelé are two synonymous names of the same species), among which nine are Trichogrammatidae and two are Scelionidae (see Table 5.1).

Among these 20 references, two did not discussed about genetic variation in behavioral traits (Ashley et al. 1974, Bennett and Hoffmann 1998), and the distribution of the 18 remaining references in the different behavioral features of egg parasitoids is the following one: optimal patch time allocation: 2; optimal clutch size: 2; optimal sex ratio: 3; optimal marking strategy: 0; optimal diet choice: 1; miscellaneous: 10. The last category regroups all behavioral traits that have not been explicitly analyzed within a behavioral ecology framework (e.g., females' walking activity).

Needless to say that this literature survey represents a very small number of published data, and thus clearly demonstrates a drastic lack of studies on the quantification of the genetic variation in behavioral traits of egg parasitoids. Important information is currently missing regarding the existence of genetic variation in

Table 5.1 List of all egg parasitoid species in which intra-population genetic variation in quantitative traits was studied

Family *Species*	References
Trichogrammatidae	
Trichogramma brassicae Bezdenko	Chassain and Boulétreau (1991), Fleury et al. (1993), Wajnberg (1993), Bruins et al. (1994), Pompanon et al. (1994), Pompanon et al. (1999), Wajnberg (1994), Wajnberg and Colazza (1998)
Trichogramma cacoeciae Marchal	Chassain and Boulétreau (1991), Pompanon et al. (1994)
Trichogramma carverae Oatman and Pinto	Bennett and Hoffmann (1998)
Trichogramma dendrolimi Matsumara	Limburg and Pak (1991), Schmidt (1991)
Trichogramma evanescens Westwood	Limburg and Pak (1991), Schmidt (1991)
Trichogramma maidis Pintureau and Voegelé	Chassain and Boulétreau (1987), Wajnberg (1989), Wajnberg et al. (1989)
Trichogramma minutum Riley	Urquijo (1950), Liu and Smith (2000)
Trichogramma pretiosum Riley	Ashley et al. (1974)
Trichogramma semifumatum (Perkins)	Ashley et al. (1974)
Trichogramma voegelei Pintureau	Mimouni (1991)
Scelionidae	
Telenomus busseolae Gahan	Wajnberg et al. (1999)
Trissolcus basalis (Wollaston)	Wajnberg et al. (2004)

behavioral decision rules adopted by egg parasitoids. In turn, this prevents, for example, starting mass breeding selection in order to improve pest control efficacy of oophagous species used in biological control programs.

5.5 Concluding Remarks and Future Directions

After decades of biological control programs designed using a trial-and-error method, behavioral ecology, by identifying the key behavioral traits implicated in the pest control efficiency of insect parasitoids and especially egg parasitoids, seems now to provide a modern, scientifically-based and formal approach leading hopefully to define optimized and more efficient pest control programs (Waage 1990, Roitberg 2007, Wajnberg et al. 2008). The information collected following such a scientific approach can help us in optimizing the choice of the correct species and population to control an indentified pest in a given environment (Wajnberg 2004, Mills and Wajnberg 2008). Moreover, quantifying the genetic variation in the key behavioral components of parasitoid reproduction strategies could, among others, provide us with the means to improve through breeding selection the efficacy of biocontrol agents released in biological control programs. This is what this chapter was about, and we have seen that, although quantifying genetic variability in insect parasitoids has been continuously presented as an important task, there is currently a drastic deficit of studies done to achieve this goal, and especially for egg parasitoids.

In this chapter, we have seen that the most important behavioral traits of parasitic wasps are implicated in (1) the way females optimally allocated their time to patches of their hosts, (2) the optimal number of progeny they should lay in each host attacked, (3) the optimal proportion of males and females they should produce, (4) the optimal marking strategy they should adopt, and (5) the optimal host acceptance decision they should develop when they are facing a choice of hosts of different quality. Actually, all these different points still remain to be analyzed in details in egg parasitoids following a behavioral ecology framework. The genetic variation in the corresponding behavioral traits still remains to be quantified and our ability to improve the pest control efficacy of oophagous insects still remains to be tested. The aim of this chapter is to stimulate research in this direction.

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