Biogeography, population genetics and mating systems of natural Nasonia populations

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Chapter 7

Summarizing Discussion

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The use of genetical methods in ecological research has offered new possibilities and lead to new insights (Lowe *et al.* 2004). Especially in research with small insects, the molecular approach gives the opportunity to study topics in the field that have so far been reserved to larger organisms (e.g. dispersal), or to the confined possibilities of the laboratory (e.g. resource allocation). While a growing amount of theory is based on primarily laboratory data of a limited number of organisms, tests of underlying assumptions under natural conditions have rarely been performed, yet. The advent of molecular tools for a larger array of organisms offers the possibilities to do so.

A prime example for missing information on ecology and natural behaviour of a tiny model organism is *Nasonia*. The aim of this thesis was to add knowledge about the field biology of *Nasonia*, which has so far mainly been used in laboratory studies and in only very few field studies (see **Chapter 1**). The main focus was on *Nasonia*'s population structure, phylogeography, reproductive strategies and dispersal abilities, to evaluate the underlying assumptions of models of adaptive behaviour. In the following I will try to merge the major findings of this thesis with previous knowledge into a more complete picture of the natural history of the *Nasonia* species complex. I will consider remaining ambiguities and open questions and point out future research topics.

A broader picture of the Nasonia *system*

The theory of reinforcement predicts that postzygotic isolation in the form of unviable hybrids, should favour selection on increased prezygotic isolation (Dobzhansky 1951). In *Nasonia*, postzygotic isolation is rather complete due to *Wolbachia* induced cytoplasmic incompatibility (Breeuwer & Werren 1990), and as there are differences in courtship behaviour, there is as well some

evidence for prezygotic isolation (van den Assem & Werren 1994; Beukeboom & van den Assem 2001). An interesting question is to what extent species divergence has progressed for other life history traits, such as sex allocation, host choice, overwintering strategies (diapause) etc.

In **Chapter 2** we showed with field data that most assumptions that are made in the recent LMC theory are fulfilled by *N. vitripennis*: local mating, random dispersal and asynchronous parasitism. Other assumptions of more basic models, such as equal clutch sizes, random mating among offspring within patches and synchronous parasitism are clearly violated. This shows that the success story of LMC research (Shuker & West 2004) is on the right track, but that there are still some poorly understood factors in this intensively studied system. When fitting the recent LMC models onto the data obtained in **Chapter 2**, we found in **Chapter 3**, that there are some factors included in these models that appear less relevant than previously thought (e.g. the total number of foundresses on a patch). Other factors seem to play a more important role (e.g. the relative clutch size of a parasitizing foundress compared to previous foundresses). The general message of this chapter is that females are limited in the cues they can obtain from their environment and these can differ from our expectations. The limited information poses boundaries to the adaptive response of the individual, as has also been acknowledged in more recent LMC research (Shuker & West 2004). A female might not have the total information on what has happened, and will happen in a patch that she is going to parasitize. This is especially true when a female *N. vitripennis* is confronted with the presence of a close relative, which I investigated in **Chapter 4**.

We found in North American field data that *N. vitripennis* does not adjust its sex ratio to conspecifics only, but reacts similarly when parasitizing hosts that are also parasitized by *N. giraulti*. This indicates that the two species have not diverged far enough yet in so far that a female is able to recognize the eggs of the competitor as different from conspecific eggs. Given that *N. vitripennis* has been found to recognize more diverged species' eggs as different (Wylie 1965; 1970), a foundress appears in principle capable of differentiating between hetero- and conspecific clutches. Our results can clearly be attributed to missing information on species identity of the eggs encountered during oviposition. From an evolutionary point of view the expectation is that an organism has

maximized the precision of adaptation. In the case of *N. vitripennis*, adaptation towards encountering a closely related species is not optimal. In the following I will discuss two hypotheses that might explain this observation.

We showed in **Chapter 6** that *N. vitripennis* is a long distance disperser that can cover at least 2 km, and that populations as far apart as 100 km are still little differentiated. This explains why we did not find differentiation on smaller scale (**Chapter 2**), and helps to demarcate what a population is in *Nasonia*. The high dispersal distance implicates the admixture of a large population that might cover areas of sympatry and allopatry of *N. vitripennis* and *N. giraulti* within North America. This high rate of admixture and therefore potential gene flow from allopatric into sympatric areas could explain the inability of *N. vitripennis* females to recognize eggs of *N. giraulti* as being different. In this scenario selection only acts in the sympatric area, but the population's adaptation is prevented or at least slowed down by gene flow out of the larger allopatric zone (Bridle & Vines 2007). However, this is only the case, when the alleles leading to recognition of the other species are selected against in the allopatric area, otherwise the capability of species recognition would spread through the whole population (Sanderson 1989). Whether the ability to recognize eggs of a heterospecific as being different comes with a fitness disadvantage when there is no closely related competitor present, has not been investigated yet. However, given that selection is only favouring species recognition in the sympatric area, it is conceivable that *N. vitripennis* cannot adapt to the regular encounters with *N. giraulti* and is therefore not able to evolve recognition of the species differences. We could show in **Chapter 4** that there is a high proportion of multiparasitism (*N. vitripennis* and *N. giraulti* parasitizing the same host) among hosts of nests that contain both species, which indicates that the selection pressure on species recognition should be high in these nests. However, to generally evaluate the strength of selection on species recognition in nature, more detailed data on the distribution of both species in North America is required. Especially degrees of sympatry and allopatry of the two species need to be determined in more detail. Another interesting line of further research is to screen for natural variation in species recognition and to artificially select for it.

Another assumption in *Nasonia* research was that all three species originate from North America. However, this has never been investigated thoroughly. In **Chapter 5** we found indication that the North American *N. vitripennis* population is much younger than the European population. This raises the question whether there was sympatric speciation of all three species in North America, or whether both *N. longicornis* and *N. giraulti* evolved in North America while *N. vitripennis* is of Eurasian origin and invaded the New World more recently. So far, the differences in *Wolbachia* infections among the three *Nasonia* species were thought to be the driving force for the speciation process. However, the fact that the distribution ranges of *N. longicornis* and *N. giraulti* do not overlap, and that *N. vitripennis* could have its origin outside of North America, poses doubt to the hypothesis that the differences in *Wolbachia* infection are cause, and not consequence of the speciation.

The immigration scenario would as well fit the results that *N. vitripennis* is not recognizing *N. giraulti* as being different when parasitizing a host, as well as the high levels of diapause of *N. vitripennis* in North America compared to European populations, and to *N. giraulti* in the same location (**Chapter 4**). It is conceivable that there was no selection on recognizing a closely related competitor as being different, in the original (allopatric) habitat (e.g. Europe). Missing adaptations of *N. vitripennis* towards encountering *N. giraulti* when parasitizing a host can be interpreted as evidence for the non-American origin of this cosmopolitan species. As for diapause, one argument accounting for the differences between the two species is that unknown factors play a role in a foundress' decision to produce diapause. Future research has to show which factors are influencing diapause production in *Nasonia*. Seen in the light of a recent immigration of *N. vitripennis* to North America, the diapause production of *N. vitripennis* in North America could be high, because the environmental cues that announce the advent of winter might be different between North America and the region of origin. For both observations, missing species recognition and high diapause production, it is conceivable that due to a rather short time of *N. vitripennis* living in North America, in combination with the high gene flow over large areas, selection might not have had enough time to shape the response of the immigrant species to the conditions in its new habitat. Another possible reason for the missing adaptation of *N. vitripennis* to the new

environment in North America could be the reduced genetic variation after the bottleneck that accompanied the founder event during the colonization of the New World. It is thought that reduced genetic variation decreases the adaptive potential of a population (Baker 1965), but it is still unclear how strong the reduction of adaptive potential after a bottleneck event really is (Dlugosch & Parker 2008). To further evaluate the validity of these hypotheses more data on the factors influencing sex allocation as well as diapause and the underlying genetics are required. Further research also has to reveal how quickly selection can act on these traits and how much variation there is in the cues that are used within and between populations from various latitudes.

Taken together I consider the most probable hypothesis of speciation in the *Nasonia* system as follows: the two sister species *N. giraulti* and *N. longicornis* developed independently from *N. vitripennis* in North America, while the *N. vitripennis* is an Eurasian species that spread to the New World more recently. The consequences of this rather recent event are the low precision of adaptation towards the local climate (diapause production) and towards the presence of a close relative in the habitat (sex ratio adaptation). The high gene flow over large distances and the presumably reduced adaptive potential after the founder event prevented a rapid adaptation.

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