Chapter 7

Synthesis

Evolutionary ecology aims to understand the interactions between species and their environment by incorporating evolutionary processes. An important objective of evolutionary ecology is to describe and understand how organisms adapt to heterogeneous environments. We therefore need to know the causes and effects of variation in traits that influence fitness in such environments. Organisms have evolved various strategies to cope with environmental variation, including genetic adaptation and phenotypic plasticity (Lynch & Gabriel 1987; Stearns 1989; Meyers & Bull 2002). Phenotypic plasticity is the ability of one genotype to express different phenotypes in different environments (Bradshaw 1965) and is represented in the slope of a reaction norm (de Jong 1990).

Empirical studies have shown that there is genetic variation in the slope and mean elevation of reaction norms of various traits, such as age at maturity, growth rate (Gutteling et al. 2007), egg hatching (van Asch et al. 2007), and diapause incidence (Winterhalter & Mousseau 2007). The level of phenotypic plasticity in a trait is therefore expected to respond to local selection pressures depending on the encountered environmental regime (Scheiner 1993; Price et al. 2003). Evidence of temporal and spatial habitat heterogeneity selecting for specific levels of phenotypic plasticity already exists (Ellers & van Alphen 1997; Pfennig & Murphy 2002; Hassall et al. 2005; Blondel 2007). The aim of this thesis was to test the hypotheses that (i) the selective advantage of such differentiation in the level of plasticity is large enough that it can occur between populations on a small spatial scale, (ii) patterns in plasticity are different for life history traits and morphological traits, and (iii) the patterns in phenotypic plasticity can be adaptive.

Population divergence in phenotypic plasticity has been studied occasionally, however these studies have mainly been restricted to geographically isolated populations (Heschel et al. 2004; Hassall et al. 2005; Lehmann & Rebele 2005). The specific question raised in Chapter 2 was whether natural selection on phenotypic plasticity is strong enough to maintain differences between parapatric populations in the presence of gene
Differences in phenotypic plasticity were investigated in the springtail *Orchesella cincta* from neighbouring habitats with distinct thermal conditions. This springtail inhabits the litter layer of the soil and is found in a variety of habitats. Forest and heath habitats were considered because these two habitats differ strongly in the amplitude of daily temperature fluctuations but are also naturally co-occurring. Amplitude of temperature fluctuations is more buffered in the forest habitat by the canopy cover and litter layer compared to the more exposed heath. However, mean temperature does not differ between the habitats. The trait under consideration was juvenile growth rate and the reaction norms of the forest populations were steeper than the reaction norms for heath populations at two replicated sampling sites. Hence, growth rate showed a lower level of plasticity in the thermally more variable heath habitat. The results of this study clearly demonstrate that reaction norms can be habitat-specific and that local selection pressures are strong enough to maintain these differences despite homogenizing gene flow.

To test whether there is a general trend of life history traits being more buffered against thermal fluctuations in thermally variable habitats, an additional experiment was set up to measure the response of other life history traits (Chapter 3). Also, thermal reaction norms for males and females were compared to assess whether life history responses to temperature are sex-specific. The plastic response in age at maturity to temperature differed between the sexes, but not between the two ecotypes. Weight at maturity showed differential plastic responses between the sexes as well as between ecotypes. In fact, females from heath populations are able to maintain nearly the same weight at maturity across a temperature range of 10ºC. These results are in agreement with the results described in Chapter 2. In *O. cincta*, some life history traits (but not all) are more buffered against thermal variation, i.e. more canalized in heterogeneous habitats than in more stable habitats.

No genetic distinction was observed between forest and heath populations based on microsatellite markers (Chapter 2). Apparently, there is strong homogenising gene flow between the populations and there is therefore no indication that one of the populations is more isolated from the others due to, for instance, environmental barriers. The fact that differentiation in thermal responses can be maintained despite the presence of high gene flow, strongly suggests ecotypic differentiation of thermal responses to be caused by natural selection and not by genetic drift. Similar results have been described before in e.g. marine systems (Luttikhuizen et al. 2003; Zane 2007) and amphibians (Orizaola & Laurila 2008).
Environmental canalization, i.e. insensitivity of traits to environmental perturbations (Stearns *et al.* 1995; Wagner *et al.* 1997; Debat & David 2001), can be the result of selection pressures opposing the reaction norm. The observed canalization of the thermal reaction norms for life history traits (Chapter 2, 3) can be interpreted as a direct effect of selection due to fluctuating temperatures. Indirectly, selection for canalization of one trait across temperatures may also affect the reaction norms of other traits. A large body size may only be maintained at the cost of a longer juvenile period, therefore high plasticity in one trait automatically results in high plasticity of the other trait. Therefore, thermal reaction norms for several life history traits are correlated. Indeed, a quantitative genetic study on *O. cincta* has demonstrated a significant genetic correlation between thermal reaction norms for developmental and juvenile growth rate (Driessen & Ellers unpublished data). This illustrates the necessity of an integrated approach when studying the evolution of life history traits.

Because the adaptive value of plasticity is different for fitness traits and non-fitness traits (sensu Richards *et al.* 2006), different patterns in the level of plasticity for these traits in response to variable environments are expected. Predictable environmental variation can select for increased phenotypic plasticity of morphological and physiological traits (Bradshaw 1965; de Jong 1995; Roff 2002), while fitness traits such as reproduction and survival should be insensitive to environmental variation and show environmental canalization. However, until now, this hypothesis has not been explicitly tested in a natural system. I therefore assessed levels of phenotypic plasticity in diverse *Drosophila serrata* populations along a latitudinal cline ranging from a temperate, variable climate to a tropical, stable climate (Chapter 4). The reaction norms for developmental rate over the 16-22°C temperature range, were flatter (more canalized) for the temperate populations than for the tropical populations. However, slopes for the reaction norms of the two morphological traits, were steeper (more plastic) in the temperate versus the tropical populations over the entire thermal range. These opposing latitudinal patterns in plasticity for fitness and morphological traits most likely reflect contrasting selection pressures along the tropical-temperate thermal gradient.

The biological context of the experiment described in Chapter 4 is very different from the previous two experiments (Chapter 2, 3). Obviously, fruitflies are a very different type of organism, as they are holometabolous insects, with a much faster life cycle and greater dispersive capabilities. More importantly, I compared distinctly separated populations with little gene flow among them. Genetic drift could therefore
lead to differences between populations without having an adaptive value. Two lines of evidence contradict this nonadaptive interpretation. First, the observed pattern in level of plasticity showed a clinal change as opposed to the idiosyncratic pattern expected to be caused by random genetic drift. Second, the fact that similar patterns for canalization of life history traits in response to variable habitats are found in different organisms and over very different spatial scales, is a strong indication that this is caused by parallel selection rather than random drift. Indeed, buffering of life history traits in response to climate change was recently described in Antarctic mammals and birds (Forcada et al. 2008).

The results of Chapters 2, 3 and 4 strongly suggest ecotypic differentiation of thermal responses to be caused by natural selection and not by genetic drift. However, this does not directly prove the adaptive value of these responses. To test whether the observed patterns in plasticity are adaptive, it is essential to demonstrate that the observed plasticity is beneficial in the environment in which it is exhibited. To test whether the ecotype-specific reaction norms described in Chapters 2 and 3 are beneficial to the populations living in these ecotypes, I measured population growth under fluctuating thermal regimes in climate rooms, mimicking the thermal conditions of forest and heath. Temperature is considered one of the most important mediators of phenotypic plasticity in ectothermic organisms, resulting in predictable changes in e.g. timing of reproduction, egg size and body size. Although the fluctuations themselves had a very strong effect on population growth, surprisingly, no difference in population growth was recorded for the populations from the two ecotypes. Under all thermal regimes, populations from heath and forest performed equally well. Apparently, amplitude of temperature fluctuations alone is not the major factor of discrimination between the two habitats. I discuss in Chapter 5 that an ecotype is defined by many other factors than temperature fluctuations alone. Temperature fluctuations will cause variation in many other factors, and the additive effect of these varying environmental factors most likely shapes the local selective pressures on these populations.

In Chapter 6 I consider whether plasticity in egg size is an adaptive response to temperature or is caused by physiological constraints. Egg size is a particularly interesting trait in life history evolution because it is simultaneously a maternal and progeny character; mothers determine egg size, which in turn can substantially affect the fitness of the progeny resulting from these eggs (Bernardo 1996; Fox & Czesak 2000). Like in many ectothermic organisms, egg size responds plastically to temperature in \textit{O. cincta}. The
larger eggs laid at lower temperatures were found to have a higher survival and the juveniles that hatch form these eggs are also larger (Chapter 6). This can create a ‘head start’ for these juveniles under difficult conditions, thereby increasing the mother’s fitness under cold conditions. Also, after exposure to temperature shocks, survival of larger eggs was much higher that for smaller eggs. This summarizes the trade-off between number of eggs and egg size: large eggs often have a higher fitness (Fox 1994), whereas small eggs are relatively cheap and allow the production of large clutches (Roff 2002). The increased resistance to thermal stress may be an important protective strategy in uncertain environments (Haccou & Iwasa 1995; Hassall et al. 2006). Under fluctuating thermal conditions large eggs may represent an adaptive risk-spreading tactic, because they are better able to withstand unfavourable conditions (Hopper 1999). The results indicate that large eggs have an advantage in cold or stressful environments, and that egg size plasticity can be adaptive as a conservative bet-hedging strategy.

In conclusion, differences in thermal variation between habitats over a small spatial scale can select for specific reaction norms. The level of plasticity of traits has been shown to respond to local selection pressures, even in the presence of gene flow. These differences are not only habitat specific, but can also be sex-specific. Contrasting latitudinal patterns in plasticity and environmental canalization of life history and morphological traits were found. This suggests that statements about overall levels of plasticity of a population are probably meaningless. Instead, testing specific hypotheses about the role of phenotypic plasticity in adaptation to variable environments and climate change is likely to be a more productive approach. It is however also stressed by these results, that not temperature fluctuations alone are of vital influence, but the additive effect of variation in all environmental features. It will become more important to test predictions on specific ecological grounds than making general predictions. The results of the studies described in this thesis indicate that there is adaptive potential in plasticity of many life history traits to respond to increased environmental variation caused by e.g. climate change.

An increasing number of studies attempts to extrapolate the findings on evolution and acclimation of thermal performance to the possible effects of climate change. A prime example is the research on thermal sensitivity in great tits, which is proven to be under natural selection because of climate change (Nussey et al. 2005). Unexpectedly and due to constraints not yet understood, thermal sensitivity in these passerines has not responded to selection so far. The authors suggest that continued
selection on plasticity can act to alleviate the mismatch between breeding times of the birds and their caterpillar prey. Another possibility is that selection on the level of plasticity in the passerines is not as strong as it is for the springtails (Charmentier et al. 2008). One of the main findings of this thesis is the ecotypic differentiation of plasticity in *O. cincta* in response to fluctuating temperatures. Springtails have a reduced ability to escape unfavourable temperature conditions (Bahrndorff et al. 2009b), and local populations will have to respond to severe local selection pressures. Being able to respond to fluctuating conditions is therefore also dependent on the selective pressures on organisms in their current habitat. Given the importance of adequate plastic responses under fluctuating conditions and its significance in the context of global warming, there is an urgent need to improve our understanding of current patterns in phenotypic plasticity shaped by natural thermal regimes.

The complexity of natural thermal environments is daunting. One of the prime difficulties in thermal research is to create a simplified standard environment in the lab that still captures the most essential features of the natural thermal regime. The ecological value of extrapolating thermal adaptation research to mitigate the effects of climate change critically depends on this. Therefore, more studies need to report the effect of performing experiments under fluctuating thermal regimes, even if the results are negative. The fact that temperature fluctuations did not create an advantage for ecotype-specific reaction norms that were thought to be shaped by thermal fluctuations (Chapter 4) can mean two things: there is no difference between the ecotypes in the considered trait, or the discriminative factor between the ecotypes is not temperature fluctuation (or at least not exclusively). There is agreement as to the need for field validation of laboratory experiments, and the use of multiple proxies for thermal performance. It is important to understand the selective forces driving plastic responses to temperature and to generalize these. This thesis is another step towards a better understanding of the ecological consequences of phenotypic plasticity, but in the spirit of good scientific practice, it still raises other questions to stimulate progress in this fascinating research field.
References


Bradshaw A.D. (1965) Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics*, 13, 115-155


Driessen G. & Ellers J. (unpublished data) Temperature-induced plasticity is genetically correlated between life-history traits in a soil dwelling arthropod. In:


saproxylic 'giant' springtail at Tallaganda in the Great Dividing Range of southeast Australia. *Molecular Ecology*, 13, 3329-3344


References


Stearns S.C. (1989) The evolutionary significance of phenotypic plasticity - Phenotypic sources of variation among organisms can be described by developmental switches and reaction norms. *Bioscience*, 39, 436-445


