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## The maintenance of variation in avian personality

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# Chapter 7

## General discussion



### **Introduction**

The increase of the human population has led to the loss of natural habitat and of species. This loss of species may be caused by limited variation within a species restricting the ability of species to cope with environmental changes (Lande 1988). Hence, it is important to study if and how the variation in traits within a species is maintained (Sih *et al.* 2004b; Turelli & Barton 2004; Bell 2007).

I concentrated on the maintenance of variation in avian personality in this thesis. Personality is a suite of traits which are consistent across situations and time and which are often found to be correlated (Koolhaas *et al.* 1999; Gosling 2001; Reale *et al.* 2007). One of the mechanisms assumed to maintain variation in personality is natural selection balanced over time. However, the association between personality and fitness in the field has until now been studied without taking into account the direct social environment of an individual. In territorial species individuals interact mostly with their closest neighbours. Therefore, introducing the social environment in terms of personalities present around a focal breeding animal could be highly important in understanding the role of selection pressures acting on different phenotypes within a species or population.

The main aim of the studies presented in this thesis was to test how the social environment affects fitness, how it interacts with personality and whether this social environment is a major factor influencing the maintenance of variation. The novelty of this approach is that we have tested the importance of neighbour personality on the fitness of individuals with different personality, and thus on selection pressures which are important for the maintenance of variation in personality.

Selection pressures can be based on social and non-social factors. One of the selection pressures based on social interactions is negative frequency-dependent selection (nFDS), which is proposed by contemporary theories to be one or sometimes the main factor maintaining variation in personality (Sih *et al.* 2004b; Penke *et al.* 2007b; Reale *et al.* 2007; Wolf *et al.* 2008b). Negative FDS is a type of selection acting on the interaction between different phenotypes resulting in the rarer phenotype having the highest fitness (Svensson & Sheldon 1998; Sinervo & Calsbeek 2006). The reason for this may be e.g. less competition, because this rare phenotype may have different food searching strategies than others, and thereby a higher chance to gain food from the common source. A similar situation appears often in mating, when the rare phenotype is more attractive and thereby having the highest fitness (Bleay *et al.* 2007). Individuals with such a phenotype may also be less at risk from predation, since predators may have developed a “searching image” of the most common prey on which they concentrate (Bond & Kamil 2002). When the frequency of this phenotype increases above a certain threshold, another phenotype becomes the rarer one and gains in turn the advantage of increased fitness (Sinervo & Calsbeek 2006; Hedrick 2007; Wolf *et al.* 2008b). Fitness therefore depends on interactions between an individual’s phenotype and the phenotypes present in its social environment. Frequency-dependent fluctuations of this advantage in fitness are able to maintain variation in a trait.

Having a long-term study of great tits (*Parus major*) where the majority of birds have been characterized for their personality allowed us to analyze the impact of selection pressures on yearly fitness in dependence on the individual social environment represented in this thesis by phenotypes around the territory of the focal breeding bird.

### **Life-history traits**

When studying the maintenance of variation in personality we need to have information on the life history of the focal species and to take into account that selection could differ between individuals of different sex, age or origin. The life of great tits in their first year when they are juveniles differs compared to when they are older than one year (Drent 1984; Naef-Daenzer *et al.* 2001). For juveniles it is important to survive the period of strong selection directly after becoming independent of their parents, to gain a territory in order to get a partner and to survive their first winter. For adults that maintain their territories and pair bonds it is important to survive the winter and reproduce again, as you can see in Figure 1. Therefore, we concentrated on yearly fitness expressed by three components: i) local adult survival, ii) reproductive success (number of juveniles a breeding pair produced that recruited into the next generation) and iii) local juvenile survival (Table 1, Figure 1). The first two components explain yearly fitness of adult birds. Local juvenile survival was defined as survival of an individual juvenile in the study area until first breeding (Figure 1).

Although we know that selection on juveniles is important (Drent 1984; Naef-Daenzer *et al.* 2001) knowledge of the processes involved in selection acting on personality in juvenile age is limited (Smith & Blumstein 2008). In particular, the lack of a direct personality test in the nestling phase of passerines hampered research on fitness aspects in the juvenile stage. Personality was therefore measured after the nestlings had fledged and had become independent from their parents, which was too late for proper analyses, or indirectly by taking the personality of the parents based on genetic background of personality (Dingemanse *et al.* 2004; Quinn *et al.* 2009). Therefore, we developed a test to study selection on passerine juveniles. We measured juvenile personality by conducting a handling stress test (HS) based on the increase in breath rate during handling of the 14-day-old great tit nestlings. The HS test is associated with the novel environment test, a standard personality test in adults. This test is described in **Chapter 4**. Using this novel method we could assess new knowledge to the impact of personality on survival of the passerine juveniles. We also could distinguish between age classes and thereby concentrate on an important question: what is the impact of the social environment on different age classes and on important life-history traits at a particular age.

### **Social environment matters but its impact varies**

In **Chapter 2** we concentrated on the impact of the social environment on adult survival and reproductive success independent of their own personality. We found that personality of neighbours surrounding the breeding territories of great tit pairs was associated with the reproductive success. The direction and strength of this relationship differed between years.

In contrast to reproductive success we did not detect this effect in adult survival (Chapter 2). In Chapter 3 we introduced the parental personality and thereby FDS in the model. For the reproductive success we obtained the same results as in Chapter 2 and again did not detect this effect in adult survival. Hence, the social environment alone was associated with the fitness of breeding birds via the reproductive success as shown in Table 1 and Figure 1. This could be surprising since one would expect that the impact of parental personality on the number of recruits should be stronger than the impact of neighbours. However, sometimes the effect of the environment is so large that it overrules individual differences in behaviour. E.g. a hyper-aggressive male water strider may drive all females out of the group thereby decreasing the mating activity of all females independent of their behavioural type (Sih & Watters 2005). In the blue-banded goby (*Lythrypnus dalli*) individuals determine their sexual phenotype on basis of a hierarchical rule: if individuals are subordinate they express themselves as females, if individuals are dominant they express themselves as males (Rodgers *et al.* 2007). In great tits neighbours are likely to affect parental condition e.g. through fights for territory before breeding, which may affect parental care and hence condition of their juveniles.

In **Chapter 5** we tested whether the survival of individual juveniles was affected by their own personality. By specifically testing the interaction between the juvenile's own personality with the effect of the personalities present around the parental breeding territory, we also tested for nFDS. A juvenile's own personality at day 14 after hatching, as measured by the handling stress (HS) test, predicted individual local juvenile survival. This is a novel result regarding passerine personality and is coherent with results of studies done with other species, which can easily be tested as juveniles (Wilson *et al.* 1993; Cote & Clobert 2007). However, we did not detect an impact of the social environment, and neither did we detect indications for nFDS via local juvenile survival.

Our results show that the social environment has different impacts on life-history traits important for a given age: we found an association with the reproductive success represented by number of recruits but not with juvenile survival.

### **Negative frequency-dependent selection**

We have established that the personality of the social environment has different impacts on various life-history traits. However, the mechanism proposed to maintain variation in personality traits is negative frequency-dependent selection (nFDS). Therefore, in **Chapter 3** we asked if FDS acts as a way to maintain variation in personality types. Because great tits are a territorial species we tested weak nFDS acting on the individual scale, which means that an individual with a personality opposite to its direct neighbours should have the highest fitness. We found for the seven years of data that we have, that there are year differences in the type and in the direction of selection that acted on personality. However, we found evidence for very weak nFDS in one year only. In some years we detected directional selection dependent only on frequency and in some years there was no selection dependent on frequency. In one year we even found strong positive frequency-dependent

selection (pFDS), where the most common phenotype has the highest fitness and so pFDS leads to the loss of variation. Hence, FDS acts on personality through adult survival on a local scale but nFDS has only marginal effect. As already mentioned above we tested the impact of nFDS on juvenile survival in Chapter 5, where we did not detect signs of nFDS and an effect of the social environment was absent. Variation in local juvenile survival could only be explained by the personality of the individual itself.

These results indicate that selection via survival can vary between juvenile and adult ages as indicated in Table 1 and Figure 1. The life history of a great tit differs greatly between juveniles and adults (Perrins 1979; Drent 1984), which can cause changes in selection on one life history trait, in our case on survival. Age differences in selection were also found for North American squirrels (*Tamiasciurus hudsonicus*) where the effect of the mother's personality had a different impact on different age phases of the juveniles' life (Boon *et al.* 2007). In bighorn ewes (*Ovis Canadensis*) selection was induced by a predator but only for some age categories (Reale & Festa-Bianchet 2003).

### **Balancing selection**

Our results fit best with the theory of balancing selection, which is a concept that gathers together mechanisms which are supposed to maintain variation in many traits and also in personality (Turelli & Barton 2004; Hedrick 2007). There is a genetic and an environmental form of balancing selection. The genetic form includes mutation-selection balance, heterozygote advantage and antagonistic pleiotropy. The environmental form includes negative frequency-dependent selection (nFDS) and environmental heterogeneity.

I concentrated on the role of nFDS. However, nFDS appeared only once between other selections dependent on frequency and with a weak effect. Hence, variability in selection pressures and age differences in the impact of selection pressures seemed to be more efficient for the maintenance of variation in personality than nFDS alone. Fluctuation of selection pressures indicates fluctuating environmental conditions and hence environmental heterogeneity, which is another environmental factor in balancing selection. We detected the impact of environmental heterogeneity in all life-history traits tested: adult survival, reproductive success and also juvenile survival (Table 1, Figure 1) and tried to explain the fluctuations by yearly variability in environmental variables important for great tits. However, beech-mast crop and population density, which are two well known environmental variables influencing overall survival did not explain these fluctuations in selection on personality. These results do not signify the unimportance of beech-mast crop and density-dependent selection for selection on personality. Most likely these factors affect selection dependent on frequency indirectly because a combination of complex environmental situations acts on great tits in the wild. There are many environmental variables like predation (Reale & Festa-Bianchet 2003), the timing of the peak in caterpillar biomass (Verhulst & Tinbergen 1991; Visser *et al.* 2006) or snow cover (van Balen 1980) which affect great tit fitness and which we have not tested.

Although we did not test for genetic effects of balancing selection, I propose that heterozygote advantage may be important for the maintenance of variation. We detected disassortative mating (Table 1, Figure 1), in which mated pair-members are less similar to each other than expected by chance. Moreover, we found that next to FDS the patterns of selection differed for the sexes (Table 1, Figure 1). Selection differing between sexes can lead to disassortative mating and thereby help to maintain variation. If e.g. fast exploring males and slow exploring females have higher survival in one year, then the chance to mate disassortatively increases. Disassortatively mated birds have heterozygote juveniles which survive better because of their heterozygote genome. Because our birds have a strong preference to mate disassortatively, I suggest that heterozygote advantage may be of importance in our population.

Results of the long-term data analyses presented till now show that the concept of balancing selection plays a role in the maintenance of variation in personality. Researchers often concentrate on impact of one selection apart from others but the mechanisms proposed in the concept of balancing selection do not affect individuals separately but act together. The chain and interactions of these mechanisms may have a much stronger effect on maintenance of variation in personality than nFDS alone. Fluctuations in environmental conditions may trigger other selection pressures and one of them may be negative frequency-dependent selection. These selection pressures may affect only one age category (adults or juveniles). Moreover, their impact may differ between sexes and also between life history traits.

### **Experimental proof of the descriptive results**

The central theme of this thesis is the impact of the social environment on fitness, and whether frequency-dependent processes are able to maintain variation in personality in the wild. We found that the social environment was associated with fitness in a territorial passerine and frequency-dependent processes are among the processes that are responsible for maintaining variation in personality. However, nFDS was very weak. We also proposed that environmental heterogeneity is of major importance because it may affect selection pressures.

The results presented until now were observational data in which we detected nFDS in adult survival in some years but not in other years. Therefore, experiments are needed to determine the causes of nFDS in the wild. We conducted an experiment influencing the social environment. In **Chapter 6** we divided our area in two plots and experimentally removed tits with extreme fast exploratory score from one plot and extreme slow exploratory score from the second plot. Therefore, the remaining tits experienced changes in their social environment. This experiment was repeated in the second year but we swapped the experimental plots (by creating a slow environment in former fast environment). Based on the results of former chapters we expected that changes in neighbour exploratory behaviour could cause differential selection on personality types between years. Moreover, we also expected strong age differences in selection. Hence,

because we based our analyses on the individual scale we expected to detect FDS in adult survival but not in reproductive success. Our results supported this prediction, and we detected FDS acting on personality in adult survival of breeding birds, but this was only true for one out of the two years. As expected we did not detect FDS in the reproductive success in the experiment. FDS in adult survival differed between the sexes: with negative FDS in females and positive FDS in males (Table 1, Figure 1). Since the analysis of the descriptive long-term data have shown that the direction of selection on personality changed with variable environmental circumstances between years and that the direction is mostly opposite in the sexes, it can be expected that nFDS and pFDS might alter in both sexes over time if the experiment continued over more years. Hence, our experiment confirmed the age and sex differences in selection that act on personality. Negative FDS was again very weak which contradicts the predictions from theoretical models. Moreover, habitat heterogeneity probably caused strong differences in selection between the two years.

**Table 1.** Mechanisms of balancing selection tested in the thesis. We tested adult fitness which consists of adult survival and reproductive success (number of recruits a pair produced) and we also tested survival of juveniles.

Personality: own personality of adult and juveniles or in case of reproductive success personality of parents, social environment: mean personality of direct male neighbours, nFDS: negative frequency-dependent selection – interaction of personality with the social environment when the rarer phenotype has highest fitness, Env. Heterogeneity: heterogeneity in non-social and social environment which causes fluctuations in selections, Sex: male or female, Disassort. mating: mated pair-members are less similar to each other than expected by chance. These birds have heterozygote juveniles which can gain from heterozygote advantage, which is one of mechanisms of the balancing selection.

	Fitness component	Personality	Social env.	nFDS (P×SE)	Env. heterogen.	Sex	Disassort. mating
Adults	Adult survival	Y	N	Y	Y	Y	Y
	Repr. success	N	Y	N	Y	NA	NA
Juveniles	Juvenile survival	Y	N	N	Y	NA	NA

### Practical implications for personality research

Our results show the important but variable impact of the social environment on individuals throughout their life. The social environment affects the development of many traits. In particular, behavioural traits are not inflexible but develop during the life through e.g. gene×environment interactions or learning (Schluter *et al.* 1991; Penke *et al.* 2007b), (Figure 1).

Differences in selection pressures are likely partly caused by age, which determines the behaviour of an individual and thereby the life-history trait on which selection acts. For example sexual selection is relevant for adult but not for juvenile great tits. On the same



principal nFDS can be relevant only for one age group. This indicates the importance of personality tests conducted at a juvenile age. Personality tests of passerine nestlings and knowledge that personality affects survival already in juvenile age is an important step forward for personality research because it changes our view on selection and the maintenance of variation of personality. Until now, most studies on selection concentrated on adult survival, showing that there were large differences in mortality between years. The handling stress test and the discovery of the importance of own personality for juvenile passerines showed that we now have to concentrate on all ages.

Because adult great tits are territorial we used two scales for studying FDS. We tested nFDS on the individual scale (direct neighbours) and compared this to the population scale. We detected FDS only on the individual scale probably because of the territoriality of the adults. In most studies interested in nFDS this was tested on a population scale in which an individual is supposed to interact with all individuals in the population and not only with their direct neighbours (but see e.g. Bleay *et al.* (2007)). This shows that the life history of a species and the scale on which individuals experience the non-social and social environment is very important for detecting nFDS. Selection can act on a population scale in a species which is not territorial like e.g. *Drosophila* larvae (Fitzpatrick *et al.*) but on a more individual scale in a species which is territorial like great tit.

These results have important consequences for the methodology of all personality, behavioural and selection studies. If we test an individual only once in its life or study only one life history trait, we may gain misleading results because behaviour may be strongly context dependent (Sih & Watters 2005; van Oers *et al.* 2005b; Reale *et al.* 2007). Our results stress the importance of the social and non-social context and the importance of repeated measures on an individual. Although repeating behavioural tests make the behaviour of the experimental animal generally bolder in the test it is worth to test individuals more times in life if possible, as already proposed by Bell *et al.* (2009) and Reale *et al.* (2007).

We should be aware that we can see the context as the non-social and social environment but also as the age of an individual. Age is related to variation in important life-history traits; selection mechanisms and scale on which these mechanisms act on personality (see Figures 1 and 2). A researcher should decide on what scale to measure behaviour between individuals and its consequences for fitness, or if possible to test selection on behaviour in different social scales to get a broader and more realistic picture about lifetime fitness of an individual and selection acting on the focal species.

### **Practical implications for ecology**

Because fluctuations in the environment cause variability in selection mechanisms, a population should ideally not have a uniform personality composition but individuals should vary in their traits. Therefore, we plead for creating protected areas with a variable environment. If an environment is uniform over long time the best fitting individuals for this uniform environment will be selected since they have highest fitness. This could be

dangerous in a long-time scale because these individuals could get extinct if the habitat changed. In programs for reintroducing a locally disappeared species there should be reintroduced individuals with different personalities because they have different styles of coping with challenges (McDougall *et al.* 2006). The variation within a species should be high because then usually some individuals are able to react adequately to environmental change. Hence, both a variable environment in protected areas and the composition of the reintroduced population could help the species to survive and to maintain the variation within a species.

There are large differences in selection pressures acting on individuals in different age classes/life-history stages. However, usually only young animals are released in the wild during reintroduction. Therefore, we should understand how different social environments and selections act on this age category specifically. In fact, also the social environment might be extremely important for reintroduction. During the first reintroduction event there are only a few juvenile individuals introduced in the area. These individuals experience the same age class and low density. However, age variation and density should improve during repeated reintroductions in the area. The consequence is that the social environment will change and will have different impact for both already “resident” and newly introduced animals. Reintroducing individuals with the personality type fitting to these conditions could increase their chance to survive.

The complex system of selection mechanisms calls for a sensitive attitude to environmental variability in nature and more knowledge of how variation is maintained in the wild. To assure effective protection of ecosystems we need to study the fitness of individuals throughout important life periods since many selection pressures act on an individual differentially during its life. By combining knowledge of species and ecosystem we could create an efficient species protection, which would include the variation in both personality and environment. We could increase the chance of these animals surviving and keep the variation of a species on a sufficient level by careful weighing of all important factors like non-social and social environment, personality of individual animals, and life-history and scales related to age.

### **General conclusions**

This study shows that evolutionary processes may depend upon variation and fluctuations in local conditions, especially the composition of the social environment (Van Gossum *et al.* 2001; Bleay *et al.* 2007; Takahashi & Hori 2008), (Figure 1). I suggest that the concept of balancing selection is appropriate for explaining the maintenance of variation in personality. I propose that social and non-social environmental heterogeneity does not only cause different directions of selection acting on personality, but also triggers variation in the types of selection. Since the non-social environment fluctuates in time and space with strong effects on density and the composition of the social environment of an individual, different selection forces often act together and their interactions contribute to the maintenance of variation in personalities in the wild. One of these selection pressures may be negative frequency-dependent selection. However, this thesis denies the hypothesis of nFDS as the main mechanism maintaining variation in personality. More probably may personality be affected in some years by nFDS but other selection mechanisms are more important to maintain variability in personality in the wild. Moreover, I also stress the importance of age and sex, which affect direction and type of selection pressures and which together with mating processes, contribute to maintaining variation in personality. In conclusion, this thesis shows that the complex situation in the wild, with environmental variability and hence variation of selection types, points to the importance of understanding these phenomena in the field and the correct use of this knowledge in nature protecting programs.

**Figure 1.** Conceptual model summarizing the relationships between personality and components of fitness for adult and juvenile great tits. The scheme shows novel knowledge gained by the studies described in this thesis. Whole scheme shows variation in the whole system from non-social to social environment which triggers different selections and thereby maintains variation in personality.

The scheme is divided in three parts: breeding season in the 1. year, winter season in the 1. year and breeding season in the next (2.) year. Bubbles represent states and conditions important for life history of adult and juvenile great tits in the breeding season. Dotted line indicates that part of juveniles of disassortatively mated parents is heterozygotic, therefore they may gain heterozygote advantage. Numbers like e.g. Ch4,5 represent chapters in which is the phenomenon described.



