The maintenance of variation in avian personality

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Chapter 1

General introduction

Introduction

There is increasing interest in the ecological problems that are caused by the growing human population. This growth has led to increased energy and land use, followed by an intensification of industry causing environmental pollution and global warming. The extended depletion of rain forests and spreading of cities have caused an inevitable loss of nature and increased habitat fragmentation (Turner 1996; Aubad *et al.* 2010; Pease 2010). As a consequence, the variation of the biological environment decreases due to the extinction of species (Turner 1996; Pimm 1998; Pimm & Raven 2000; Aubad *et al.* 2010; Jenkins *et al.* 2010).

Every species, humans included, has to cope with these continuous environmental changes. We can study the reactions to environmental changes at different scales; from whole ecosystem to individual differences (Sinervo & Calsbeek 2006). Ecosystems consist of species that can be subdivided into several populations. The composition of these populations may vary because of, for example, different environmental conditions in the past and thereby different selection pressures acting on their variation and adaptability to environmental challenges. The maintenance of large phenotypic and genetic variation within species or populations is important in a variable and changing world.

Therefore, it is important to understand the mechanisms that are responsible for maintaining this variation. If the environmental change is not abrupt but slow, individuals within populations may be able to catch up with these changes. Not all individuals are the same in their strategies and hence some individuals will react appropriate to these changes and others not. Therefore, their individual success depends on the type of environmental change and on their plasticity. The way populations react to changes will thus depend on the composition of phenotypes. If the majority of individuals in one or a few populations cannot adapt and the population becomes extinct, then immigrants from another population may re-colonize the area (Hanski & Heino 2003).

The viability of populations or species may be severely reduced if the change in the environment is too fast for micro-evolution to catch-up or if variation within a species becomes too small. If the variation among individuals within a species is restricted, most individuals react in similar ways. This uniformity in reactions can thus pose a severe threat to a species. If environmental changes are abrupt and irreversible, the majority of individuals within a species are not able to adapt to this directional selection fast enough. In the extreme situation local populations and sometimes the whole species are not flexible in coping with environmental changes and may become extinct with decreasing variation within populations (Lande 1988).

To understand the causes and speed of extinction of a species and, more importantly, how to prevent it, we need to know how ecosystems work and which mechanisms affect selection and maintain variation in populations and species. Therefore ecological and evolutionary studies are needed to find out how diversity is maintained in natural populations. Ecological studies uncover bonds and trade-offs within and between species which can be tested and embedded within evolutionary theories and then used for the protection of nature (Caswell 1983; Pfister 1998). We should be able to predict the future development of the studied species and make general predictions about development of other species with this knowledge. Studies in undisturbed ecosystems may reveal the mechanisms acting on variation in species; especially important is the information about genetic and phenotypic variation within species and how this is maintained. This enables us to predict the development of species compositions in already disturbed areas. We could then use this information to develop strategies for successful species protection or even set up programs for endangered species to maintain diversity in the wild (Lande 1988; Karlsson *et al.* 2008).

Processes maintaining variation in traits within a species

One of the key processes that are proposed to maintain variation between individuals within a species is balancing selection. Balancing selection is often only associated with genetic processes, but balance between phenotypes can be maintained also by other processes. I use in this thesis a concept which includes genetic and environmental forms and also frequency-dependent selection (Turelli & Barton 2004; Hedrick 2007). The genetic form is represented by genomic mutations (Roff 1998a), antagonistic pleiotropy and heterozygote advantage. Antagonistic pleiotropy signifies that genetic polymorphisms have a positive effect on one trait, but simultaneously a negative effect on another trait (Hedrick 1999). Heterozygote advantage is a process in which individuals with a heterozygote genome have the highest fitness (Dobzhansky & Pavlovsky 1960). Heterozygotes may be reintroduced in the population through disassortative mating, where mated pair-members are less similar to each other than expected by chance. However, these genetic effects alone are often not powerful enough to maintain variation. Therefore, environmental heterogeneity as a non-social aspect and negative frequency-dependent selection as a social aspect of the environment can contribute to the maintenance of variation. Environmental heterogeneity causes selection to vary in space and/or time (Kassen 2002; Ernande & Dieckmann 2004; Karlsson *et al.* 2008) and thus maintains variation through fluctuating selection. Environmental fluctuations either lead to individuals that are plastic in their phenotype or that vary in genotype (Gabriel *et al.* 2005; Hedrick 2006; Robinson *et al.* 2008). In the latter case fluctuating conditions contribute to the maintenance of genotypes in the population. Individuals have not only to cope with the non-social environmental heterogeneity but also with variation in their social environment. Frequency-dependent selection (FDS) is one of the selective forces that act through social interactions where fitness of a certain phenotype is dependent on the frequency of the interacting phenotypes (Svensson & Sheldon 1998; Sinervo & Calsbeek 2006). If negative FDS (nFDS) acts, fitness increases in the rarer phenotype because this phenotype gains advantage from e.g. a relatively lower impact of competition or higher preference of mates. As their fitness increases after some time the number of these rarer individuals increases. Thereby another phenotype becomes rarer and gains in turn the advantage of decreased competition. Frequencies oscillate and establish the balance in a rate leading to the stable coexistence between these phenotypes within a population (Hori 1993; Roff 1998b; Bond & Kamil 2002; Sinervo & Calsbeek 2006). In contrast, positive FDS (pFDS) increases fitness in more common phenotype, which leads to loss of variation (Iwasa & Pomiankowski 1995; Sinervo & Calsbeek 2006).

Relationships within species may be rather complex ranging from cooperation to competition and thus different selection pressures may interact depending on the non-social circumstances and will therefore contribute to the maintenance of variation (Sinervo & Calsbeek 2006). For example, fluctuating food supply usually triggers density-dependent selection. Because socially induced selections are observed in high densities when individuals are forced to interact, density-dependent selection is closely related to FDS (Sokolowski *et al.* 1997; Sinervo & Calsbeek 2006; Bleay *et al.* 2007). Also disassortative mating and heterozygote advantage were found acting together with nFDS (Penn & Potts 1999; Takahashi & Hori 2008). Hence, different forms of balancing selection may reinforce each other in the maintenance of variation.

Animal personality

Individuals may differ in many traits on which selection may act, like sex, age and physiological, morphological and behaviour traits. All these traits or suites of traits shape an individual to use particular strategies on which selection acts, determining the individual fitness in different ecological conditions and thereby the relative increase or decrease of particular phenotypes. One of such suite of traits in which individuals differ is personality.

Animal personality can be defined as a mechanism influencing physiological and behavioural reactions. Hence, traits affected by personality are correlated and consistent across situations and time (Koolhaas *et al.* 1999; Gosling 2001; Reale *et al.* 2007). Personality is relatively stable but individual phenotypes can change to a certain level during the development along the reaction norm of a genotype (Dingemanse *et al.* 2010). However, this plasticity is limited and we can follow a shift but not a complete change of responses (Sih *et al.* 2004a; van Oers *et al.* 2005a). For example, food rationing affected exploratory behaviour of two lines of great tits selected for slow and fast exploratory behaviour (Carere *et al.* 2005). Slow chicks became much faster compared to their parents but fast chicks had a similar score to their parents. Six months later the juveniles of the slow line were still relatively fast and fast line became even faster. Juveniles of blue tits (*Cyanistes caeruelus*) fed with additional taurine as neonates took significantly greater risks when investigating novel objects than controls and it increased their success at a spatial learning task. Early diet therefore has downstream impacts on behaviour of juveniles (Arnold *et al.* 2007).

Personality traits are under natural (Reale *et al.* 2007) and sexual selection (Van Oers *et al.* 2008; Schuett *et al.*). Personality is an important factor influencing individual fitness (Reale *et al.* 2007; Smith & Blumstein 2008). We can use this knowledge for instance in nature conservation for developing programs for endangered species or for reintroducing threatened species back to the wild. Often in these programs individuals are selected for a particular behaviour such as shyness or boldness. Hence, variation of the reintroduced population is artificially decreased and this therefore decreases the chance of a species to succeed in environment which changes in time and space (Bremner-Harrison *et al.* 2004; McDougall *et al.* 2006; Watters & Meehan 2007). Personality plays an important role in social interactions influencing position in the hierarchy (Verbeek *et al.* 1996; Dingemanse & de Goede 2004; Harris *et al.* 2008; McNamara *et al.* 2009). Social status may then affect the mate bond and the quality of the territory. These social interactions operating during competition and cooperation between conspecifics are the mechanisms important for social selection as nFDS acting on personality traits (Dall *et al.* 2004; Wolf *et al.* 2008b; McNamara *et al.* 2009). Theoretical models have shown that negative frequency-dependent selection (nFDS) is a powerful mechanism for maintaining genetic variation in personality traits (Reale *et al.* 2007; Wolf *et al.* 2008b). Therefore the frequency of individuals with a certain personality in the social environment of a focal individual is often proposed to be important for the maintenance of variation by nFDS. However, unfortunately most personality studies interested in nFDS have been carried out with laboratory and domestic animals.

The most complete evidence of selection on different personalities in wild animals comes from work on the great tit (*Parus major*) (Dingemanse & Réale 2005; Reale *et al.* 2007). However, until now the impact of the social environment in terms of frequency of personality types has been ignored in this species.

Study system

The great tit (*Parus major*) is a common non-migratory passerine, which breeds in secondary holes and artificial nest boxes in all types of wooded areas in Europe and parts of Asia and North Africa (Perrins 1965). In March-April females lay 5-12 eggs and after 14 days of incubation altricial juveniles hatch (Perrins 1965). Both parents feed juveniles. Parental care is very important for growth, fledging weight and thus survival of the nestlings (Naef-Daenzer & Keller 1999). Parental care affects their survival later in life (Both *et al.* 2005), but also the survival of the parents themselves (Norris *et al.* 1994; Svensson & Nilsson 1997). Also the quality of the territory of a male with its asocial and social attributes plays an important role for adult survival and reproductive success.

At the age of 16-23 days nestlings fledge and stay together with their parents for approximately three weeks until the parents stop taking care for them (Drent 1984). In the first days after fledging there is strong selection on juvenile survival. The mortality rate of juvenile great tits is 5-10% per day in the first four days after fledging (Naef-Daenzer *et al.* 2001). The time directly after becoming independent of their parents is another critical phase for the survival of juveniles. In this period the mortality increases temporarily up to 30–50% (Drent 1984; Naef-Daenzer *et al.* 2001), mainly because of predation and lack of experience. After achieving independence from parents fledglings form hierarchical flocks and disperse between flocks and areas. Thereby juveniles are redistributed over a large area (Drent 1984). In September (at the end of their first moult) the surviving juvenile males try to establish dominance areas which develop into areas with spatial intolerance (territories)