Interactions Between Behaviour And Genetics In Wild And Domestic Bird Populations

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Introduction

The match between an animal and its environment is determined by its ability to cope with challenges in that environment, and therefore by its personality. Animal personality can be defined as a coherent set of behavioural and physiological responses that is consistent over time and across situations (van Oers, Klunder and Drent 2005), and is also referred to as animal temperament (Réale, Reader, Sol *et al.* 2007) or coping style (Koolhaas, Korte, De Boer *et al.* 1999). Animals with different personalities display differences in traits like aggression, fearfulness, exploration and boldness in social and non-social conditions (Réale, Reader, Sol *et al.* 2007). Therefore, an animal's personality largely determines its response to environmental challenges. It depends on the environmental circumstances, which personality type has an advantage and this may vary over time, depending on the stability of the environment. Personality traits can be favoured by both natural and artificial selection, if they result in increased fitness or productivity (Biro and Stamps 2008), and therefore play an important role in both wild and domestic populations. Here, we review how personality traits affect and are affected by natural and artificial selection by focusing on studies from both wild and domestic bird populations. Further, we will also explore how artificial selection affects personality and fitness traits in a domestic population. We will use the great tit (*Parus major*) and the laying hen (*Gallus gallus domesticus*) as our model species.

Avian personality

Birds exhibit behaviour and social organizations which are at least equal in complexity to mammals. Birds are widely distributed, highly diversified, yet they are generally more conspicuous and approachable in natural environments than many other vertebrates. These attributes resulted in birds providing in key model organisms for behavioural biologists. Also captive bird populations proved to be extremely valuable in studies related to the genetics of behaviour (Berthold and Querner 1981, Jensen, Buitenhuis, Kjaer *et al.* 2008, Jones and Hocking 1999, Rodenburg, Komen, Ellen *et al.* 2008). Thus, given these advantages, it is not surprising that also most studies on personality have been conducted on birds. The study of personality traits in birds can be translated into a natural context more easily than in other taxa, allowing studies on ecological and evolutionary aspects. Especially birds of resident species can be followed individually, often throughout their lives. Moreover, their behaviour can be measured both under standardised conditions in captive situations, and on the same

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individuals in their natural environment and most of all their fitness can be measured. The ample possibilities for conducting behavioural tests under laboratory conditions furthermore allows testing consistent differences in individual behaviour within and across contexts in an excellent manner (Dingemanse, Both, Drent *et al.* 2002, Martins, Roberts, Giblin *et al.* 2007, Schuett and Dall 2009, van Oers, de Jong, van Noordwijk *et al.* 2005). Studies on avian personality cover aspects ranging from the genetic variation that is linked to personality (Fidler, van Oers, Drent *et al.* 2007, Gil and Faure 2007, van Oers, Klunder and Drent 2005) and to the fitness consequences of personality in natural populations (Dingemanse, Both, Drent *et al.* 2004). Further, in domestic populations the effects of domestication on personality traits have been studied (Jensen, Buitenhuis, Kjaer *et al.* 2008, Mignon-Grasteau, Boissy, Bouix *et al.* 2005), as well as the relationship between personality traits and maladaptive behaviours, such as feather pecking in laying hens (Rodenburg, Buitenhuis, Ask *et al.* 2003, Rodenburg, Buitenhuis, Ask *et al.* 2004). Birds are also used as examples in mathematical models to investigate possible solutions to the evolutionary background of personality (Wolf, van Doorn, Leimar *et al.* 2007) and are used for detailed studies on the physiological background of behavioural consistency (Carere, Drent, Privitera *et al.* 2005, Fucikova, Drent, Smits *et al.* 2009, Kralj-Fiser, Scheiber, Blejec *et al.* 2007). Long before the current interest in animal personality developed, the importance of taking the uniqueness of individuals into account had already been recognized, and most of such studies used birds as model species.

Behaviour and genetics in great tits

The great tit (*Parus major*) has grown to become one of the most important model species to study the effects of personality traits from an ecological and evolutionary perspective. Previously, much of the research on personality traits was based on humans and laboratory rodents. The fact that these are not wild populations makes them less suitable to study the effects of personality on fitness traits and on the evolutionary processes that have shaped personality traits (van Oers, de Jong, van Noordwijk *et al.* 2005). In great tits, variation in exploratory behaviour was found (Verbeek, Drent and Wiepkema 1994) and this is used as a proxy for personality (Groothuis and Carere 2005). Based on this difference between the so-called fast and slow explorers in combination with the reaction towards a novel object, a selection experiment on fast and slow early exploration was started in the laboratory in 1994 (Drent, van Oers and van Noordwijk 2003) and a selection experiment on risk taking behaviour in 2001 (van Oers, Drent, de Goede *et al.* 2004). Furthermore, genetic parameters for exploratory behaviour and for risk-taking behaviour were estimated using a back cross design (van Oers, Drent, de Jong *et al.* 2004). It was shown that exploration and risk taking behaviour in great tits had moderately high heritabilities: for exploration, a narrow sense heritability was found of 0.54 (Dingemanse, Both, Drent *et al.* 2002, Drent, van Oers and van Noordwijk 2003). Significant heritabilities were confirmed in a natural population, where the broad sense heritabilities ranged from 0.22-0.39 (Dingemanse, Both, Drent *et al.* 2002). For risk taking behaviour, similar heritabilities were found, ranging from 0.19 to 0.32 (van Oers, Drent, de Goede *et al.* 2004). Furthermore, strong genetic correlations were detected between early exploratory behaviour, boldness and risk-taking behaviour, confirming the existence of personalities in this species (van Oers, de Jong, Drent *et al.* 2004). The genetic correlation was, however, expressed in a context-dependent way. This

was shown when it was investigated how much risk fast and slow-explorers took in a social and a non-social situation. Slow explorers were more affected by a social companion compared to fast explorers, showing that phenotypic correlations could fluctuate according to the environment they were measured in.

One burning question in natural populations is how variation in personality traits is maintained. These personality differences turned out to have fitness consequences that varied over years and between sexes (Dingemanse, Both, Drent *et al.* 2004). This confirms that the effects that personality traits have on survival depend strongly on environmental conditions: in one year it may pay off to be fast exploring, in another year to be slow exploring. These fluctuating selecting pressures alone could be responsible for the maintenance of genetic variation in natural populations. Another important factor is that personality types mate disassortatively (Both, Dingemanse, Drent *et al.* 2005). As a consequence pairs that consist of members with different personalities vary in the success in which they raise chicks. Slow females that are paired to slow males and fast females that are mated assortatively do best: they raise offspring with highest fledging weight (Both, Dingemanse, Drent *et al.* 2005), which is a good indicator of future reproductive success. These same pairs, however, also happened to have the highest chance of having extra-pair offspring in their broods (i.e. offspring sired by males other than the social male), a phenomenon that occurs in about 25% of all broods of the socially monogamous great tit (van Oers, Drent, Dingemanse *et al.* 2008).

One of the future challenges in genetic research in natural populations is to link the quantitative variation in these personality traits with variation in actual genes. Some careful expeditions in the great tit, have shown that selection for fast or slow exploration also resulted in genetic changes: selection resulted in mutations in the dopamine receptor gene *DRD4* (Fidler, van Oers, Drent *et al.* 2007, Korsten, Mueller, Hermannstadter *et al.* 2010). This gene has been related to variation in novelty seeking or exploratory behaviour in a variety of animals, including humans. The association between exploratory behaviour and the *DRD4* polymorphism were confirmed in an independent wild-caught hand reared sample, and also in wild birds in the same population (Korsten, Mueller, Hermannstadter *et al.* 2010). However, in three other populations of wild Great tits in the UK, Netherlands and Belgium, this was not the case, indicating that gene-behaviour associations are not always that straithforward in quantitative traits (Tschirren and Bensch 2010). Future research will therefore have to focus on more unbiased searches for candidate genes. A first start is already made by the detection of over 20,000 novel single nucleotide polymorphisms, which will be used for QTL analyses in natural populations (van Bers, van Oers, Kerstens *et al.* 2010). These studies show that personality traits in the great tit clearly have a genetic basis, and that fitness traits are affected by trait variation, which is a prerequisite for evolutionary change.

Behaviour and genetics in laying hens

Domestication of the chicken started 6,000 to 8,000 years ago. For the past 2,000 years, chickens have been kept for eggs and meat. Only in the past 50-60 years, intensive selection on increased meat and egg production has taken place, resulting in a large increase in productivity: a Jungle fowl hen will lay about 60 eggs per year, a modern laying hen more than 300 (Anonymous 2001). This change in productivity has been accompanied by changes in behaviour: domestic White Leghorn hens have been shown to be less fearful and to have a

lower foraging motivation than Red Jungle Fowl (the wild ancestor), when kept under similar conditions (Schutz, Forkman and Jensen 2001). Domestic laying hens also display behavioural problems such as feather pecking and cannibalistic pecking. The occurrence of these behaviours, however, seems unrelated to the process of domestication, as it can also be seen in Red Jungle Fowl kept indoors in floor pens (Rodenburg 2010, van Rooijen 2010). Interestingly, it has been shown that the propensity to develop feather pecking is related to personality traits. Rodenburg et al. (2004) showed that chicks that showed more freezing behaviour in an open-field test at 5 weeks of age were more likely to develop feather pecking as adults at 30 weeks of age. Similarly, Jones et al. (1995) showed that chicks from a low feather pecking line vocalized and walked sooner in the open field than chicks from a high feather pecking line. The estimated heritability for open-field activity in young birds was 0.49 ± 0.13 (Rodenburg, Buitenhuis, Ask *et al.* 2004), which is relatively high for a behavioural trait. Similar to the work in great tits, the existence of different personalities has been studied in laying hens, especially in relation to feather pecking (Korte, Beuving, Ruesink *et al.* 1997, Korte, Ruesink and Blokhuis 1999, van Hierden, Koolhaas, Kost'al *et al.* 2005). Although the results were not as consistent as the results from great tits and rodents (Groothuis and Carere 2005), differences between high and low feather pecking birds were found in coping with stress, resembling proactive and reactive coping styles (Koolhaas, Korte, De Boer *et al.* 1999). Interestingly, it was found that the serotonergic system plays an important role in the development of feather pecking, and that line differences in feather pecking may originate from differences in the central serotonergic system (van Hierden, de Boer, Koolhaas *et al.* 2004, van Hierden, Koolhaas and Korte 2004, van Hierden, Korte, Ruesink *et al.* 2002).

Effects of selection for low mortality

Recently, we started a selection experiment selecting on low mortality in group housing, aiming to reduce feather pecking and cannibalism (Ellen, Muir and Bijma 2007), based on the methods developed by Bijma et al. (2007, 2007). In this experiment, we also studied changes in behaviour and physiology in response to selection, comparing the low mortality line with an unselected control line. Major changes were detected in behaviour and physiology, but also in growth and onset of egg production. It was shown that selection for low mortality led to birds that are less fearful, both at young age (Rodenburg, Uitdehaag, Ellen *et al.* 2009) and at adult age (Bolhuis, Ellen, Van Reenen *et al.* 2009), and that have a reduced response to stress (Rodenburg, Bolhuis, Koopmanschap *et al.* 2009). Further, changes were detected in the peripheral serotonergic system: birds from the low mortality line had higher whole-blood serotonin concentrations and a lower platelet serotonin uptake (Bolhuis, Ellen, Van Reenen *et al.* 2009). This possibly reflects brain serotonergic neurotransmission, which has been related to the predisposition of a bird to develop damaging behaviour (van Hierden, de Boer, Koolhaas *et al.* 2004). This relationship between feather pecking and the serotonergic system was recently confirmed in genetic studies (Biscarini, Bovenhuis, Parmentier *et al.* 2010, Flisikowski, Schwarzenbacher, Wysocki *et al.* 2009). Flisikowski et al. (2009) performed an association study in high and low FP lines and found an association between *DEAF1*, a gene for a regulatory factor of the serotonergic system, and FP. Further, similar to the results found in great tits, mutations in the dopamine D4 receptor were detected. Similarly, Biscarini et al. (2010) found an association between

the gene for the serotonin receptor *HTR2C* and feather damage, which was significant across a population of nine pure-bred selection lines.

Apart from changes in behaviour and physiology, selection for low mortality resulted in changes in growth and onset of egg laying (Figure 1). Selection for low mortality resulted in hens that had a lower body weight at 20 weeks of age compared with control hens ($F_{1,33}=4.83$; $P<0.05$; Figure 1, left panel). Furthermore, they had a later onset of egg laying compared with control hens ($F_{1,33}=7.72$; $P<0.01$; Figure 1, right panel). Interestingly, at 35 weeks of age hens from the low mortality line were heavier than control birds (1647 vs. 1598 g; $F_{1,33}=5.28$; $P<0.05$) and this difference remained throughout the remainder of the laying period.
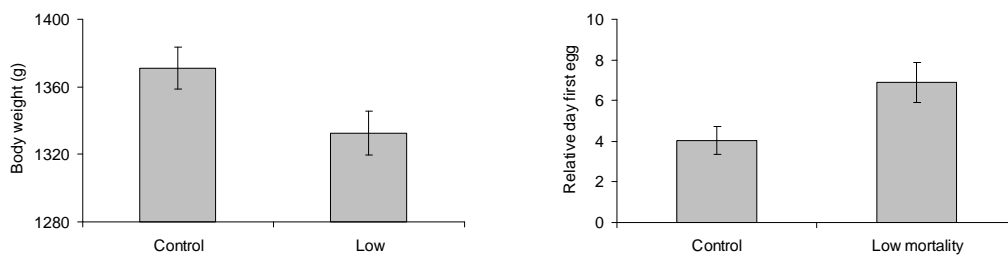

Figure 1: Body weight (left panel) and onset of egg laying (right panel) at 20 weeks of age in the control line and the low mortality line (third generation of selection)

These results show that selection did not result in smaller birds, but in a delayed growth and maturation. Similarly, Jensen et al. (2005) showed in a genetic study that feather pecking was phenotypically linked to early sexual maturation and fast growth. It may that by selecting on early onset of egg production, problems with feather pecking have increased in recent years. The results from this selection experiment in laying hens may also be of value for a comparison with results from wild populations: selecting for low mortality, e.g. for the fittest birds, resulted in reduced fearfulness and stress sensitivity, in changes in the serotonergic system and in reduced growth rate and a delayed sexual maturation, indicating a trade-off between survival and growth. Of course, in the case of artificial selection of domestic animals we have to keep in mind that the selection environment has much less variation compared with wild populations. This may also result in less genetic variation in personality traits.

Conclusion

When comparing the studies on behaviour genetics in great tits and laying hens, it is fascinating to see that two fields of study that seem quite far apart have so much in common. We think that increased collaboration between animal ecologists and applied animal scientists and animal breeders could be very fruitful. The work that has been done on great tits shows that personality traits strongly affect fitness in wild populations. At the same time,

involvement of the dopaminergic system in both exploratory behaviour in the great tit (Fidler, van Oers, Drent *et al.* 2007, Korsten, Mueller, Hermannstadter *et al.* 2010) and feather pecking behaviour in the laying hen (Flisikowski, Schwarzenbacher, Wysocki *et al.* 2009), indicates that the interaction between personality and environment in great tits and laying hens may not be so very different at all. As indicated previously, personality traits can favour both natural and artificial selection if they result in increased fitness or productivity (Biro and Stamps 2008), and therefore play an important role in both wild and domestic populations.

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