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University of Turku

# EVOLUTIONARY QUANTITATIVE GENETICS OF ANIMAL PERSONALITY IN THE WILD

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*“No one supposes that all the individuals of the same species are cast in the same actual mould. These individual differences are of the highest importance for us, for they are often inherited”*

Charles Darwin, *Origin of Species*

## ABSTRACT

Individuals within populations often show repeatable behavioural differences which reflect variation in personality. In contrast to human personality, which has been extensively studied by psychologists for several decades, animal personality has only recently drawn the attention of behavioural ecologists. Animal personality is now known as a widespread phenomenon in nature and has been increasingly studied over the last 15 years due to its important ecological and evolutionary implications. Importantly, the mere existence and maintenance of personality, when individuals are expected to be behaviourally flexible, remains a puzzle which needs to be solved. The bulk of animal personality studies aims at understanding the evolution and causation of animal personality, and has shown that personality is often related to individual performance such as survival and reproductive success. In this context, quantitative genetics provide a framework to study the evolution of animal personality. This is because personality traits vary continuously within populations and can be considered as quantitative traits comparable to size, determined by many genes which are inherited according to Mendelian rules. Unfortunately, the uptake of ideas and concepts of quantitative genetics to the study of animal personality has been slow and questions related to personality development, although essential to understand its evolution, have been understudied. The main aim of my thesis is to provide a quantitative genetics view of personality in a wild population of blue tits (*Cyanistes caeruleus*). The research presented in this thesis addresses a range of classical themes in evolutionary quantitative genetics in the context of animal personality evolution, that is, heritability, genetic correlations, (correlated) selection and plasticity. Indeed, quantitative genetic approaches were applied to two behavioural responses to handling measured in adults and nestlings and showed that that these two responses are heritable and reflect aspects of blue tits' personality. Although these personality traits are genetically correlated in nestlings, the genetic correlation between them disappears in adults because of developmental plasticity. In addition, the personality traits measured in adults are linked to their survival and reproductive success, and one of these traits shows an age-related decline which is consistent with predictions from evolutionary theories of senescence. Finally, a variance-partitioning description of assortative mating shows that the approach traditionally used for estimating assortative mating in fixed traits is largely inappropriate when applied to labile traits such as behaviour. Alternative approaches allowing for a better estimation of assortative mating and other sources of phenotypic resemblance between mated partners are then introduced. In addition to providing some methodologies and examples to facilitate the use of quantitative genetics in the study of personality, this thesis shows the merits of adopting this framework, which has the potential to move personality research further. This is because applying quantitative genetics to the study of animal personality not only enables answering questions that have been overlooked, such as age-related plasticity, but also gives insight into potential mechanisms maintaining variation in personality.

## TIIVISTELMÄ

Saman populaation yksilöiden välillä on toistuvia käyttäytymiseroja, jotka kuvaavat yksilöiden välisiä persoonallisuuseroja. Psykologit ovat tutkineet ihmisen persoonallisuutta usean vuosikymmenen ajan, kun taas käyttäytymisekologit ovat vasta viime aikoina kiinnittäneet huomiota eläinten persoonallisuuksiin. Nykyään eläinten persoonallisuuden tiedetään olevan yleinen ilmiö luonnossa, ja koska persoonallisuuspiirteillä on tärkeitä ekologisia ja evolutiivisia seurauksia, aiheen tutkimus on lisääntynyt viimeisen 15 vuoden aikana. Silti on epäselvää miksi persoonallisuuseroja on yleensä olemassa, ja miksi niitä ylläpidetään tilanteissa joissa yksilöiden käyttäytymisen oletettaisiin olevan joustavaa. Suurin osa alan tutkimusta, mikä pyrkii ymmärtämään syitä eläinten persoonallisuuseroille ja niiden evoluutiolle, on osoittanut, että persoonallisuus on usein sidoksissa yksilön suorituskykyyn, kuten selviytymiseen ja lisääntymismenestykseen. Kvantitatiivinen genetiikka tarjoaakin puitteet eläinten persoonallisuuden evoluution tutkimiseen, sillä persoonallisuuspiirteet vaihtelevat populaatioiden sisällä ja niitä voidaan pitää kvantitatiivisina piirteinä samaan tapaan kuin eläimen kokoa, joka määräytyy mendelistisesti perittyjen geenien kautta. Kvantitatiivisen genetiikan ideoiden ja konseptien omaksuminen eläinten persoonallisuustutkimukseen on kuitenkin ollut hidasta. Lisäksi persoonallisuuden kehittymistä on tutkittu vain vähän, huolimatta sen välttämättömyydestä persoonallisuuden evoluution tutkimiselle. Väitöskirjani tarkoituksena on tarjota kvantitatiiviseen genetiikkaan perustuva näkemys eläinten persoonallisuudesta käyttäen sinitiaisten (*Cyanistes caeruleus*) luonnonpopulaatiota. Tämän väitöskirjan tutkimukset käsittelevät evolutiivisen kvantitatiivisen genetiikan klassisia teemoja, kuten perinnöllisyyttä, geneettistä korrelaatiota, valintaa ja plastisuutta eläinten persoonallisuuden evoluution näkökulmasta. Kvantitatiivisen genetiikan metodeja käytettiin analysoimaan kahta eri käyttäytymisvastetta, jotka mitattiin aikuisilla ja poikasilla niitä käsiteltäessä. Havaittiin, että nämä kaksi käyttäytymisvastetta sekä periytyvät että heijastavat sinitiaisen persoonallisuutta. Vaikka kyseiset persoonallisuuspiirteet ovat geneettisesti korreloituneita poikasilla, korrelaatio häviää aikuisilla. Tämä johtuu todennäköisesti kehityksen plastisuudesta. Aikuisilla sinitiaisilla persoonallisuuspiirteet ovat yhteydessä eloonjäämiseen ja lisääntymismenestykseen. Toinen piirteistä kuitenkin heikkenee iän myötä ja on näin ollen yhtenevä vanhenemisen evoluutioteorian oletusten kanssa. Tämä väitöskirja kuvaa valikoivan pariumisen varianssin jakaantumista kvantitatiivista genetiikkaa hyödyntäen. Kuvaus osoittaa, että menetelmät, joita on perinteisesti käytetty valikoivan pariumisen arvioimiseen pysyvistä piirteistä ovat suurelta osin soveltumattomia muuttuvien piirteiden, kuten persoonallisuuden tutkimiseen. Väitöskirja esittelee myös vaihtoehtoisia lähestymistapoja, joiden avulla voi erottaa toisistaan valikoivasta pariumisesta ja muista syistä johtuvan lisääntymisparien ilmiöiden yhteneväisyyden. Kvantitatiivisen genetiikan menetelmien ja käytännön esimerkkien lisäksi tämä väitöskirja esittelee myös kyseisen metodologian hyödyt. Kvantitatiivisen genetiikan käyttö edistää eläinten persoonallisuustutkimusta, sillä se ei ainoastaan vastaa huomiotta jääneisiin kysymyksiin, kuten ikään liittyvään plastisuuteen, vaan lisää myös ymmärrystä mekanismeista, jotka ylläpitävät persoonallisuuden vaihtelua.

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## LIST OF ORIGINAL PUBLICATIONS AND AUHOR CONTRIBUTIONS

This thesis is based on the following publications referred to in the text by their Roman numerals:

- I** **Class, B.**, Kluen, E. & Brommer, J.E. (2014). Evolutionary quantitative genetics of behavioral responses to handling in a wild passerine. *Ecology and Evolution*, **4**, 427–440.
- II** **Class, B.** & Brommer, J.E. (2015). A strong genetic correlation underlying a behavioural syndrome disappears during development because of genotype-age interactions. *Proceedings of the Royal Society B*, **282**, 20142777.
- III** Brommer, J.E. & **Class, B.** (2015). The importance of genotype-by-age interactions for the development of repeatable behavior and correlated behaviors over lifetime. *Frontiers in Zoology*, **12**, S2.
- IV** **Class, B.** & Brommer, J.E. (2016). Senescence of personality in a wild bird. *Behavioral Ecology and Sociobiology*, **70**, 733–744.
- V** **Class, B.**, Dingemanse, N.J., Araya-Ajoy, Yimen G. & Brommer, J.E. (2017). A statistical methodology for estimating assortative mating for phenotypic traits that are labile or measured with error. *Methods in Ecology and Evolution*, **38**, 42–49.

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BC =Barbara Class; JEB= Jon E Brommer; EK= Edward Kluen; NJD= Niels J Dingemanse; YA-A =Yimen Araya-Ajoy



# I. INTRODUCTION

## 1.1 Animal personality in behavioural ecology

Anybody who spends sufficient time observing animals might notice that individuals of the same species differ in their behaviour, just as humans do. Interestingly, these behavioural differences between individuals, termed “personality” are not restricted to domestic animals and have also been found in the wild across a variety of taxa ranging from gastropods and arthropods to mammals and birds (Gosling et al. 2001). Although animal personality research has a long history which started in the early days of ethology (van Oers & Naguib 2013), it is only in the end of the 20th century that personality in wild animals started to receive attention from behavioural ecologists. Because animal personality is a widespread phenomenon in nature which has ecological and evolutionary implications, animal personality research has been increasing continuously (Réale et al. 2010) and has been integrated into evolutionary biology and different fields of ecology, ranging from community ecology (Quinn 2015) and population dynamics (Tuck et al. 2015) to conservation (Sinn et al. 2014), social networks (Krause et al. 2010) and spatial ecology (Harrison et al. 2015).

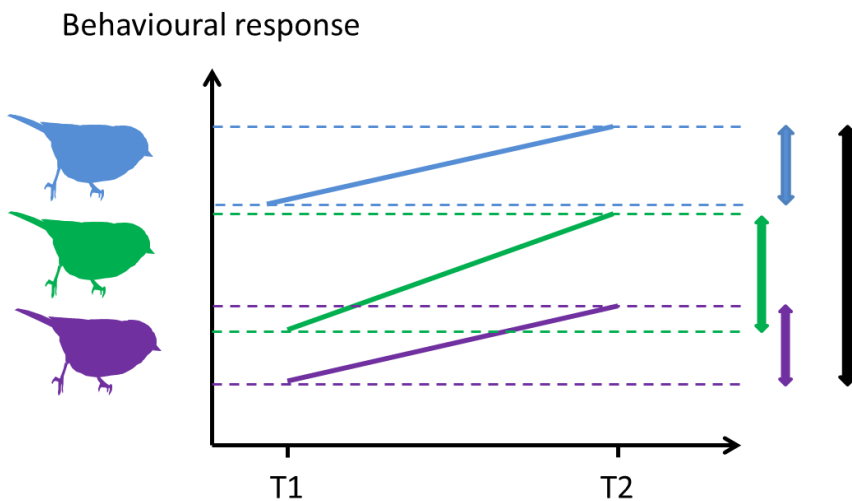
In behavioural ecology, animal personality is commonly defined as behavioural differences between individuals that are maintained over time and across situations (Réale et al. 2007). For instance, in a population, individuals differ in their behaviour in that some individuals tend to always take more risks than other individuals and these differences are largely maintained across repeated measurements and in different contexts (e.g. presence or absence of predator cues). The presence of personality can be tested by measuring repeatedly the behavioural response of individuals over time or in different contexts (Figure 1).

Although each individual can vary in its response between two measurements ( $\sigma_{within}^2$ ), individuals vary in their average response ( $\sigma_{between}^2$ ) and the rank orders are largely maintained. The total variance observed in the population ( $\sigma_{total}^2$ ) is the sum of the variances between and within individuals and the presence of personality variation in a population can be tested by estimating behavioural repeatability (R) (Nakagawa & Schielzeth 2010):

$$R = \frac{\sigma_{between}^2}{\sigma_{total}^2} \quad (1)$$

Note that R is similar to the intra-class correlation metric used in other fields such as in psychology. A repeatability significantly different from zero means that a significant part of the total variance for a trait in the population is caused by differences between

individuals and hence that this trait reflects an aspect of personality of these individuals. Repeatability has been found in various species, where individuals of different ages or sexes have been tested in different settings (e.g. wild, field enclosure, lab) and contexts (e.g. predation risk, population density) for any type of behavioural response (e.g. emergence time, distance travelled, agonistic behaviour), with these responses sometimes being grouped into distinct categories labelled as boldness, exploration, activity, aggressiveness, and sociability (Réale et al. 2007). In a meta-analysis, Bell et al. (2009) showed that the repeatability of behaviour is on average 37%, which means that 37% of the observed variation in behavioural traits is caused by differences between individuals, with the rest being caused by environmental or unexplained (residual) variation.



**Figure 1:** Schematic illustration of the behavioural responses of three individuals that have been measured at two different times (T1 and T2). Individuals vary in their average response (elevation of each bird) and each individual can vary in its response between two measurements (length of the double-headed arrows or slope of the response). The black double-headed arrow represents the total variance observed in the population.

In addition, different behavioural traits have often been found to correlate within populations, forming what are called “personality axes” in psychology and “behavioural syndromes” in ecology (Sih et al. 2004). Personality axes and behavioural syndromes constitute an important feature of personality but differ in that personality axes attempt to describe variation in personality using different latent factors upon which different behavioural traits load whereas a behavioural syndrome simply refers to a suite of behavioural traits that are correlated across individuals. While the former has been mainly studied in humans and non-human primates before being extended to domestic and wild animals, the latter appeared more recently in behavioural ecology. For example, human personality traits are grouped into five axes (conscientiousness, agreeableness,

neuroticism, openness, and extraversion) which may or may not be shared by other species (Gosling & Mehta 2013). In contrast, behavioural syndromes are commonly reported as phenotypic correlations between pairs of traits (e.g. boldness and aggression or time of emergence and activity) and are, on average, positive (Garamszegi et al. 2012).

Interestingly, the mere existence of personality in animals implies that individuals cannot express the entire range of behavioural responses that are expressed in the population (see double-headed arrows in figure 1). In addition, a behavioural syndrome consisting of a positive correlation between boldness and aggressiveness implies that an individual cannot be the boldest and the least aggressive in the population. This means that individuals are to some extent constrained in their behavioural responses, which challenges the expectation of individuals flexibly adjusting their behaviour to cope with any change in external or internal factors. Tinbergen's (1963) four questions (current utility, mechanism, ontogeny and phylogeny) constitute a framework that is generally adopted by behavioural ecologists to understand the existence of any specific behaviour and can be applied to the study of personality. To date, much of empirical studies in behavioural ecology have focused on the first question, and measured the fitness consequences of personality in natural or captive populations.

Some hypotheses for the existence and maintenance of personality include purely phenotypic mechanisms such as stable-state differences, state-behaviour feedbacks, and negative frequency-dependence (Dall et al. 2004, Sih & Bell 2008, Wolf et al. 2007, Wolf et al. 2008, Luttbeg & Sih 2010, Wolf & McNamara 2012, Sih et al. 2015, reviewed in Brommer & Class 2017b). These hypotheses derive from the individual optimization theory based on the idea that each individual's phenotype is optimal and results from a balance between the benefits and costs that are determined by its own state (Brommer & Class 2017b). Other hypotheses that have been gaining popularity and empirical support invoke natural selection, be it frequency-dependent, correlational, or spatiotemporally heterogeneous, to explain the maintenance of personality variation (Dingemanse & Réale 2013). These hypotheses will be detailed below. Importantly, the presence of genetic variation underlying personality variation is a necessary condition for personality traits to respond to selection which therefore has to be tested.

## **1.2 Evolutionary quantitative genetics applied to personality**

### ***1.2.1 Heritability of personality***

Quantitative genetics provide a framework for studying the evolution of personality. This is because personality varies continuously within populations, and can be considered as a quantitative trait comparable to size or offspring production. Hence, provided that personality is heritable and under selection, quantitative genetics will allow making predictions regarding its evolution. In the situation of a behavioural trait measured

repeatedly in different individuals, the response *beh* of an individual *i* measured at time *t* can be described using the equation:

$$beh_{it} = \mu + \mu_F + ind_i + \varepsilon_{it} \quad (2)$$

where  $\mu$  is the mean behaviour over all the individuals measured,  $\mu_F$  is the deviation from the mean due to fixed effects (e.g. sex of the individual),  $ind_i$  is the individual-specific deviation from the overall mean and  $\varepsilon_{it}$  is the residual deviation for each individual at each observation. These two deviations are assumed to be independent and normally distributed with a mean of zero and a certain variance  $\sigma^2$  noted as  $ind \sim N(0, \sigma_{ind}^2)$  and  $res \sim N(0, \sigma_{res}^2)$ , where  $\sigma_{ind}^2$  is equivalent to between-individual variance,  $\sigma_{res}^2$  is equivalent to within-individual variance and the phenotypic variance  $\sigma_{phen}^2$  resulting from their sum is equivalent to the total variance introduced in the previous section (Falconer & MacKay 1996).

$$\sigma_{phen}^2 = \sigma_{ind}^2 + \sigma_{res}^2 \quad (3)$$

Note that for fixed traits (e.g. skeleton size in adult birds) that can be measured without error, the residual variance is usually very small and hence the phenotypic variance mostly reflects the variance in individual-specific deviations, while in labile traits such as behaviour, residual variance accounts for a substantial part of the phenotypic variance. As in the previous section, repeatability is calculated as the ratio of the individual-specific variance on the phenotypic variance. However, some of the individual-specific variance is due to differences in the genes that individuals inherit from their parents while the remaining variance is due to environmental factors that are kept constant within individuals (e.g. long-lasting effects of early-life environment).

The advantage of using a quantitative genetics approach is that it allows further partitioning of the variance between individuals into its genetic and environmental causes. Indeed, quantitative traits are assumed to be encoded by many loci that are inherited according to Mendelian rules and that act additively such that the genotypic value of a trait is the sum of the contribution of each loci on this trait. The individual-specific deviation of individual *i* results from the sum of its breeding value ( $a_i$ ) and the environmental effects that are conserved across repeated measures (permanent environmental effects,  $pe_i$ ), and both deviations are assumed to be independent and identically distributed and noted as  $a \sim N(0, \sigma_a^2)$  and  $pe \sim N(0, \sigma_{phen}^2)$ :

$$ind_i = a_i + pe_i \quad (4)$$

$$beh_{it} = \mu + \mu_F + a_i + pe_i + \varepsilon_{it} \quad (5)$$

Using a quantitative genetic approach, it is thus possible to partition further the variance in individual-specific values into variance caused by additive genetic effects and permanent environment variance. The phenotypic variance is thus the sum of these two variance components and the residual variance (Falconer & MacKay 1996).

$$\sigma_{phen}^2 = \sigma_a^2 + \sigma_{pe}^2 + \sigma_{res}^2 \quad (6)$$

By convention, non-additive genetic sources of phenotypic variance such as dominance variance (due to interactions within loci) and epistatic variance (due to interactions between loci) and their interaction are assumed to be negligible, although they are likely to be more important for behaviours than morphological traits (Meffert et al. 2002, Stirling et al. 2002). These effects are challenging to estimate due to high and specific data requirements, and thus focusing on additive genetic effects, while keeping in mind that non-additive genetic effects are ignored, may be a reasonable first step.

Because only traits that are heritable can respond to selection and thus evolve, much emphasis is generally laid on estimating additive genetic variance in traits and their heritability ( $h^2$ ), which is the ratio of additive genetic variance on the phenotypic variance (Falconer & MacKay 1996):

$$h^2 = \frac{\sigma_a^2}{\sigma_{phen}^2} \quad (7)$$

Heritability of personality traits has been measured in the wild and in the lab using different approaches. These approaches all hinge on the fact that related individuals look more similar than unrelated individuals because they share some of their genes, the most commonly used approaches being parent-offspring regressions, full-sib analyses (Dingemanse et al. 2002), selection lines (Drent et al. 2002) and animal models (detailed below) which have gained popularity over the recent years. Overall, the heritability of behaviours is lower than the heritability of morphological traits but similar to the heritability of life-history traits (Stirling et al. 2002). A more recent meta-analysis showed that heritability is generally low for behavioural traits (0.14), but additive genetic variance accounts for 52% of the between-individual variance in behaviour (“heritability of personality”, Dochtermann et al. 2015).

### ***1.2.2 Genetic correlations between personality traits***

As previously mentioned, suites of behavioural traits have been shown to covary between individuals. As for phenotypic variance, the phenotypic covariance between traits can be decomposed into additive genetic, permanent environment, and residual covariance (Dochtermann & Roff 2010). For instance, two behavioural traits (*beh1* and *beh2*) can be described separately:

$$beh1_{it} = \mu^{beh1} + \mu_F^{beh1} + a_i^{beh1} + pe_i^{beh1} + \varepsilon_{it}^{beh1}$$

$$beh2_{it} = \mu^{beh2} + \mu_F^{beh2} + a_i^{beh2} + pe_i^{beh2} + \varepsilon_{it}^{beh2} \quad (8)$$

where the deviations  $a$ ,  $pe$ ,  $\varepsilon$  stem from identical and independent distributions (Searle 1961) and follow a bivariate normal distribution (BVN):

$$\begin{bmatrix} a_i^{beh1} \\ a_i^{beh2} \end{bmatrix} \sim BVN(0, \Sigma_a), \Sigma_a = \begin{bmatrix} \sigma_a^{2^{beh1}} & \sigma_a^{beh1-beh2} \\ \sigma_a^{beh1-beh2} & \sigma_a^{2^{beh2}} \end{bmatrix}$$

$$\begin{bmatrix} pe_i^{beh1} \\ pe_i^{beh2} \end{bmatrix} \sim BVN(0, \Sigma_{pe}), \Sigma_{pe} = \begin{bmatrix} \sigma_{pe}^{2^{beh1}} & \sigma_{pe}^{beh1-beh2} \\ \sigma_{pe}^{beh1-beh2} & \sigma_{pe}^{2^{beh2}} \end{bmatrix}$$

$$\begin{bmatrix} \varepsilon_i^{beh1} \\ \varepsilon_i^{beh2} \end{bmatrix} \sim BVN(0, \Sigma_{res}), \Sigma_{res} = \begin{bmatrix} \sigma_{res}^{2^{beh1}} & \sigma_{res}^{beh1-beh2} \\ \sigma_{res}^{beh1-beh2} & \sigma_{res}^{2^{beh2}} \end{bmatrix}$$

$$\Sigma_{phen} = \Sigma_a + \Sigma_{pe} + \Sigma_{res} = \begin{bmatrix} \sigma_{phen}^{2^{beh1}} & \sigma_{phen}^{beh1-beh2} \\ \sigma_{phen}^{beh1-beh2} & \sigma_{phen}^{2^{beh2}} \end{bmatrix}$$

$$\Sigma_{ind} = \Sigma_a + \Sigma_{pe} = \begin{bmatrix} \sigma_{ind}^{2^{beh1}} & \sigma_{ind}^{beh1-beh2} \\ \sigma_{ind}^{beh1-beh2} & \sigma_{ind}^{2^{beh2}} \end{bmatrix} \quad (9)$$

where:

$\sigma$  is the covariance between both behaviours

$\Sigma$  is the variance-covariance matrix on the different levels.

$\sigma_a^{beh1-beh2}$  denotes the genetic covariance resulting from either linkage disequilibrium (association between genes coding independently for different traits, due to drift, selection, or assortative mating) or pleiotropy (a subset of genes influencing one trait influences another trait).

$\sigma_{pe}^{beh1-beh2}$  denotes the permanent environment covariance due to environmental effects that are conserved across repeated measurement and affecting both traits simultaneously

$\sigma_{res}^{beh1-beh2}$  denotes the residual covariance between traits due to external processes affecting both traits simultaneously, for instance if traits are measured at the same time by the same observer or in the same environment.

$\sigma_{ind}^{beh1-beh2}$  denotes the covariance between traits that is due to individual-specific effects and is the sum of the covariance on the additive genetic and permanent environmental levels.

Correlations are more often used in the study of behavioural syndromes than covariances because they are unitless measures of the strength of association between two traits on the different levels. The phenotypic correlation ( $Cor_{phen}^{beh1-beh2}$ ) between two behaviours results from the sum of the correlations on different levels, weighed by the proportion of the phenotypic variance that these levels explain (Dingemanse et al. 2012):

$$Cor_{phen}^{beh1-beh2} = \frac{\sigma_a^{2beh1}}{\sigma_{phen}^{2beh1}} * \frac{\sigma_a^{2beh2}}{\sigma_{phen}^{2beh2}} * Cor_a^{beh1-beh2} + \frac{\sigma_{pe}^{2beh1}}{\sigma_{phen}^{2beh1}} * \frac{\sigma_{pe}^{2beh2}}{\sigma_{phen}^{2beh2}} * Cor_{pe}^{beh1-beh2} + \frac{\sigma_{res}^{2beh1}}{\sigma_{phen}^{2beh1}} * \frac{\sigma_{res}^{2beh2}}{\sigma_{phen}^{2beh2}} * Cor_{res}^{beh1-beh2} \quad (10)$$

Behavioural syndromes can be reported as correlations on the phenotypic, individual and genetic levels, although the latter is the most relevant metric for studying the evolution of personality. Indeed, estimating the additive genetic (co)variance matrix for behaviour, commonly termed G matrix ( $\Sigma_a$ ), is important for predicting the response of multiple behaviours to selection, because genetic correlations, especially when caused by pleiotropy, can impede the independent evolution of traits and thus constitute evolutionary constraints (Dochtermann & Dingemanse 2013). Estimating genetic correlations between traits requires large amounts of data which can be challenging especially in natural populations. Therefore, most studies rather use the phenotypic correlation because it is assumed to be a reliable proxy for the genetic correlation and does not require any pedigree information or repeated measures. This assumption, called the Cheverud's conjecture, has been tested for behavioural traits by Dochtermann (2011), who found that, although similar in sign, phenotypic correlations typically underestimate genetic correlations between behaviours. In contrast, correlations on the individual-level might be a better proxy for genetic correlations between behaviours because approximately half of the between-individual variance is due to additive genetic effects (Dochtermann et al. 2015). In addition, the between-individual correlation per se is of interest to behavioural ecologists since the existence of personality depends on the sole presence of between-individual variation in behaviour (Dingemanse et al. 2012). Although estimating it only requires repeated measures for individuals without pedigree information, this requirement might still represent a considerable sampling effort which is why many studies take the "individual gambit" and only estimate phenotypic correlations (Brommer 2013). Contrary to expectations, it has been recently shown that phenotypic correlations between

behaviours indeed constitute a good proxy for between-individual correlations (Brommer & Class 2017), although the reason for this is not yet clear.

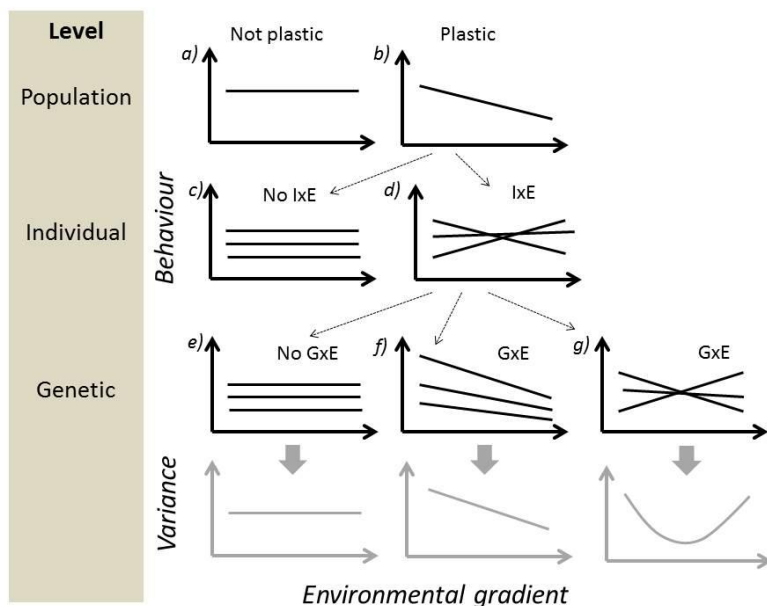
### ***1.2.3 Plasticity in personality***

The previously-mentioned hypotheses for the evolution of personality, combined with empirical studies focusing on a specific ontogenetic stage or limited to one population in which individuals share relatively similar environments, might give the false impression that personality is long-term stable and context-general. In fact, behavioural traits are labile, which means that individuals can plastically adjust their behaviour to variations in their internal state (age, energy stock) or external environment (predation risk, temperature). Personality traits can thus be plastic and repeatable at the same time. Plasticity in personality traits has received an increasing interest of the recent years and quantitative genetics provides a framework for studying it (Dingemanse et al. 2010). This is because behavioural plasticity can be seen in a population on different levels: i) the population mean can change in response to environmental variation ii) individuals can vary in their response to the same environmental variation iii) individuals' plastic responses themselves can be heritable (Figure 2, Brommer 2013b). Two approaches are commonly used to study plasticity: the reaction norm approach and the character-state approach.

The reaction norm approach is a function-valued trait approach in which the trait values on different levels are allowed to vary as a function of an environmental variable. Reaction norms are generally used in ecology and genetics to represent the diversity of phenotypes that can be produced by one genotype across an environmental gradient (or other gradients such as age or time). The reaction norm approach can be visualised by plotting for every individual (or genotype) its phenotypic values against an environmental gradient or across (in general two) different situations. Reaction norms are not necessarily linear but for simplicity are represented as linear slopes in Figure 2. Every line (or individual or genotype) of the reaction norm is characterized by its elevation and its slope. In the context of personality research, each line's elevation (intercept at the mean-centered environment, Nussey et al. 2007) represents each individual's (or genotype's) "personality" and each slope represents each individual's (or genotype's) plastic response. Hence, individuals can vary in their elevation and in their slopes. Between-individual variation in elevation (or intercept) indicates that the behavioural trait is repeatable and between-individual variation in slopes indicates that there is between-individual variation in plasticity or individual-environment interaction (IxE)(Figure 1d). Whether this between-individual variation in plasticity is due to plasticity itself being heritable (GxE) can be investigated by testing whether the same pattern is found on the genetic level (Figure 2f,g). Finding evidence for IxE but not for GxE means that individuals differ in their plasticity because of experiencing consistently different environmental factors (PExE). These factors can be past environmental effects that are long-lasting (e.g. maternal effects) or environmental effects experienced by the individual that are consistent



across measurement events. One important feature of reaction norms is the covariance between slope and elevation. This covariance can generate changes in individual or genetic variance over the environmental gradient. For instance, a positive covariance between elevation and slope can be seen when lines are “fanning out” and generates an increase in variance. A negative covariance can be seen when lines are “fanning in” or crossing (Figure 2 f, g). This will generate a decrease in variance, sometimes followed by an increase when lines are crossing. Therefore, IxE and GxE generate changes in individual and additive genetic variances and hence changes in repeatability and heritability estimates at different points of the environmental gradient.



**Figure 2:** Schematic illustration showing behavioural plasticity on different levels. For simplicity, only linear plasticity is drawn here, but the same hierarchical structure applies to non-linear relationships. On the population level, (a) the environment-specific mean behaviour may be invariant across the environmental gradient, but (b) may also vary. On the individual and genetic levels, deviations from these environment-specific means are considered. (c) All individuals show the same deviation from the average behaviour at every value of the environmental gradient, and there is no between-individual variation in plasticity (no IxE). Alternatively, (d) individuals differ in their environment-specific deviation from the environment-specific means, showing variation in plasticity (IxE). Despite the presence of IxE, (e) Genotype – environment interaction (GxE) may be absent, or (f) GxE occurs without the ranking of genotypes changing across environment (reaction norms not crossing within the environmental gradient), or (g) GxE where the ranking of genotypes changes (reaction norms cross). As a result of GxE, additive genetic variance can change across the environmental gradient. For instance, it can decrease when lines are “fanning in” (f) or it can show a curvilinear pattern (g). (Reproduced from Brommer & Class 2017b. In: Vonk, Weiss & Kuczaj (eds) *Personality in nonhuman animals*. doi:10.1007/978-3-319-59300-5. ISBN:978-3-319-59299-2)

The reaction norm approach cannot be used when behavioural responses have been measured across more than two discrete contexts and when these cannot be ordered. An alternative is to use the character-state approach to test for IxE and GxE (Brommer 2013b). This approach is a multivariate approach in which the same trait measured into  $n$  different contexts is considered as  $n$  different response variables. Hence, in the same way as multiple behaviours can be correlated on different levels, the same behaviour can be correlated across contexts on the phenotypic, individual or genetic levels. For instance, a cross-context correlation close to 1 on the individual level means that individual ranks are largely maintained across the different contexts while a cross-context correlation different from 1 indicates changes in individual ranks (IxE). The cross-context correlation can be negative when individual ranks are reversed between the two contexts (if individuals that have the highest scores in context 1 have the lowest scores in context 2 and vice versa). The same applies to cross-context correlations on the genetic and permanent-environment levels. Note that this approach should be used for a reasonable number of contexts because its dimensionality increases greatly with  $n$ .

There is empirical evidence for IxE and GxE in personality traits using these two approaches. For instance, different literature reviews showed that the cross-environmental correlation of rankings for personality traits is generally moderate (median estimate =0.4, Brommer 2013b) or varies from very low to very high values in fish (Killen et al. 2016), which suggests that IxE might be common. Random regressions have been used more often to test for IxE in personality traits and individuals have been shown to vary in their plasticity as a function of food availability (Konttiainen et al. 2009), predation risk (Mathot et al. 2011), temperature (Betini & Norris 2012), time of the year (Dingemanse et al. 2012b), brood size (Nicolaus et al. 2012), number of trials (Ensminger & Westneat 2012), or reproductive status (Favreau et al. 2014). On the genetic level, evidence for heritable behavioural plasticity mainly comes from selection experiments where animals from different lines selected for high and low personality scores differ in their plasticity (Koolhaas et al. 1999, Øverli et al. 2005, Carere et al. 2005). However, evidence for GxE in personality traits based on the two approaches described above remains scarce (Dingemanse et al. 2012b), presumably due to a lack of power (Brommer 2013b).

#### ***1.2.4 Evolutionary theories explaining the existence and maintenance of personality***

There is now abundant evidence that personality traits are heritable and related to fitness (Smith & Blumstein 2008) and thus can respond to selection. Because directional selection tends to erode additive genetic variance, the existence of heritable personality variation within populations raises a “classical” question in evolutionary quantitative genetics: what mechanisms can prevent the erosion of additive genetic variation for personality traits and thus maintain their existence? Below, I shortly review the main mechanisms that have been proposed and their empirical support (also see Brommer & Class 2017b).

*Mutation-selection balance*

Under the mutation-selection balance scenario, genetic variation in personality traits is maintained thanks to mutations occurring at every generation which restores the loss of additive genetic variance caused by stabilizing selection, where individuals deviating from the optimal phenotype are eliminated (Zhang & Hill 2005, Nettle 2006, Penke et al. 2007). One empirical study in humans supports the mutation-selection theory for personality traits (Verweij et al. 2012).

*Disruptive selection and sexual selection*

Genetic variation in personality traits can be maintained by disruptive selection if individuals expressing extreme phenotypes (compared to the population mean) achieve a higher fitness than individuals with intermediate phenotypes (Lynch & Walsh 1998). Disruptive selection for personality traits has been shown empirically in eastern chipmunks (Bergeron et al. 2013) and in garter snakes (Brodie 1992). Assortative mating can be considered as a source of disruptive selection on personality if males and females that are assortatively mated regarding their personalities achieve a higher reproductive success than disassortative pairs. Differences in reproductive success between assortative and disassortative pairs have been found in the wild and in the lab and in diverse taxa (Dingemanse et al. 2004, Both et al. 2005, Sinn et al. 2006, Spoon et al. 2006, Schuett et al. 2011, Gabriel & Black 2012, Ariyomo & Watt 2013, Kralj-Fišer et al. 2013, Harris et al. 2014, David et al. 2015).

*Sexual antagonistic selection*

Genetic variation in personality can be maintained by sexual antagonistic selection when a behavioural trait that is positively genetically correlated across sexes is selected for in opposite directions in males and females (Rice & Chippindale 2001). Cross-sex genetic correlations are on average high ( $0.77 \pm 0.09$ ) for behavioural traits (Poissant et al. 2010) suggesting that intersexual conflicts are likely to occur in these traits. Sexual antagonistic selection on personality has been found in great tits (Dingemanse et al. 2004) and in comb-footed spiders (Pruitt & Riechert 2009).

*Balancing selection*

Environmental factors generally vary in time and/or space, generating antagonistic selection pressures over time/space which can maintain between-individual variation in behaviour (Nettle 2006, Penke et al. 2007, Koolhaas et al. 2007, Dingemanse & Réale 2013). For instance, different personality types are favoured under high or low predation risk, shy individuals being more likely to survive than bold individuals when predation risk is high, while bold individuals are more likely to outcompete shy individuals over resource acquisition when the predation risk is low. Because predation risk can vary in time or space, different personality types will be favoured in different circumstances and overall both phenotypes will achieve a similar fitness. This hypothesis is generally well supported by studies in wild and captive populations showing that fluctuations in food abundance (Dingemanse et al. 2004, Montiglio et al. 2014, Both et al. 2005, Kontiainen et al. 2009, Quinn et al. 2009, Le Coeur et al. 2015, Vetter et al. 2016), density (Cote et al. 2008, Le Galliard et al. 2015, Quinn et al. 2009, Nicolaus et al. 2016), predation risk (Réale & Festa-Bianchet 2003), and environmental variability in time (Réale et al. 2009, Taylor et al. 2014) or space (Monestier et al. 2015) can act to maintain variation in personalities by alternatively selecting different personality types over time/space. Under negative frequency-dependent selection, which can be considered as a type of fluctuating selection, the fitness of individuals expressing a heritable behavioural tactic decreases as the frequency of individuals expressing the same tactics in the population increases. At equilibrium, the different phenotypes achieve equal fitness payoffs and genetic variation underlying personality can be maintained. Empirical evidence for this mechanism maintaining behavioural variation however remains scarce and only a few studies showed frequency-dependent selection on heritable personality traits (Fitzpatrick et al. 2007, Pruitt & Riechert 2009). Finally, non-equilibrium dynamics can also be considered as a form of fluctuating selection which can maintain phenotypic variation in personality that may (or may not) be associated with genetic variation (Wolf & Weissing 2010).

*Genotype-Environment or Genotype-Age Interaction*

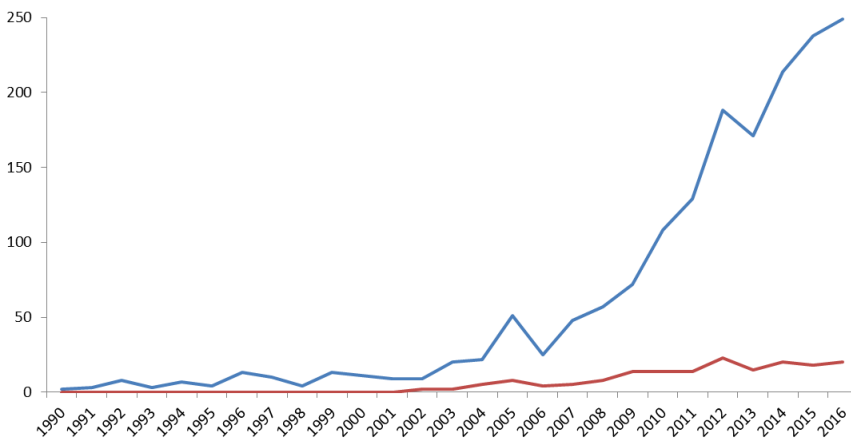
Genotype-environment or genotype-age interactions can maintain genetic variation in personality when there is additive genetic variation for plasticity in behavioural traits and when different phenotypes are favoured in different environments or at different ages. Provided there is no perfect plastic response for any given genotype and that environmental conditions vary within individuals, there would be no optimal genotype but instead a range of genotypes that achieve a similar fitness and would be maintained in the population (Roff 1997). As discussed above, there are still few empirical studies showing Gx $E$  in behaviours but evidence for Ix $E$  is accumulating.

*Pace-of-life syndromes*

While the mechanisms described above can also be invoked to explain the existence and maintenance of behavioural syndromes, one hypothesis, which is at the intersection of the phenotypic mechanisms mentioned in the first section and the genetic mechanisms detailed above, is becoming increasingly popular: the pace-of-life syndrome (POLS) (Réale et al. 2010b). Although it was first used to describe between-species differences in life-history and physiology, the POLS framework has recently been extended to within-species differences and personality variation. Under the POLS hypothesis, variation in personality traits can be maintained because personality coevolved with life-history and physiological traits. Hence, individuals vary in their life-history strategies, behaviour and physiology which together form a “pace-of life” syndrome allowing them to either live a “fast” (early reproduction, short-lived) or a “slow” life (late reproduction, long-lived). Overall, individuals with slow or fast POLS would achieve an equal fitness and the different POLS would be maintained in the population. Importantly, this hypothesis generates predictions regarding the sign of the associations between behavioural, life-history and physiological traits. For instance, individuals that are on average bolder, or fast explorers are predicted to mature and reproduce earlier, have a lower body condition, weaker immune system, a higher metabolism and a shorter lifespan. There has been a strong interest in studying POLS since Réale et al. (2010b) introduced the idea of including personality to POLS. However, empirical evidence for this hypothesis remains equivocal (Brommer & Class 2017b), which suggests that the links between behavioural, life-history and physiological traits might not be universal but vary between systems due to different selection pressures, as already pointed out by Réale et al. (2010b). These mixed results might also be due to inappropriate methodologies, most studies looking at correlations between behaviour and life-history or physiological traits, although the link between these traits and the general pace-of-life of individuals was not formally tested. Setting up a general framework for testing for POLS would greatly help in moving further towards an understanding of the existence and maintenance of personality variation.

## II. CHALLENGES AND AIMS OF THE THESIS

Although quantitative genetics has proven to be a valuable approach to the understanding of evolution and is commonly used in evolutionary biology studies, the uptake of the ideas and concepts of quantitative genetics in the study of animal personality has been slow. Indeed, while the number of studies on animal personality has increased spectacularly since 2006, and is now reaching 250 published articles per year, the number of studies reporting heritability in personality traits has been slowly increasing and reached a maximum of 20 published articles per year (Figure 3). One likely reason for this is that the detection of heritability, genetic correlations and GxA in fixed traits usually requires substantial amounts of data in order to reach sufficient statistical power, and these requirements can be even higher for behavioural traits because they are labile and generally have a low heritability. These data requirements include information on the population pedigree and/or repeated measures for individuals, which can be challenging to obtain for certain systems and take considerable time and effort to collect, particularly in the wild. The advantages of studying evolution of traits in wild populations are however numerous compared to artificial populations. Applying quantitative genetics to wild populations indeed allows for a better understanding of the evolution of traits (their variation and the selective forces acting on them) in a complex and realistic context, where extrapolations from artificial experiments often do not hold (Kruuk et al. 2014). Fortunately, the data required for such analyses can be collected in relatively common settings, as evidenced by the increasing application of quantitative genetics to ecological or behavioural studies in natural populations over the last decade (Kruuk et al. 2014).



**Figure 3:** Number of articles using the keywords “personality” (blue line) and “personality AND heritab\*” (red line) published from 1990 to 2016 (search performed on Web of Knowledge, refining for studies in zoology, ecology, evolutionary biology, and veterinary sciences).

The main aim of my thesis is thus to provide a quantitative genetics view of personality in a wild population of passerines breeding in nest boxes, which is a “classical” study system in ecology. In addition to providing some methodologies and examples to facilitate the use of quantitative genetics in the study of personality, this thesis also aims at showing the merits of adopting this framework, which has the potential to move personality research further. For instance, the question of the ontogeny of personality has been largely overlooked by behavioural ecologists and would deserve more attention. Indeed, studying ontogeny, one of Tinbergen’s four questions, is essential to reach a deeper understanding of the evolution of animal personality and its mechanisms. Fortunately, quantitative genetics already provides approaches that can be applied to the study of personality development, since development can be viewed as age-related plasticity. In addition, and as already mentioned, behavioural traits differ from morphometric traits in that a considerable part of their phenotypic variation is due to residual variation and plastic responses. Hence, some of the metrics that are widely used for estimating quantitative genetic parameters in morphometric traits might not be appropriate when applied to behaviour. This might be the case for the assortative mating correlation, a common metric used in the calculation of heritability which has important evolutionary consequences. The work presented in my thesis addresses the following questions:

1. Are behavioural responses to handling heritable and genetically correlated? (**Chapter I**)
2. What are their consequences for survival and reproductive success? (**Chapter I**)
3. Is there age-related plasticity in personality?
  - a) Does personality remain constant during development? (**Chapter II,III**)
  - b) Does personality undergo senescence? (**Chapter IV**)
4. How to estimate assortative mating for personality traits?(**Chapter V**)

### III. MATERIAL AND METHODS

#### 3.1 Study species

Three chapters of this thesis (**I, II, IV**) are based on a long-term data set collected in a wild population of blue tits (*Cyanistes caeruleus*), a small passerine from the *Paridae* family, which is a common resident breeder throughout temperate and subarctic Europe. Blue tits are often found in habitats consisting of deciduous and mixed woodlands with a large proportion of oak and usually breed in tree holes although they readily use nest boxes. The data used in this thesis was collected in a population breeding in nest boxes and established in 2003 near the city of Tammissaari in South-Western Finland (60°01' N, 23°31' E). Before the work presented in this thesis, data on this population has been collected for a doctoral thesis on animal personality (Kluen 2012) and other studies (e.g. Brommer 2004, Pitala et al. 2009, Fresneau et al. 2014). In this population, blue tits generally start laying eggs in the end of April, although the first egg is laid on average in early May (mean laying date on 4<sup>th</sup> of May, sd=6 days), and the clutch size consist of 8-14 eggs (mean=10.2, sd=1.6). Females generally start incubating eggs after laying the penultimate egg and the incubation period lasts 13 days during which they are provisioned by males. In blue tits, both parents take part in the provisioning of nestlings, which mainly consume caterpillars. Young blue tits generally fledge on the third week after hatching (18-22 days old), and females sometimes initiate second but smaller broods, while males continue providing parental care to the fledglings.

#### 3.2 Study site

The study site consists of approximately 10km<sup>2</sup> of boreal forest, which is mainly composed of Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), downy and silver birch (*Betula pubescens* and *Betula pendula*), and differs from other study sites used for *Paridae* in Western Europe in that the oak is very rare and therefore plays no role in food availability during the breeding season. The number of boxes in the study site varied between years due to destruction by forestry activities, natural degradation, and predation by woodpeckers, but boxes were regularly replaced so that this number remained between 330 and 400 over the years. Nest boxes had a 26 mm diameter entrance-hole to only allow blue tits and coal tits (*Periparus ater*) (Dhondt & Eyckerman 1980) and were attached to trees using a rope at approximately 1.5m high.

#### 3.3 Population monitoring

Every year approximately 100 broods were monitored during the breeding season, which lasts from late April to mid-July. Starting from the last week of April, each box was checked at weekly intervals to establish i) the laying date (based on the assumption that females lay one egg a day, Perrins 1979), ii) the clutch size, and, when the clutch size was



complete and incubation had started, iii) predict the hatching date (calculated as laying date + clutch size + 13-1). Starting from one day before the expected hatching date, nests were visited daily in the afternoon, and on the day of hatching (day 0) nestlings were weighed together to estimate the average mass of the brood, which was used for the cross-fostering protocol performed on day 2 (see below). Between day 5 and day 9, adults were caught in the box while feeding the young. They were identified thanks to a metal ring on their left leg, or were ringed if previously unringed. The sex was determined on the basis of the presence or absence of a brood patch, which only females have, and the age was determined based on the coloration of their primary coverts as either one year old or older (Svensson 1992). Morphometric and behavioural measurements were taken at the same time following the protocol described below. On day 9, nestlings were weighed and ringed to allow lifetime identification, and, on day 16, morphometric and behavioural measurements were taken using the same protocol as for adults. This protocol was not performed in nestlings from second broods, which were only ringed. The percentage of ringed nestlings which survived and bred in the population on subsequent years (recruitment rate) is on average 5% (mean=0.05, sd=0.03). No information on the occurrence of natal dispersal outside of the study site is available for this population so the recruitment rate is likely to be lower than the true survival rate of the nestlings during their first year.

### **3.4 Morphometric and behavioural measurements**

After an adult individual was taken out of the bag in which it was kept, morphometric measurements were taken (following the same order for each individual). First, tarsus length (measured twice) and head size (measured from the back of the skull to the tip of the bill) were measured using a sliding calliper (accuracy, 0.1 mm). Then, wing length and tail length were measured using a ruler. During these measurements, the aggressive behaviour of the bird (biting, pecking, flapping wings) was observed and scored from 1 (passive from the beginning) to 5 (fighting continuously), reflecting the propensity of the bird to calm down during the morphometric measurements. For instance, a bird fighting during the measurement of the tarsus -a measurement which can be quite uncomfortable for the bird- and calming down thereafter is given a score of 3. This behavioural response is called “handling aggression” (HA) and has been measured from 2006 onwards. After the morphometric measurements, the bird was held still on its back and breath rate (BR) was recorded twice, defined as the time it took for the bird to take 30 breaths. BR was then calculated as the average of these two measurements and expressed as a number of breaths per second. BR can be considered as a measure for the bird’s stress response to handling (Carere & van Oers 2004), and has been measured from 2007 onwards. Finally, the bird was weighed using a 20g Pesola spring balance (accuracy, 0.1 g) before being released. The handling of each bird, when performed by an experienced observer, takes approximately 5 minutes. The measurement of nestlings’ morphological and personality traits followed a similar protocol which only differed in that BR was measured before the

other traits. Until 2011, nestlings were all taken from the nest on day 16 and placed individually in small paper bags which were randomized prior to morphometric and behavioural measurements. After 2011 this procedure changed, so that all the nestlings were placed together in a large paper bag. This change, however, did not affect the measurement of HA and BR in nestlings because the genetic correlation between each behaviour before and after 2011 does not differ from unity (**Chapter I**).

Personality traits in this population were the subject of a previous doctoral thesis (Kluen 2012) and additional behavioural traits have been studied such as neophobia-related behaviours in a cage test (Kluen et al. 2012), measured from 2008 to 2010 (abandoned thereafter due to logistical constraints) and nest-defence behaviours measured since 2007 (Fresneau et al. 2014). Although some of these traits were found to be repeatable and thus reflect aspects of the birds' personality (Kluen et al. 2012, Fresneau et al. 2014), the present thesis focuses on the two handling behaviours described above because they provide numerous advantages. Firstly, both traits have been measured since 2006 and 2007, and thus phenotypic data spans 7 to 8 generations, which facilitates the use of quantitative genetic analyses. Importantly, phenotypic data for HA and BR covers the lifespan of individuals from early life (nestlings) to late adulthood, which allows studying personality within individuals throughout their ontogeny. Furthermore, these two behaviours can readily be compared with behavioural traits commonly studied in the personality and coping style literature. Indeed, HA can be considered as a measure of docility (Réale et al. 2007) - a high HA indicating a low docility- and proactive individuals are expected to be less docile (Koolhaas et al. 2007). In addition, BR is commonly measured as a stress response because it is mediated by the activation of the parasympathetic system which is generally higher in reactive individuals (Koolhaas et al. 1999, Carere et al. 2001). Finally, analyses performed in **Chapter I** showed that HA and BR are heritable and related to individuals' performance (see Results section), which was not the case for nest defence behaviour (unpublished results). Hence both traits allow studying the evolution and ontogeny of personality and are the focus of chapters **II** and **IV**.

### 3.5 Cross-fostering

A reciprocal cross-fostering procedure was carried out from 2007 to 2010 on the second day after hatching. During this procedure, an equal number of nestlings were swapped between pairs of nests, called "dyads", which were formed based on similar hatching dates, average weights of hatchlings, and, if possible, brood sizes. If the brood sizes differed between two nests in a dyad, the number of nestlings which were swapped was approximately half the size of the smallest brood. Before the procedure, each nestling was weighed and marked by clipping a unique combination of its toe nails. The choice of which nestlings were cross-fostered was done random-systematically by first tossing a coin for the heaviest nestling in one nest and then alternating the cross-fostering treatment down the size-hierarchy of the brood.

## 3.6 Statistical analyses

### 3.6.1 Analyses of the fitness consequences of personality traits

#### *Survival selection analysis*

A capture-mark-recapture (CMR) analysis was performed using the software MARK (White & Burnham 1999) in **Chapter I** to test whether individuals' survival probability of surviving from one year to the next was affected by their personality traits. Logistic regressions, where individuals' probability of surviving ( $\phi$ ) and being captured ( $p$ ) was a function of personality, age, sex, year and their interactions, were fitted for HA and BR separately. The first measure of each personality trait was used for each individual, but, in case measurements were missing, the individual was given the sex-specific mean value for this trait (Cooch & White 2012). CMR models are based on the encounter history of each individual consisting of a suite of 1s and 0s for each year; 1 for a year during which the individual was encountered and 0 otherwise. After confirming that the data met the assumptions from the Cormack-Jolly-Seber model (CSJ) using a Goodness-of-fit test, all the possible combinations of covariates and their interactions were tested for  $p$  while the full model was fitted for  $\phi$ . These models were compared using Akaike Information Criterion (AICc), and the model with the lowest AICc was considered the best model. The best model for  $p$  was then fitted while the same procedure was performed to find the best model for  $\phi$ .

#### *Recruitment selection analysis*

Generalized linear mixed models were fitted in **Chapter I** to study the effects of parents' personality traits and their interaction on the recruitment probability of their genetic and foster offspring. These models were fitted for HA and BR separately, and included only information on broods that were cross-fostered to separate genetic from environmental effects of parents' personality traits. In these models, each nestling's recruitment status (1 if recruited, 0 if not) was modelled as a function of its genetic and foster parents' personality traits, the interaction between its genetic parents' personality traits, the interaction between its foster parents' personality traits, and the year, while nest of origin and nest of rearing were fitted as random effects to account for heterogeneity across these levels. These models assumed a binomial error distribution and a logit link and were run in R (R Development Core Team 2013) using the "glmer" function from the package "lme4" (Bates 2005). Each covariate was standardized by its mean and standard deviation to allow comparison of the effect sizes and properly model the interactions. A positive interaction between the values of males and females forming pairs indicated recruitment selection for assortative mating. This means that pairs where both the male and the female have an above-average personality score achieve a higher reproductive success (their offspring have a higher probability to recruit) than pairs composed of average parents. The statistical

significance of fixed effects was calculated by comparing models with and without each variable using LRT, where the likelihood was approximated using Laplace integration (Bolker et al. 2008).

### 3.6.2 Quantitative genetics analyses

#### *Animal model*

HA and BR were considered as quantitative traits which vary continuously in the population. An animal model, which is a type of linear mixed-effect model, was used to estimate additive genetic, permanent environment, and residual variances for both traits. The covariance between HA and BR on these levels was estimated using a multivariate animal model. The animal model uses information on the relatedness between individuals based on the population pedigree (Lynch & Walsh 1998, Kruuk 2004) and is noted:

$$y = X\beta + Z_A\mathbf{u}_A + Z_{PE}\mathbf{u}_{PE} + \boldsymbol{\varepsilon}$$

where  $y$  is a vector containing all observations on all individuals (here HA and BR separately or jointly),  $\beta$  is a vector of one or more fixed effects (here observer, sex, age and year),  $X$  represents a design matrix (of 0's and 1's) relating the appropriate fixed effects to each individual. The vector  $\mathbf{u}_A$  denotes additive genetic effects which are fitted as random effects, and  $Z_A$  is the design matrix relating the appropriate additive genetic effects to each individual. Similarly,  $Z_{PE} \mathbf{u}_{PE}$  denotes the random effect structure on the permanent environment level and finally,  $\boldsymbol{\varepsilon}$  is a vector of residual errors. The additive genetic (co)variance matrix (also called G matrix) and its elements was estimated using information on the coefficient of coancestry  $\theta_{ij}$  between individuals  $i$  and  $j$ , as derived from the pedigree (see below). The mixed model was solved using Restricted Maximum Likelihood (REML), as implemented in ASReml and ASReml-R (VSN International, Hemel Hempstead, U.K., Butler et al. 2009).

Multivariate animal models were used in **Chapters I** and **II**, where they allowed the calculation of the G matrix for HA and BR in adults (**Chapter I**), or as a character-state approach (**Chapter II**) to estimate cross-ontogeny correlations for HA and BR. In animal models, the statistical significance of fixed effects is tested using a Wald test while the statistical significance of additive genetic (co)variances is tested by constraining each of these (co)variances in different models that are compared with the initial model using a likelihood ratio test (LRT) with one degree of freedom (Wilson et al. 2010).

Multivariate mixed models were also used to analyse simulated assortative mating data in **Chapter V** where they allowed estimation of the correlation between hypothetical personality traits in males and females on the between-pair and within-pair levels (by

fitting pair identity as a random effect). Simulations were performed in R and these models were run using the package “asreml”.

### *Random regression (animal) model*

Random regression models were fitted in **Chapter IV** to study age-related plasticity in HA and BR separately. Random regression models are linear mixed models which allow the variance in random effects to vary as a function of a continuous variable, here being age (Wilson et al. 2007b), and can be used to test for IxA, GxA and PExA in personality traits. For instance, in a random regression modelling individual-level plasticity, the behavioural response *beh* of individual *i* measured at time *t* is modelled as:

$$beh_{i,t} = \mu + Age_{i,t} + FIXED_{i,t} + f_{ind}(x, Age) + \varepsilon_{i(t)}$$

where  $\mu$  is the overall fixed-effect mean,  $Age_{i,t}$  the mean-centred age effect (fitted as a factor) and  $FIXED_{i,t}$  a vector of additional fixed effects (here sex, year and observer) associated with individual *i* at measure time *t*. The random regression function  $f_{ind}(x, Age)$  is an orthogonal polynomial of order *x* on the individual level and captures deviation from the mean effect of Age (Henderson 1982). The presence of IxA in *beh* can be statistically tested by comparing models with increasing values of *x* using LRT (cf. Brommer et al. 2010b). While a zero-order polynomial ( $x=0$ ) only models individual variation in intercepts, a first order polynomial ( $x=1$ ) allows estimating individual variation in intercepts, linear slopes and the covariance between them. Therefore, there is evidence for IxA if the model where  $x>0$  significantly improves the model fit compared to  $x=0$  (Wilson et al. 2008; Brommer et al. 2010b; Charmantier et al. 2014). If a significant IxA is found, the function  $f_{ind}(x, Age)$  can be further partitioned into  $f_a(x, Age)$  and  $f_{pe}(x, Age)$  describing orthogonal polynomials of order *x* on the level of additive genetic and permanent environment effects respectively. Lastly,  $\varepsilon_{i,t}$  is the residual for individual *i* at the time it is measured. Residual errors can be age-specific (heterogeneous) or correlated across ages (homogeneous, noted as  $\varepsilon_i$ ). This can be tested by comparing the fit of models with heterogeneous and models with homogeneous residuals using LRT.

Because the age at the time of measurement is heterogeneously distributed in the population, an overall effect of age on personality on the population level can be due to either selecting removing certain individuals from the population (between-individual level) or individuals changing as they age (within-individual level) (Kreft et al. 1995, van de Pol & Verhulst 2006). While the former indicates the action of selection on personality traits, the second indicates age-related plasticity in behaviour. Whether population-level change in personality is due to selective disappearance or individual plasticity was first investigated by replacing the fixed effect variable  $Age_{i,t}$  by each individual’s mean age and age at the time of measurement centred on its mean. The statistical significance of each age

variable was then tested using a Wald test. If there was age-related plasticity on the level of the population, individual mean-centred age was used as the age variable in the random regression function to allow for a more accurate estimation of the random regression parameters (Hofmann & Gavin 1998, Nezlek 2001, Enders & Tofighi 2007, Blozis & Cho 2008, Curran & Bauer 2011, Ke & Wang 2014, Wang & Maxwell 2015). The random regression analysis in **Chapter IV** was performed in ASReml.

#### *Population pedigree*

The population pedigree used for these analyses is a social pedigree, where nestlings hatched in the same nest are assumed to be full siblings, all sired by the male who provides care for them (social father). However, errors in paternal links are likely to occur when using a social pedigree because some of the offspring in a nest may have been sired by another male than the social father (extra-pair paternity). Although the rate of extra-pair paternity in this population is not yet known, it has been estimated between 7% and 25% in nine blue tit populations (Brommer et al. 2010). Based on simulation, this level of extra-pair paternity is likely to cause relatively small error in the estimation of the quantitative genetic parameters (Charmantier & Réale 2005). This was also shown by simulations performed in **Chapter II**.

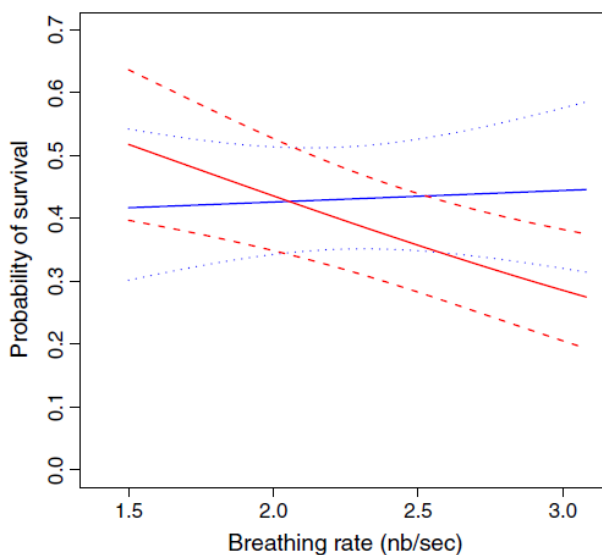
## IV. RESULTS AND DISCUSSION

### 4.1 Heritability and selection on two behavioural responses to handling (I)

In the first chapter of this thesis, we investigated whether HA and BR, two behavioural responses expressed during handling, are heritable and under selection in adults. Indeed, a previous study carried out in this population showed that these two traits are repeatable ( $R = 0.40 \pm 0.05$  for HA and  $0.18 \pm 0.05$  for BR, see Klueen et al. 2014) and thus reflect aspects of blue tits' personality. Using univariate and multivariate animal models, we first showed that HA and BR constitute heritable aspects of the birds' personality ( $h^2 = 0.35 \pm 0.07$  and  $0.20 \pm 0.07$  respectively) that are uncorrelated on the genetic level ( $-0.02 \pm 0.20$ ). Both traits are thus heritable and can respond to selection independently. We found that repeatability is about 40% for both traits, which is in line with what has been found for behavioural traits (37%, Bell et al. 2009). For BR, the "heritability of personality" (defined by Dochterman et al. 2015 as the ratio of VA on VI) is 48%, which is very close to the average heritability of personality and implies that additive genetic effects and permanent environmental effects, due to parental or long-term environmental effects (including positive feedback loops), equally determine the between-individual variation in this trait. In contrast, 81% of the between-individual variation in HA is due to additive genetic effects, which is within the range that can be expected for aggression and antipredator behaviours (Dochterman et al. 2015). These heritability estimates mirror those obtained for the same traits in nestlings in the same population (Brommer & Klueen 2012). We found a positive residual correlation ( $0.18 \pm 0.05$ ) between HA and BR, which also found by Klueen et al. 2014, but no genetic correlation between them. This positive residual correlation might be due to measurement error or correlated plasticity, both traits being measured during the same day and handling event. The absence of a behavioural syndrome between HA and BR in adults contrasts with Brommer and Klueen (2012), where these traits were strongly genetically correlated. Whether this behavioural syndrome disappears due to selection or age-related plasticity was investigated in **Chapter II**.

We then analysed whether each trait was under survival selection and found that the apparent survival probability in the population depended mainly on the year and on the interaction of sex and BR. Indeed, females with a higher BR had a lower probability to survive from one year to the other while the males' probability of survival, although slightly higher than females', was not affected by BR (Figure 4). In contrast, HA did not affect the apparent survival probability. Although we can only speculate about what causes the negative impact of a high BR on females' survival probability, it could be argued that this might not be caused by an increased predation risk because BR does not affect the probability of being captured. Birds that are not caught on some years may indeed be more cautious, and would be less likely to be predated. Alternatively, the negative impact of BR

on females' survival could be caused by a lower competing ability over food resources during winter (Nilsson et al. 2011).

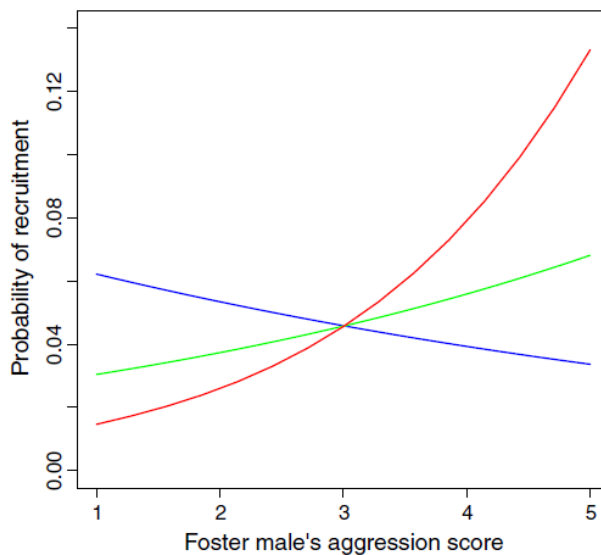


**Figure 4:** Probability of apparent survival of adult blue tit males and females as a function of their breath rate (n of breaths/s) based on capture–mark–recapture (CMR) analysis of encounter data covering 2007–2012, as reported in Table 2. For clarity, we plot the survival selection only for the year 2007, but this pattern was the same in the other years (except for differences in average survival between years), as there was no significant interaction with year (Table 2). Solid lines represent the values estimated by the binomial model for males (blue) and females (red) and the dashed lines represent the 95% confidence intervals. The CMR analyses was based on values of breath rate standardized to zero mean and unit SD, but we, here, plot the relationship of apparent survival and breath rate on the data scale, based on values (1.4–3.0 breaths/s) which contain 95% of its observed distribution. (Reproduced from Class et al. 2014. *Ecology and Evolution* 4:427-440. doi:10.1002/ece3.945; see original publication I).

In a third step, we investigated whether each personality trait affected individuals' reproductive success through genetic or parental effects and whether there was selection for assortative mating based on these personality traits. We found that the offspring's probability to recruit was affected by the year and increased with foster fathers' HA, especially when paired with females with similar HA scores (Figure 5). There was indeed a significant interaction between foster parents' HA scores, indicating the presence of selection for assortative mating mediated by parental effects. In addition, birds mated assortatively regarding their HA score (Pearson's correlation between males and females' first HA score  $r=0.19$ ; 95% CI: [0.067, 0.31]), and a positive impact of foster fathers' HA was also found on the nestlings' mass at 16 days old, which has been shown to impact their survival probability after fledging (e.g. Garnett 1981, Tinbergen & Boerlijst 1990, Naef-



Daenzer et al. 2001, Monrós et al. 2002). Finally, the effect of genetic parents' HA was systematically non-significant and BR did not influence in any way the offspring's recruitment probability. These results are in agreement with other studies in the wild showing that partners with similar personalities achieve higher reproductive success (Both et al. 2005, Gabriel & Black 2012, David et al. 2015). In this study we demonstrated that this positive effect of personality on the offspring recruitment is independent from genetic effects (the genetic quality of parents or their genetic compatibility), but is instead caused by parental effects which were previously shown in a lab population of zebra finches (Schuett et al. 2011). We can exclude a bias in the apparent recruitment of offspring due to effects of foster parents' HA on their offspring's natal dispersal because foster parent's HA had no effect on the natal dispersal of the recruits within the study site. Therefore, several non-exclusive hypotheses can be proposed to explain these results. These hypotheses include a better foster male's ability to obtain good territories (Nilsson & Smith 1985, Naef-Daenzer et al. 2001), a higher investment of males in parental care (Dickens et al. 2008, Grieco 1999), a higher investment of females mated with these males in parental care (Mutzel et al. 2013), or a better synchronization of partners over parental care (Spoon et al. 2006, Royle et al. 2014).



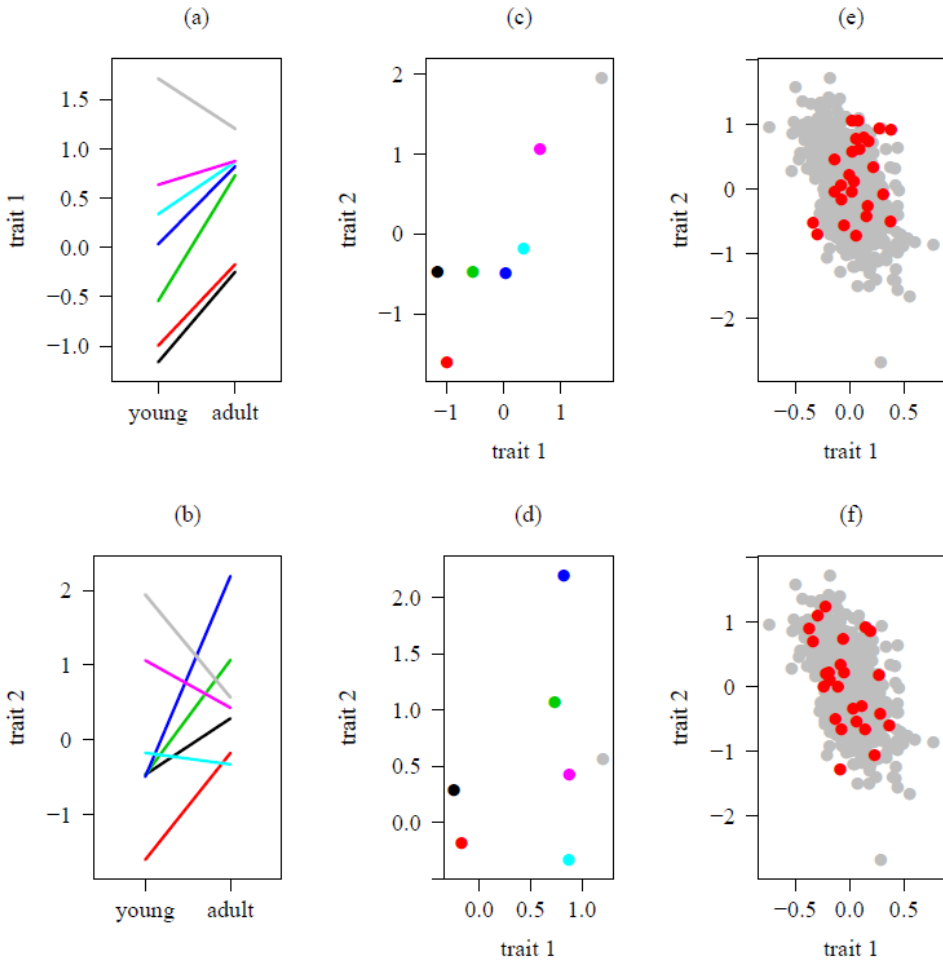
**Figure 5:** Illustration of the effect of foster parents' handling aggression on the offspring's probability of recruitment as based on reciprocal cross-fostering carried out in 2007–2010, derived from the model coefficients reported in Table 3. Recruitment selection is plotted here for the year 2007 only, but is qualitatively the same in other years since there was no interaction with year (Table 3). The analysis was based on handling aggression standardized to zero mean and unit SD, but is here plotted on the data scale. The probability of recruitment was calculated for foster fathers paired with highly aggressive (score = 5, red), intermediate (score = 3, green) and nonaggressive (score = 1, blue) females. (Reproduced from Class et al. 2014. *Ecology and Evolution* 4:427–440. doi:10.1002/ece3.945; see original publication **I**).

## 4.2 Developmental stability of a behavioural syndrome (II)

In **Chapter II**, we investigated the developmental stability of a behavioural syndrome caused by a genetic correlation. Indeed, the previous finding that HA and BR were uncorrelated in adults despite their strong genetic correlation in nestlings ( $r_A = -0.50 \pm 0.15$ , Brommer & Klun 2012) was puzzling and deserved further investigation. Adopting a quantitative genetic approach to the study of personality development can provide some insights into what causes behavioural syndromes. For example, a behavioural syndrome that is consistent over an individual's ontogeny can indicate either that the genetic architecture is strictly maintained, or that a functional link exists between them, referred to as structured pleiotropy (De Jong 1990). In the first case, there is no GxA, while in the second there can be GxA, albeit the relative rankings of genotypes for both traits are maintained across age classes such that their correlation is unchanged. Two possible mechanisms can explain changes in genetic correlations over the course of development: selection and plasticity. Selection, by favouring certain combinations of traits, can eliminate a genetic correlation between two traits if this genetic correlation is caused by linkage disequilibrium. Under this scenario, nestlings in which the genes coding for HA and BR were associated would thus disappear from the population before adulthood. Secondly, the genetic correlation between the two behaviours can be caused by GxA occurring in one or both traits (Figure 6). Indeed, the expression of genes determining one or both behaviours might have changed over time, for instance turning "on" or "off" or changing in their effect sizes, which would have changed each individual's breeding value for one or both behaviours and thus their genetic correlation.

Using a character-state approach, we first confirmed the previous finding that the genetic correlation between HA and BR was strongly negative in nestlings ( $-0.49 \pm 0.09$ ) and did not differ from zero in adults ( $0.07 \pm 0.16$ ). We then demonstrated that the genetic correlation did not disappear due to selection, because the genetic correlation between HA and BR offspring did not statistically differ between recruited and non-recruited nestlings but did differ significantly between nestlings and adults. In contrast, we found evidence for GxA because the cross-ontogeny correlation for HA and BR, although positive ( $0.38 \pm 0.10$  for HA and  $0.50 \pm 0.11$  for BR), differed significantly from 1. The hypothesis that the genetic correlation between HA and BR disappeared during ontogeny because the two behavioural traits underwent GxA was further supported by our simulations. Genetic correlations between traits can constitute evolutionary constraints (Lynch & Walsh 1998), and a meta-analysis suggested that genetic correlations between behavioural traits might constrain their independent evolution to higher extent than for life-history traits (Dochtermann & Dingemanse 2013). Altogether, our results show that genetic correlations underlying behavioural syndromes can change during the ontogeny because of developmental processes, and thus that behavioural syndromes might not be as evolutionarily constrained as previously thought. Because the assumption of the lifelong stability of behavioural syndromes might lead to inaccurate predictions of their

evolutionary trajectories, this study underlines the importance of considering personality and behavioural syndromes at multiple ontogenetic stages and calls for incorporating quantitative genetics to the study of personality from a lifetime perspective.



**Figure 6:** Theoretical plot illustrating the notions of consistency over the ontogeny, genotype-age interaction (GxA) and selection on the genetic correlation between trait 1 and trait 2. In (a,b), each line represents one individual, which is reported as a point in (c,d). In (a), the rank order of the individuals' breeding values for trait 1 remains stable across ontogeny. In (b), the rank order of the breeding values for trait 2 is different in young and adults because of GxA. As a consequence, the positive genetic correlation between trait 1 and trait 2 in young individuals (c) disappears in adults (d). Figures (e) and (f) represent the breeding values of nestlings that recruited (red) or not (grey), assuming a 5% recruitment probability. In (e), the breeding values of the two traits are not negatively correlated in recruits, which is why the genetic correlation is 0 when these individuals are measured as adults. In (f), the individuals are selected randomly and thus the correlation stays negative when they are measured as adults. (Reproduced from Class & Brommer 2015. *Proceedings of the Royal Society B*. 282:20142777. doi:10.1098/rspb.2014.2777; see original publication II).

### 4.3 Consequences of behavioural plasticity for the life-long stability of personality (III)

Although age-related plasticity in personality has been well studied by psychologists and animal breeders, it has largely been overlooked by behavioural ecologists. This chapter aims at drawing the attention of behavioural ecologists to the occurrence of IxA and GxA in behaviour and its consequences for repeatability and heritability across ages and for the stability of behavioural syndromes. Indeed, individual differences in plasticity that are heritable can be expected whenever there is a population-level change in the expression of behavioural trait. For instance, average personality changes over the lifetime of individuals have been well documented in humans (McCrae et al. 2000) and non-human species (Suomi et al. 1996, King et al. 2008, Sinn et al. 2008, Kubinyi et al. 2009, Réale et al. 2009, Dammhahn 2012, Selmann et al. 2012, Massen et al. 2013, Fisher et al. 2015, Hall et al. 2015).

In this chapter, we first provide a quantitative genetic description of GxA and of the methods used for its detection, which is similar to what I described earlier in this thesis for GxE. Importantly, we show that the occurrence of IxA (or GxA) can cause changes in between-individual (or genetic) variance and changes in behavioural rankings of individuals (or genotypes) across ontogenetic stages (see Figure 2 for GxE). The occurrence of IxA (or GxA) can hence alter behavioural repeatability (or heritability) across ages. We then reviewed empirical evidence for age-related changes in repeatability as well as estimates of cross-ontogeny correlations for single behaviours. The direction of the age-related changes in repeatability has been difficult to predict: a lower repeatability in juveniles than in adults can be expected due to ongoing developmental changes, but the opposite can also be expected due to highly constrained developmental trajectories in juveniles (Biro & Stamps 2008). One meta-analysis did not find any difference in repeatability in juveniles and adults (Bell et al. 2009), but mostly included studies which focussed on only one ontogenetic stage. Based on the very few studies estimating repeatability in both juveniles and adults, we found that repeatability was on average slightly lower for juveniles than for adults, although the difference was small, only concerned vertebrates (e.g. David et al. 2012, Petelle et al. 2013), and some studies (Fratkin et al. 2013, Bajer et al. 2015) found opposite results. The few available estimates do not, therefore, allow us to draw any conclusion about potential age-related changes in repeatability. In contrast, studies reporting phenotypic correlations of behaviours across ages were more abundant. Using both significant and non-significant estimates, we found that the cross-ontogeny correlations of behaviours are generally positive and on average moderate (0.3). These results are consistent with the predictions from GxA or IxA causing rank-order changes, and thus cross-ontogeny correlations lower than 1 for behaviours. However they do not constitute evidence for GxA or IxA because we only included estimates on the phenotypic level which constitute most of the estimates available for

behaviours. To date, **Chapter II** constitutes rare evidence for a low cross-ontogeny correlation between behaviours on the genetic level.

From a theoretical point of view, correlations between behaviours are also expected to change as a result of IxA or GxA. This was empirically shown in **Chapter II**, where two behaviours forming a behavioural syndrome undergo GxA, which causes their genetic correlation to disappear. In this study, we used simulations to demonstrate that a behavioural syndrome caused by a strong genetic correlation between behaviours in juveniles can decrease, disappear, or change sign if at least one of the traits undergoes GxA between during the part of the ontogeny considered. A few empirical studies indeed found changes in the magnitude (e.g. Guenther & Trillmich 2012) or the sign (e.g. Kanda et al. 2012) of phenotypic correlations between behaviours over age, although here again they do not constitute direct evidence for GxA.

To summarize, this chapter showed the importance of considering age-related plasticity in behaviour in personality research because of its consequences for repeatability, heritability and the stability of behavioural syndromes over the lifetime. Our review of the available studies using phenotypic data suggests that IxA and GxA might be common, although direct evidence remains scarce. In contrast, the relative roles of environmental vs. genetic effects for lifetime changes in personality have been well documented in humans (Bergen et al. 2007, Bornovalova et al. 2009, Kandler 2012, Kandler et al. 2013). In order to encourage future studies of IxA and GxA in behaviour, we also detailed two quantitative genetic approaches, namely the character-state approach, which was used in **Chapter II**, and the random regression approach, which we implemented in **Chapter IV**. The latter approach has recently been used to investigate IxA in behaviour (Fisher et al. 2015, Polverino et al. 2016).

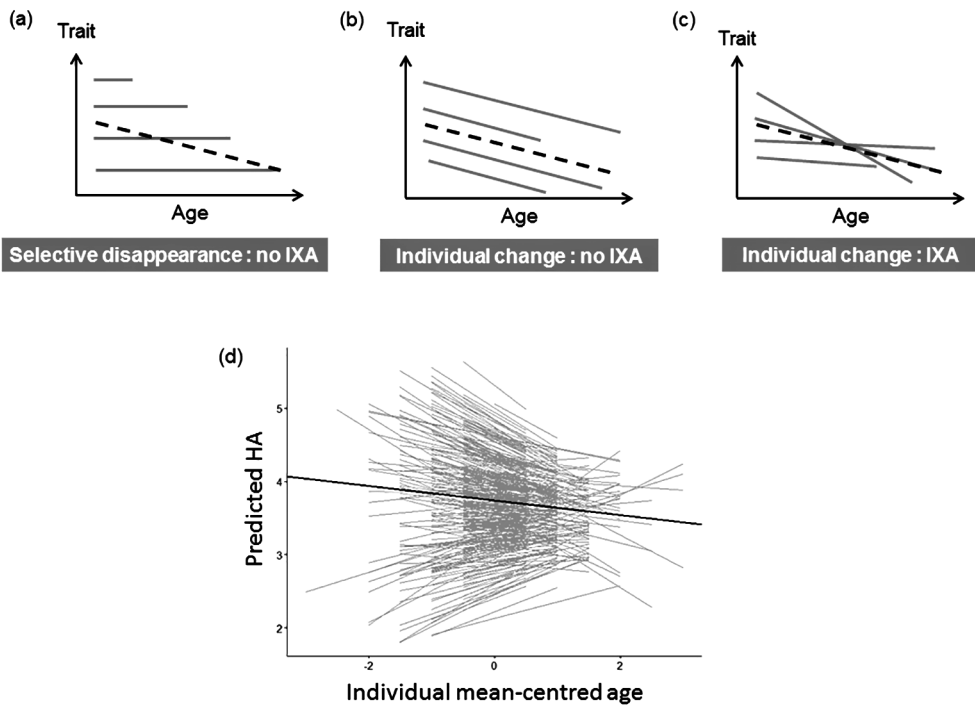
#### **4.4 Senescence in two behavioural responses to handling (IV)**

In this chapter, we investigated the life-long stability of HA and BR and tested for the presence of IxA and GxA using the random-regression approach introduced in **Chapter III**. This approach has often been used to study senescence, which is defined as a decline in the fitness of individuals as they age (Medawar 1952, Williams 1957, Hamilton 1966) and has been found across many animal taxa (Nussey et al. 2013, Jones et al. 2014). Evolutionary explanations for the occurrence of senescence predict that traits that are positively linked with fitness will show an age-related decline associated with GxA (Promislow et al. 1996, Wilson et al. 2008, Charmantier et al. 2014). These explanations hinge on the fact that selection becomes weaker as individuals age because relatively few individuals live long enough to get old. As a result, deleterious mutations decreasing individual performance in late life may accumulate due to random processes (Medawar 1952) or may invade the population because they increase individual performance in early life (Williams 1957). The consequence of either of these processes is the presence of

additive genetic variation in the rate of ageing, or GxA, which can be considered as the “fingerprint” of evolved senescence (Wilson et al. 2008, Charmantier et al. 2014). Because most personality traits are heritable (Dochtermann et al. 2015) and linked with fitness (Smith & Blumstein 2008), just as HA and BR in this population (**Chapter I**), they might also undergo senescence, which can be investigated by first testing whether traits that are positively related to fitness decline with age and then testing if individuals or genotypes differ in their rate of ageing. Alternatively, the asset protection principle predicts that personality traits increasing reproductive success will increase over age as the individual’s residual reproductive value decreases (Clark 1994, Wolf et al. 2007). We found that HA decreases linearly over age in the population and that this decrease is unlikely to be due to selective disappearance of highly aggressive individuals or to habituation, but rather caused by age-related plasticity (Figure 7). This population-level decline in HA, which is positively related to reproductive success in males, contrasts with the asset protection principle, but is consistent with predictions from the senescence hypothesis. In addition, the random regression approach applied to HA further showed that individuals differ in their rate of age-related decline (Ix<sub>A</sub>), but failed to provide support for GxA, presumably because of low power. Interestingly, we found an age-related decrease in between-individual variance in HA, which, if associated with a decline in additive genetic variance, contrasts with both theoretical predictions (Charlesworth & Hughes 1996) and empirical studies finding a stable or increasing additive genetic variance over age (Brommer et al. 2007, Wilson et al. 2007, Brommer et al. 2010b). Alternatively, this decline in between-individual variance could be caused by a decline in permanent environment variance, although most of the individual variance in slopes (0.26) seems to be due to additive genetic effects (0.21) rather than permanent environment effects (0.04). However, it is important to keep in mind that this pattern was found on the individual-centred age scale, which makes its interpretation difficult. Altogether, these results show an age-related decline associated with individual differences in plasticity in a personality trait, and suggests the occurrence of senescence in this trait. An important next step to confirm this hypothesis and rule out the possibility of selection favouring an age-related decrease in HA will be to test whether the link between HA and fitness is constant over age.

In contrast, we did not find any age-related change in BR, which raises the question of which personality traits are expected to undergo senescence. Because the occurrence of senescence in reproductive success or survival has not been formally tested in this population, we can only speculate about possible causes for why HA would undergo senescence but not BR. For example, in great tits (*Parus major*), a closely related species, fertility declines after the first year of reproduction (Bouwhuis et al. 2009) while mortality remains relatively constant (Jones et al. 2014). This pattern is in line with our findings in that the personality trait showing a senescent decline is the one associated with reproductive success while the personality trait associated with survival does not change with age. This potential link between senescence in fitness traits and personality would

deserve further investigation in this population, but also empirical work in other systems to test for its generalization. For instance, personality traits could show different ageing patterns depending on how strongly they relate to the fitness component showing the strongest age-related decline.



**Figure 7:** Predicted patterns for age-related changes in a behavioural trait (a-c) and results obtained for handling aggression (HA)(d). Plots (a) to (c) are theoretical representations of the different individual patterns (grey lines) possibly underlying a population-level decline in a behavioural trait over age (dashed black line). In (a), the mean population decline over age is caused by the disappearance of individuals with high values of the trait (between-individual effect). In (b), all the individuals express age-related plasticity (within-individual effect). In (c), individuals vary in age-related plasticity: there is an individual-age interaction (IXA). In (d), predicted individual and mean values of HA are plotted as a function of individual mean-centred age. Grey lines representing individual values were derived from model 3 and plotted for the 406 individuals who have multiple measurements for HA. The black line represents the mean HA as a function of individual mean-centred age. (Modified from Class & Brommer 2016. *Behavioral Ecology and Sociobiology* 5:733-744. doi:10.1007/s00265-016-2096-0; see original publication **IV**).

#### 4.5 A quantitative genetic view of assortative mating for labile traits (V)

This last chapter demonstrates that the metric used for estimating assortative mating in wild populations in ecology and evolutionary studies, including quantitative genetic analyses, can be biased when applied to labile traits such as behaviour. Indeed, assortative mating is commonly calculated as the correlation between males and females phenotypes across mated pairs (Jiang et al. 2013), and it is generally assumed that the phenotypic resemblance of partners resulting from non-random mate choice captures associations in “intrinsically determined” trait values (Kirkpatrick & Barton 1997;  $m = h^2r$ , where  $m$  is the correlation between breeding values and  $r$  the phenotypic correlation, see Falconer & Mackay 1996). However, using a variance partitioning description for labile traits (or traits measured with error), we show that the correlation between phenotypes of paired individuals does not only arise due to the correlation between their individual-specific values (“true assortative mating”), but can also be due to (short term) shared environmental effects on the phenotypes of paired individuals or correlated measurement error. Importantly, these processes are likely to be common for labile traits, which respond plastically to environmental factors often varying in time and space, and we show that their relative contribution to the phenotypic correlation between mated partners depends on the repeatability of the traits (Figure 8). For instance, the phenotypic correlations between “fixed” traits that are highly repeatable ( $R \sim 1$ ) in males and females will mostly reflect the correlation between their individual-specific values. In contrast, most behavioural traits are less than 50% repeatable, and hence the correlation between the phenotypes of mated individuals will mostly reflect covariance due to shared environmental effects or correlated measurement error.

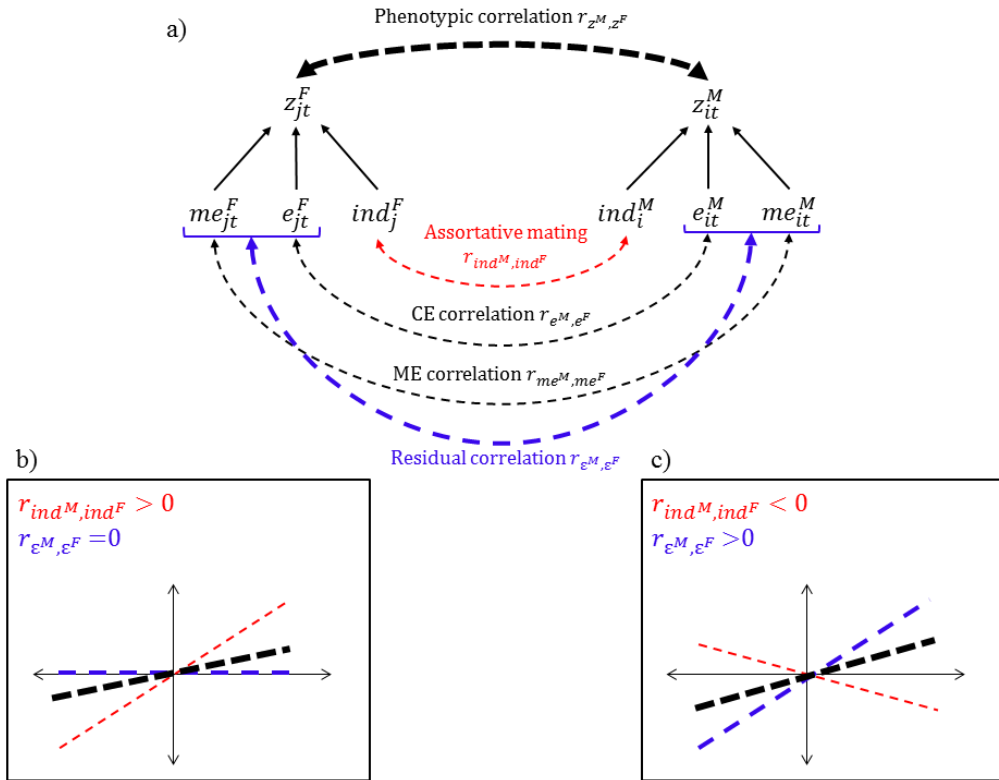
We introduced different statistical approaches which can be used to estimate assortative mating in labile traits, or in traits measured with error: i) The correlation between mean phenotypes of males and females of each unique pair (CIM), ii) The correlation between randomized values of individuals (CIR) iii) Between- and within-pair correlations derived from bivariate mixed-effects models. One critical aspect for the performance of these different approaches is the number of replicated measures on the individual level for the CIM and CIR approaches, and on the pair level for the bivariate mixed model approach. Although the amount of replication on both levels is similar if individuals forming pairs always survive and remate, they are likely to be different in most natural populations where individuals mate with different partners due to divorce or to the death of their previous partner. We thus investigated the relative performance of the introduced approaches using simulations of assortative mating in two hypothetical populations (the “immortal albatross” and the “bluish tit”) characterized by stable or unstable pair compositions and monitored once or twice per breeding season for a few (3) years or for many (10) years. Data was generated and analysed using each approach for scenarios where the phenotypic correlation between males and females was due either to the



correlation between their individual-specific values (assortative mating only scenario) or to shared environmental effects (common environment only scenario).

As predicted, we found that the performance of both individual-level approaches critically depends on the number of replicates within individuals, while the performance of the pair-level approach depends on the number of replicates within pairs. Importantly, both CIM and CIR approaches are biased towards the phenotypic correlation when the number of replicates is low, which in the “common environment only” scenario increases the risk of spuriously detecting assortative mating when it is absent (Type I error). In contrast, the bivariate mixed model approach, although the most conservative, provides consistently unbiased estimates of assortative mating, common environment correlation, and residual correlation. Therefore, the bivariate mixed model was the best approach for this worked example, and we showed that adopting a study design where repeated measures are taken on the level of the pair drastically increased its statistical power. Because the performance of each approach depends on the characteristics of the population (e.g. repeatability of the trait, rates of mortality and divorce, population size), we advised the use of simulations to: i) choose the best statistical approach given the data already collected, or ii) choose the best sampling design and the best statistical approach based on the characteristics of the population and the trait repeatability.

Recently, there has been an increasing interest in estimating assortative mating based on personality traits and estimating its impact on fitness (Dingemanse et al. 2004, Both et al. 2005, Sinn et al. 2006, Spoon et al. 2006, Schuett et al. 2011, Gabriel & Black 2012, Ariyomo & Watt 2013, Kralj- Fišer et al. 2013, Harris et al. 2014, David et al. 2015). Indeed, assortative mating has been proposed as a mechanism contributing to the evolution and maintenance of personality (see above). Therefore, the field of animal personality research would benefit from adopting a variance-partitioning approach allowing to accurately estimating assortative mating and assessing the importance of environmental and residual covariance for the phenotypic resemblance between partners. In addition, we argue that the approaches described in this paper are not restricted to assortative mating for repeatedly expressed traits such as behaviour, physiology, or metabolism but can be applied to a wider range of traits, contexts, and mating systems. We do, however, point out some issues, such as that the occurrence of permanent environmental effects that are correlated between partners and indirect (genetic) effects (e.g. when partners’ personalities converge after mating) can be confounded with assortative mating in the pair-level approach introduced here. Solving these issues would require either partitioning the between-pair covariance further to the genetic and permanent environmental levels, or, because phenotyping individuals before and after they form pairs can be difficult, further developments of statistical approaches using data of individuals mating repeatedly with different partners.



**Figure 8:** Correlations at multiple levels shape the overall phenotypic correlation between paired individuals. In a), phenotypes of paired males and females ( $z_{it}^M, z_{jt}^F$ ) are determined by individual-specific values ( $ind_i^M, ind_j^F$ ), environmental effects ( $e_{it}^M, e_{jt}^F$ ) and measurement error ( $me_{it}^M, me_{jt}^F$ ), where 1/3 of the phenotypic variation is due to individual differences and the remainder to residual variation ( $\varepsilon = me + e$ ). Correlations can exist at each level (dashed arrows); the phenotypic correlation equals (Eqn. 2)  $r_{z^M, z^F} = 1/3 * r_{ind^M, ind^F} + 2/3 * r_{\varepsilon^M, \varepsilon^F}$ . The phenotypic correlation thus b) underestimates or c) overestimates the correlation caused by assortative mating. (Reproduced from Class et al. 2017. *Methods in Ecology and Evolution* 38:42-49. doi:10.1111/2041-210X.12837; see original publication **V**).

## V. CONCLUSIONS AND FUTURE DIRECTIONS

This thesis addressed a range of classical themes in evolutionary quantitative genetics in the context of animal personality evolution. Indeed, the first four chapters of this thesis applied quantitative genetic approaches to personality traits measured in the wild to estimate their heritability (**I**) and the genetic correlation between them (**II**, **III**), study their plasticity across the ontogeny (**II**, **III**, **IV**), and whether selection acts on them (**I**, **IV**) or on their correlation (**II**). The most important findings of chapters **I**, **II**, and **IV** are: i) HA and BR, two behavioural responses to handling measured in adult and nestling blue tits, are heritable and linked with adults' performance in the wild. While BR decreases females' survival, HA increases males' reproductive success, especially when paired with females that are similar in their HA score. This positive interaction of both parents' HA on their reproductive success suggests the presence of selection for assortative mating, which is mediated by parental care only; ii) Although HA and BR are genetically correlated and form a behavioural syndrome in nestlings, their correlation disappears in adults not because of correlated selection but because of developmental plasticity, and more specifically genotype-age-interactions; iii) HA in adults declines within individuals over their lifetime, and individuals vary in their rates of decline, which suggests the occurrence of senescence in HA.

Altogether, these findings raise the question of the maintenance of additive genetic variance in HA and BR, given that both traits are under directional selection. Although this thesis does not provide clear evidence for any of the evolutionary mechanisms potentially maintaining additive genetic variation in personality, the results obtained suggest that some of them may be occurring in this population. For instance, there is selection for assortative mating based on HA on the phenotypic level, which, if present on the genetic level could help maintain additive genetic variation in HA in the population. In addition, there is evidence for GxA during the first year of life in blue tits which may help maintaining additive genetic variation in HA and BR if selection favours different phenotypes in nestlings and in adults. In contrast, selection analyses in **Chapter I** showed no evidence for fluctuating selection on personality because there was no significant interaction between personality and year. Because these analyses only included a few years of data, new selection analyses including a now longer study period could be performed in future studies. Furthermore, selection for personality traits differs between the sexes but does not act in opposite directions. Although each trait is highly genetically correlated across the sexes (unpublished results), these results do not support sexually antagonistic selection as a mechanism maintaining additive genetic variation in HA and BR. Finally, whether HA or BR are part of a pace-of-life syndrome has not yet been tested and would deserve proper investigation.

Importantly, three chapters of this thesis focused on the ontogeny of personality to underline its importance for studying the evolution of personality, and to encourage further

empirical work on this question using the tools provided by quantitative genetics. Personality changes over the lifetime of individuals have been well reported and the sources of between-individual variation in these changes investigated in humans and non-human primates. In contrast, behavioural ecology studies, despite an increasing interest in estimating the sources of between-individual variation in behaviour, are mostly focused on a limited part of the ontogeny of their subjects. While behavioural ecology studies would benefit from adopting a lifetime perspective, psychology studies have implemented quantitative genetic approaches such as random regression analyses, but do not report lifetime changes in the amount of additive genetic or between-individual variance (Mroczek & Spiro 2003, Terracciano et al. 2005). Studying lifetime changes in personality using a quantitative genetic framework in different taxa would allow comparative studies of personality development and provide valuable insights into the evolution and phylogeny of this fascinating phenomenon.

Finally, the fifth chapter of this thesis shows that the approach traditionally used for estimating assortative mating in “fixed” traits is largely inappropriate when applied to labile traits such as behaviour. Fortunately, alternative approaches are available to accurately estimate assortative mating and other sources of phenotypic resemblance between mated partners, which are often assumed to be absent in quantitative genetic analyses (Falconer & MacKay 1996). Further developments of these approaches might enable the answering of new questions such, as the occurrence of indirect genetic effects between partners, or the niche-specialization hypothesis (Dingemanse & Araya-Ajoy 2015). One important aspect of this last chapter is that it questioned one assumption that is traditionally made for fixed traits but might not be appropriate for behaviour. Another important assumption that is often made, mostly by convenience, is the minor role of dominance genetic variance in quantitative traits (Lynch & Walsh 1998). In fact, a substantial amount of dominance variance can be expected in personality traits because they are closely related to fitness, (Mousseau & Roff 1987, Crnokrak & Roff 1995). Although dominance variance was found in personality in humans (Eaves et al. 1998, Keller et al. 2005, Pilia et al. 2006), captive primates (Adams et al. 2012), and from various laboratory or agricultural populations (reviewed in Wolak & Keller 2014), estimates from wild populations remain scarce. This is because estimating dominance variance requires a large amount of data on specific types of relatives, which can be difficult to collect in wild populations. Avian study systems such as the blue tit population studied for this thesis, characterized by relatively large family sizes, extra-pair offspring, and pedigree records for many generations, are nevertheless good candidates for estimating dominance variance (Wolak & Keller 2014). Accounting for dominance variance in personality traits in the wild will not only allow for a better estimation of its different variance components, but is also of interest due to its many evolutionary implications, especially in the mechanisms maintaining additive genetic variation in personality (Roff 1997, Wolak & Keller 2014).

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