Adaptive causes of among-individual differences in behaviour *from theory to data*

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To my sister,

for your unconditional support and love.

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Summary

Phenotypic variation is the basis of evolution because it acts as the raw material for selection. However, when a trait is under selection, favoured alleles may get fixed in the population and phenotypic variation could be eroded. Thus, to understand how variation in phenotypic traits can be maintained represents a central challenge in evolutionary biology. The overall aim of my PhD project was to study the evolutionary and behavioural ecology of among-individual variation in labile traits such as behaviour. The studies presented in this thesis were specifically planned to combine theoretical models and empirical data to obtain a better insight into the mechanisms explaining the existence and maintenance of individual differences in behaviour (i.e., animal personality). I addressed empirical questions using both observational and experimental data collected in the field and the lab in wintering and breeding great tits (*Parus major*).

Behavioural ecologists have often focused on studying population-average levels of phenotypic plasticity. While it might be insightful in some cases, one should not ignore the multilevel nature of phenotypic variation in labile traits, such as behavioural or life-history traits. **Chapter 1** is an opinion paper where my colleagues and I discussed the application of state-dependent behaviour theory to the study of animal personality, and expanded these ideas to broaden the conceptual framework of adaptive individual variation in behaviour. Particularly, our aim was to expand classic optimality models to specifically focus on among-individual differences in behaviour. Additionally, we presented new ideas about experimental design and provided insights into the statistical approach to empirically test the postulated models about among-individual differences in behaviour.

Life-history theory posits that trade-offs are a likely mechanism maintaining phenotypic variation among individuals, assuming that variation already exists among individuals. Life-history theory also postulates that trade-offs might exist at some but not other hierarchical levels (e.g. within- but not among-individuals). In **Chapter 2**, we investigated whether a behavioural trade-off exists between two decision-making (cognitive) traits, thereby explaining the maintenance of variation in cognition, a presumed driver of variation in animal personality. To do so, we carried out a lab experiment to study a trade-off between accuracy in taking a decision and speed with which that decision was taken. We showed that speed-accuracy trade-offs were indeed level-specific: trade-offs between speed and accuracy existed among-individuals but not within-individuals. Our result thus demonstrated that birds that on average took faster decisions also were more

often wrong in their decisions than birds that on average took slower decisions. Furthermore, we also demonstrated that failure to correctly account for level-specific patterns of covariance can lead to biased inferences about the existence of trade-offs (i.e. we found no trade-off at the population level). This study thus exemplified the importance of partitioning the phenotypic variance among different hierarchical levels (i.e. of considering the hierarchical structure of labile traits) and supports the notion that trade-offs indeed have great potential in acting as mechanisms generating among-individual variation in behaviour.

Following up with the notion of trade-offs as a cause of phenotypic variation among individuals, in **Chapter 3** we investigated the factors that determine energy management in wintering great tits. Birds such as the great tit would face the bad winter conditions by increasing their fat reserves. However, birds must simultaneously avoid predation from aerial predators (e.g. hawks), giving rise to a trade-off between avoiding predation and avoiding starvation during periods of harsh environmental conditions. In **Chapter 3**, we studied the relationship between foraging activity at feeders and daily mass gain in wild wintering great tits. Our results demonstrated that birds foraged and gained mass early during the day, as predicted by theory when the starvation-predation risk trade-off is mass-dependent and starvation risk outweighs predation risk. We concluded that increased energetic demands experienced by small birds in winter might favour individuals avoiding risk of starvation rather than predation avoidance. Furthermore, the hypothesized trade-off did not explain the existence of among-individual variation in behaviour because individuals did not differ in how they resolved the starvation-predation risk trade-offs, i.e. all birds gained mass in the similar manner throughout the day. This result suggests a different process (e.g. another trade-off) as the underlying mechanism explaining the observed variation in foraging behaviour among individuals.

In **Chapter 4**, we jointly tested the two distinct bodies of theory explaining the maintenance of among-individual variation. On the one hand, evolutionary ecologists expect phenotypic integration in situations where correlational selection favours optimal combinations of functionally-related traits. On the other hand, optimality models developed by behavioural ecologists predict that an individual’s behaviour will vary as a function of its state (e.g. body condition, size), thus also predicting that particular combinations of state and behaviour maximize fitness. Both the state-dependent personality theory and correlational selection concept, therefore, imply that selection favours phenotypic integration and simultaneously leads to a flat fitness surface. In **Chapter 4,** we combined these two approaches and investigated patterns of phenotypic integration between morphology and behaviour based on predictions derived from two optimality models (the “asset protection” and “state-dependent safety” model). To test this hypothesis of “state-dependent personality”, we explored patterns of covariance for multiple morphological traits (body mass, wing length, tarsus length and bill length; encapsulating two dimensions of “state”: structural size and energetic reserves) and two behaviours (aggressiveness and exploration) in free-living great tits in spring. Our results demonstrated the existence of a behavioural module “risk-taking behaviour” that covaried with each of two morphological (state) modules (“body size” and “energy reserves”), thereby providing support for both optimality models simultaneously. We thus demonstrated the existence of state-dependent personality using for first time a multivariate approach. Furthermore, our results suggest that phenotypic integration in situations where correlational selection favours optimal combinations of functionally-related traits is a potential mechanism explaining among-individual variation in behaviour.

Overall, my thesis highlighted the relevance of embracing the multi-level nature of behaviour for a full understanding of the adaptive causes of behavioural variation among individuals. This is particularly necessary because behaviour also varies substantially within individuals. While I investigated these questions in the context of animal personality, my work aimed at achieving a general understanding on the importance of acknowledging that variation in labile traits can be due to among-individual and/or within-individual processes. Therefore, the framework presented throughout my thesis could be readily applied to other labile traits such as physiological and life-history traits.

General Introduction

Multi-Level Phenotypic Variation in Labile Traits

Phenotypic variation is the basis of evolution because it acts as the raw material for selection (Darwin, 1859). However, when a trait is under selection, favoured alleles may get fixed in the population and phenotypic variation could be eroded. A central challenge in evolutionary biology is therefore, to understand how variation in phenotypic traits can be maintained (e.g. Endler, 1986; Lack, 1961; Wilson, 1998); and a full understanding of phenotypic evolution necessarily requires acknowledging the multi-level nature of phenotypic variation (Westneat, Wright, & Dingemanse, 2015).

Early studies investigating the causes of phenotypic variation among individuals have largely focused on "fixed traits", traits that are expressed only once in an individual's lifetime and vary solely among individuals. A classic example of a fixed trait is the morphological defence structures induced by the presence of predators. For instance, some species of *Daphnia* develop costly and life-long protective helmets, but only when coexisting with predatory fish (e.g. Tollrian 1995). Among-individual variation in fixed traits can be caused by genetic differences and by early-life environmental differences that have permanent effects on an individual's phenotype (Fig 1). These early-life environmentally-induced modifications of development and growth result in irreversible phenotypic variation in adulthood, a phenomenon known as "developmental plasticity" (Schlichting & Pigliucci, 1998).

In the past decade, however, evolutionary ecologists have increasingly focused on phenotypic traits that are repeatedly expressed throughout the life of an individual. These traits are called "labile traits" (Dingemanse et al. 2010). Examples of labile traits are repeatedly expressed life-history (e.g. timing of reproduction and the number of offspring) and physiological traits (e.g. body mass or energy reserves). In the case of labile traits, variation exists among- *and* within- individuals (Westneat et al., 2015) (Fig 1). Among-individual variation in labile traits can be caused by genetic and environmental differences. Environmental differences can originate among-individual variation in two ways: via irreversible plasticity in response to early-life permanent environmental effects and via reversible plasticity in response to environmental variables that affect individuals in adulthood and that do not exhibit carry-overs (Fig 1). In both cases, the environmental conditions differ among individuals. Furthermore, labile traits allow individuals to adjust their responses to environmental conditions that vary within individuals. Hence, within-individual variation in labile traits results in response to environmental differences that have non-permanent effects and change over short time spans (i.e. environmental conditions are reversible) (Piersma & Drent, 2003) (Fig 1).

Considerable research effort has been devoted to identify the conditions under which selection would favour the expression of reversible versus irreversible plasticity (Gabriel et al. 2005; Gabriel 2006; Botero et al. 2015, reviewed by Forsman 2015). The distinction between these two types of plasticity, and as corollary, acknowledging the existence of different variance components at the phenotypic level is important. This is because only among-individual variation that is underpinned by additive genetic differences is able to respond to selection. Thus, investigating the evolution of multilevel nature of labile traits will enhance our understanding of the ecological and evolutionary dynamics of natural populations (Forsman 2015).

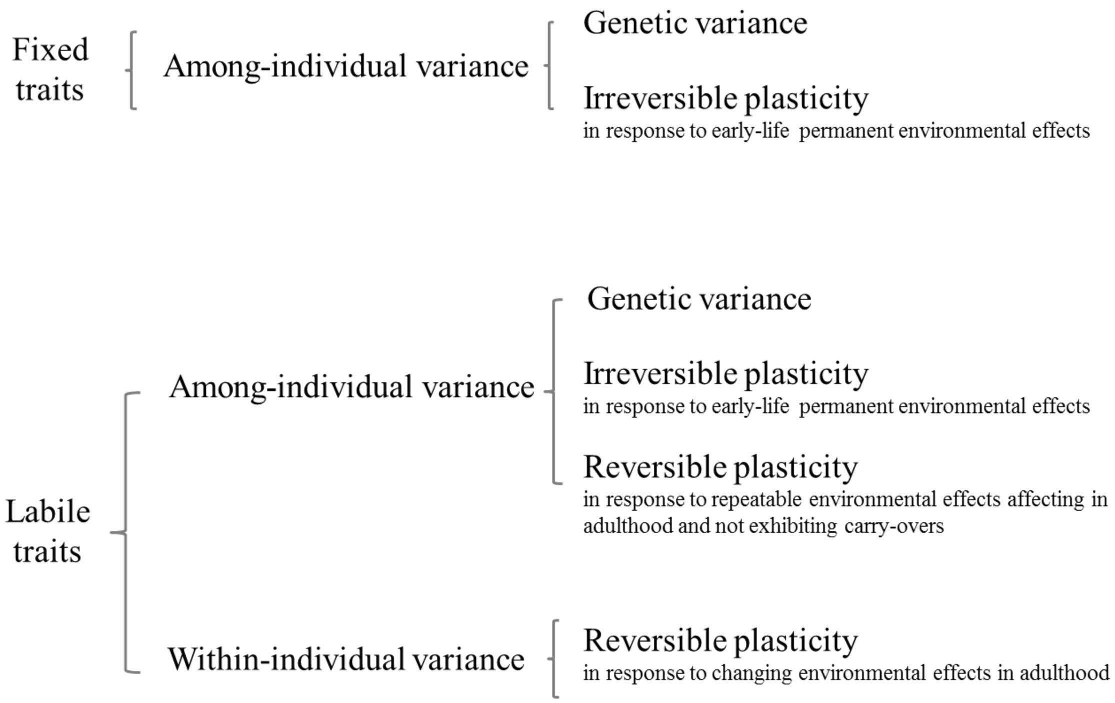

Figure 1. *Schematic summary of the processes generating phenotypic variation in fixed and labile traits. The scheme depicts how genetic and environmental differences can lead to variation among- and within-individuals.*

The framework of phenotypic plasticity developed for labile traits such as physiology and life history can as well be applied to behaviour (Dingemanse et al., 2010; Stamps & Groothuis, 2010). Behavioural traits encompass both genetic and environmental differences that generate among- and within-individual variation

(Dingemanse et al., 2010). In the field of behavioural ecology, variation among individuals in their behavioural response is usually referred to as “animal personality” (Dingemanse et al., 2010). Among-individual differences in behaviour have been observed in many species, ranging from microbes to humans (Gosling & John 1999; Sih et al., 2004; Réale et al., 2007) and have been described for a number of different behaviours (Bell, Hankison, & Laskowski, 2009; Réale, Dingemanse, Kazem, & Wright, 2010). Furthermore, animal personality has been found to be heritable (Van Oers, De Jong, Van Noordwijk, Kempenaers, & Drent, 2005; Réale et al., 2007) and to affect fitness (Dingemanse & Reale, 2005; Smith & Blumstein, 2008), being potentially subject to evolutionary change.

Trade-Offs as a Fundamental Mechanism in the Maintenance of Among-Individual Variation

Within single populations, individuals plastically adjust their responses to the environment (i.e. differences in deviations to mean behaviour), and at the same time, show repeatable differences in behaviour (i.e. differences in mean behaviour). While this “multilevel nature” of phenotypic variation in behavioural traits is commonly acknowledged, it is not yet clear why among-individual differences in behaviour actually exist (Dall et al., 2004; Sih et al., 2004; Sih, Bell, Johnson, & Ziemba, 2004; Dingemanse & Reale, 2005; Dingemanse & Wolf, 2010; Wolf & Weissing, 2010). Labile traits allow individuals to alter their phenotype to match the current environment, and therefore, have evolved to respond to reversible temporal environmental changes. Thus, the subsequent question must arise: why do individuals show consistency in their behavioural responses when plasticity is available to deal with changing environmental conditions?

The study of the origin and maintenance of animal personality has indeed stimulated the development of several theoretical models and hypotheses (Dall et al., 2004; Sih et al., 2004; Dingemanse & Reale, 2005; Dingemanse & Wolf, 2010; Wolf & Weissing, 2010). These models were developed to address the particular problem of repeatable among-individual differences in otherwise very plastic behaviours. In general terms, however, the study of phenotypic variation in natural populations necessarily revolves around the classic idea of trade-offs. Trade-offs represent the “costs paid in the currency of fitness when a beneficial change in one trait is linked to a detrimental change in another” (Stearns, 1989). The relevance of trade-offs hinges on the notion that they limit the amount of resources that an individual can allocate to single traits. This notion, while basic, is essential. If there were no trade-offs, and therefore, no limits to trait expression, selection would ultimately optimize all traits correlated with fitness (Stearns, 1989). The consequences of such fitness maximization would be the evolution of a single population of "Darwinian demons", e.g. individuals that would simultaneously live and reproduce *ad infinitum*. Since Darwinian demons do not seem to exist, trade-offs must be ubiquitous.

Another important notion is that trade-offs can often be hidden due to environmental effects. The “resource-allocation model” (van Noordwijk & de Jong, 1986) postulates that trade-offs between traits can be masked by heterogeneity across individuals in resource acquisition (van Noordwijk & de Jong, 1986; Stearns, 1992; Reznick, Nunney, & Tessier, 2000). In that case, the expected negative genetic correlations between two costly traits will remain hidden in “raw” phenotypic data. The idea is that the absolute amount of resources available is assumed to vary across individuals, e.g., some individuals have access to more resources than others. Thus, while all individuals will face the same allocation trade-off, the absolute amount of resources allocated to each trait will vary among individuals according to their absolute total amount of resources. The “resource-allocation model” is therefore able to predict when variance in acquisition of resources will swamp variation in allocation of resources, and thereby, trade-offs will be unobservable.

While trade-offs played a fundamental role in the development of life-history theory, they are also central in the study of animal personality. Trade-offs are often implicitly assumed as the underlying mechanism explaining among-individual variation in behaviour, both from the perspective of behavioural ecology and evolutionary quantitative genetics. From an adaptive theory perspective, researchers assume that selection optimizes behaviour but do not aim to formally test that assumption. The main goal of adaptive theory is to predict an individual’s behaviour by studying its optimal behavioural responses to environmental change (Parker & Maynard-Smith, 1990). From an evolutionary perspective, researchers have mainly focused on evolutionary dynamics and how behaviour responds to selection. Thus, the main aim is to understand how selection favours one particular behavioural strategy over another (Westneat & Fox, 2010). From both perspectives the study of among-individual differences in behaviour has extensively stimulated the development of theoretical models and hypotheses. Several non-mutually exclusive hypotheses have been proposed to explain the ultimate causes of among-individual variation in behaviour (Dall, Houston, and McNamara 2004; Sih, Bell, and Johnson 2004; Wolf et al., 2007; Wolf, van Doorn, and Weissing 2008; Dingemanse and Wolf 2010; Luttbeg and Sih 2010; Dingemanse and Reale 2013; **Chapter 1**). Below I introduce both, the adaptive theory and evolutionary quantitative genetics perspectives on the study of among-individual variation in behaviour:

– Adaptive theory perspective of among-individual differences in behaviour

Over the past decade, there has been considerable (mathematical and verbal) theoretical work on the existence of among-individual differences in behaviour from an adaptive perspective (Dall, Houston, & McNamara 2004; Sih, Bell, & Johnson 2004; Wolf et al. 2007; Wolf, van Doorn, & Weissing 2008; Dingemanse & Wolf 2010; Luttbeg and Sih 2010; Dingemanse & Reale 2013, **Chapter 1**). Behavioural ecology theory is traditionally based on optimality theory (Krebs & McCleery, 1984). Optimality theory assumes that the fitness of an individual's behavioural action is maximised by natural selection (Houston & McNamara, 1999). Thus, given enough time and standing phenotypic variation, selection will lead to optimal behavioural responses. Furthermore, optimality theory is based on the notion that each individual expresses the behaviour that is optimal given its state (Houston & McNamara, 1999). State is broadly defined as any feature that affects the costs and benefits of an individual's behavioural actions (e.g., energy reserves, metabolism, predation risk, age, information state, social rank, etc.; Houston & McNamara 1999, **Chapter 1**). The general idea of state-dependent behaviour models is that each individual's phenotype is optimal and results from a balance between the fitness benefits and costs (Houston & McNamara, 1999) . Trade-offs underlying the costs and benefits in optimization theory are fundamental, typically involving the "resource allocation" model (see above). Adaptive hypotheses have primarily focused on explaining differences in behaviour due to feedback dynamics between behaviour and state. In the case of positive dynamics between behaviour and state, even small initial among-individuals differences in state will be reinforced, giving rise to individual differences in behaviour that are maintained through time (Dingemanse & Wolf 2010; Luttbeg & Sih 2010, **Chapter 1**).

– Evolutionary quantitative genetics perspective of among-individual differences in behaviour

Evolutionary quantitative genetics is based on the "(multivariate) breeder's equation", and therefore, focuses on understanding two main aspects: the heritability and genetic correlations underlying the (co)variation of traits, and how selection acts on these traits (Lande & Arnold, 1983). These two aspects have the potential to provide important insights into the evolutionary responses and constraints acting on behavioural (co)variation (Falconer & Mackay, 1998; Lynch & Walsh, 1998). In the specific case of among-individual differences in behaviour, it has been repeatedly shown that animal personality is heritable (Stirling, Réale, & Roff, 2002; Van Oers et al., 2005, Réale et al., 2007) and related to fitness (Dingemanse & Reale, 2005; Smith & Blumstein, 2008). Therefore, behavioural differences among individuals are potentially under selection (Smith & Blumstein, 2008). Several hypotheses have been developed to explain how among-individual variation in behavioural traits can be maintained, instead of being eroded. These hypotheses are often based on complex patterns of covariances between behaviour and fitness. For instance, it is well known that there are trade-offs between life-history traits (see above), and different behavioural types might resolve trade-offs differently. Thus, within a single population, certain life-history strategies will be related to individuals with a particular behavioural type (e.g., "pace-of-life syndrome hypothesis", Réale et al., 2010). Furthermore, antagonistic selection pressures over time or space represent another important mechanism explaining the maintenance of animal personality (Koolhaas, De Boer, Buwalda, & Van Reenen, 2007; Penke, Denissen, & Miller, 2007; Dingemanse & Reale, 2013). Spatio-temporal fluctuating selection occurs when the direction of selection on animal personality is temporally or spatially fluctuating according to, for instance, environmental factors such food availability or density (Dingemanse, Both, Drent, & Tinbergen, 2004; Quinn, Patrick, Bouwhuis, Wilkin, & Sheldon, 2009). Another mechanism explaining among-individual behavioural variation is correlational selection. In such a scenario, several multivariate phenotypic combinations would do equally well and result in a fitness "ridge" ((Brodie, 1992; Sinervo & Svensson, 2002).

Research Goal

The main goal of my PhD project was to study the behavioural and evolutionary ecology of wild populations, and thus individual variation in behaviour, environmental effects, and the interaction between them. More specifically, I aimed to reconcile theoretical models and empirical data to obtain a better insight into the mechanisms explaining the existence and maintenance of among-individual differences in behaviour. These questions were addressed using both long-term observational data and short-term experimental work under field and lab conditions in wild great tits (*Parus major*).

Study System: the Great Tit as a Model in Evolutionary and Behavioural Ecology

For the empirical components of the thesis, I studied great tits. Historically, birds have made a major contribution to evolutionary theories concerning the development and maintenance of phenotypic variation (e.g. Grant and Grant 1991). Among birds, the great tit is one of the most well studied species, being a model system in ecology and evolution. Indeed, the great tit has a long history of being a model species; it was the focus of the first long-term individual-based field studies of vertebrates started in 1912 in The Netherlands by Wolda and Kluijver (Kluijver, 1951). Its success as a model species probably resulted from its tractability as a nest box breeder, allowing to be monitored in a (semi)standardized fashion over long periods of time. Furthermore, great tits breed in large numbers (i.e. have high population density) in nest box populations, allowing to carry out extensive experimental (e.g. Pettifor et al., 1988; Tinbergen & Daan 1990) and descriptive work (e.g. **Chapter 4**) while simultaneously accruing large sample sizes. Besides its suitability for field studies under natural conditions, its success as a model species can also be attributed to the fact that great tits can be easily kept in captivity and performing natural behaviours. Indeed, wild-caught great tits have previously been used in many captive experiments over extensive time periods (e.g., Krebs, Kacelnik, & Taylor 1978; Wansink & Tinbergen 1994; Marchetti & Drent 2000; Lange & Leimar 2004; van Oers et al., 2004, **Chapter 2**). Great tits thus make an ideal study system because of the extensive information available on their basic population ecology and their high suitability for field and lab studies.

The great tit is a passerine bird from the family Paridae. It is a territorial hole-nesting breeder inhabiting wooded areas throughout Europe, as well as parts of Asia and North Africa, being one of the most common Palearctic species. The species breeds between March and June. The great tit is socially monogamous (Kolliker, Brinkhof, Heeb, Fitze, & Richner, 2000), though commonly engages in extra-pair reproduction (Brommer, Korsten, Bouwman, Berg, & Komdeur, 2007). Females lay on average about nine, and maximally fifteen eggs. Whereas only the females incubate the eggs, both sexes provide parental care. Female great tits are known to adjust their breeding timing to spring temperatures. More specifically, individual females often advance their laying date in warm springs (McCleery & Perrins, 1998; Visser, Both, & Lambrechts, 2004). This response to temperature is the result of phenotypic plasticity (Visser et al., 2004) and considered adaptive. It allows birds to synchronize their phenology with the temperature-dependent hatching times and growth rates of the caterpillars, main food resource for nestlings provisioning (Visser, Noordwijk, Tinbergen, & Lessells, 1998; Visser & Holleman, 2001). Seminal contributions to the topic made use of the extensive long-term information available on the basic population ecology of great tits (e.g. Visser et al., 1998; Nussey, Postma, Gienapp, & Visser, 2005; Charmantier et al., 2008); and currently, breeding timing in female great tits provides a textbook example of adaptive phenotypic plasticity in response to climate change in wild populations.

In addition to general knowledge about their breeding ecology, other detailed information of great tits is also well known, such as their physiology (e.g. metabolic rate, Broggi et al., 2007; hormonal profiles, van Oers et al., 2011); cognitive abilities (e.g. innovation rate and problem-solving, Cole & Quinn 2012; Morand-Ferron, Cole, & Quinn

2015); and morphology (e.g. van Balen 1967; Gosler 1987). Furthermore, great tits are a highly suitable species to study behaviour. Initial studies focused on exploring population-level variation in many sorts of behavioural responses: classic work on foraging (e.g. Smith & Dawkins 1971; Krebs, Kacelnik, & Taylor 1978), life-history decisions (e.g. Perrins 1965; Perrins & McCleery 1989), aggressiveness (e.g. Lange & Leimar 2004), singing behaviour and territoriality (e.g. Krebs et al., 1977)... More recently, the great tit became a model species for studies on repeatable individual differences in behaviour (e.g., Groothuis & Carere 2005). This is because one of the earliest studies of the ecological and evolutionary relevance of individual differences in behaviour was carried out in great tits (Dingemanse, Both, Drent, van Oers, & van Noordwijk, 2002). This early work described individual differences in exploration behaviour (i.e. activity in an unfamiliar environment), that were later on found to be related to other behavioural traits such as dominance (Dingemanse & de Goede, 2004) or risk-taking behaviour (Stuber et al., 2013), and hormonal profiles (e.g. van Oers et al., 2011). Since this early work there has been an explosion of scientific output related to animal personality in great tits and many other animal taxa (for a review of empirical work see Réale, Dingemanse, et al., 2010).

The Research group "Evolutionary Ecology of Variation" at the Max Planck Institute for Ornithology in Seewiesen, where I carried out this PhD thesis, has been monitoring 12 nest box populations of great tits in Southern Germany (Bavarian Landkreis Starnberg; 47º 58' N, 11º 14' E) since 2010 (Fig 2). Each plot consisted of a regular grid of 50 boxes, with 50 meters between adjacent boxes. The study area contains a total of 600 nest boxes. Every breeding season, from April until June, all boxes are checked (bi)weekly to determine the date of the first egg, onset of incubation, and clutch size. When the nestlings are six days old, they are weighed, marked with an aluminium ring and blood sampled. Parents are caught with a spring trap in the nest box on the next day, measured, blood sampled, and marked with a unique combination of colour and aluminium rings, if caught for the first time. Weight, tarsus, wing and bill length are measured in adults and fourteen-day-old nestlings. As part of the general fieldwork protocol, we also systematically quantify territorial aggressiveness and exploration behaviour in spring (for further details see **Chapter 4**).

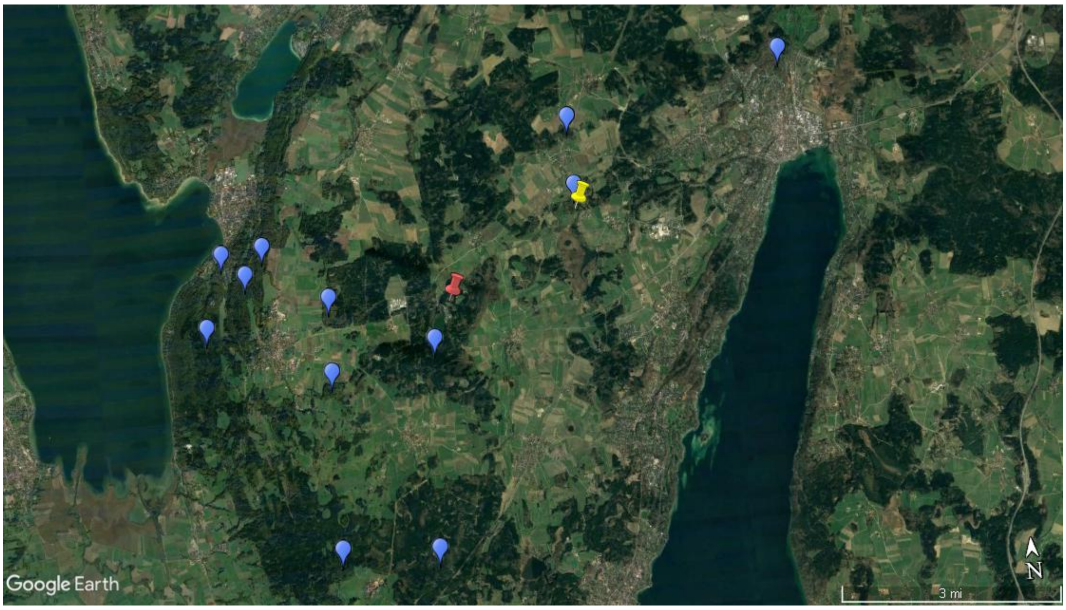

Figure 2. *Study sites of all the Chapters of the PhD thesis. The geographic position of the Max Planck Institute for Ornithology, where* ***Chapter 2*** *was carried out, is depicted in red; the field site of* ***Chapter 3*** *is depicted in yellow; and the 12 plots where data for* ***Chapter 4*** *was collected are depicted in blue. Image was overlaid on a Google Earth image.*

Besides the standard data collection during the breeding season, the research group has also been studying great tits in winter conditions. My colleagues and I have done experimental short-term work using automated identification systems (i.e. RFID antennas and PIT-tags) and bird feeders to quantify foraging activity (**Chapter 3**) and risk-taking behaviour (Mathot, Nicolaus, Araya-Ajoy, Dingemanse, & Kempenaers, 2014). The experimental winter data is complemented with a systematic behavioural test of the exploration behaviour in wintering great tits (see Dingemanse et al., 2002, **Chapter 2**). Therefore, besides general knowledge on breeding patterns and standard morphological data, long-term information on several behavioural traits is available for our great tit population (e.g., **Chapter 4**). These characteristics, and especially, the long-term behavioural data, make our population unique and exceptionally suitable for a study into the evolutionary and behavioural ecology of individual differences in behaviour in the wild.

Thesis Outline

The overall aim of my PhD project was to study the evolutionary and behavioural ecology of individual variation in labile traits. The studies described below were specifically planned to further the understanding of the adaptive cause of behavioural differences among individuals. This thesis combined theoretical and empirical approaches. In addition, I addressed empirical questions using both long term (observational) data and experimental work carried out in field and lab conditions in wintering and breeding great tits.

First I discussed the application of the theoretical models for adaptive individual variation **(Chapter 1)**, to then introduce a conceptual framework of the main factors and mechanisms that contribute to an adaptive explanation of animal personality. In particular, my colleagues and I discussed how positive feedbacks between state and behaviour can lead to among-individual variation in behaviour. The remainder of the thesis, **Chapters 2-4**, presented a series of empirical studies. With these studies I aimed to investigate different mechanisms explaining why we observe individual differences in behaviour. Specifically, **Chapters 2 and 3** focused on behavioural trade-offs as the mechanism maintaining phenotypic variation. I investigated whether the existence of a trade-off between decision-making behaviours (**Chapter 2**), and between foraging and mass gain (**Chapter 3**) would ultimately cause the maintenance of individual variation. Both chapters were short-term empirical studies and applied different approaches (i.e. lab and field conditions) to quantify behavioural trade-offs in wintering birds. **Chapters 4** focused on phenotypic integration among functionally related traits caused by correlational selection as the mechanism explaining state-dependent personality.

In the next sections of the thesis I will present the studies that are part of my PhD (**Chapters 1-4**) and then, discuss how my findings highlight the relevance of embracing the multi-level nature of behaviour for a full understanding of the adaptive causes of phenotypic variation among individuals. Additionally, I will also expose some of the general assumptions that are made when working with phenotypic data and applying a trait-by-trait approach. Although I focused in explaining adaptive patterns of among-individual variation in behavioural traits, my findings are readily applicable to other labile traits such as life-history and physiology.

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Chapter 1

Animal personality and state–behaviour feedbacks: a review and guide for empiricists

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ABSTRACT

An exciting area in behavioural ecology focuses on understanding why animals exhibit consistent among-individual differences in behaviour (animal personalities). Animal personality has been proposed to emerge as an adaptation to individual differences in state variables, leading to the question of why individuals differ consistently in state. Recent theory emphasizes the role that positive feedbacks between state and behaviour can play in producing consistent among-individual covariance between state and behaviour, hence state-dependent personality. We review the role of feedbacks in recent models of adaptive personalities, and provide guidelines for empirical testing of model assumptions and predictions. We discuss the importance of the mediating effects of ecology on these feedbacks, and provide a roadmap for including state–behaviour feedbacks in behavioural ecology research.

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STATE–BEHAVIOUR FEEDBACKS AND THE EMERGENCE OF PERSONALITY DIFFERENCES

The past decade has seen tremendous interest in animal personalities (Dall, Bell, Bolnick, & Ratnieks, 2012; Sih, Bell, Johnson, & Ziemba, 2004; Wolf & Weissing, 2012), stemming from accumulating evidence for individual repeatability and significant correlations between various behaviours (e.g., boldness, aggressiveness, activity, exploration, or sociability). Empirical studies show that animal personalities and behavioural syndromes (correlations across contexts) vary as a function of ecology (Bell et al., 2009; Garamszegi, Markó, & Herczeg, 2012); for example, aggressiveness and boldness are often positively correlated but the strength of this correlation varies depending on the predation regime (Bell & Sih, 2007; Dingemanse, Dochtermann, & Wright, 2010). Variation in syndrome structure also exists across different temporal scales; for instance, early experiences (e.g., exposure to stressors) can have large effects on the development of personality structure but such effects can either be temporary or permanent (Stamps & Groothuis, 2010; Stamps & Groothuis, 2010; Buwalda, Stubbendorff, Zickert, & Koolhaas, 2013;). Understanding the processes explaining the emergence of personality differences and variability of syndrome structure within and among species represents a major current topic in adaptive personality research.

Although personality has been examined in numerous species, most studies are descriptive in nature, documenting patterns of behavioural structure. Over the past few years, however, theory has been developed to explain the existence of animal personalities from an adaptive perspective. Most of this theory invokes adaptive state-dependent behaviour, explaining personality as an adaptive outcome of among-individual differences in state (Biro & Stamps, 2008; Dingemanse & Wolf, 2010; Wolf & Weissing, 2010). Building on earlier work by Rands, Cowlishaw, Pettifor, Rowcliffe, & Johnstone (2003) and Dall, Houston, & McNamara (2004) recent models have focused on the joint emergence and maintenance of among-individual differences in behaviour and state, and how such differences are promoted by positive feedbacks between behaviour and state. These models (both mathematical and verbal) have generated testable predictions for a broad range of scenarios. The time is now ripe for more tests of the predictions of those models. Here, we present a framework that unifies the logic of numerous recent models in a fresh way and paves the way for rigorous testing of these models. Specifically, we: (i) describe the core idea underlying all feedback loops thereby uniting numerous mechanisms and models; (ii) discuss how this core idea can integrate the study of proximate and ultimate mechanisms, potentially over ecological, developmental, and evolutionary time scales; (iii) summarize predictions of these models on variation in animal personalities; and (iv) offer guidance to empiricists for studying state–behaviour feedbacks, and for testing predictions on how these feedbacks relate to personalities.

FEEDBACK LOOPS AND VARIATION IN PERSONALITIES – THE CORE CONCEPT

Although behaviour in principle can be infinitely flexible, behavioural repeatability can potentially be explained by among-individual differences in slower-changing or even fixed state variables, in combination with adaptive state- dependent behaviour (Dall et al., 2004; Dingemanse & Wolf, 2010; Luttbeg & Sih, 2010; Wolf & Weissing, 2010, Table 1). Individuals thus differ in behaviour because they differ in state and adjust their behaviour in an adaptive fashion to these differences. In behavioural ecology, the state of an individual includes any features that affect the cost and benefits of its behavioural actions (Houston & McNamara, 1999). Often, these involve labile characteristics of the focal individual such as its energy reserves, condition or vigour, reproductive value, physiology (metabolic rates, hormone levels, or immune state), morphology, or colour, age, or size. They could also include the individual's information state, skill set, social rank, or role. Importantly, state variables are not restricted to features of the focal individual but include also characteristics of its social environment (e.g., its local density or sex ratio, or the behaviour or other traits of its social partners), or aspects of its ecological environment (e.g., its predators, competitors, or parasites). Consistent differences among individuals in any of these features can, in combination with adaptive state-dependent behaviour, explain consistent differences among individuals in behaviour.

When state variables are themselves labile, the question shifts to: what explains consistent individual differences in both the labile state variables and behaviour? Recent models emphasize that positive feedbacks between state variables and behaviour can link the co-evolution or co-development of state and behaviour that can then drive divergence and persistence of long-term differences in both (Fig 1, Box 1, Table 1), thus resulting in consistent among-individual variation in behaviour (cf. personality) and state. By contrast, negative feedbacks result in convergence in state and behaviour, and thus no long-term persistence of differences in either. Note that with feed-backs, the state variable no longer needs to be inherently stable or slow-changing – feedbacks between two potentially rapidly changing variables can stabilize both. Whether feedbacks are positive or negative depends on the selective landscape. Positive versus negative feedbacks should evolve by means of positive versus negative correlational selection for optimal combinations of state and behaviour. Positive feedbacks, in particular, are favoured if a behavioural tendency produces a change in a state variable that increases the net benefit of maintaining or even increasing that behavioural tendency (cf. adaptive phenotypic plasticity; Box 1). In the following section, we summarize models and ideas on state variables, feedback dynamics, and predictions about variation in personality (Box 1, Table 1).

Box 1. Feedbacks: integration of proximate and ultimate approaches

Animal behaviourists commonly distinguish between proximate versus ultimate approaches for explaining observed behaviour (but see Laland, Sterelny, Odling-Smee, Hoppitt, & Uller, 2011). The usual idea is that proximate explanations invoke underlying mechanisms; for example, how physiology, hormones, neurosensory, or cognitive mechanisms might explain observed behaviours. By contrast, adaptive, ultimate approaches attempt to explain behavioural patterns using cost–benefit considerations; animals exhibit behaviours that enhance fitness. The state–behaviour models described here integrate these two by solving for the best behaviour given the organism’s state (the proximate mechanism). That is, these models explicitly unify adaptive (ultimate) and mechanistic (proximate) views. To choose which model to use to explain observed behaviours in a given system, the behaviourist must match their system to the relevant state variable (see Guide for empiricists). One important point is that because the models emphasize feedback loops, the emphasis is on the joint unfolding of the back-and-forth feedback between the organism’s behaviour and its physiology (or other state variables) on short-term, developmental, or evolutionary time scales (i.e., state is a proximate underpinning of behaviour, and vice versa). Because many of the models track changes in behaviour and a state variable (e.g., condition, energy reserves, or RRV) over long periods of time, the models make predictions on the development of behaviour (and state variables) over ontogeny (Sih, 2011). With positive feedbacks, early experiences (that affect early differences in state) have large effects on later ‘personality type’, whereas with negative feedbacks even large differences in early state are predicted to have little effect on later personality. Thus the state–behaviour feedback framework suggests that developmental sensitive time windows (where experiences during the window govern later phenotypes) are not an invariant feature of a developmental system, but are instead an adaptive outcome of positive feedback loops. Finally, note that this framework substantially expands the usual view of what is a ‘proximate mechanism’. Instead of focusing primarily on physiology or neuroendocrine mechanisms (and perhaps associated genetic mechanisms), the relevant state variables could be any factor that influences adaptive behaviour and, in turn, is influenced by the behaviour. As noted in the text this can include a broad range of individual traits, as well as traits of other individuals (e.g., social partners), or even of other species (e.g., parasites).

FEEDBACK LOOPS: AN OVERVIEW OF MODELS AND MECHANISMS

Various models of feedbacks between state and behaviour have been proposed (Table 1). In the following sections we discuss three main types: (i) state–behaviour feedbacks involving intrinsic state variables; (ii) state–behaviour feedbacks involving extrinsic state variables; (iii) co-evolutionary feedbacks.

(i) State–behaviour feedbacks involving intrinsic state variables

We use intrinsic state variables to mean state variables that are features of the same individual that is expressing the behaviour; for example, an individual's level of fat reserves, hormones, metabolic rate, residual reproductive value (RRV, see below), etc.

Feedback loops involving risk–reward and life history trade-offs. Perhaps the most widely recognized mechanism explaining personality differences connects variation in life history strategies to personalities where the key state variable is the individual's RRV, roughly speaking, it's expected future reproductive success (or 'assets') (Wolf et al., 2007a). According to the asset protection principle (Clark, 1994), the higher the assets of an individual, the less willing that individual should be to risk its life for a given benefit, as the assets of an individual determine what it stands to lose in the case of death. Differences in assets are thus predicted to give rise to differences in all kind of risk-related behaviours like boldness and aggressiveness, with higher-asset individuals being more cautious. Positive feedbacks occur if: (a) being cautious means reducing current reproductive effort and investing instead in future reproduction (thus increasing RRV), and conversely, (b) if the risky behaviour of low-asset individuals tends to increase current reproductive success, but at the cost of decreases in future RRV (e.g., via exposure to parasites) (Wolf, van Doorn, Leimar, & Weissing, 2007b). In essence, positive feedbacks favour either a fast lifestyle associated with bold, aggressive, risky behaviour and rapid reproduction, or a slow lifestyle with cautious behaviour and delayed reproduction (Réale, Garant, et al., 2010). Asset protection, however, can also produce negative feedbacks if, for example, being bold results in increased assets (e.g., increased energy reserves) while being cautious results in an erosion of assets. This negative feedback would tend to produce convergence in assets and behaviour, and thus no long-term persistence of differences in personality.

While the above arguments are based on the prediction that high-asset individuals are more cautious, higher assets in the form of higher condition can also favour higher risk-taking (Luttbeg & Sih, 2010). For example, prey often enjoy state-dependent safety where larger, stronger, more vigorous prey are better at escaping from or defending against predators, and thus suffer lower costs of predation risk while foraging than weaker prey (see Luttbeg & Sih, 2010 for references). The lower cost allows high condition animals to forage actively and thus continue to bring in the energy to maintain their high condition. By contrast, animals in poor condition should not take risks if they can be easily captured. Because they hide instead, they take in little energy and stay in poor condition (i.e., animals in poor condition make the best of a bad job). Similar logic can generate positive feedback loops involving state-dependent resistance against parasites (Kortet, Hedrick, & Vainikka, 2010). Hosts in better condition might have more effective immune systems that allow them to be bold and active (and thus gain the energy to stay in good condition) even if this exposes them to more parasites.

Condition-dependent foraging success can also generate positive feedback loops (Wilson, Grimmer, & Rosenthal, 2013). Game theory predicts that if the costs of fights are high then only animals in good condition (with high resource holding potential, RHP) should be aggressive, while those in poor condition should be unaggressive since they have a low chance of winning. High RHP, aggressive individuals then gain resources that keep them in superior condition, while low RHP, unaggressive individuals settle for less and remain in poor condition and thus unaggressive. An extreme case of this phenomenon involves condition-dependent cannibalism as the mechanism that generates the positive feedback that maintains individual differences in condition and behaviour (Kishida et al., 2011). Finally, risk in the sense of uncertainty (e.g., about the best foraging options, breeding sites, etc.) can generate feedbacks between energy reserves and behaviour. Individuals that sample and learn about alternative foraging options can potentially gain more energy in the long-term but suffer short-term costs due to sampling (i.e., checking the state of an option that is currently unprofitable (Dall & Johnstone, 2002; Mathot & Dall, 2013). Under high immediate risk of starvation, individuals in the poorest energetic state are expected to sample because the only means of achieving sufficient energy intake is to locate the most profitable feeding options, that is, ‘sampling for survival’ (Mathot & Dall, 2013). Because sampling will allow individuals with low energy reserves to build reserves, the feedback between sampling behaviour and energy reserves is negative, and individual differences in energy reserves and sampling behaviour will tend to erode over time. The situation reverses to a positive feedback loop when there is a low immediate risk of starvation. Then, individuals with lower energy reserves should not sample, because sampling errors will significantly increase their probability of starvation. Instead, only individuals with high energy reserves are expected to be able to afford the ‘luxury’ of sampling, because for them, the short-term costs of sampling are not enough to increase their probability of starvation (Mathot & Dall, 2013).

Feedbacks involving an individual’s skill set or experience. An individual’s skill set is another key state variable. Often, the more experience an individual has with a particular behaviour, the better the individual gets at performing that behaviour which makes it advantageous for the individual to stick to that behaviour (Pearce, 2013; Wolf & Weissing, 2010). This positive feedback between behaviour and the experience that an individual has with this behaviour thus favours consistency. Moreover, when selection on different behavioural alternatives is negatively frequency-dependent, this feedback is predicted to promote consistent, among-individual differences in behaviour (Wolf et al., 2008); note that frequency-dependent selection alone does not predict consistency (Wolf, Van Doorn, & Weissing, 2011).

The behaviour-experience feedback can also work for more complex behavioural phenotypes associated with differences in social roles, social niches, or positions in a social network (Bergmüller & Taborsky, 2010; Krause, James, & Croft, 2010); that is, personality differences can be understood as social niche specializations (Bergmüller & Taborsky, 2010; Montiglio, Ferrari, & Reale, 2013). Here, the state variable is the individual's social role, niche, or position. More broadly, the key state variable can be any ecological or social situation that is experienced by focal individuals (see below, feedbacks involving extrinsic state variables). Positive feedbacks can emerge if different social roles-niches-positions drive differences in behaviour that in turn reinforce the individual's social role-niche-position. For example, subordinate individuals might forage in low-quality patches to avoid competing with dominants over food, however, this patch choice can then prevent them from gaining the resources required to gain dominance, thereby reinforcing their subordinate position. This is a special case of the general idea that situation choice facilitates the evolution of specialization (Rosenzweig, 1987).

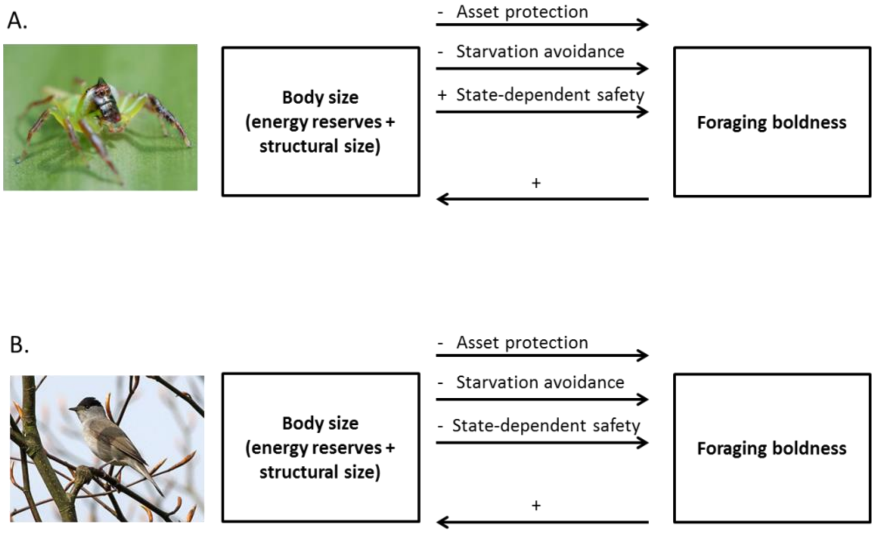

Figure 1. *Illustration of how multiple mechanisms can simultaneously shape feedbacks between state and behaviour. Foraging boldness allows individuals to accrue more resources and increase their body size (either through growth or accumulation of energy reserves). However, the effect of body size on behaviour differs depending on the mechanism underlying the relationship. Asset protection predicts a negative feedback that drives large individuals to avoid risky behaviours, and starvation avoidance predicts negative feedback that drives small individuals to take risks while foraging. Additionally, depending on the species, larger body size/energy reserves can provide safety benefits*

(e.g., larger jumping spiders, Phidippus princeps, are better at escaping predators (Stankowich, 2009); panel A) or reduce their escape performance (e.g., larger blackcaps, Sylvia atricapilla, have reduced predator evasion (Kullberg, Fransson, & Jakobsson, 1996); panel B). When the different mechanisms produce loops with differing directions (A), the net direction of the feedback between state (e.g., body size) and behaviour (foraging boldness) will depend on the relative importance of each of these mechanisms, which varies as a function of predation risk and resource level (i.e., the feedback outcome can be explained as match/mismatch between risk and rewards (Luttbeg & Sih, 2010)). Photos obtained via Wikimedia commons.

Hormone–behaviour feedbacks. Individual differences in hormone levels can drive differences in behaviour. Behaviour, in turn, can affect hormone levels. For example, high testosterone can increase aggressiveness, but aggressive behaviour can also drive up testosterone levels, giving rise to a positive feedback. Positive feedbacks also exist between social behaviours and oxytocin (Calcagnoli et al., 2014; Lukas et al., 2011; Neumann, 2009), and between behaviour, life histories, and corticosterone responses (Del Giudice, Ellis, & Shirtcliff, 2011; Koolhaas, de Boer, Coppens, & Buwalda, 2010). Of course, neuroendocrine systems themselves are characterized by feedbacks (Korte, Koolhaas, Wingfield, & McEwen, 2005; Romero, Dickens, & Cyr, 2009) and these feedbacks can potentially stabilize personalities even if behaviour does not strongly affect hormones (Koolhaas et al., 2010).

Hormones can also serve as an important mediator of feedbacks between other intrinsic or extrinsic state variables and behaviour. For example, behaviour–parasite feedbacks (discussed below) are often mediated by effects of parasites on host hormone levels (Adamo, 2013; Lafferty & Shaw, 2013) and, in some cases, appear to involve adaptive parasite manipulation of host neuroendocrine pathways (Lim, Kumar, Hari Dass, & Vyas, 2013; Perrot-Minnot & Cezilly, 2013). Progress in understanding feedbacks between behaviour and multiple, interacting components of the overall neuroendocrine system should be invaluable for better understanding personalities.

(ii) State–behaviour feedbacks involving extrinsic state variables

Other models emphasize that state variables that shape an individual's personality need not be a trait of the focal individual, but can instead be a characteristic of a conspecific, members of another species (e.g., parasites), or some other external factor such as an environmental contaminant.

An example involves the feedback between the predictable part of a focal individual's behaviour (cf. its 'personality') and the responsiveness of its social partners. If the focal individual's behaviour is consistent (and thus predictable), this favours social partners that are paying attention (responsive). Conversely, if social partners are responsive, this can favour the focal individual being predictable. Being predictable can be favoured if it allows an individual to build a reputation (e.g., for being aggressive or cooperative) that manipulates a socially responsive partner's behaviour in a mutually beneficial way (e.g., to back off without a fight, or to cooperate (Wolf & McNamara, 2013; Wolf et al., 2011). Similarly, the behaviour–predictability feedback is predicted to promote consistency (via a form of correlational selection that favours individuals continuing to do what they have done in the past) in leader–follower situations (Johnstone & Manica, 2011; Wolf & McNamara, 2013) and in contexts of social niche specialization (Bergmüller & Taborsky, 2010). Other feedback loops involving the reciprocal behaviours of two or more individuals include effects of the aggressiveness of individual X on individual Y and vice versa (Wilson, Gelin, Perron, & Reale, 2009), and personality-dependent, predator–prey behavioural response games (Pruitt, Stachowicz, & Sih, 2012).

A fascinating example of where the state variable is another species involves parasites. Individual differences in encounters with parasites due to small differences in behavioural tendencies or just to chance can affect the individual's subsequent behaviour (Barber & Dingemanse, 2010; Coats, Poulin, & Nakagawa, 2010; Kortet et al., 2010) in ways that generate long-term, consistent, among-individual differences. If carrying a parasite load increases host energy demands without reducing host vitality, the result can be an increase in activity or exploratory behaviour (to 'feed' the parasite) that further increases parasite loads (i.e., positive feedback). Parasites can also manipulate host behaviour to enhance parasite transmission to the next host (Poulin, 2013). For example, parasites can make their hosts more active or bold, thus picking up more parasites until the host's highly conspicuous behaviour causes them to be noticed and eaten by the parasite's next host (Lafferty & Morris, 1996). As this process unfolds, the positive feedback loop can help explain the persistence of consistent personalities. Conversely, a negative feedback loop can exist if parasites weaken their hosts (and thus reduce host activity) or reduce their host's tendency to be sociable (thereby reducing encounters with other infected hosts).

Finally, state–behaviour feedbacks involving non-living, extrinsic factors can also generate personality. For example, if environmental chemicals influence behaviour in ways that increase the likelihood of being further exposed to chemicals, then even chance variation in initial encounters with contaminants, such as pesticides, heavy metals, or pharmaceuticals, could generate lasting among-individual differences in behaviour (Brodin, Fick, Jonsson, & Klaminder, 2013; Montiglio & Royauté, 2014)

(iii) The joint evolution of behaviour and state variables

Most of the models discussed above assume that animals adjust their behaviour to their state in an adaptive way (e.g., animals with higher assets increase their fitness by being more cautious). Most also assume, however, that the converse need not hold; that is, while behaviour affects the state variable (e.g., bolder foraging increases energy reserves), the state variable is not adjusting adaptively to the behaviour. An alternative view explicitly models how behavioural consistency can emerge from the co-evolution or co-development of an adaptive, integrated phenotype where both the behaviour and state respond adaptively to the other. For example, in the classic hawk– dove game, in the absence of a co-evolving state variable, selection favours individuals that exhibit behavioural inconsistency (i.e., individuals that switch between hawk and dove behaviours in repeated interactions). If, however, behaviour co-evolves with physiological state variables (e.g., metabolic capacity), the result is the evolution of alternative, consistent personalities with associated differences in physiology: low-metabolism individuals that are unaggressive versus high-metabolism individuals that are aggressive (Wolf & McNamara, 2012). High metabolic capacity helps animals win fights that bring in the energy to offset the costs of maintaining a high metabolic capacity. Extending the scenario to allow for a second behavioural trait (boldness) that is also affected by the physiological state variable, this model predicts the co-evolution of positive correlations between metabolic rate, aggressiveness, and boldness. Although this model is couched in terms of co-evolving physiological state variables, the underlying concepts apply to any co-evolving morphological, cognitive, or life history trait that affects the costs or benefits of behavioural actions (Wolf & McNamara, 2012). Thus this model formalizes the basic logic underlying the Pace of Life syndrome (Réale, Garant, et al., 2010)or life history-productivity syndrome (Biro & Stamps, 2008) ideas that posit the co-evolution of fast versus slow general lifestyles including physiology, behaviour and life histories, and of fast/slow cognition syndromes (Sih & Del Giudice, 2012).

MULTIPLE SIMULTANEOUS FEEDBACK LOOPS

Several of the above examples illustrate how a single mechanism (e.g., asset protection or starvation avoidance) can generate either positive or negative feedbacks depending on other factors. In other cases, state-dependent behaviour can be simultaneously shaped by mechanisms with contrasting feedback patterns (Fig 1). When the feedbacks do not all operate in the same direction, the net direction of the feed-back loop will depend on the relative contribution of each mechanism, which is likely to vary as a function of ecological conditions (e.g., predation risk, food availability, etc.) (Luttbeg & Sih, 2010).

GUIDE FOR EMPIRICISTS

We next provide a guide for studying state–behaviour feedback loops and for testing predictions on how those loops influence animal personalities (Boxes 2 and 3). While one could start with a model and search for a system that appears to fit that model, we assume, for this guide, that the empiricist is already studying a particular system and seeks to identify and test models that can potentially explain variation in the structure of personality in that system.

Because the various models revolve around different state variables, it is important to identify which state variables are good candidates for a state–behaviour feed-back loop in one's system. Although feedback loops are dynamic processes that play out over time within an individual, they should often also generate among-individual state–behaviour correlations. For example, if hosts that are more active pick up more parasites that then make those hosts even more active, we expect development of an among-individual, positive (host activity vs. parasite load) correlation. A first step can thus be to screen for among-individual state–behaviour correlations. When some data are available on temporal consistency, focus on state variables that have a similar level of temporal consistency as behaviour. For example, behaviours that exhibit life-long stable differences among individuals are more likely to be connected to stable state variables (e.g., morphology, life history type, or a stable social role) than with day-to-day variation in the social environment. Identifying good candidate state variables leads the empiricist to one or a few of the models in Table 1. Next, check to make sure that your system fits key assumptions of those models.

Having identified relevant state variables, if possible, manipulate these experimentally (e.g., alter energy reserves or parasite loads) to assess effects on behaviour. Following behaviour over longer periods of time will provide insights into feedbacks. Even after the initial manipulation, positive feedback loops should be associated with sustained changes in individual behaviour over time, whereas negative feedback loops should be associated with individuals returning to their original, pre-manipulation behaviour (and state). If the model makes predictions on how mediating factors (e.g., local density, risks, or resources) should affect personalities on an ecological time scale, experimentally manipulate these mediating factors. Take feedback loops into account when planning data collection and statistical analyses. Empirical studies often treat some of the state variables described above as nuisance parameters, and try to correct for these, potentially removing the signature of feedback loops from the data. We thus suggest that empiricists should not follow the common practices of standardizing the social environment experienced by individuals, or to statistically standardize for individual body size or energy state when assessing individual behavioural variation. Ideally, collect longitudinal datasets, measuring individuals' state and behaviour repeatedly over relevant time scales (i.e., time series). We next describe statistical methods for quantifying feedback loops and their outcomes.

Quantifying within-individual loops

In principle, feedback loops can be characterized as an individual property, and thus vary among individuals (Zucchini, Raubenheimer, & MacDonald, 2008). For testing within-individual feedback loops, repeated measurements of individuals' behaviour and state are essential. Statistically, feedbacks within a single individual may be captured with a 'double' phenotypic equation where behaviour ($y_{t,b}$; b for behaviour) and state ($y_{t,s}$; s for state) at time t are both response variables (Box 3). The key difference with classic phenotypic equations (Dingemanse et al., 2010; Westneat, Hatch, Wetzel, & Ensminger, 2011) is that some variables are both predictor and response. Within-individual feedback loops leave various traces in empirical data when captured in action. First, among-individual variation in state and behaviour should increase over time with positive feedback and result in positive correlations between individual intercepts and slopes of temporal reaction norms ('fanning-out'; left and middle panels of Fig 2A,D). When the effect of (current) state on (current) behaviour ($\lambda_{s\rightarrow b}$) and (current) behaviour on (future) state ($\lambda_{b\rightarrow s}$) are both positive (Fig 2D, right panel), state and behaviour shift in the same direction within the same individual, causing positive 'within-individual correlations' (Dingemanse & Dochtermann, 2013). When $\lambda_{s\rightarrow b}$ and $\lambda_{b\rightarrow s}$are both negative, state and behaviour shift in opposite directions, causing negative within-individual correlations (Fig 2A, right panel). Along the same lines, negative loops also leave distinct patterns of (co)variance, for example, negative intercept– slope correlations ('fanning-in'; left and middle panels of Fig 2B,C). Parameters$\lambda_{s\rightarrow b}$ and $\lambda_{b\rightarrow s}$) can also be estimated directly, for example, using structural equation modelling (Box 3).

Individual divergence due to positive feedback would typically cease at some point in time either because of biological floors or ceilings to both state and behaviour, because behaviour is open for modification only during certain developmental stages (J. A. Stamps & Groothuis, 2010) or because the effect of state on behaviour (or vice versa) is non-linear.

At such ‘end stages’, within-individual correlations would decrease to zero and be replaced by stable ‘among-individual correlations’ (Dingemanse & Dochtermann, 2013).

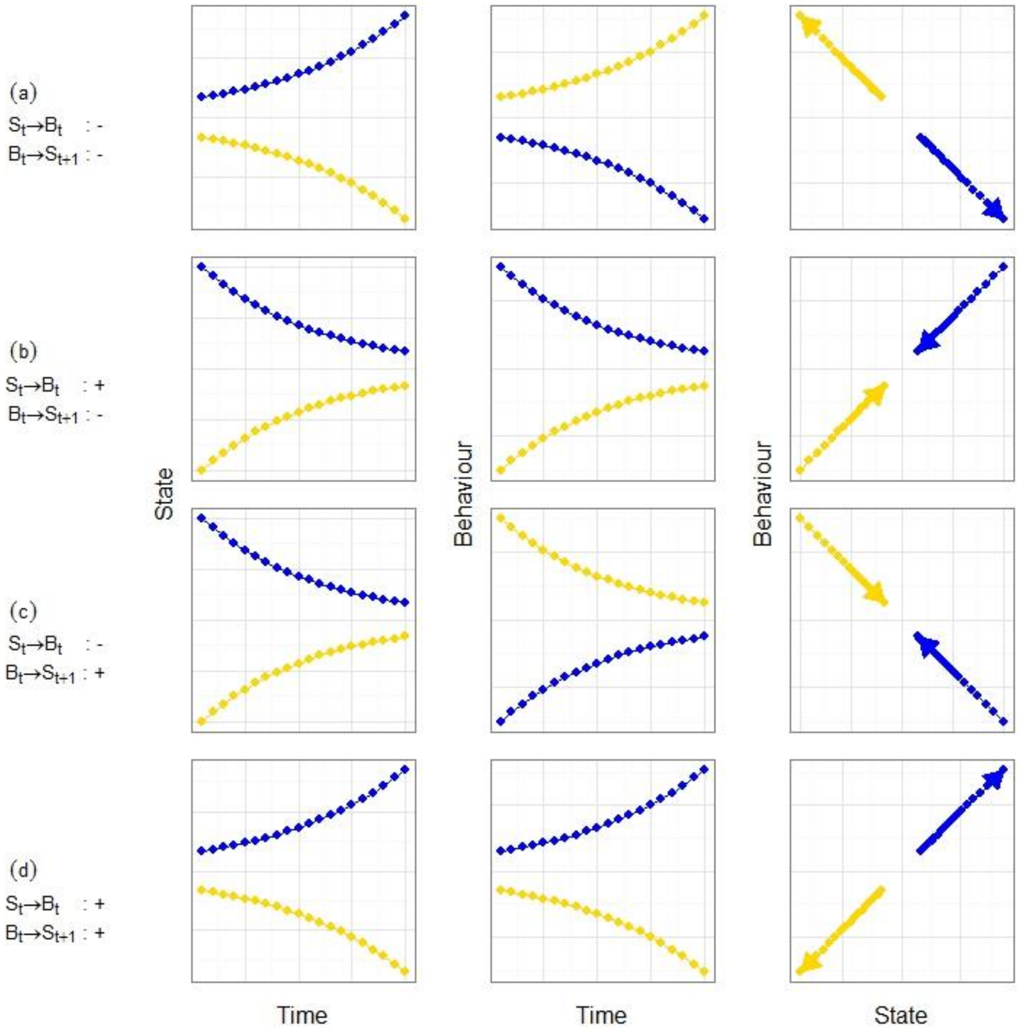

Figure 2. *Patterns of variation in temporal reaction norms for state (s) (left panel) and behaviour (b) (middle panel) while within-individual feedback loops are ‘in action’. All scenarios are drawn from the simple equations given in Box 3, with starting values of 0.1 (blue individuals) and _0.1 (yellow individuals) for state at time t for 20 time steps. Scenarios A through D differ in value of* $\lambda_{s\to b}$ *and* $\lambda_{b\to s}$ *respectively (“-“ = -0.3; “+” = +0.3), resulting in either positive (A,D) or negative (B,C) loops. Different scenarios come with specific predictions for pattern and direction (arrows) of within-individual covariance in state and behaviour leading to within-individual correlations while feedback loops are ‘in action’ (right panel). We note that negative feedback can, depending on parameter settings, also result in cycling or chaos; those scenarios are not depicted but would not result in among-individual differentiation (state-dependent personality).*

Box 2. A worked example

To illustrate our guide to empirically testing state–behaviour feedback loops, we provide an example with cannibalism as the focal behaviour and gape size in salamander larvae as the state variable.

(i) Identify the system and the mechanism. The first step is to identify a system and a mechanism that fits the system. In this case, we focus on a state-dependent foraging strategy model as the mechanism and larval salamanders as the species. Many salamander larvae exhibit size-dependent cannibalism, especially under high population densities. These interactions induce an increase in gape size within populations that allows conspecific predation, and also an increase in foraging efficiency since conspecifics represent a rich resource. However, under high predation risk, salamander larvae reduce their foraging activity in order to avoid risky encounters. The relative importance of each mechanism will influence the net direction of the feedback loop.

(ii) Predictions. See the predictions for positive and negative feed-backs of this model ('State-dependent foraging strategy') in Table 1 in main text.

(iii) Experimental approach. The most straightforward experimental test is to manipulate the body size of salamander larvae (e.g., by experimentally increasing food availability) as a proxy for gape size to investigate whether this manipulation results in the predicted effect on cannibalistic behaviour, and vice versa. In some cases, experimental manipulations of state and/or behaviour may not be feasible or even necessary. Non-experimental studies can also be suitable tests of state–behaviour feedback loops since natural variation in both variables can provide enough initial differences among individuals to initiate the dynamics. For instance, Kishida et al., (2011) empirically studied this mechanism and system based on baseline initial variation among individuals. A complementary experimental test is to manipulate the ecological conditions to test for predicted changes in the feedback loop direction. Theoretical models allow us to predict the feedback outcome based on match/mismatch between risk and rewards (Luttbeg & Sih, 2010). For instance, feedbacks between gape size and cannibalism can vary as a function of predation risk and resource level. One experiment can keep resource levels constant (here, salamander larvae density) and manipulate predation risk by adding larval dragonflies (top predators of amphibian larvae). The ecological prediction is that positive feedbacks should predominate in conditions of intermediate ecological favourability while negative feedbacks should predominate in highly favourable or highly unfavourable conditions (Luttbeg & Sih, 2010). In both cases, manipulative or not, repeated measurements of behaviour and state of the same individual and for different individuals are essential. Salamander larvae present continuous growth until metamorphosis, and therefore, changes in size (and gape size) can be measured daily over the entire larval period. In terms of behaviour, cannibalistic tendency can also be assessed regularly over the same period. The required data (i.e., number of measurements) will depend on the effect size of each variable, and consequently, on the statistical power.

(iv) Statistical analysis. To analyse the relationship between number of salamanders cannibalized and gape size, we can use a 'reaction norm' approach (Dingemanse et al., 2010; Nussey, Wilson, & Brommer, 2007) where time is fitted as the environmental (x) axis (Dingemanse et al., 2012) to estimate how cannibalistic behaviour and gape size change within individuals over time. We would, as a first step, statistically fit a random regression mixed-effect model that would enable us to estimate the statistical parameter (cf. intercept/slope correlation) that informs us on whether state and behaviour indeed showed patterns of 'fanning-out' (cf. among-individual divergence) or 'fanning-in' (cf. among-individual convergence) as expected when there were feedback loops in action (see Fig 2 in main text). As a second step, we would fit a bivariate random regression model, where cannibalistic behaviour and gape size were both fitted as the two response variables, and quantify the covariance between the slopes of the two temporal reaction norms (for guidelines, see Dingemanse & Dochtermann, 2013). In the presence of feedbacks (whether positive or negative), the slopes of the reaction norms for behaviour and gape size would be correlated. See the text, Box 3, and Fig 2 in main text for more details.

Quantifying among-individual feedback loops

Positive within-individual feedback loops lead to within- individual covariance between state and behaviour while the loop is in action. Among-individual correlations represent the final outcome of this process (i.e., stable, state- dependent personality differences); these among-individual correlations are, notably, of non-genetic origin. However, feedback loops can also occur at longer (evolutionary) time scales, and thus result in among-individual correlations due to the evolution of genetic correlations between the heritable parts of state and behaviour. On such an evolutionary time scale, long-term experiments could be used on short-lived organisms to quantify joint changes in breeding values of behaviour and state over multiple generations. Similarly, phylogenetic analyses comparing populations or species could be used to study the joint evolution of state and behaviour. Provided that feedbacks are indeed a function of ecological condition, a final approach would be to compare genetic correlation structures across populations (or species) experiencing different ecologies.

Box 3. Feedbacks in equations and statistical analyses of phenotypes

Feedbacks between phenotypic traits are often described mathematically using multivariate phenotypic equations with simultaneous relationships (Gianola & Sorensen, 2004; Wu, Heringstad, & Gianola, 2010). A simple example is represented by the following ‘double’ equation (Equation 1):

$$y_{ts} = y_{t-1,s} + \lambda_{b\rightarrow s} y_{t-1,b} + e_{ts} \qquad \text{(Eqn. 1a)}$$

$$y_{tb} = \lambda_{s\rightarrow b} y_{ts} + e_{tb} \qquad \text{(Eqn. 1b)}$$

where y_{ts} and y_{tb} represent, respectively, state and behaviour of a single individual at time *t*. Here, the first part of the equation (Eqn. 1a) captures the notion that an individual’s current state is equal to its previous state ($y_{t-1,s}$) apart from a modification due to its previous behavioural action ($y_{t-1,b}$), where the dependence of current state on previous behaviour is given by $\lambda_{b\rightarrow s}$. The second part of the equation (Eqn. 1b) captures the notion that an individual’s current behaviour is a function of its current state (y_{ts}), where the dependence of current state on previous behaviour is given by $\lambda_{s\rightarrow b}$. Both models have residuals (e_{ts}, e_{tb}) and would in reality also incorporate a multitude of fixed effects (e.g. age) that are ignored here for simplicity.

The magnitude and sign of the feedback loop (L) between state and behaviour can be quantified by multiplying the effect of current state on current behaviour ($\lambda_{s\rightarrow b}$) with the effect current behaviour on future state ($\lambda_{b\rightarrow s}$). An important characteristic of equation 1 is that positive feedback will result in an infinite increase in individual differentiation over time (Fig 2a,d). In reality, we would expect biological floors and ceilings to both state and behaviour, resulting in the stabilisation of individual differentiation with time. Statistically, this can be implemented by specifying non-linear effects of state on behaviour (and vice versa).

The simultaneous relationships between state and behaviour exemplified in our worked example can be quantified statistically using structural equation modelling for datasets where state and behaviour have both been assayed repeatedly on the same individual (Gianola & Sorensen, 2004; Wu et al., 2010). The approach can also be extended to quantify individual differences in feedback loops when implemented in a mixed-effect modelling framework (Zucchini et al., 2008); such variation is expected because ecological conditions should shape the magnitude and sign of feedbacks in nature (Luttbeg & Sih, 2010). Finally, cases where a focal individual's behaviour represents the state of another individual (cf. interacting phenotypes) can be captured by fitting a single phenotypic equation with two random effects (individual and social partner identity), where the feedback loop can be calculated directly from the covariance between the two random effects (McGlothlin, Moore, Wolf, & Brodie, 2010).

CONCLUDING REMARKS

In this paper, we highlighted a parsimonious explanation for state-dependent personality due to positive feedbacks between state and behaviour. We reviewed theoretical models on the role of feedback loops in shaping behavioural variation both within and among individuals. The models discussed in this paper indicate that the direction and strengths of feedback loops will often depend on the ecological conditions. We clarify that positive feedback loops can lead to adaptive personalities (among-individual covariance between state and behaviour) whether of genetic or non-genetic origin. We further provide guidelines for empirical testing of adaptive theory (Box 3). We hope our conceptual framework for explaining variation in personalities proves useful for guiding future integration of theoretical and empirical work in this exciting field with many outstanding questions (Box 4) to be addressed in the near future.

Box 4. Outstanding questions

- Feedbacks and distribution of personality types. Feedbacks would, in their simplest form, result in dichotomous among-individual variation in behaviour (see Fig 2 in main text), hence discrete personality types. What are the mechanisms that prevent the emerging among-individual variation to become dichotomous? What is the timescale over which feedback loops act? Is there an end-point to positive feedback and why? At what developmental stages do feedback loops exist, and why?
- Selection on feedback loops. Feedback loops imply that state is a function of behaviour and vice versa. Such functions are commonly viewed as reaction norms (Niels J Dingemanse et al., 2010; D H Nussey et al., 2007). Do individuals differ in state–behaviour and behaviour–state reaction norms, whether in intercepts or slopes? And are components of these reaction norms correlated? How does selection act on these reaction norms (Box 1). _ Ecology of feedback loops. Are feedback loops a function of ecological conditions (e.g., competitive regimes, predators, food availability), and if so, which ecological factors are of key importance? Can temporal or spatial variation in ecological conditions explain variation among individuals in magnitude and sign of feedback loops?
- Which combinations of behavioural and state variables show feedback? Theory has been developed for specific combinations of states and behaviours (see Table 1 in main text). How general are the associated predictions? Do they apply to specific behaviour–state combinations or more generally?
- Ecological versus evolutionary time scales. Feedbacks can occur both within single individuals and across individuals, leading to among-individual correlations of non-genetic versus genetic origin, respectively. When should feedback loops evolve at each of those time scales? Do feedback loops differ between time scales; if so, why?
- Fitness consequences of state–behaviour feedbacks. Do positive (divergent) feedbacks generate among-individual differences in fitness, or do they produce alternative state–behaviour combinations with equal fitness, and under what conditions? Does the strength or direction of the feedback loop predict changes in individual fitness proxies through time?

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Table 1: Overview of mechanisms and models generating dynamic feedbacks between state and behaviour.

Mechanism	State ↔ Behaviour	Predicted feedback	Assumptions	Key factors	Type[d]	Refs
1. Feedbacks involving intrinsic state variables						
Asset protection	RRV[a] ↔ Willingness to take risks[b]	*Positive feedback:* emerge in scenarios where more risky actions increase assets. *Negative feedback:* emerge when more risky actions decrease assets. Thus, individuals with low RRV are more willing to take risks, while individuals with high RRV avoid risk in order to protect their assets.	Risky actions increase or decrease assets compared to less risky actions; these effects can work via fecundity or mortality.	Effect of risky actions on fecundity and mortality schedule.	M	(Luttbeg & Sih, 2010; McElreath, Luttbeg, Fogarty, Brodin, & Sih, 2007; Wolf et al., 2007a, 2007b)
Starvation avoidance	Energy reserves ↔ Sampling[c]	*Positive feedback:* under low starvation risk, only individuals with high energy reserves can 'afford' to sample, which allows them to track resources and maintain higher long-term intake rates than non-samplers. *Negative feedback:* under high starvation risk, individuals with low reserves sample for survival. Sampling allows them to build energy reserves, eroding among-individual differences in energy reserves and sampling.	Sampling behaviour involves immediate costs (e.g. sampling errors), but allows higher long-term intake rate through tracking of resources	Probability of energetic shortfall	M	(Mathot & Dall, 2013)
Starvation avoidance	Energy reserves ↔ Boldness while foraging	*Positive feedback:* Individual with lower energy reserves is more willing to take risks, but never increases in state relative to individuals with high reserves because individuals with high reserves always forage as part of a pair, allowing them to	Foraging in pairs is advantageous because it lowers predation risk and/or increases energetic gain	Social environment (i.e. solitary versus group foraging)	M	(Harcourt, Ang, Sweetman, Johnstone, & Manica, 2009; Luttbeg & Sih, 2010; Rands et al., 2003)

		forage more efficiently. *Negative feedback:* Poor condition individuals are forced to be bold because of the need to forage, and foraging builds energy reserves. High condition individuals are less bold and therefore they do not increase reserves as quickly.				
State-dependent safety	Size, energy reserves, condition, vigour ↔ Boldness in foraging context	*Positive feedback:* Individuals in good condition behave more boldly, thereby increasing in condition	Individuals with higher state face lower risk of predation while being bold.		M	(Luttbeg & Sih, 2010)
State-dependent immune function	Host immune function ↔ Boldness, activity	*Positive feedback*: High resource intake leads to efficient immune function, and individuals with efficient immune function are better able to cope with the potential exposure to parasites that results from high foraging effort (e.g. boldness and activity).	High resource-intake rates lead to efficient immune function.		V	(Kortet et al., 2010)
State-dependent foraging strategy	Gape size ↔ cannibalistic behaviour	*Positive feedback*: Individuals with larger gape-size are more cannibalistic, thereby increasing in size and reinforcing their tendency to be cannibalistic. *Negative feedback:* Predation risk reduces cannibalism since predators preferentially attack cannibalistic individuals, which become less active, and thus, less likely to encounter potential cannibalism victims. Consequently, there is no reinforcement of cannibalism or size differences.	Cannibalism increases growth rate due to an increase in foraging efficiency. Predation risk reduces cannibalism either through non-consumptive effects or through consumptive .	Predation risk	E	(Kishida et al., 2011)

Learning /Skill	Experience with responsiveness ↔ Responsiveness	*Positive feedback*: Initial differences in responsiveness are maintained.	Individuals that have been responsive in the past face lower costs (or higher benefits) of being responsive again.	M	(Wolf et al., 2008)
Winner-loser effects	Winning/losing experience ↔ Aggressiveness	*Positive feedback:* Individuals that have recently experienced a “win” in an agonistic encounter are more likely to initiate future agonistic encounters. Individuals initiating agonistic encounters have a higher probability of winning, reinforcing individual differences in winning-experiences and aggressiveness. The strength of the loop would probably differ between winners and losers since winner effects are distinct from loser effects, and often have memory times.	Initiating an aggressive encounter increases the likelihood of winning.	V	(Chase, Bartolomeo, & Dugatkin, 1994)
Hormone-mediated perception of hunger	Insulin levels↔ Feeding behavior	*Positive feedback:* High levels of insulin lead to overeating due to increased perception of hunger, and weight gain increases insulin levels.	High insulin levels trigger overeating behavior	E	(Rodin, 1985)
State-dependent energy assimilation efficiency	BMR ↔ behaviours that increase resource acquisition	*Positive feedback:* Large metabolic machinery (e.g. stomach, intestines) is necessary to process high volumes of energy. Acquiring and processing high volumes of energy facilitates the maintenance of energetically costly organs that are needed for energy	High energy processing ability promotes expression of behaviours that increase energy acquisition rate	V	(Biro & Stamps, 2010; Biro & Stamps, 2008; Careau & Garland, 2012; Careau, Thomas, Humphries, & Réale, 2008)

		processing.				
2. Feedbacks involving extrinsic state-variables						
Aggressiveness mediated by other individuals’ aggressiveness	Aggressiveness’ individual 1 ↔ Aggressiveness’ individual 2	*Positive feedback:* Individuals that are more aggressive are more likely to elicit aggressiveness in others.	Recursive effect in interacting phenotypes		V	(McGlothlin et al., 2010)
Parasite mediated changes in energy expenditure	Parasite infection ↔ boldness/activity	*Positive feedback:* Parasite infection increases energetic needs, favouring high levels of boldness/activity to secure resources. Animals that are more bold/active are more likely to encounter and become infected by parasites.	Parasite infection imposes non-negligible energetic costs.		V	(Barber & Dingemanse, 2010)
Anthropogenic contaminants (ACs)	Exposure to AC ↔ risky behaviours	*Positive feedback:* Animals that are exposed to ACs decrease survival or increase reproductive effort, favouring an increased expression of risky behaviour. This further exposes them to ACs, reinforcing differences in survival/reproductive effort. *Negative feedback*: Toxic effects of exposure to ACs lead to overall decrease in risky-behaviours, reducing future exposure to ACs.	Exposure to ACs changes optimal allocation of energy to growth, reproduction and maintenance AND/OR has toxic effects that impair the function of the organism.	Toxicity	V	(Montiglio & Royauté, 2014)
3. Joint evolution of behaviour and state-variables						
Coevolutionary diversification	Model applies to diverse range of behaviours and state variables	*Positive feedback:* promotes the evolutionary emergence of correlated differences in state and behaviour	State variable affects the cost and/or benefits of behaviour; behavioural trait is under negative frequency-dependent selection	Increases in the evolving state variable are costly to individuals.	M	(Wolf & McNamara, 2012)

[a] RRV = residual reproductive value, i.e. future fitness expectations

[b] any behaviour that increases access to resources at the cost of an increased risk of mortality

[c] investment of time and/or energy to reduce uncertainty about alternative foraging options

[d] Type of paper from which predictions were derived: M = Model, V = Verbal argument, E=Empirical

Chapter 2

A multi-level approach to quantify speed-accuracy trade-offs in great tits (*Parus major*)

Maria Moiron, Kimberley J. Mathot, and Niels J. Dingemanse

ABSTRACT

Animals often face a conflict between the speed and accuracy by which a decision is made. Decisions taken quickly might be relatively inaccurate, whereas decisions taken more slowly might be more accurate. Such “speed-accuracy trade-offs” receive increasing attention in behavioural and cognitive sciences. Importantly, life-history theory predicts that trade-offs typically exist only at certain hierarchical levels, such as within rather than among individuals. We therefore examined within- and among-individual correlations in the speed and accuracy by which decisions are taken, using a foraging context in wild-caught great tits (*Parus major*) as a worked example. We find that great tits exhibit among-individual variation in speed-accuracy trade-offs: some individuals predictably made relatively slow but accurate decisions, whereas others were predictably faster but less accurate. We did not, however, find evidence for the trade-off at the within-individual level. These level-specific relationships imply that different mechanisms acted across levels. These findings highlight the need for future work on the integration of individual behaviour and cognition across hierarchical levels.

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INTRODUCTION

An important research objective in evolutionary and behavioural sciences is to understand why phenotypic variation is maintained despite selection (Hallgrímsson & Hall, 2005). A classic explanation for the persistence of phenotypic variance is the occurrence of trade-offs in the simultaneous investment in multiple traits that are costly to produce (Reznick, Nunney, & Tessier, 2000b; Stearns, 1992; van Noordwijk & de Jong, 1986a). Though developed as part of life-history theory (Stearns, 1992), trade-offs are also commonly evoked to understand variation in behavioural decision-making and other phenotypic traits (e.g. risk-taking behaviours can be explained by a starvation-predation risk trade-off (Houston, McNamara, & Hutchinson, 1993; Lima, 1986) or male fertilization-related behaviours and a trade-off between within-pair and extra-pair reproduction (Webster, Pruett-jones, Westneat, & Stevan, 1195)). Decision-making trade-offs arise when a beneficial increase in the performance of one trait decreases the performance in another. One well-known cognitive trade-off occurs between speed and accuracy of behavioural decisions (Chittka, Dyer, Bock, & Dornhaus, 2003; Chittka, Skorupski, & Raine, 2009). 'Slow' decisions allow for time to collect and assess environmental information and consequently, allow for decisions based on relatively accurate information. By contrast, 'fast' decisions allow for less time to assess environmental state, and consequently, enable quick decisions based on less accurate information. Because of this "speed– accuracy trade-off", multiple alternative strategies might persist within the same population.

The study of speed-accuracy trade-offs has mainly focused on the within-individual level. That is, within the same individual, positive changes in speed typically co-occur with negative changes in accuracy (Chittka et al., 2009). Speed-accuracy trade-offs are also increasingly evaluated at the among-individual level, for example in studies of animal personality (Sih & Del Giudice, 2012). Among-individual trade-offs would imply that individuals that take, on average, fast decisions also, on average, take inaccurate decisions. Such among-individual differences in average behaviour imply individual repeatability in both speed and accuracy. Support for trade-offs at this level is, however, inconclusive (Chittka et al., 2003; Ducatez, Audet, & Lefebvre, 2014; Mamuneas, Spence, Manica, & King, 2014; Proulx, Parker, Tahir, & Brennan, 2014; Wang, Brennan, Lachlan, & Chittka, 2015): both evidence, and lack of evidence, for the existence of a trade-off between speed and accuracy have been reported. For example, among-individual speed-accuracy trade-offs have been observed in different taxa (e.g. bumblebees (Chittka et al., 2003); birds (Ducatez et al., 2014); fish (Wang et al., 2015)) though other studies (in fish) failed to detect it (Mamuneas et al., 2014; Proulx et al., 2014).

Why some studies fail to find a trade-off between speed and accuracy represents an important research question. One prominent explanation known from the life-history literature is that different mechanisms contribute to correlations at different levels (Reznick et al., 2000b; Stearns, 1992; van Noordwijk & de Jong, 1986a). When a single mechanism is underlying the relationship at all levels, one can expect similar magnitudes and signs of correlations across all levels. In contrast, when mechanisms are level-specific, this could result in correlations with conflicting directions across different levels. The latter scenario occurs, for example, in situations where individuals have to trade-off investment in multiple costly actions while individuals simultaneously differ in their access to or acquisition of energy. For instance, in the classic example of resource acquisition and allocation of money invested in buying houses and cars in humans, a positive covariance at the among-individual level is expected between these two costly traits because rich people have enough money to buy both a big house and a big car (Reznick et al., 2000b; van Noordwijk & de Jong, 1986a). Simultaneously, a negative covariance at the within-individual level is expected since money spent on a house cannot be spent on buying a car. House and car size are thus expected to correlate *positively* among individuals but *negatively* within individuals. Analogously, the same rationale can be applied to speed-accuracy trade-offs, where we might expect the covariance between cognitive traits to differ across hierarchical levels.

In the recent literature, the idea that there may be repeatable individual differences in speed-accuracy trade-offs, and therefore, that individuals may consistently differ in cognition, which refers to the way individuals acquire, process, store, or act on information, has attracted some theoretical attention (Sih & Del Giudice, 2012). Sih and Del Giudice (2012), for example, hypothesized that variation in cognition functionally underpins variation in personality (defined as repeatable among-individual variance in behaviour; Dingemanse and Dochtermann, 2013). This hypothesis is based on the ‘coping style’ literature and poses that individual differences in behaviour fall on a ‘fast–slow’ gradient along the bold–aggressive–active–exploration axis. Thus, animals that are bolder, more aggressive, proactive and/or exploratory take more risks but can also gather more rewards (Coppens, de Boer, & Koolhaas, 2010). The overarching hypothesis is that cognitive traits also fall on this ‘fast–slow’ gradient where fast explorer individuals should take faster decisions but slow-explorer individuals should make more accurate choices, that is, fast explorer individuals should favour speed over accuracy (Guillette, Hahn, Hoeschele, Przyslupski, & Sturdy, 2014; Sih & Del Giudice, 2012).

The goal of this study was to estimate sources of variation in decision-making behaviour at the within- and among-individual levels, to examine whether there was a trade-off between speed and accuracy, and whether this trade-off existed at multiple hierarchical levels. We expected a trade-off to exist both among- and within-individuals. We also expected relationships with exploratory tendency (Sih and Del Giudice 2012), where we predicted that fast exploring individuals would be faster in taking a decision but also less accurate. These questions were applied to a foraging context using great tits (*Parus major*) as a model. To accomplish this, we screened wild-caught great tits in a novel environment task to assess their exploration behaviour (Dingemanse, Both, Drent, van Oers, & van Noordwijk, 2002). Birds were then repeatedly subjected to a foraging task to repeatedly assess their decision speed and accuracy.

MATERIALS AND METHODS

Collection of study subjects and housing conditions

We used 31 wild-caught adult great tits (16 males and 15 females). The great tit is a common Palearctic passerine species, and a model for the study of repeatable individual differences in exploration behaviour (e.g. Dingemanse et al. 2002). Wild-caught great tits have previously been used in captive experiments over extensive time periods without showing signs of stress or abnormal behaviour (Lange & Leimar, 2004; te Marvelde, Webber, Meijer, & Visser, 2012; Wansink & Tinbergen, 1994) while exhibiting similar behaviours as observed in the wild (e.g. Krebs, Kacelnik, and Taylor 1978; Wansink and Tinbergen 1994; Marchetti and Drent 2000; Lange and Leimar 2004; van Oers et al. 2004). Furthermore, it has been recently shown that the great tit genome presents an overrepresentation of genes related to neuronal functions, learning and cognition in regions under positive selection (Laine et al., 2016), which makes this species an excellent animal models for studies in behaviour and cognition. Birds were caught between October and November 2014 in Seewiesen, Bavaria, southern Germany. Birds were transported to the laboratory within 30 minutes, weighed to the nearest 0.1 g, after which standard morphological measurements were taken (e.g. tarsus, bill and wing length). A maximum of 4 individuals were taken per capture to ensure that all behavioural testing (detailed below) could be completed within 6 days of capture for any given individual. Sex and age of birds were determined based on plumage characteristics (Jenni & Winkler, 1994); to allow individual identification, birds were provided with an aluminium number ring. Birds were housed individually in home cages of 100 × 40 × 50 cm with five walls and a wire-mesh front. Each cage contained two food bowls, one water bowl and six perches, and was situated in a laboratory room with natural daylight conditions (i.e. laboratory facilities were lighted by the natural day light available through the full length windows immediately in front of the cages). Human disturbance was kept to a minimum. Birds were provided with water and mealworms (larvae of *Tenebrio molitor) ad libitum*, and released at the capture site at the end of the experiment.

Exploratory tendency assessment

The day following capture, between 07h00 and 07h30, we measured the exploration behaviour of each bird. Exploration behaviour has been previously shown to predict willingness or ability to perceive changes in the environment in great tits (Nicolaus et al., 2015; Stuber et al., 2013; Verbeek, Drent, & Wiepkema, 1994). Each bird was individually tested in a novel environment containing 5 artificial trees. Following the standard procedure established for this species (Dingemanse, Bouwman, et al., 2012), we introduced each bird into the room without handling by darkening the cage with a curtain, opening the sliding door, turning on the light in the test room and briefly lifting the curtain, after which all birds flew into the room. Birds were then scored based on movement (the total number of flights and hops) in the experimental room during a 2-minute period where faster explorers had higher exploration scores than slow explorers. After the exploration test, birds were returned to their home cages.

Decision-making task

We measured each individual's decision-making behaviour repeatedly within a single experimental session. Each evening between 17h00 and 17h30, one bird was randomly selected and taken from its home cage to an individual cage adjacent to the experimental room. The selected bird had *ad libitum* access to water but was food-deprived until the start of the experiment the following morning, during which time the focal bird was tested individually. Thus, birds had no access to their normal food for 14 hours, a duration that was necessary to ensure a high motivation to search for food but at the same time is nearly identical to the natural non-feeding periods in free living tits in winter, as they do not feed from dusk to dawn. During experiments, no food was available other than that provided at the feeding stations.

The foraging trials were conducted in the experimental room where the exploration test (see above) was previously conducted (Fig 1). The experimental room consisted of one perch, one water bowl and two wooden trays spaced 1.5 m from each other supporting a white food bowl (11 × 7.5 × 3.5 cm) (hereafter, "feeder"). The experimental room was kept on the same light cycle and temperature as the holding room, in both cases matching the natural photoperiod. At one side of the experimental room, there was a one-way screen from where we continuously monitored and scored the subject's behaviour. During the experiment, the laboratory room was equipped with two feeders which consisted of two identical operant feeding stations (i.e. requiring the same technique to pick up food) placed at one wall of the lab room, and located 1.5 m apart. Through two sliding doors in the wall, both feeders were placed inside the experimental room with the aid of a wooden board and without the experimenter being visible to the bird (Fig 1). There were two types of feeders: a low-reward feeder which contained half of a mealworm and a high-reward feeder which contained two mealworms. Each day each feeder's reward size (i.e. right or left location) was switched; therefore it was fixed for a single bird but varied over the course of the experiment to exclude any side preference effects among individuals (left, n = 16; right, n = 15; alternating by bird identity number). The order that a bird was selected to undertake the experiment among the 4 possible days was also randomized ("experimental sequence"). We tested for any effect of experimental sequence or of preference for a feeder location by including the sequence order and the side of the high reward feeder (left or right) as a predictor in our models to demonstrate that among-individual differences in our behavioural trait measures were not caused by those factors (see results reported in the Supplementary Material).

The experimental session started at 8h00 when we opened the sliding shutter connecting the home cage (where they had stayed since their exploratory tendency assessment) to the experimental room. Birds were moved from the home cage to the experimental room without handling by darkening the cage that was to be left by placing a piece of cloth in front of it (Dingemanse et al., 2002). This procedure enabled us to not add extra stress caused by additional handling. Furthermore, once a focal bird was inside the experimental room, it was left undisturbed for 30 minutes in order to familiarize to the room. After this time, we started the training phase of the experiment where each bird was subjected to 16 foraging trials. The purpose of the training was to familiarize the birds with picking up food at feeders with the two different reward sizes. This was done by presenting a single feeder at each trial, forcing birds to make use of that location and therefore, to experience both food rewards over time. Thus, for these initial 16 trials, the bird was presented either with the low-reward feeder, containing a half mealworm per visit, or with the high-reward feeder, containing two mealworms per visit. We applied the same randomization scheme to all the birds. The order by which feeders were presented was therefore randomly allocated before the start of the experiment but both the low-reward and high-reward feeder were presented eight times exactly. After the bird took the food out of the feeder, independent of whether the bird was still processing the food, we removed that feeder from the experimental room. The maximum trial length was 2 hours (all 31 birds took all the food in each trial within that time range). Five minutes later, a refilled feeder was placed back in the experimental room. During the first five trials the feeder was uncovered so that the bird could see the reward and get familiar with the reward setup. After the fifth trial the feeder was fully covered by a cardboard lid so birds could not visually assess the reward size. Once these first 16 training trials were concluded, the experiment continued with the testing phase. This phase consisted of another 6 trials where the two feeders were presented simultaneously. As during the training phase, the low-reward feeder contained half a mealworm and the high-reward feeder contained two mealworms. As soon as the bird touched one of the feeders or cardboard lid, we considered the bird as having made a decision. The other feeder was immediately removed from the experimental room, while the ‘chosen’ feeder was left in the room so that the bird could acquire the food. As during the training phase, the refilled feeders were placed back into the experimental room 5 minutes after the bird had taken a decision. By the end of the experiment, when a focal bird had completed a total of 22 trials, it was returned to its home cage where it was provided with *ad libitum* access to food and water.

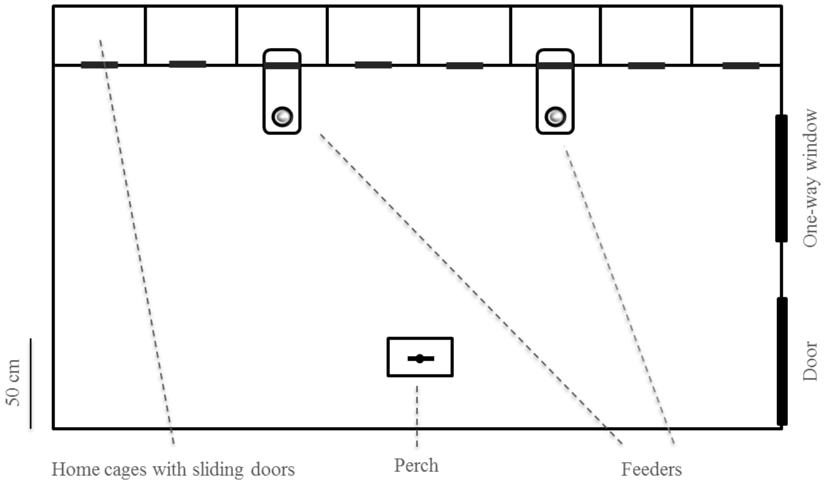

Figure 1. *Illustration of the experimental setup: a perch was placed in-between two sliding doors through which two feeders were presented. A sliding door also connected the home cage to the experimental room (3. 95L × 2.35W × 2.30 H m) (scale bar).*

Measures of decision speed and accuracy

We were interested in the time needed to take a decision when both feeders were presented at the same time (“decision time”), and the accuracy of the decision taken. The training phase gave birds the opportunity to learn about the different rewards. Decision time (a proxy for decision speed) was computed as time (in seconds) elapsed between the moment that the feeders were made available in the experimental room and the moment that the bird touched one of them (our measure of feeder choice, see above). Shorter decision times thus indicate faster decision-making. Decision accuracy was defined by whether the bird made the correct decision, that is, whether it chose the high-reward feeder (yes = 1, accurate, no = 0, inaccurate).

Statistical analyses

We applied a mixed-effect modelling framework to estimate sources of variation in both behaviours at both the within and among individual levels (following Dingemanse & Dochtermann 2013), and to quantify trade-offs between speed and accuracy within and among individuals. First, we investigated sources of variation in decision time and decision accuracy separately. To do so, we constructed two separate univariate mixed-effect models, one where our response variable was decision time (in seconds) and another where our response variable was decision accuracy (right or wrong choice) (Table 1). Sex (factor: male or female), age (factor: first-year adult or older adult), and exploration behaviour (covariate: total number of flights and hops) were fitted as fixed effects. Random intercepts were included for individual identity, enabling us to partition the total phenotypic variance into variance attributable to individual identity versus residual within-individual variance. We calculated "adjusted" repeatability of decision time and accuracy as the among-individual variance divided by the total variance not attributable to fixed effects (Nakagawa & Schielzeth, 2010). Decision time was log-transformed and modelled with Gaussian errors. Decision accuracy was modelled with binomial error structure where residual variance is taken to be $\pi^{2/3}$ (Nakagawa & Schielzeth, 2010).

Based on current theory, we predicted a clear cause-effect relationship between our variables: time to take a decision ("decision time"; predictor) should influence the accuracy of that decision ("decision accuracy"; response). Furthermore, we took into account that the effects of decision time on decision accuracy could vary within versus among individuals (see Introduction) (van de Pol & Wright, 2009). For example, within-individual changes in decision accuracy should result from within-individual phenotypic plasticity in decision time (*sensu* van de Pol and Wright 2009 ; Westneat et al. 2011), whereas among-individual effects of decision accuracy may also include effects of personality-related traits as well as effects attributable to repeatable variation in conditions due to the experimental design (i.e. the high-reward feeder location varying exclusively among individuals) (van de Pol & Verhulst, 2006). We thus used a within-subject centring approach to separate the within-individual from among-individual effects of decision time (fixed effect predictor variable) on accuracy (response variable), and tested whether the estimate of this fixed effect differed within vs. among individuals (e.g., van de Pol and Verhulst 2006; van de Pol and Wright 2009). Following van de Pol and Wright (2009) we calculated 1) the mean value of decision time for each individual and 2) the observation's deviation from the focal individual's mean value. We then built a model where decision accuracy was fitted as a binary response variable to which the among- and within-individual components of decision time were fitted as fixed effects. We also fitted exploration behaviour as a fixed effect into this model to test whether this behaviour mediated the trade-off (Table 2). Individual identity was included as a random effect. Finally, we tested whether the among- and within-individual effects of speed on accuracy differed statistically. To do so, we calculated the difference between the parameter estimates of the within- and among-individual effect of decision time, and assessed whether its credible interval overlapped zero.

All statistical analyses were carried out using the packages “lme4” and “arm” of the statistical freeware R-3.1.2 (R Development Core Team, 2014). To obtain parameter estimates, we used the *sim* function to simulate values from the posterior distributions of the model parameters. Model fit was assessed by visual inspection of the residuals. Based on 5000 simulations, we extracted 95% credible intervals (CI) around the mean (Gelman & Hill, 2007), representing the uncertainty around our estimates. Assessment of statistical support was obtained from the posterior distribution of each parameter. We considered an effect as “strongly supported” if zero was not included within the 95% CI, while estimates centred on zero provide strong support for the absence of an effect. However, in the cases where zero was included within the 95% CI, but where these was a clear skew in the distribution of the 95% CI, we considered the support for that effect as “unknown” as it was neither “strongly supported” nor “strongly not supported” (e.g. Dingemanse et al. 2012).

RESULTS

During the 6 trials of the decision-making task, birds chose on average, the correct feeder significantly more than would be expected by chance (binomial test: number of successes = 117, number of trials = 186, $P < 0.001$; alternative hypothesis: true probability of success is not equal to 0.5). Mean decision accuracy was 0.63 (SE = 0.48, min=0, max=1); there was some support that decision accuracy improved over time within the average individual (effect of trial: 0.12, 95%IC = -0.06, 0.32). Mean decision time was 119.2 seconds (SE=343.1, min=1; max=3899); there was weak support that decision time also decreased over time within the average individual (effect of trial: -0.03, 95%IC = -0.12, 0.05). Neither decision speed nor accuracy differed between sexes or age-classes (Table 1). Furthermore, we found inconclusive support for the prediction that fast explorers spent less time to make a less accurate decision owing to credible intervals of these effects slightly overlapping zero (Table 1 and Fig S1). Decision time was repeatable (R= 0.68; 95% CI: 0.61, 0.75) as was decision accuracy (R=0.26; 95% CI: 0.18, 0.34). These findings imply that both cognitive traits harbored both within and among-individual variation.

Table 1. Sources of variation in (a) decision accuracy (binary variable: correct vs. incorrect choice) and (b) log-transformed decision time (seconds).

	Decision accuracy	Decision time
Fixed effects	β (95% CI)	β (95% CI)
Intercept	0.30 (-0.69, 1.27)	3.98 (2.82,5.11)
Sex	-0.83 (-2.03,0.34)	-0.96 (-2.33, 0.44)
Age	0.51 (-0.68, 1.73)	-0.08 (-1.49, 1.35)
Exploratory tendency	0.05 (-0.02, 0.12)	-0.04 (-0.11, 0.04)
Random effects	σ^2 (95%CI)	σ^2 (95%CI)
Individual	0.93 (0.57, 1.39)	2.23 (1.76, 2.89)
Residual	$\pi^{2/3}$	1.09 (0.89, 1.34)
Repeatability	*R* (95% CI)	*R* (95% CI)
	0.23 (0.16, 0.31)	0.67 (0.59, 0.75)

We present fixed (β) and random (σ^2) parameters, and adjusted repeatabilities (*R*), with their 95% credible intervals. The reference categories for categorical variables are “male” for “sex” and “older adult” for “age”.

Decision time and accuracy covaried among-individuals as expected: we found strong support for a positive correlation between an individual’s mean values for decision speed and accuracy (see the Supplementary Material for an alternative analysis following Lüdtke et al. (2008) that confirms this finding based on a bivariate mixed-effects modelling approach). Faster birds (i.e. birds with a lower mean decision time) were more likely to take less accurate decisions (Table 2, Fig 2). In contrast, there was strong support for a lack of correlation between decision time and accuracy within-individuals: moment-to-moment changes in decision speed did not predict moment-to-moment changes in accuracy within the same individual (Table 2, Fig 2). Importantly, there was strong support for level-specific relationships between decision time and accuracy as the 95% CIs of parameter estimating the difference between the among-individual minus the within- individual effect of decision time did not overlap zero (mean: 0.58; 95% CI: 0.13, 1.05). This finding implies that more than one mechanism needs to be invoked to explain the covariance between these two cognitive traits in our dataset.

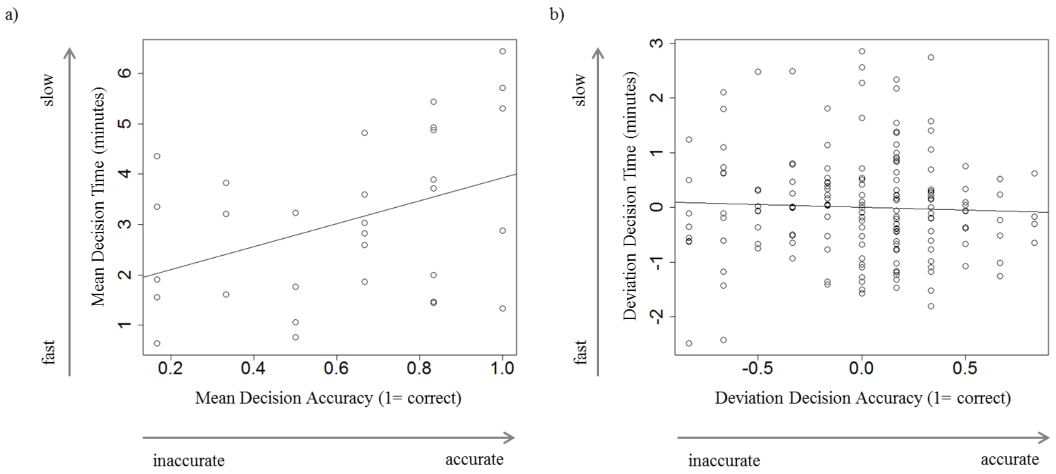

Figure 2. *The effect of decision time on decision accuracy (a) among and (b) within individuals. We plot here (a) each individual's average level of decision time and accuracy over 6 repeated observations (i.e. the among-individual relationship), and (b) each instance's deviation of decision time and accuracy from the individual's mean (i.e. the within-individual relationship).*

DISCUSSION

We investigated the presence of trade-offs between speed and accuracy in a foraging context in great tits, and asked whether such trade-offs varied across hierarchical levels. As predicted and in line with previous studies (e.g. Chittka et al. 2003), we detected a speed-accuracy trade-off at the among-individual level: some birds, on average, made slow but accurate decisions over repeated observations of their decisions, while others, on average, made fast but less accurate choices. At the same time, contrary to earlier evidence and our own expectations, we did not find empirical support for the presence of within-individual correlations in decision time and accuracy: within-individual moment-to-moment changes in decision time did not predict moment-to-moment change in accuracy. Importantly, among- and within-individual effects differed statistically, implying that there was strong evidence for different mechanisms governing trade-off across these two hierarchical levels.

Level-specific associations between decision speed and accuracy

We expected the trade-off between speed and accuracy to occur both among and within individuals provided that they were governed by a single mechanism. In contrast to expectations, the within-individual trade-off was not revealed by our data analysis. There are several methodological and biological reasons why within-individual trade-offs may not have been detected.

We start by discussing two key methodological reasons. First, within-individual trade-offs may have existed but may have been masked by measurement error (Dingemanse & Dochtermann, 2013). This would represent a valid explanation if measurement error explained a major proportion of the within-individual variation in both speed and accuracy (for a statistical argument, see Dingemanse, Dochtermann, and Nakagawa 2012). Given that we collected accurate measurements under laboratory conditions, we forcefully reject this explanation. Second, we might not have had enough statistical power to detect patterns of within-individual covariance. We also find this explanation highly unlikely because statistical power to detect correlations is much higher at the within- compared to the among-individual level (Dingemanse & Dochtermann, 2013); we were able to detect significant effects at that among-individual level, implying that we must have been able to detect trade-offs at the within-individual level as well. We therefore assume that there were instead multiple biological mechanisms causing level-specific patterns of covariance.

Table 2. Estimates of among- and within-individual effects of decision time, and among-individual effects of exploratory tendency on decision accuracy.

	Decision accuracy
Fixed effects	β (95% CI)
Intercept	-1.53 (-2.82, -0.16)
Decision time	
Among-individual effect	0.49 (0.17, 0.81)
Within-individual effect	-0.09 (-0.44, 0.26)
Exploration tendency	0.07 (0.00, 0.141)
Random effects	σ^2 (95%CI)
Individual ID	0.60 (0.36, 0.93)
Residual	$\pi^{2/3}$

Estimated effects (β; mean and σ^2; variance) are reported with their 95% credible intervals.

We propose two biological mechanisms explaining level-specific patterns of covariance between speed and accuracy. First, given the presence of empirical evidence for within-individual trade-offs in other studies of cognition (Chittka et al., 2003), and growing awareness that trade-offs (e.g. between life-history traits) may be context-specific (Sgrò & Hoffmann, 2004), a key biological explanation centres on the notion that another biological process may have obscured our ability to detect the trade-off at the within-individual level. Specifically, the overall lack of correlation at the within-individual level may have been due to an individual-level character mediating the magnitude of the trade-off within individuals. In the context of our foraging paradigm, we can imagine that the trade-off might only have been expressed within individuals that were in poor body condition. This would imply that among-individual variation in body condition might have predicted the strength of the trade-off within individuals, and that failure to have modelled this cross-level statistical interaction obscured our interpretation. In order to test this post hoc explanation, we re-ran our analysis after including a term that modelled the interaction between an individual's average body mass and its within-subject centred decision times. However, our statistical model did not support this idea (see Supplementary Material).

A second biological explanation for level-specificity would imply that the within-individual speed-accuracy trade-off did not exist. Given the experimental setup of our study, we view this as the most likely explanation for our finding of level specificity. Specifically, our experimental design probably gave rise to a dual role of decision accuracy. That is, among-individual variation in decision accuracy might reflect differences in both how well the task was learned (the genuine "decision accuracy") and willingness to sample (Mathot, Wright, Kempenaers, & Dingemanse, 2012). By contrast, within-individual variation in accuracy might instead solely have reflected willingness to sample. An "inaccurate" decision might thus not reflect inaccuracy *per se* but rather an active sampling decision, and therefore not covary with decision time within-individuals. We view this explanation as relatively likely because the experiment was set up in a way that caused each feeder's reward to be constant over the foraging trials experienced by an individual. Individuals that delayed their choice (i.e. took slower decisions) would not necessarily acquire better information since they had already learned what the good feeder was. To unequivocally disentangle the effect of sampling and learning on our measure of decision accuracy, it would have been necessary to measure decision-making traits in multiple independent tasks (e.g. Chittka et al. 2003). For example, performing a series of independent foraging tasks would allow us to explore the strength of the trade-off under different conditions. Previous studies imply that the speed-accuracy trade-off depends on the difficult of the task and also if errors (i.e. incorrect choices in the current experiment) were punished (Chittka et al., 2003, 2009). With our experimental design, the position of the feeders did not vary among the six experimental trials (i.e. their 'correct' decision was not changing) and incorrect choices were not penalized. We demonstrated that, on average, birds did learn to discriminate the correct option in our set-up; however, individuals may exhibit variation in learning speed which in turn, may have influenced the quantification of cognitive traits (Guillette et al., 2014; Guillette, Reddon, Hurd, & Sturdy, 2009). Nonetheless, this uneven effect on the performance of individuals can still be considered as evidence for the existence of among-individual variation in decision-making behaviour, independent of whether it is due to learning, sampling, or other processes. In fact, the goal of the training involved in this study was to provide all individuals with the same opportunities to learn the different food rewards rather than training the individuals to perform the task with the same level of accuracy). If all individuals had performed the task accurately in each foraging trial, we would not have observed any among-individual variation in decision accuracy and would therefore not have been able to investigate speed-accuracy trade-offs at the among-individual level.

Sources of variation in decision speed and accuracy

Our study also examined sources of variation in cognitive traits. A recent conceptual framework hypothesized a link between variation in cognition and personality (Sih & Del Giudice, 2012). This prediction is based on the hypothesis that behavioural types might also differ consistently in cognitive traits. We found inconclusive statistical support for the notion that individual-level exploratory tendency mediated the among-individual trade-off between decision time and accuracy. The distribution of credible intervals around the estimated effects of exploration behaviour on speed and accuracy were such that the data failed to strongly support either the presence or the absence of personality-related differences in cognition. This finding indicates that a larger data set would have been required to draw firm conclusions.

Hierarchical thinking: the merit of the approach

The variance partitioning approach represents an important means to better understand the hierarchical structuring of labile phenotypic characters (Araya-Ajoy & Dingemanse, 2014; Westneat et al., 2015a). Here, we applied the approach to investigate the hierarchical structuring of trade-offs. Quantification of trade-offs is generally challenging because their existence may often be obscured by other biological processes (Hadfield, Nutall, Osorio, & Owens, 2007; Morrissey, 2014; Sgrò & Hoffmann, 2004; van Noordwijk & de Jong, 1986). Indeed, as we showed in the current study, decision speed and accuracy traded off only among-individuals. Importantly, if we would not have partitioned the covariance between these two cognitive traits across the two hierarchical levels, we would likely have drawn erroneous conclusions (for statistical arguments, see van de Pol and Wright 2009; Dingemanse and Dochtermann 2013). Indeed, when we re-ran our original statistical model (presented in Table 2) to include the unpartitioned effect of decision speed on accuracy (instead of its among- and within-individual components), the strength of support for the existence of trade-offs was substantially decreased as the 95% CIs of the unpartitioned effect included zero (i.e., effect of the 'raw' decision time on accuracy: 0.19; 95% CI: -0.05, 0.43).

The current study utilized a variance partitioning approach to investigate whether short-term (i.e. within-day) repeatable individual differences in speed predicted short-term repeatable individual difference in accuracy, while simultaneously considering within-day within-individual patterns of covariance between these two cognitive traits. An exciting avenue for future study would be to expand this paradigm to investigate patterns of covariance between cognitive traits at higher hierarchical levels. For example, it would be insightful to understand whether long-term individual differences in speed would also negatively covary with long-term difference in accuracy, since evidence for level specificity would shed light on the proximate (temporal) mechanism causing trade-offs between cognitive traits. Along the same lines, the hierarchical structure of such analyses may be expanded to study trade-offs at the population or species level, where patterns of covariance are likely governed by different mechanisms. For instance, information sampling as a mechanism can act at the within-individual receptor cell level, at the central nervous processing system level or at the within-population group level (e.g. as might be the case in social insects or human societies), and speed-accuracy trade-offs may occur at any of these organizational levels (Bogacz, Wagenmakers, Forstmann, & Nieuwenhuis, 2010; Chittka et al., 2009; Jandt et al., 2014). In short, this study calls for the exploration of speed-accuracy trade-offs across a wider range of hierarchical levels as this would help us understand the types of environmental and genetic factors mediating the covariance between cognitive traits.

Concluding remarks

This study demonstrated that two cognitive traits, decision speed and accuracy, involved in a foraging context, varied both within and among individuals as did the covariance between them. The multi-level structuring of these cognitive traits underlines the need to incorporate level-specificity in biological hypotheses explaining the maintenance of this variation (Araya-Ajoy & Dingemanse, 2014; Westneat et al., 2015a). Our foraging paradigm applied to great tits demonstrates the need for such considerations, as level-specific effects of trade-offs resulted in level-specific patterns of covariance between these cognitive traits. This study thereby illustrates the usefulness of considering the contribution of multiple biological mechanisms in understanding phenotypic variation in cognitive and other labile phenotypic traits.

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Electronic Supplementary Material of Chapter 2

Text S1. Assessment of body condition

For our experiments, we used 31 adult great tits that were caught between October and November 2014 in Seewiesen, southern Germany. Birds were transported to the laboratory within 30 minutes, weighed to the nearest 0.1 g after which standard morphological measurements were taken (e.g. tarsus, bill and wing length). The day following capture we measured the exploratory behaviour of birds between 07h00 and 07h30. Each individual's body weight (nearest 0.1 g) was measured prior to assessing exploratory behaviour. This latter weight measure is the "body mass" data that we used in our analyses (see Discussion and Table S2-S3).

Text S2. Alternative analyses of the among-individual speed-accuracy trade-off

We verified that the reported support for the among-individual correlation was not an artefact due to bias that sometimes occurs when using within-subject centering approaches (Lüdtke et al., 2008). To do so, we applied a bivariate mixed-modelling model approach where speed and accuracy were both simultaneously fitted as response variables. This bivariate model revealed that decision speed was indeed significantly positively correlated with decision accuracy at the among-individual level (among-individual correlation = 0.53, 95 % 95% CI =0.18, 0.86).

We used the following methodology for this alternative statistical analysis: we estimated the among-individual correlation between decision speed and decision accuracy using a Markov-chain Monte-Carlo bivariate mixed-effects model in the R package MCMCglmm (Hadfield, 2010). With this alternative approach, it was not possible to estimate within-individual correlations because of the properties of the binomial distribution of decision accuracy. This bivariate mixed-effects model included random intercepts for individual identity. We ran the model for 33,000,000 iterations, with a thinning interval of 3,000, and a burn-in of 30000. This yielded effective sample sizes of 10990 for all (co)variances. We visually inspected plots of the traces and posterior distributions as well as calculated the autocorrelation between samples to ensure that all models yielded unbiased estimates. We ran the model using an inverse gamma prior. We calculated the among-individual correlation of decision speed and accuracy by dividing the among-individual covariance between the two traits by the square root of the product of the among-individual variances.

Table S1. Effects of experimental sequence and preference for a feeder location

Sources of variation in (a) decision accuracy (binary variable: correct vs. incorrect choice) and (b) log-transformed decision time (seconds). We used the same statistical model as detailed in the Main text (Table 1) with the difference that here we fitted the experimental sequence (covariate; order of experimental day ranged from 1 to 4) and feeder location (factor: high reward vs. low reward) as fixed effects. Estimate effects (β; mean and σ^2; variance) are reported with their 95% Credible Interval. The reference category for the feeder location variable is "the right location" as opposed to "the left location".

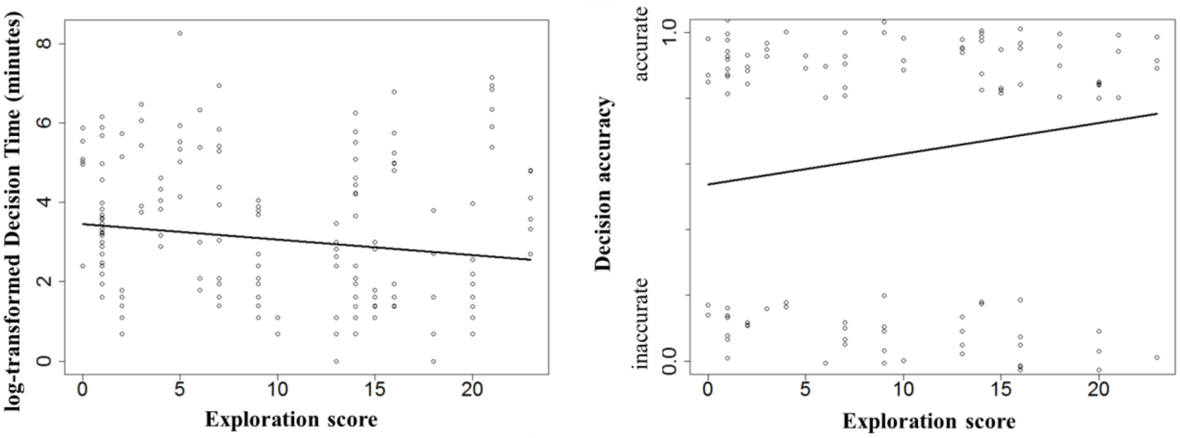
	(a) Decision accuracy	(b) Decision time
Fixed effects	β (95% CI)	β (95% CI)
Intercept	0.52 (-0.65, 1.75)	3.95 (2.60, 5.30)
Experimental sequence	0.08 (-0.39, 0.54)	-0.17 (-0.70, 0.33)
Feeder location	-0.11 (-1.11, 0.90)	-0.91 (-2.07, 0.20)
Random effects	σ^2 (95%CI)	σ^2 (95%CI)
Individual ID	1.14 (0.69, 1.64)	2.20 (1.78, 2.80)
Residual	$\pi^{2/3}$	1.08 (0.89, 1.34)
Repeatability	*R* (95% CI)	*R* (95% CI)
	0.27 (0.18, 0.34)	0.67 (0.58, 0.74)

Table S2. Effects of body mass

We examine the effect of among- and within-individual variation in decision time on accuracy. We used the same statistical model as detailed in the Main text (Table 2) with the difference that here we fitted body mass (covariate; in grams) and the interaction between body mass and the within-individual component of speed as fixed effects. Estimated effects (β; mean and σ^2; variance) are reported with their 95% credible interval. Notably, the reported evidence for the absence of evidence for mass-mediated within-individual trade-offs was also found when tarsus (a measure of structural size) and its interaction with within-subject centred decision speed were fitted as fixed effects, or when residuals of the relationship between mass (response) and tarsus (predictor) were used instead (Results not shown), implying that these findings are not biased by variation in structural size.

	Decision accuracy
Fixed effects	β (95% CI)
Intercept	-0.59 (-1.65, 0.44)
Decision time	
Among-individual effect	0.41 (0.10, 0.73)
Within-individual effect	-0.10 (-0.45, 0.27)
Body mass	0.04 (-0.41, 0.50)
Body mass × Decision time within individuals	-0.05 (-0.45, 0.37)
Random effects	σ^2 (95% CI)
Individual ID	0.84 (0.51, 1.29)
Residual	$\pi^{2/3}$

Figure S1. Effect of Exploration on Decision Speed and Decision Accuracy



Chapter 3

To eat and not be eaten: diurnal mass gain and foraging strategies in wintering great tits

Maria Moiron, Kimberley J. Mathot, and Niels J. Dingemanse

ABSTRACT

Adaptive theory predicts that the fundamental trade-off between starvation and predation risk shapes diurnal patterns in foraging activity and mass gain in wintering passerine birds. Foragers mitigating both types of risk should exhibit a bimodal distribution (increased foraging and mass gain early and late in the day), whereas both foraging and mass gains early (versus late) during the day are expected when the risk of starvation (versus predation) is greatest. Finally, relatively constant rates of foraging and mass gain should occur when the starvation–predation risk trade-off is independent of body mass. Using automated feeders with integrated digital balances, we estimated diurnal patterns in foraging and body mass gain to test which ecological scenario was best supported in wintering great tits *Parus major*. Based on data of 40 consecutive winter days recording over 12 000 body masses of 28 individuals, we concluded that birds foraged and gained mass early during the day, as predicted by theory when the starvation– predation risk trade-off is mass-dependent and starvation risk outweighs predation risk. Slower explorers visited the feeders more often, and decreased their activity along the day more strongly, compared with faster explorers, thereby explaining a major portion of the individual differences in diurnal patterning of foraging activity detected using random regression analyses. Birds did not differ in body mass gain trajectories, implying both that individuals differed in the usage of feeders, and that unbiased conclusions regarding how birds resolve starvation–predation risk trade-off require the simultaneous recording of foraging activity and body mass gain trajectories. Our study thereby provides the first unambiguous demonstration that individual birds are capable of adjusting their diurnal foraging and mass gain trajectories in response to ecological predictors of starvation risk as predicted by starvation–predation risk trade-off theory

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INTRODUCTION

Small passerines rely on body reserves as their main means of energy storage in winter (Witter & Cuthill, 1993). Body reserves act as ‘insurance’ against detrimental effects of interrupted food supplies, and are therefore predicted to decrease the risk of starvation (Dall, 2010; Houston & McNamara, 1993; Lima, 1986). Carrying body reserves, however, also comes with associated costs in the form of increased risk of predation. Extra body reserves increases predator exposure because it decreases manoeuvrability or take-off ability (Brodin, 2001; Gosler, Greenwood, & Perrins, 1995; Walters et al., 2017). Individual foragers have to resolve this predation-starvation risk trade-off to maximize overwinter survival (Houston & McNamara, 1993; Houston, McNamara, & Hutchinson, 1993). For small passerines, adaptive models predict that this trade-off can be resolved by individuals varying the amount of reserves carried (thus varying their body mass) both within days (e.g., between dawn and dusk) and among days (e.g., across successive days or between seasons) as a form of adaptive phenotypic plasticity (Houston & McNamara, 1993; Houston et al., 1993; McNamara, Houston, & Lima, 1994). Species inhabiting seasonal environments, for instance, down-regulate their mass from winter to summer as predicted by theory (Lehikoinen, 1987). By contrast, comparatively few studies have empirically tested theoretical predictions regarding adaptive short-term (i.e., within day) regulation of body mass, particularly in the wild (Lilliendahl, 2002; Macleod, Gosler, & Cresswell, 2005; Thomas, 2000).

Adaptive theory predicts that small passerine birds should increase their body mass (i.e., build up energy reserves) between dawn and dusk to survive the night, predicated on the fact that small birds lose mass overnight (e.g., Lima 1986; Houston and McNamara 1993; Bednekoff and Houston 1994; McNamara, Houston, and Lima 1994). Previous work on body mass trajectories carried out under laboratory conditions has already demonstrated that birds are able to plastically adjust their body mass under artificially increased risk of starvation or predation (e.g., Bednekoff and Krebs 1995; Lilliendahl et al. 1996; Lilliendahl 1998; Brandt and Cresswell 2009). Diurnal mass regulation has also been demonstrated in the wild but remains relatively understudied (Lilliendahl, 2002; Macleod, Gosler, et al., 2005; Thomas, 2000). Furthermore, mass regulation has never been studied in conjunction with foraging activity, which is expected to be the behavioural driver of these fattening patterns. Studies conducted directly in natural populations are of vital importance because the evolution of body mass regulation has ultimately been moulded by natural selection in an ecological context that may not be adequately mimicked in the laboratory. This implies that field-based confirmation of adaptive theory would be particularly insightful. Field studies are, moreover, extremely suitable for testing a wide range of general predictions related to how diurnal body mass regulation varies as a function of abiotic (e.g., day length, and night temperature) and biotic (e.g., food availability and predation risk) factors.

Diurnal variation in body mass trajectories is ultimately thought to result from plastic adjustments in foraging behaviour over the day (Houston et al., 1993). While the former has at times been used as a proxy for the latter, foraging activity *per se* has received relatively less attention in studies of the starvation-predation risk trade-off (Bonter, Zuckerberg, Sedgwick, & Hochachka, 2013). Importantly, theoretical models of optimal foraging predict a bimodal distribution of foraging activity in situations where the risk of starvation and the risk of predation are both of relatively high importance (McNamara et al., 1994; Pravosudov & Lucas, 2001). Under such ecological conditions, individuals should restrict most of their foraging activity to right after dawn and right before dusk. These patterns are expected because early in the day body reserves are at their lowest, and birds thus need to rapidly build up extra reserves to insure against the possibility of food being unavailable later in the day; right before dusk, by contrast, body reserves will only expose a forager to increased (i.e., mass-dependent) predation risk for a relatively short period of time (McNamara et al., 1994). A different type of diurnal pattern would be expected when starvation risk is of relatively much greater importance than predation risk (McNamara et al., 1994). In such ecological conditions, mass should be gained as early in the day as possible, to insure against later unavailability of food. Once sufficient mass (energy reserves) is acquired, birds should reduce their exposure to predators by seeking a refuge and avoid foraging for the rest of the day. The opposite pattern would be expected when predation risk is of relatively much greater importance. In that case, nearly all mass gain should be delayed until towards the end of the day (McNamara et al., 1994). Finally, when the starvation-predation risk trade-off is independent of mass (i.e. the level of energy reserves have no effect on either predation or starvation risk), a constant mass gain over the day is expected (i.e. the “risk- spreading theorem”, Houston, McNamara and Hutchinson 1993). In other words, theory predicts that the ecological conditions (i.e., the combination of levels of risk of predation and starvation) should affect both foraging and mass gain trajectories, and thereby calls for field studies that quantify both aspects under natural conditions. Previous work on free-living birds has focused on documenting either foraging activity (Bonter et al., 2013) or diurnal mass trajectories (Lilliendahl, 2002; Macleod, Gosler, et al., 2005) and has therefore not considered how the trade-off between avoiding risk of starvation and predation simultaneously shapes both traits.

A practical problem associated with testing predictions derived from adaptive foraging theory is the difficulty of measuring mass gain and foraging behaviours directly in the wild. Research on diurnal patterns in body weight in small passerine birds has often relied on measurements made during capture (e.g., Lehikoinen 1987; Gentle and Gosler 2001), which may consequently change birds' perception of predation risk, and thereby affect any subsequent measurement (Macleod & Gosler, 2006). For instance, great tits (*Parus major*) change their foraging behaviour in response to human disturbance (e.g., catching and handling) in a similar way as they would after encountering predators (Macleod & Gosler, 2006). Fortunately, technological developments, in the form of electronic balances capable of automatically registering both individual identity (by means of reading Passive Integrated Transponder (PIT) tags and Radio-Frequency Identification (RFID) antennas) and body mass, provide the opportunity to gather vast amounts of repeated measures on both foraging and mass trajectories on large numbers of individuals in the wild without requiring repeated capture and release (Bonter et al., 2013; Macleod, Gosler, et al., 2005). These technological advances enable research on starvation-predation trade-offs to empirically test predictions that go beyond population-level predictions because they allow testing key aspects of theory that require the estimation of among- and within-individual variation. For example, do individuals differ in how they resolve the starvation-predation risk trade-off, and if so which phenotypic traits mediate individual-level variation? Similarly, is there within-individual variation (e.g. among days or years) in how this trade-off is resolved, and if so, which ecological factors vary to cause such effects?

Differences in how individuals resolve the starvation-predation risk trade-off could arise if birds differ either in perceived or in actual starvation and/or predation risk. Such individual differences could be caused by individuals experiencing different environmental conditions or related to individual-specific phenotypic attributes such as sex, size or behavioural type. Individual-specific phenotypes affecting the ability to monopolize resources (e.g., aggressiveness, size, or sex affecting dominance) likely affect the risk of starvation (Koivula, Orell, Rytkönen, & Lahti, 1995; Krams, 2000; Lange & Leimar, 2004; Verhulst & Hogstad, 1996), while individual-specific phenotypes affecting exposure to predators (e.g., risk-taking behaviours, like willingness to foraging alone or in the open) may affect risk of predation (Abbey-Lee, Mathot, & Dingemanse, 2016). Furthermore, at the within-individual level, variation in the optimal resolution of the trade-off should exist because of variation in abiotic factors, like (night) temperature and day length, which affect the energetic requirements for self-maintenance and the time window available for foraging, respectively (Cuthill, 2000; Krams et al., 2010; Thomas & Cuthill, 2002; Witter & Cuthill, 1993). Seasonal changes in diurnal body mass patterns are therefore expected because when conditions become harsh, such as in winter, birds may face greater energetic requirements and adjust their diurnal mass gain strategies accordingly.

In this study, we quantified among- and within-individual variation in body mass and foraging activity in a wild population of great tits. Using custom-made automated weighing-feeding systems, we recorded 12 678 feeder visits of 28 individual great tits over 40 consecutive winter days. Our first objective was to quantify the total amount of phenotypic variation in body mass and foraging activity, and to partition this variation into its underlying within- and among-individual components. Our second objective was to investigate the shape of the diurnal mass gain and foraging activity patterns. We tested whether birds concentrated their mass gain and foraging activity (i) either around dawn and dusk (as predicted when both starvation and predation risk are of high importance), (ii) around the first half of the day (as predicted if starvation risk is greatest), (iii) around the last half of the day (as predicted if predation risk is greatest), (iv) or evenly over the day (as predicted by the risk-spreading theorem) (Houston et al., 1993; McNamara et al., 1994). Our third objective was to assess whether differences in body mass and foraging activity trajectories were a function of individual-specific phenotypic attributes or abiotic environmental conditions predicted to affect the optimal resolution of the starvation-predation risk trade-off.

MATERIALS AND METHODS

The study was carried out in a forest plot in Bavaria, south-western Germany (47^{o}58’ N, 11^{o}14’ E). Birds were captured with mist nets and marked with one aluminium and three colour rings if not previously marked. Directly following capture, we recorded the behaviour of the captured individual for a 2-min period in a 61 L × 39 W × 40 H cm cage, where the total number of hops among different sections of the cage (see Fig 1 in Stuber et al. 2013) was used to measure its activity (Araya-Ajoy et al., 2016). Activity in a novel environment, labelled ‘exploration behaviour’, represents a proxy for risk-taking behaviour as it correlates with anti-predator boldness (Stuber et al., 2013). After the behavioural test, we determined sex and age based on plumage characteristics and took standard morphological measurements (e.g. tarsus and wing length). Finally, each bird was implanted with a PIT-tag subcutaneously in the back above the scapula (Nicolaus, Bouwman, & Dingemanse, 2008), and released at its capture site. Previous work on great tits has shown that our protocol of PIT-tag implantation has no effect on survival (or other fitness components) (Nicolaus et al., 2008).

Automated weighing-feeding system

We used an automated weighing-feeding system ('feeder'; designed by Dorset, The Netherlands) to automatically weigh PIT-tagged birds when visiting the feeder. The system consisted of an electronic scale placed at the feeder entry suspended to one side. Thus, when a bird landed on the scale to feed, its tag was detected and the bird weighed (see Supplementary Material for a detailed description of feeder programming and functioning). Feeders were filled with peanut kernels, which were ground into tiny fragments because complete kernels might quickly be picked up and consumed elsewhere (i.e., within protective cover away from the feeder) and thus result in insufficient time at the platform to acquire an accurate weight measurement.

Study design

In July 2015 two simple (non-automated) feeders baited with *ad libitum* sunflower seeds were placed in the forest plot for 3 months to attract and familiarize birds with the set-up. One week prior to the onset of data collection (10 November 2015), these two simple feeders were replaced by two feeders with the weighing-feeding system described above. We used two feeders to cover a greater area of the study plot and thus, to increase the number of individuals with potentially access to the feeders. The study ran for 40 days (10 November 2015 to 20 December 2015). The two feeder sites consisted of small shrubs surrounded by mature beech woodland with similar habitat characteristics of forest structure, cover and exposure to weather.

Environmental data

We used daily weather data from a nearby weather station (Rothenfeld weather station, 4 km distance from study site, Agrarmeteorologie Bayern, www.am.rlp.de). We extracted average temperatures for each day (i.e. average temperature during day-time and preceding-night of focal day). Daily sunrise and sunset times were acquired from the website www.timeanddate.com, using the nearest available location to the field site (Starnberg city; 6 km distance from study site). Day length was subsequently calculated for each day by subtracting sunrise times from sunset times.

Statistical analyses

We used a reaction norm approach to quantify variation in body mass and foraging activity within and among individuals. In both cases, we first fitted a model estimating population-average and individual-specific (linear and nonlinear) effects of time of day (Model 1), and then expanded the focal model to additionally quantify whether reaction norm variation was attributable to environmental covariates (temperature, day length; Model 2) and individual-level phenotypic traits (sex, size, exploration behaviour; Models 3a-c).

Analyses of body mass Variation in body mass was normally distributed and modelled using random-regression mixed-effects models that assumed Gaussian errors. The initial model focused on testing for (non)linearity of diurnal variation in mass regulation, and therefore fitted both the linear and quadratic effect of time of day (expressed in decimal fractions of hours after sunrise; continuous variable) as fixed effects (Model 1). The mixed-effects model further included random intercepts for individual identity (28 levels) as well as random slopes with respect to the linear and quadratic effects of time of day. Covariances between random terms (i.e., intercept–linear slope, intercept–quadratic slope, and linear slope–quadratic slope covariances) were also modelled. We further estimated individual repeatability as the among-individual variance divided by the total phenotypic variance (Nakagawa & Schielzeth, 2010). This initial analysis thereby enabled us to fully quantify how individuals differed in the (non)linearity of diurnal body mass trajectories.

As a second step, Model 1 was expanded to test whether within-individual variation in reaction norm components could be attributed to environmental variation (Model 2). Average daily temperature and day length were therefore included as fixed-effects, as well as their two-way interactions with (non)linear time of day effects. We included the mean temperature of the focal day in our analyses because temperature variables are usually highly correlated and this variable has been used in previous studies (Bonter et al., 2013; Macleod, Gosler, et al., 2005).

As a third step, Model 2 was expanded to test whether among-individual variation in reaction norm components could be attributed to individual-specific traits (Model 3a-c). The following individual-level traits were included as fixed effects: sex (factor: male or female), size (covariate: tarsus length centred within-sex) and exploration behaviour (covariate: total number of hops among cage locations). Tarsus was centred within sex to break the collinearity between sex and size caused by the species' sexual dimorphism (Gosler & Harper, 2000). We also included all two-way interactions between phenotypic traits and the linear, or quadratic, component of time of day, to test for phenotype-dependent variation in diurnal mass changes (see Introduction). Including all traits (and their two-interactions) as predictor variables into the same model would have caused an over-parameterized model; we therefore decided to evaluate the effects of each trait separately (Models 3a, 3b, 3c). Exploration behaviour data was missing for three out of 28 individuals and those individuals were given the average population phenotypic value (re-analysis of the data excluding these three individuals did not change our findings, results not shown). Owing to evidence for age-related variation in body mass (Gosler & Harper, 2000), we also considered including age (first-year vs. older) as a predictor variable. Inclusion of age was, however, not possible because our sample harboured insufficient variation (only two out of 28 individuals were first-year birds).

Analyses of foraging activity We defined foraging activity as a binary variable by quantifying whether an individual was present (yes/no) at the feeder within 1-hour time blocks (for a detailed discussion of our reasons for this definition of foraging activity, see Supplementary Material). Foraging activity (0 = absent from the feeder within a given time block, 1 = present at the feeder) was modelled with a Binomial error structure where residual variance was taken to be $\pi^2/3$ (Nakagawa & Schielzeth, 2010). Days where a focal bird was not present at all were removed because this would cause uninterpretable variation in reaction norm slopes. Variation in foraging activity was subsequently modelled by fitting Models 1 through 3c as described above for our analyses of body mass.

General modelling procedures All covariates included in our models were mean-centred and standardized to the standard deviation units. We evaluated the importance of considering temporal autocorrelations but we chose not to control for it in our models (for statistical approaches and results, see Supplementary Material). Statistical analyses for the univariate models were carried out using the packages “lme4” and “arm” of the statistical freeware R-3.3.2 (R Development Core Team, 2016). To obtain parameter estimates, we used the *sim* function to simulate values from the posterior distributions of the model parameters. Model fit was assessed by visual inspection of the residuals. Based on 5000 simulations, we extracted 95% credible intervals (CI) around the mean (Gelman & Hill, 2007), representing the uncertainty around our estimates. Assessment of statistical support was obtained from the posterior distribution of each parameter. We considered an effect as “significant” if zero was not included within the 95% CI, while estimates centred on zero were considered to provide strong support for the absence of an effect.

RESULTS

Over the course of the study, we recorded 12 678 visits from 28 PIT-tagged individual great tits (20 males and 8 females). The population-average body mass was 18.96 g (SD: 1.03). An individual bird was recorded on average 20.61 on days (range: 1 to 40) and the probability that an individual bird was recorded on a given day was not influenced by sex, size, behavioural type, temperature or day length (results not shown). The mean number of visits per individual per day was 21.92 (range: 1 to 68). Mean daily temperature was 4.05°C (range: -4.64°C to 13.45°C) and mean day length was 8.69 hours (range: 8.37 h to 9.52 h).

Diurnal mass gain trajectories

Individuals differed substantially in their average body mass over repeated observations as indicated by the existence of among-individual variation in reaction norm intercepts (Model 1, Table 1). The repeatability of body mass was high (R = 0.88; 95% CI: 0.87, 0.89). Body mass increased relatively steeply early in the morning and levelled off towards the end of the day, as revealed by a positive linear and negative quadratic effect of time of day (Model 1, Table 1, Fig 1a). Interestingly, individuals did not differ in their diurnal patterns of body mass gain (black lines in Fig 1a), as indicated by a near-zero among-individual variance in linear and quadratic reaction norm slopes with respect to time of day (Model 1, Table 1).

Temperature and day length both affected the average body mass of individuals within days as well as its diurnal pattern: on colder days and on shorter days, individuals had higher body mass (indicated by the main effects of temperature and day length; Model 2, Table 1). Furthermore, birds increased their body mass more steeply over the day when days were short (indicated by the interaction between day length and linear time; Model 2, Table 1). Both these environmental factors also affected the non-linear nature of mass gain over the day (indicated by their interactions with quadratic time; Model 2, Table 1). When days were colder, birds showed a more pronounced increase of mass gain compared to warmer days.

As expected for this size-dimorphic species, males and structurally large individuals were heavier than females and structurally small individuals (main effect of sex and tarsus; Model 3a-b, Table 1) while heavier birds did not differ from leaner birds in exploration behaviour (no support for a main effect of exploration behaviour; Model 3c, Table 1). In line with our finding of a complete lack of among-individual variation in diurnal body mass trajectories (see above), neither sex, exploration behaviour, nor within-sex variation in body size explained variation in how body mass changed over the day (i.e., none of the interactions between (linear or quadratic) time and individual-specific attributes (sex, tarsus, exploration) deviated from zero; Table 1; Model 3a-c).

Daily foraging strategies

Individuals differed in how often they visited the feeders, indicated by the existence of among-individual variation in reaction norm intercepts for foraging activity (Model 1, Table 2). Individual repeatability of foraging behaviour was, simultaneously, relatively low (R = 0.14; 95% CI: 0.11, 0.17). Foraging activity further showed a non-linear pattern over the day (Table 2, Fig 1b). Birds started to feed just before sunrise (maximum 25 min before sunrise), after which they increased their foraging activity over the course of the morning. Foraging activity remained relatively stable during the rest of the day but subsequently declined abruptly in the hour before sunset. Interestingly, individuals differed in how steeply their foraging activity declined over the day (as indicated by nonzero among-individual variation in linear reaction norm slopes) and in how peaked their foraging activity was (among-individual variation in quadratic reaction norm slopes, Model 1; Table 2; Fig 1b). Patterns of among-individual covariance among intercepts and (linear and quadratic) slopes implied that birds visiting the feeders relatively more often showed stronger decreases in foraging activity (as indicated by a negative intercept-linear slope covariance) while such birds also had a more marked peak of foraging activity (as indicated by a negative intercept-quadratic slope covariance) (Fig 1b).

Temperature and day length both affected the average foraging activity of individuals within days as well as its diurnal pattern: on colder days and on shorter days, individuals visited the feeders more often (indicated by the main effects of temperature and day length; model 2, Table 2). Furthermore, birds increased their foraging activity more steeply over the day when days were short (indicated by the interaction between day length and linear time; model 2, Table 2). When days were shorter the birds also showed a more marked peak in their foraging activity (indicated by the interaction between day length and quadratic time; model 2, Table 2).

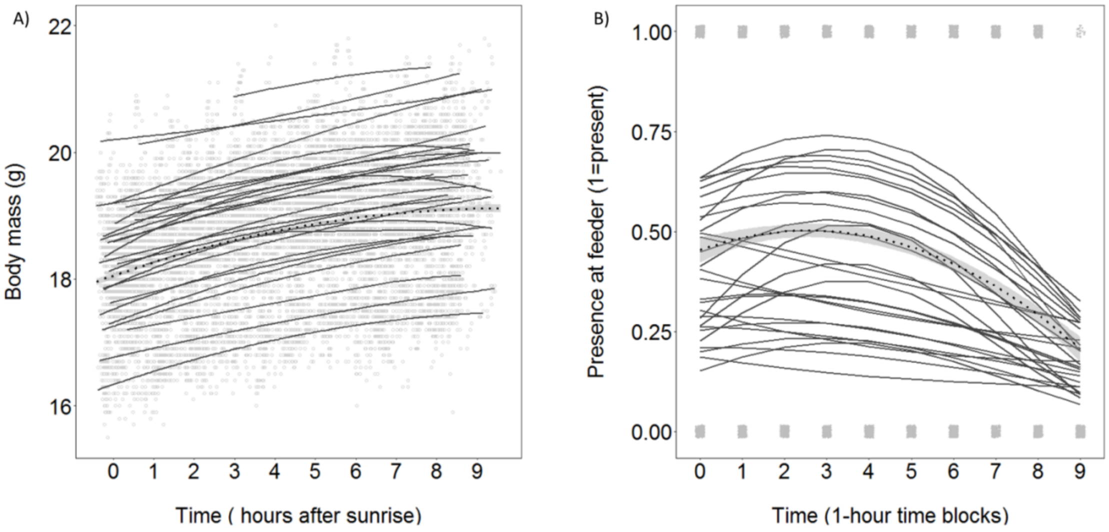

Figure 1. *Diurnal variation in winter body mass and foraging activity. We present posterior distributions of estimates from non-linear reaction norm models of body mass as a function of time of day (hours after sunrise) (A) and foraging activity and as a function of time blocks (1-hour time block) (B). Open grey circles represent raw data (jittered in vertical direction), solid lines represent single individuals, and dotted line represents population average and its shaded grey area, 95% CI.*

Relatively slow-explorers visited the feeders more often and decreased their activity along the day more strongly compared to relatively fast-explorers (non-zero main effect of exploration and linear term interaction; Model 3c, Table 2, Fig 2). Importantly, exploration behaviour explained a large amount of the covariance between the intercept and linear slope of time (as the intercept-slope covariance estimate reduced substantially between Model 1 and 2). Interestingly, exploration behaviour did not explain the intercept–quadratic slope covariance, implying that another trait that we did not measure caused this effect. None of the other phenotypic traits (sex or size) explained variation in average level of either foraging activity or foraging trajectories (i.e., no evidence for main effects of sex and tarsus and none of the interactions between (linear or quadratic) time deviated from zero; Table 2; Models 3a-b).

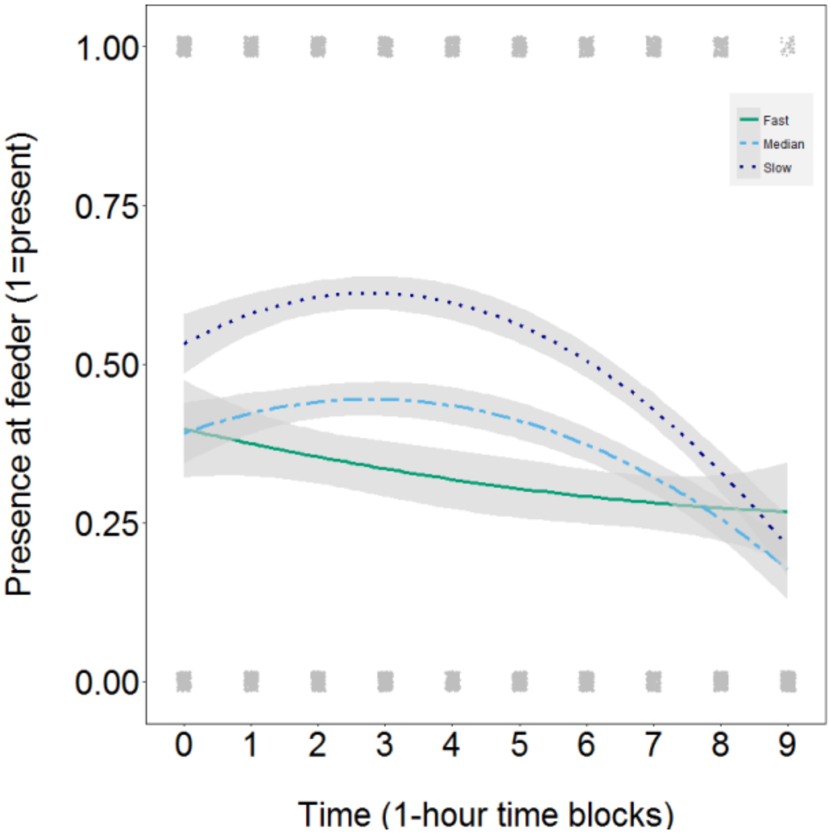

Figure 2. *Non-linear effects of exploration behaviour on daily foraging patterns. Foraging activity was measured as binary (presence of an individual at the feeder in a given time block) and time along the day was divided into 1-hour blocks. Exploration was included as continuous predictor in our analysis but is grouped in terciles (i.e. "fast" represents high explorative individuals, and "slow", low exploration scores) for illustrative purposes. Lines represent the effect of each category and shaded area, standard errors.*

Table 1. Results from random regression models performed to quantify variation in body mass (measured as a continuous variable, in grams).

	Model 1	Model 2	Model 3a	Model 3b	Model 3c
Fixed effects	β (95% CI)	β (95% CI)	β (95% CI)	β (95% CI)	β (95% CI)
Intercept	19.00 (18.63, 19.38)	19.00 (18.65, 19.42)	18.01 (17.45, 18.57)	19.04 (18.66, 19.41)	19.06 (18.62, 19.46)
Time (linear term)	0.36 (0.33, 0.39)	0.37 (0.34, 0.40)	0.38 (0.32, 0.45)	0.37 (0.34, 0.40)	0.37 (0.34, 0.40)
Time (quadratic term)	-0.06 (-0.09, -0.03)	-0.05 (-0.08, -0.02)	-0.06 (-0.11, -0.02)	-0.05 (-0.07, -0.02)	-0.05 (-0.07, -0.02)
Sex [male]	-	-	1.38 (0.73, 2.04)	-	-
Sex [male] × Time (linear term)	-	-	-0.02 (-0.09, 0.05)	-	-
Sex [male] × Time (quadratic term)	-	-	0.02 (-0.04, 0.07)	-	-
Within-sex centred tarsus	-	-	-	0.28 (-0.10, 0.73)	-
Within-sex centred tarsus × Time (linear term)	-	-	-	-0.01 (-0.04, 0.03)	-
Within-sex centred tarsus × Time (quadratic term)	-	-	-	-0.00 (-0.04, 0.04)	-
Exploration behaviour	-	-	-	-	-0.07 (-0.43, 0.28)
Exploration behaviour × Time (linear term)	-	-	-	-	-0.01 (-0.04, 0.02)
Exploration behaviour × Time (quadratic term)	-	-	-	-	-0.01 (-0.03, 0.01)
Mean Temperature	-	-0.07 (-0.08, -0.06)	-0.07 (-0.08, -0.06)	-0.07 (-0.08, -0.06)	-0.07 (-0.08, -0.06)
Mean Temperature × Time (linear term)	-	-0.00 (-0.01, 0.01)	-0.00 (-0.01, 0.01)	-0.00 (-0.01, 0.01)	-0.00 (-0.01, 0.01)
Mean Temperature × Time (quadratic term)	-	-0.01 (-0.02, -0.00)	-0.01 (-0.02, -0.00)	-0.01 (-0.02, -0.00)	-0.01 (-0.02, -0.00)
Day length	-	-0.06 (-0.07, -0.05)	-0.06 (-0.07, -0.05)	-0.06 (-0.07, -0.05)	-0.06 (-0.07, -0.05)
Day length × Time (linear term)	-	-0.04 (-0.05, -0.03)	-0.04 (-0.05, -0.03)	-0.04 (-0.05, -0.03)	-0.04 (-0.05, -0.03)
Day length × Time (quadratic term)	-	0.01 (-0.00, 0.01)	0.01 (-0.00, 0.01)	0.01 (-0.00, 0.01)	0.01 (-0.00, 0.01)
Random effects	σ^2 (95%CI)	σ^2 (95%CI)	σ^2 (95%CI)	σ^2 (95%CI)	σ^2 (95%CI)
Among-individual					
Intercept	1.03 (0.93, 1.16)	1.05 (0.97, 1.17)	0.67 (0.61, 0.79)	1.02 (0.92, 1.21)	1.07 (0.97, 1.29)
Linear term Slope	0.01 (0.00, 0.01)	0.01 (0.00, 0.01)	0.01 (0.00, 0.01)	0.01 (0.00, 0.01)	0.01 (0.00, 0.01)
Quadratic term Slope	0.00 (0.00, 0.01)	0.00 (0.00, 0.01)	0.00 (0.00, 0.01)	0.00 (0.00, 0.00)	0.00 (0.00, 0.01)
Intercept–linear slope covariance	0.01 (-0.22, 0.23)	0.15 (-0.07, 0.36)	0.32 (0.09, 0.50)	0.17 (-0.06, 0.39)	0.14 (-0.09, 0.36)
Intercept–quadratic slope covariance	0.07 (-0.17, 0.30)	0.16 (-0.09, 0.39)	0.07 (-0.19, 0.32)	0.14 (-0.10, 0.38)	0.16 (-0.09, 0.40)
Linear slope–quadratic slope covariance	-0.07 (-0.33, 0.19)	-0.08 (-0.37, 0.20)	-0.06 (-0.35, 0.22)	-0.09 (-0.37, 0.19)	-0.07 (0.36, 0.21)
Within-individual					
Residual variance	0.14 (0.14, 0.15)	0.13 (0.12, 0.13)	0.13 (0.12, 0.13)	0.13 (0.12, 0.13)	0.13 (0.12, 0.13)

Point estimates and 95% credible intervals (CI) are provided for each fixed (β; mean) and random (σ^2; variance) parameter.

Table 2. Results from random regression models performed to quantify variation in foraging activity (measured as binary trait, presence at feeder at a given 1-hour time block).

	Model 1	Model 2	Model 3a	Model 3b	Model 3c
Fixed effects	β (95% CI)	β (95% CI)	β (95% CI)	β (95% CI)	β (95% CI)
Intercept	-0.42 (-0.76, -0.09)	-0.34 (-0.68, 0.01)	-0.03 (-0.65, 0.59)	-0.33 (-0.66, 0.01)	-0.29 (-0.59, -0.03)
Time (linear term)	-0.34 (-0.41, -0.27)	-0.36 (-0.43, -0.28)	-0.43 (-0.57, -0.30)	-0.35 (-0.42, -0.28)	-0.37 (-0.43, -0.31)
Time (quadratic term)	-0.24 (-0.36, -0.12)	-0.27 (-0.39, -0.16)	-0.33 (-0.55, -0.09)	-0.27 (-0.39, -0.16)	-0.28 (-0.40, -0.16)
Sex [male]	-	-	-0.42 (-1.16, 0.30)	-	-
Sex [male] × Time (linear term)	-	-	0.11 (-0.04, 0.26)	-	-
Sex [male] × Time (quadratic term)	-	-	0.07 (-0.19, 0.33)	-	-
Within-sex centred tarsus	-	-	-	-0.17 (-0.54, 0.20)	-
Within-sex centred tarsus × Time (linear term)	-	-	-	-0.03 (-0.10, 0.05)	-
Within-sex centred tarsus × Time (quadratic term)	-	-	-	0.04 (-0.09, 0.18)	-
Exploration behaviour	-	-	-	-	-0.36 (-0.67, -0.06)
Exploration behaviour × Time (linear term)	-	-	-	-	0.08 (0.00, 0.13)
Exploration behaviour × Time (quadratic term)	-	-	-	-	0.07 (-0.05, 0.18)
Mean Temperature	-	-0.14 (-0.24, -0.04)	-0.14 (-0.24, -0.05)	-0.14 (-0.24, -0.04)	-0.14 (-0.24, -0.04)
Mean Temperature × Time (linear term)	-	-0.07 (-0.13, -0.01)	-0.07 (-0.13, -0.01)	-0.07 (-0.14, -0.01)	-0.07 (-0.13, -0.01)
Mean Temperature × Time (quadratic term)	-	0.05 (-0.02, 0.13)	0.05 (-0.02, 0.13)	0.06 (-0.02, 0.13)	0.05 (-0.02, 0.13)
Day length	-	-0.44 (-0.54, -0.34)	-0.44 (-0.54, -0.34)	-0.44 (-0.54, -0.34)	-0.43 (-0.54, -0.34)
Day length × Time (linear term)	-	0.25 (0.18, 0.31)	0.25 (0.18, 0.31)	0.25 (0.18, 0.32)	0.24 (0.18, 0.31)
Day length × Time (quadratic term)	-	0.21 (0.14, 0.29)	0.21 (0.14, 0.29)	0.22 (0.14, 0.29)	0.21 (0.14, 0.29)
Random effects	σ^2 (95%CI)	σ^2 (95%CI)	σ^2 (95%CI)	σ^2 (95%CI)	σ^2 (95%CI)
Among-individual					
Intercept	0.74 (0.54, 0.98)	0.76 (0.55, 1.00)	0.75 (0.54, 0.98)	0.76 (0.55, 1.01)	0.61 (0.45, 0.81)
Linear term Slope	0.03 (0.02, 0.04)	0.01 (0.00, 0.01)	0.01 (0.01, 0.01)	0.04 (0.02, 0.07)	0.04 (0.02, 0.06)
Quadratic term Slope	0.02 (0.02, 0.03)	0.00 (0.00, 0.00)	0.00 (0.00, 0.00)	0.03 (0.03, 0.04)	0.03 (0.03, 0.04)
Intercept–linear slope covariance	-0.61 (-0.80, -0.34)	-0.87 (-0.93, -0.77)	-0.85 (-0.93, -0.75)	-0.55 (-0.77, -0.26)	-0.06 (-0.42, 0.30)
Intercept–quadratic slope covariance	-0.61 (-0.73, -0.45)	-0.64 (-0.77, -0.45)	-0.61 (-0.76, -0.43)	-0.61 (-0.72, -0.50)	-0.55 (-0.66, -0.44)
Linear slope–quadratic slope covariance	0.74 (0.55, 0.87)	0.63 (0.42, 0.79)	0.61 (0.40, 0.78)	0.37 (0.04, 0.65)	0.05 (-0.33, 0.41)
Within-individual					
Residual variance	$\pi^2/3$	$\pi^2/3$	$\pi^2/3$	$\pi^2/3$	$\pi^2/3$

Point estimates and 95% credible intervals (CI) are provided for each fixed (β; mean) and random (σ^2; variance) parameter.

DISCUSSION

Theoretical models predict that a fundamental trade-off between risk of starvation and risk of predation shapes diurnal patterns in foraging activity and mass gain in wild passerine birds. A bimodal distribution in foraging activity and mass gain (due to peaks at the beginning and at the end of the day) is expected for foragers mitigating both types of risk. Early foraging activity and mass gain are expected when the risk of starvation is greater. In contrast, delayed foraging activity and mass gain are expected when the risk of predation is greater. A relatively constant rate of foraging and mass gain throughout the day (i.e. spread the risk) is instead expected when the starvation-predation risk trade-off is independent of body mass. In this study, we simultaneously quantified foraging activity and body mass in free-living great tits. We observed no individual differences in mass gain trajectories but birds did differ in their foraging strategies. Furthermore, we found that exploration behaviour partly explained observed among-individual differences in diurnal patterns of foraging activity, and that the diurnal patterns in both traits varied within-individuals as a function of mean day temperature and day length. Overall, our results are consistent with the birds responding to a mass dependent starvation-predation risk trade-off where starvation risk is considerably higher than predation risk.

Diurnal patterns

Diurnal mass gain was highest after dawn, and slowly decreased over the course of the day with very little mass gained in the second half of the day. This mass gain pattern matches relatively well with the actual foraging activity demonstrated in our study at the population level. This suggests that unbiased estimates of within-individual patterns for foraging activity were captured by the birds' visits to our feeders, and that the (unobserved) usage of alternative food sources (elsewhere in the forest) did not greatly bias observed population-level patterns. Birds showed an initial burst of foraging activity in the morning, decreased feeding relatively uniformly throughout the day, and terminated feeding abruptly as sunset approached. The initial rapid increase in body mass can therefore be explained by early foraging activity beginning right before sunrise (i.e. when birds would be energy-depleted following a night of fasting). For the remainder of the day, the rate of mass gain was lower. At the end of the day, we observed the opposite pattern; birds dropped their foraging activity an hour before sunset. This early termination of feeding under daylight conditions could imply that birds reached their satiation threshold (Houston & McNamara, 1993), which seems biologically unlikely. Alternatively, our results may also be explained by other mechanisms such as an increase in predation risk later in the day. Certain predators (e.g. owls and sparrowhawks) might have a late-day peak in their foraging activity (McNamara, Barta, Houston, & Race, 2005), in which case, great tits might not face a constant risk of predation over the day but instead, suffer a higher predation risk around dusk. This pattern of late-day drops in foraging activity has also been reported for other wintering birds (Bonter et al., 2013; Lima, 1988). Another possibility is that predation risk could be minimized to become zero, for example, if birds make use of refuges. After taking an increased foraging risk and gaining enough mass to survive overnight great tits can take advantage of the refuge effect (Houston et al., 1993) by seeking cover and waiting out the rest of the day with the minimum possible energy expenditure (Cresswell, 1998). Overall, of the four hypotheses proposed to explain our patterns of diurnal mass gain and foraging activity, our results are more consistent with the hypothesis of an early foraging activity and mass change due to a higher starvation risk. Therefore, we tentatively conclude that our findings imply that small birds face higher starvation compared to predation risk in winter and that the balance between avoiding the risks of starvation and predation is consequently skewed towards reducing starvation risk during those winter months.

Ecological conditions

Theory also predicts that starvation and predation risks should vary over time and between-individuals due to variation in environmental factors. Indeed, birds seem to use day length and to a lesser extent, daily mean temperature as proximate cues to assess how much foraging to perform and mass to gain. As nights become longer, there is a greater risk that reserves will be depleted before foraging can resume at dawn (Bednekoff & Houston, 1994; Houston & McNamara, 1993, 1999; McNamara et al., 1994). This tendency acts in conjunction with the temperature effect because temperatures tend to be lowest when nights are longest. Thus, given that metabolic costs increase when temperatures drop, energy reserves will be exhausted earlier in the night. To compensate for such a joint effect, birds in our population went to roost with higher body mass under inclement weather conditions (Table 1). Individuals modified their body mass gain and foraging strategies slightly to reach their targeted end-weight. For instance, birds adjusted their end-of-day mass by increasing their mass gain more steeply on shorter days and they had a more rapid mass gain on colder days (Cresswell, 1998; Macleod, Barnett, Clark, & Cresswell, 2005; Thomas, 2000). Individuals also foraged more actively (i.e. visited more often the feeders) on shorter days and under lower mean temperatures (Bonter et al., 2013). Furthermore, day length had a positive effect on the quadratic effect of time; that is, birds presented a more prominent peak of foraging activity on shorter days. This study thus provides the first clear demonstration that birds are capable of adjusting their diurnal mass gain trajectory and foraging strategy in response to ecological predictors of starvation risk as predicted by starvation-predation risk trade-off theory (Houston et al., 1993; Lima, 1986).

Individual variation in trajectories

We quantified whether and how individuals differed in their diurnal patterning of body mass and foraging activity, and whether diurnal patterns were explained by individual-level morphological and behavioural traits. We used a reaction norm framework as a heuristic tool for doing so (Dingemanse, Kazem, Réale, & Wright, 2010; Nussey, Wilson, & Brommer, 2007). These reaction norm analyses showed i) that individuals did not differ in their diurnal patterning of mass gain, ii) that individuals did differ in diurnal patterning of foraging activity, iii) and that exploration behaviour (partly) explained these among-individual differences in diurnal patterns of foraging activity. This result has, at least, two important implications. First, it demonstrates that observations of diurnal patterns of foraging activity alone do not provide a complete picture of how individuals resolve starvation-predation risk trade-offs. If we had recorded only foraging activity in the present study, as is commonly done in field studies, we might have erroneously concluded that slow explorers face higher starvation risk and/or lower predation risk relative to fast and intermediate explorers, and consequently, increase foraging activity mid-day relative to other birds. However, the observation that patterns of mass gain did not mirror patterns of foraging activity in slow explorers suggests in fact that higher foraging intensity at the feeders was required by slow explorers to achieve the same level of starvation insurance (i.e. energy reserves) compared with intermediate and fast explorers. Whether this reflects exploration-related differences in the use of alternative food sources (e.g., natural food sources in forest plots or other feeders), or exploration-related differences in energy conversion efficiency is unclear, and should be the focus of future work. Furthermore, only two out of 28 individuals were first-year birds, and only eight individuals were females (i.e. 20 males). Given that adult males are dominant over females and juvenile males at feeders (Dingemanse & de Goede, 2004), further research is required to elucidate whether the patterns of mass regulation reported here also characterizes these least dominant categories of birds.

Conclusions

Wintering great tits in our population demonstrated substantial variation in body mass and foraging strategies. Temporal patterns of mass gain matched those of foraging activity, indicating unbiased estimates of within-individual patterns for foraging activity. Furthermore, individuals differed in foraging strategies (i.e. diurnal patterning of foraging activity at the feeder) but not in their mass gain patterns. The observed differences in foraging activity suggest that birds exhibit behavioural flexibility in resolving the trade-off but nonetheless exhibit a fixed diurnal pattern in mass gain. Taken together, our findings imply that increased energetic demands experienced by small birds in winter might favour individuals prioritising avoiding risk of starvation rather than maximising predation avoidance. How the predictions of the starvation-predation risk trade off apply to other ecological scenarios, and whether observed differences between behavioural types result from individual differences risk of predation and/or starvation, should be addressed by future research in this area.

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Electronic Supplementary Material of Chapter 3

Text S1. Automated feeder functioning

The automated weighing-feeding system consisted of an electronic scale placed at the feeder entry suspended to one side. Thus, when a bird landed on the scale to feed, its tag was detected and the bird weighed. Mass was only stored (to the nearest 0·1g) when a stable reading was obtained for at least 1 second (reading rate of 60 times/second). Furthermore, on some occasions birds perched with one foot on the weighing platform causing their body mass to be substantially underestimated. To avoid such biases, we excluded all mass values that were 0.5 g lower than the maximum mass recorded within the focal hour of the measurement for the focal individual, as such a rate of mass loss would not be possible and therefore must reflect measurement error. The feeder was equipped with a RFID antenna fitted with a clock (recording date and time to the nearest second). For each visit, the feeder was programmed to remain open for 10 s, after which it closed for another 10 s, before opening again (regardless of whether another bird arrived in the meantime). Feeder closing was meant to stimulate birds to leave the feeder after a visit and thereby reduce the probability of monopolizing access. Reliability of the RFID readers was verified by comparing readings registered to the SD card with videos collected at feeders. We thus were able to confirm that the feeder-weighing system worked properly.

Table S1. Estimates of foraging activity (measured as binary variable) for analyses with different time block definitions. We calculated foraging activity as a binary variable where we quantified the presence/absence of an individual at the feeder in a given time block. We did not use bins for body mass because body mass was a continuous (normally distributed) variable. In order to test whether using different time blocks (i.e. dividing time in different arbitrary time frames) would lead to different conclusions regarding diurnal foraging patterns, we performed sensitivity tests of the discretization of the time variable from 5 to 30 and 60 minutes by running the same models with different time blocks (i.e. 10, 20 or 120 time blocks). To do so, we ran 3 univariate mixed-effects models where foraging activity (measured as binary variable, presence at the feeder per a given time block) was the response variable. We added the variable time divided in three different time blocks and its quadratic term as fixed effects. We included random intercepts and slopes for individual identity (28 levels).

	60-min interval	30-min interval	5-min interval
Fixed effects	β (95% CI)	β (95% CI)	β (95% CI)
Intercept	-0.37 (-0.64, -0.08)	-1.15 (-1.41, -0.89)	-2.83 (-3.06, -2.59)
Time (linear term)	-0.34 (-0.41, -0.28)	-0.33 (-0.40, -0.27)	-0.09 (-0.14, -0.03)
Time (quadratic term)	-0.29 (-0.35, -0.22)	-0.26 (-0.31, -0.21)	-0.15 (-0.18, -0.12)
Random effects	σ^2 (95%CI)	σ^2 (95%CI)	σ^2 (95%CI)
Intercept	0.52 (0.41, 0.65)	0.44 (0.35, 0.55)	0.37 (0.30, 0.47)
Slope	0.01 (0.00, 0.01)	0.01 (0.00, 0.01)	0.01 (0.01, 0.02)
Intercept–slope covariance	-0.83 (-0.91, -0.71)	-0.75 (-0.86, -0.58)	-0.62 (-0.77, -0.41)
Residuals			
	$\cdot\pi^2/3$	$\pi^2/3$	$\pi^2/3$

Table S2. Fixed effects estimates of models that fitted a temporal autocorrelation structure. Body mass was measured as continuous variable (in grams) and foraging activity as binary variable (presence at the feeder per a given 1-hour time block). We tested the importance of temporal autocorrelation in our data by comparing two models, one with an autoregressive - moving average correlation structure and one not controlling for any autocorrelation (Pinheiro & Bates 2000). To do so, we ran two univariate mixed-effects models where body mass was the response variable, and two univariate mixed-effects models where foraging activity was the response variable. We also added the variable time and its quadratic term as fixed effects (either “Time” as continuous variable for body mass or “Time blocks” as time divided in 1-hour block for foraging activity). We included random intercepts and slopes for individual identity (28 levels). To control for autocorrelation in our residuals, we included an ARMA (1,1) correlation structure (Pinheiro & Bates 2000). We checked the normalized residuals of our model to confirm that the ARMA correlation matrix did control for the temporal correlation. To run the models with body mass we used the R-package “lme” and for foraging activity, we used “glmmPQL” package.

	Body mass	Foraging Activity
Fixed effects	β (95% CI)	β (95% CI)
Intercept	18.96 (18.59, 19.34)	-0.32 (-0.61, -0.03)
Time (linear term)	0.40 (0.38, 0.42)	-0.46 (-0.52, -0.40)
Time (quadratic term)	-0.08 (-0.09, -0.07)	-0.31 (-0.37, -0.23)

Chapter 4

Evidence for phenotypic integration predicted by state-dependent behaviour theory in a wild bird population

Maria Moiron, Yimen G. Araya-Ajoy, Kimberley J. Mathot, Alexia Mouchet and Niels J. Dingemanse

ABSTRACT

State-dependent behaviour has been proposed as a key mechanism generating repeatable among-individual differences in behaviour (i.e., animal personality). Two hypothesized patterns of state-dependent risk-taking behaviour are based on “asset protection” and “state-dependent safety” models. Based on these two optimality models, we tested hypotheses of phenotypic integration between morphology and behaviour in a free-living population of great tits (*Parus major*) monitored for seven years. While investigating these patterns of phenotypic integration, we explicitly studied the role of body mass in the integration of morphology and behaviour, distinguishing between the body mass components of structural size and of energetic reserves. We repeatedly quantified multiple morphological (body mass, wing, tarsus, and bill length; encapsulating two dimensions of “state”: structural size and energetic reserves) and behavioural traits (aggressiveness and exploration) in >740 individual males. Structural equation modelling supported the existence of a behavioural module, “risk-taking behaviour” that covaried with each of two morphological modules “body size” and “energetic reserves”, thereby providing support for both optimality models simultaneously. Overall, we demonstrated that an individual’s morphological and behavioural traits represent expressions of an integrated phenotype, suggesting a role for state-dependent behaviour in generating animal personality in a wild bird population.

Unpublished manuscript

INTRODUCTION

State-dependent behaviour has been proposed as a key mechanism generating repeatable among-individual differences in behaviour (i.e., animal personality). Testing state-dependent models for adaptive animal personality is challenging because the states and behaviours of interest often cannot be captured adequately by simply quantifying single traits, given that in many cases, the state and behaviour are latent variables (Araya-Ajoy & Dingemanse, 2014). For example, approach distance to a dummy, probability of attack, and number of calls and songs are observable expressions of “territorial aggressiveness” in male great tits, the latter representing a latent variable that has likely evolved because correlational selection favoured phenotypic integration of behavioural traits (Araya-Ajoy & Dingemanse, 2014). Understanding how selection acts on combinations of traits therefore poses a major challenge in evolutionary ecology. Empirical evidence demonstrates that natural selection can act on many traits simultaneously, while phenotypic correlations are also widespread (Lande & Arnold, 1983). This is because natural selection favours correlations among phenotypic traits when certain combinations of traits enable an organism to accomplish a particular function (Pigliucci, 2003; Schwenk, 2001). An optimal combination of functionally-related traits is defined as phenotypic integration (Pigliucci, 2003; Sinervo & Svensson, 2002; Wagner, 2000). These functional modules arising from the evolution of phenotypic integration have the potential to ultimately respond to selection as a unit (Houle, 2001). Additionally, some functional modules might overlap with others. While the traits that form a single module are highly inter-connected, a single module may, to a certain extent, be more weakly connected to other modules, a phenomenon called “quasi-independence” (Wagner, Pavlicev, & Cheverud, 2007). The concept of functional integration and quasi-independence is well illustrated by work on *Physid* snails: shell shape ranges continuously from elongated to rotund, and individuals with different shell shapes rely on different anti-predator responses to survive attacks by their common predators, crayfish and fish (namely, usage of near-surface habitats vs. refuges) (DeWitt, Robinson, & Wilson, 2000; DeWitt, Sih, & Wilson, 1998). Under high predation pressure by crayfish, snails have narrower shells and make more use of surface habitats. In contrast, under high predation pressure by fish, snails have wider shells and make more use of refuges. This integration exists because a different optimal combination of morphological defence and anti-predator behaviour is favoured under different ecological scenarios. Given that behavioural and/or morphological traits can aggregate as integrated units across functionally different contexts, phenotypic integration has been invoked as a potential mechanism explaining the existence and maintenance of repeatable among-individual differences in behaviour, also called animal personality (Sih et al., 2004).

Here, we test a pattern of phenotypic integration between morphology and behaviour based on state-dependent behaviour theory developed in behavioural ecology (Houston & McNamara, 1999). Optimality models developed in behavioural ecology predict the adaptive integration of physiology or morphology (called "state" variables) and behaviour. The "asset protection" model predicts that individuals with the highest assets (e.g., energetic reserves), should display lower risk-taking behaviour because they have much to lose (Clark, 1994; Luttbeg & Sih, 2010). In contrast, "state-dependent safety" models predict the opposite effect; individuals with higher assets can perform higher risk-taking behaviour (i.e. take more risks) because their assets make them less vulnerable to predation (Luttbeg & Sih, 2010). Despite the contrasting relationship of physiology or morphology and behaviour, both optimality models predict covariation between traits, that is, adaptive phenotypic integration. In this study, we investigated a model of morphological and behavioural integration in a natural population of great tits (*Parus major*) breeding in 12 nest box plots. We measured six morphological and behavioural observable variables in all breeding male individuals (body mass, tarsus length, bill length, wing length, aggressiveness and exploration behaviour) for each of seven consecutive years (2010-2016). Hereafter we used the term "trait" as an observable (measured) variable and "character" as the unmeasured variable underlying the expression of functionally related observable variables (Bollen 2002).

Most of the above-mentioned optimality models have focused on the effect that assets have on risk-taking behaviour, without being explicit as to whether these assets are a measure of body size or energetic reserves. In addition to this conceptual ambiguity, most empirical tests involving "assets" use body mass as a measure of both body size and energetic reserves (Piersma & Davidson, 1991). This is because body size and body condition cannot be measured directly as they represent latent variables. Body size is defined as the structural size of an organism independent of its energetic reserves (Piersma & Davidson, 1991). Energetic reserves are the amounts of nutrients (especially fat and protein) that individuals store in order to survive periods of negative energy balance. Energetic reserves may vary with time of day and year, reproductive status, and habitat quality. Body mass certainly contains information about both body size and energetic reserves; however the failure to properly quantify and differentiate between the two variables can result in misleading interpretations. Therefore, this paper offers a statistical solution to test for the effects of both processes simultaneously. In this study, while investigating patterns of phenotypic integration between morphology and behaviour, we explicitly focussed on distinguishing between components of structural size and of energetic reserves. One hypothesis is that a risk-taking behavioural module (detailed above) is present above and beyond the general allometric covariation caused by the latent variable “body size”. In this case, body mass would simply be an expression of the latent variable “body size”; the behavioural module would thus be linked directly to “body size”, and only indirectly linked to body mass (Fig 1, Table 1, models 2-9). Alternatively, the behavioural module could be associated with the specific trait body mass (i.e., when size-independent variation in body mass represents a proxy for energetic reserves). The existence of a “energetic reserves” module can occur independently if the behaviour module is directly related to the latent variable “body size” (Fig 1, Table 1, Models 10-12) or not (Fig 1, Table 1, Models 13-18). In both cases (Fig 1, Models 10-18), “energetic reserves” would represent another latent variable that is covarying with the latent variable “body size”.

Table 1. A priori hypotheses of morphological and behavioural integration in male great tits.

Model	Hypothesis
Model 1	Null model of trait independence
Model 2	All morphological traits are part of the latent variable, and behavioural traits are uncorrelated (with each other and with the morphological traits)
Model 3	All morphological traits are part of the latent variable, and behavioural traits are correlated with each other, but not with the morphological traits.
Model 4	All traits are part of the latent variable, and there is additional covariance between behaviours independent of the latent variable
Model 5	All traits are part of the latent variable
Model 6, 8	All morphological traits are part of the latent variable and either exploration (6) or aggressiveness (8) is part of the latent variable
Model 7, 9	All morphological traits are part of the latent variable and either exploration (7) or aggressiveness (9) is part of the latent variable. There is additional covariance between behaviours independent of the latent variable
Model 10-12	All traits are part of the latent variable; and there is a causal influence of body mass on both behaviours at the same time (10), either exploration (11) or aggressiveness (12)
Model 13-15	All morphological traits are part of the latent variable; and there is a causal influence of body mass on both behaviours at the same time (13), either exploration (14) or aggressiveness (15)
Model 16-17	All morphological traits are part of the latent variable; behaviours are correlated and there is a causal influence of body mass on either exploration (16) or aggressiveness (17)
Model 18	All morphological traits are part of the latent variable; there is a causal influence of body mass on both behaviours and there is additional covariance between behaviours independent of the latent variable

In sum, in this study we tested for the existence of three quasi-independent modules; one morphological module labelled as "body size" where we predicted that all morphological traits were connected via a latent variable; one energetic module labelled as "energetic reserves" where predicted that size-independent variation in body mass is connected to the two behavioural traits; and one behavioural module labelled "risk-taking behaviour" where we predicted that exploration behaviour and aggressiveness were connected via a latent variable (Fig 1). We then examine whether these modules were part of an integrated phenotype in great tits. We explicitly investigated the role of body mass in the integration of quasi-independent modules. We tested these alternative hypotheses of phenotypic integration and state-dependent behaviour at the among-individual level, acknowledging the hierarchical structure of evolutionary characters (Araya-Ajoy & Dingemanse, 2014; Klingenberg, 2014). To do so, we used mixed effect models combined with structural equation modelling (SEM) to test the relative fit of distinct biological hypotheses of among-individual integration between morphology and behaviour (i.e., "personality"). Our results provide evidence for the existence of a behavioural module "risk-taking behaviour" that covaried with each of two morphological modules ("body size" and "energy reserves"), demonstrating that asset protection and state-dependent safety models were both supported.

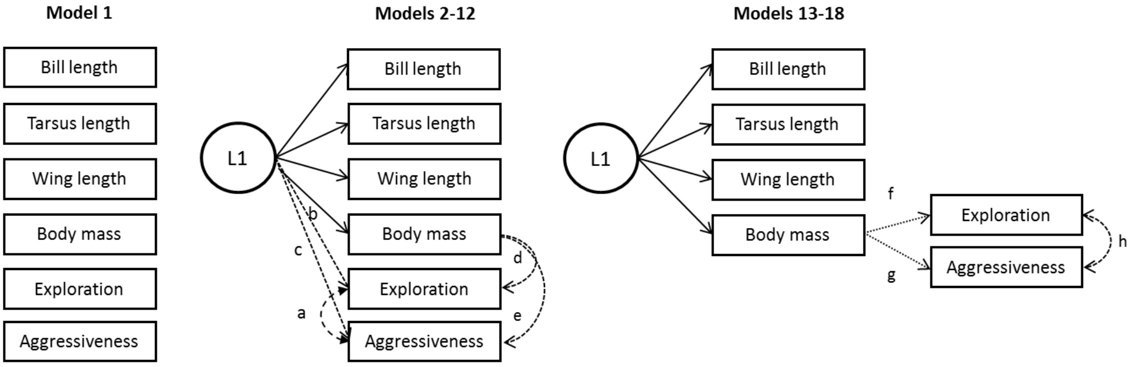

Figure 1. *Models (1–18) of hypothesized relationships between morphological and behavioural traits. Models are described in Table 1. Unidirectional arrows represent causal relationships between traits; bidirectional arrows represent undefined correlations. Solid lines represent relationships present across the whole set; dashed lines represent relationships expressed in specific cluster structures. "L1" represents a latent variable. Path "a" is active in model 3; "a-c" in model 4; "b-c" in model 5; "b" is active in model 6; "a-b" are active in model 7; "c" is active in model 8; "a" and "c" are active in model 9. Paths "a-e" are active in model 10; "a-d" is active in model 11; "a-c" and "e" are active in model 12; Path "f" and "g" are active in model 13; "f" is active in model 14; "g" is active in model 15; paths "f" and "h" are active in model 16; "g" and "h" are active in model 17; and "f-h" are active in model 18.*

METHODS

- Population and study site:

Our study was carried out in a nest box population of great tits consisting of 12 plots, established in autumn 2009 in Bavaria, southern Germany (Starnberg; 47º 58' N, 11º 14' E). Each plot consisted of a forest patch with 50 nest boxes positioned in a regular grid with 50 m between each box. The population was monitored from 2010 onwards following the same fieldwork protocol to collect morphological, behavioural and life-history data for every breeder. Our protocol consisted of checking nest boxes twice a week from April through July to determine lay date and clutch size (see Nicolaus *et al.* 2015 for more details). Once an egg was found, we assessed aggressiveness of each focal male four times; twice during the egg-laying stage and twice during the egg-incubation stage (see below). When chicks were seven days old, parents were caught with a spring trap inside the nest box, marked with a unique combination of rings if not previously marked and assessed for their exploration behaviour (see below). After the test, birds were measured and a small blood sample was taken. Sex and age (first-year vs. older breeder) were determined based on plumage characteristics, body mass was measured using a Pesola spring balance to the nearest 0.1 g, tarsus length and bill length were measured with slide callipers to the nearest 0.1 mm, and wing length (third primary) was measured with a wing ruler to the nearest 0.5 mm. We collected morphological and behavioural data for a seven-year period (2010-2016) for all first broods produced by great tit pairs in our study plots. First broods were defined as those broods initiated within 30 days of the first clutch of the year (Noordwijk, McCleery, & Perrins, 1995). All birds in the current study were adult males (n=742, total number of observations: n = 1111), given that we were only able to measure aggressiveness in males.

- Experimental protocol:

Aggressiveness: We quantified male aggressiveness by simulating territorial intrusions at each focal nest. We performed four tests per nest per year, twice during the egg-laying stage and twice during the egg-incubation stage. The aggression test consisted of a taxidermic mount of a male great tit presented on a 1.2 meter wooden pole with a playback song one meter away from the subject's nest box. Once the focal male had entered a 15-meter radius around the box, we recorded the behaviour of the individual for three minutes. Details of the experimental setup and assayed behaviours are provided in Araya-Ajoy & Dingemanse (2014). Following previous work, we used the minimum distance of the focal male to the mount as our measure of the intensity of an aggressive response for both breeding stages (Araya-Ajoy et al., 2016; Araya-Ajoy & Dingemanse, 2014, 2017). For ease of interpretation, approach distance was multiplied by −1 so that higher values represented more aggressive responses (Araya-Ajoy & Dingemanse, 2014). Observations where males did not arrive within 15 min were scored as nonresponsive. Previous work from the same population of great tits showed that the cross-context correlation (*r*) between aggressiveness expressed during the laying versus incubating stages was much lower than one (*r* ± 95% credible interval (CI) = 0.51 (0.31, 0.60)) (Araya-Ajoy & Dingemanse, 2014), indicating that aggressiveness during the two different breeding stages did not fully represent the same character (Roff, 1997). Araya-Ajoy and Dingemanse (2014) also showed that correlations between expressions of aggressiveness were tighter during the egg laying compared to the incubation stage (Araya-Ajoy & Dingemanse, 2014). For the statistical analyses presented here, we pragmatically chose to focus on aggressiveness expressed during the laying stage, using the mean of the two repeated measures collected annually during laying for each individual, thereby best approximating their individual-specific annual values (Araya-Ajoy & Dingemanse, 2017). In cases where there was only one data point available (i.e. the individual did not respond to one of the behavioural assays), we took the single score as a proxy for the mean score. Reassuringly, our decision to use the mean score of aggressiveness during laying stage (vs incubation) did not alter our conclusions (Results not shown).

Exploration behaviour: We assayed exploration behaviour of adults directly following capture when their nestlings were seven days old. For two minutes, we recorded the behaviour of the captured individual in a 61 L × 39 W × 40 H cm cage adapted from the classic "novel environment test" (for more details see Stuber *et al.* 2013). The total number of movements between different sections of the cage (see Fig 1 in Stuber *et al.* 2013) was used to measure an individual's activity in a novel environment, labelled "exploration behaviour" (Araya-Ajoy et al., 2016).

- Statistical analyses:

We conducted three sets of statistical analyses. First, we explored the sources of variation for each of the six measured traits (i.e. body mass, wing length, tarsus length, bill length, aggressiveness and exploration). To do so, we partitioned the phenotypic variation across multiple levels using mixed-effect models. Univariate models were used to determine the magnitudes of sources of variation, and informed us on relevant terms to be included in the multivariate model. As a second step, we estimated patterns of covariance among traits at different hierarchical levels using a multivariate extension of the model. Finally, we fitted structural equation models (SEMs) to study the hypothesized causal relationships between the phenotypic traits at the among-individual level. Aggressiveness was squared-root transformed (Araya-Ajoy & Dingemanse, 2014) and morphological traits were log-transformed as their relationships are expected to be linear on this scale (Houle, Pélabon, Wagner, & Hansen, 2011). We modelled all six variables assuming a Gaussian error distribution and scaled each to standard deviation units (i.e. mean centred and variance standardized) to facilitate comparison of the relative magnitudes of variance components across traits.

Univariate mixed-effects modelling

We ran univariate mixed-effect models, where each trait (i.e., body mass, tarsus length, wing length, bill length, aggressiveness, or exploration) was fitted as the response variable. Time of day (i.e. expressed in decimal fractions of hours after sunrise) of the measurement was included as fixed effect. Because we were only interested in variance components, we will not discuss fixed effect estimates further (they are listed in Table S1). We fitted random intercepts for the identity of the plot (n=12 levels), year (n=7 levels), plot-year (the unique combination of plot and year, n=84 levels); individual (n=742); and observer (n=40). Observer identity was not fitted for models where aggression was the response variable, because those used the mean value of two behavioural assays (see above). This decision was justifiable as a previous study showed that observer identity did not explain significant variation in aggressiveness (Araya-Ajoy & Dingemanse, 2014). Univariate analyses were performed using the R-packages "lme4" and "arm" implemented in R v. 3.3.3 (Team R Core 2017). We used the "sim" function to simulate posterior distributions of the model parameters. Based on 5000 simulations, we extracted the mean value and 95% CI (Gelman & Hill, 2007). Model fit was assessed by visual inspection of the residuals.

Multivariate mixed-effects modelling

We estimated among-trait covariance at the among-individual, among-observer and within-individuals-among-year levels, using a multivariate mixed-effects model. To do so, we fitted all six traits as response variables and individual and observer identity as random effects. To avoid over-parameterization, we only included those random effects that explained substantial variation in the univariate analyses (i.e. individual and observer identity; see Table S1). The resulting among-observer and within-individuals among-years covariance matrices were not important to our study question and thus not discussed further (Results not shown). The multivariate mixed-effects model was fitted using a Bayesian framework implemented in R v. 3.3.3 (Team R Core 2017) with the R-package MCMCglmm (Hadfield, 2010). We used an inverse gamma prior and ran 3,005,000 iterations per model, with a burn in period of 5000 and a thinning interval of 3000 iterations.

Posterior means and 95% CI were estimated for covariances and correlations. We also checked whether our estimates were a function of the choice of prior, which was not the case.

Structural equation modelling

To test the relative fit of alternative biological hypotheses of phenotypic integration, we applied structural equation modelling to 18 *a priori* conceived scenarios assessing how the different traits were associated among individuals (Fig 1, Table 1). Of the 18 models, model 1 represents a (biologically unrealistic) statistical "null" expectation; models 2-9 represent different scenarios of phenotypic integration and quasi-independence between body size and risk-taking modules; and models 10-18 represent hypotheses of body size as a module and causal influences of body mass (as proxy for the "energetic reserves" module) on the risk-taking module. We used the among-individual correlation matrix estimated with the multivariate mixed-effects model to test our SEM hypotheses with the R-package "SEM" in R v. 3.3.3 (Team R Core 2017). We then compared the model fit using the Akaike information criterion (AIC) (Burnham & Anderson, 2004) and evaluated the relative support based on AIC differences relative to the best-fitting model (ΔAIC).

RESULTS

All phenotypic traits (i.e., body mass, tarsus length, wing length, bill length, exploration behaviour and aggressiveness) showed considerable variation among individuals (Table S1). In addition, most morphological traits were strongly correlated (Table 2). In general, heavier birds had longer tarsi, wings and bills suggesting that all were expressions of a common latent variable (i.e., representing "body size"). Furthermore, individuals that were on average relatively aggressive toward conspecifics were also relatively active in a novel environment (i.e. more "explorative") suggesting the existence of the hypothesized behavioural character "risk-taking behaviour" (Table 2).

SEM comparisons identified model 10 as best explaining the among-individual correlation matrix (as it had the lowest AIC value; Table S2). Model 10 posited the overall phenotypic integration of two quasi-independent modules, representing "body size" and "risk-taking", respectively. The overarching latent variable included paths affecting the expression of all traits with an additional covariance between the behavioural traits (i.e. that was independent of the latent variable "body size") (Model 10; Fig 2). Furthermore, variation in body mass not attributable to the latent variable "body size" was negatively linked to both behavioural traits, implying that the amount of energetic reserves was also linked (independent from body size) to "risk-taking behaviour".

Table 2. Among-individual correlation estimates (with associated 95% CI) between six morphological and behavioural traits. Values in bold face indicate significant correlations, owing to with 95% CI not overlapping zero.

	Body mass	Exploration	Aggressiveness	Tarsus length	Wing length
Exploration	-0.02 (-0.16, 0.12)				
Aggressiveness	-0.12 (-0.32, 0.08)	**0.28 (0.02, 0.49)**			
Tarsus length	**0.54 (0.44, 0.64)**	**0.18 (0.04, 0.31)**	-0.10 (-0.31, 0.07)		
Wing length	**0.31 (0.18, 0.45)**	-0.01 (-0.18, 0.16)	0.06 (-0.15, 0.31)	**0.20 (0.08, 0.34)**	
Bill length	**0.19 (0.03, 0.35)**	**0.24 (0.07, 0.43)**	0.11 (-0.16, 0.38)	**0.25 (0.08, 0.38)**	-0.02 (-0.20, 0.16)

DISCUSSION

This study investigated patterns of among-individual integration between morphology and behaviour (i.e., "personality") in free-living male great tits. We found evidence for an overall integration between behaviour and morphology mediated by two distinct mechanisms: one integration mechanism between behaviour and morphology acted through the overarching latent variable "body size" while another integration mechanism was mediated by size-independent variation in body mass (i.e., an "energetic reserves" module). By using structural equation models we effectively disentangled multiple ways by which body mass was involved in the integration between morphology and behaviour. Our statistical approach therefore allows us to provide firm support for both optimality models simultaneously.

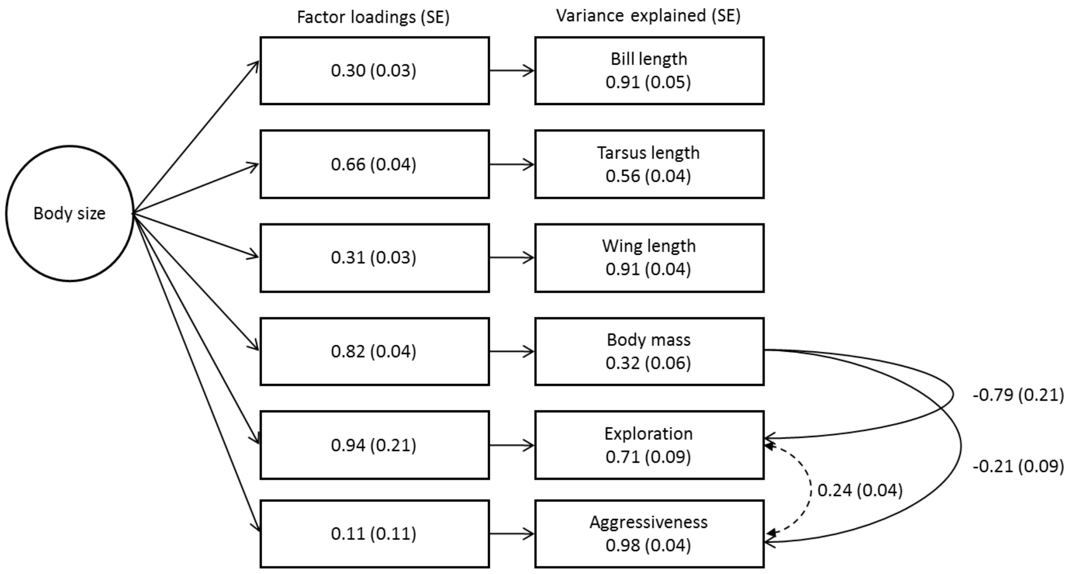

Figure 2. *Parameter estimates of the structural equation model that best fitted our data (Model 10). For each trait, we report the variance explained by the SEM structure and factor loadings with the corresponding standard error (SE) in parentheses. Solid lines represent causal relationships, and dashed lines are connecting the behavioural traits between them (i.e. constituting the latent variable "Risk-taking behaviour").*

While theoretical studies have attracted extensive empirical attention to the link between "state" features (e.g. body size, energetic reserves) and behavioural expressions (Houston & McNamara, 1999), there are very few empirical studies that addressed state and behavioural traits as evolutionary characters. Our study investigated such a key aspect and tested for among-individual integration between morphology and behavioural characters predicted by adaptive behavioural ecology theory (Brodie, 1992; DeWitt et al., 2000). Additionally, body features like size or energetic reserves have been among the most frequently invoked state variables in state-dependent behaviour theory. Models based on those body features predict that the energy that an organism obtains typically depends on its size or reserves, and the organism's body features will be influenced by its behavioural responses (Houston & McNamara, 1999). The central problem in testing these models is the difficulty of empirically quantifying body size and energetic reserves, given that both are latent variables. A common approach to measure any of these two distinct body features is by quantifying the total mass of an individual. Notably, in this study we found that body mass played two distinct roles in the overall integration between morphology and behaviour. On the one hand, behaviour and morphology were integrated within an overarching latent variable representing size-related behaviour. Individuals that defended their territories more strongly against conspecifics and explored their environment more actively also had higher mass and longer tarsi, wings and bills. Thus, risk-takers were also relatively large individuals. At the same time, behaviour was additionally linked to the portion of body mass that was independent of "body size" (e.g., energetic reserves). Individuals that defended their territories more vigorously against conspecifics and explored their environment more actively also had a lower size-independent body mass. Thus, risk-takers had lower energetic reserves compared to risk-avoiding individuals.

Our evidence for phenotypic integration of behaviour and morphology is particularly insightful given the considerable theoretical and conceptual literature that suggests such links (Houston & McNamara, 1999). The support for quasi-independence between the "body size", "energetic reserves" and "risk-taking behaviour" modules fits with predictions derived from theoretical models of state-dependent behaviour. We had predicted that if integration had evolved as an asset protection mechanism, individuals with more "assets" such as energetic reserves or body size would be more cautious. In contrast, if integration had evolved as a state-dependent safety mechanism, individuals with higher assets would be better at avoiding high predation risk, and therefore, take more risks (Luttbeg & Sih, 2010). Our study showed support for a state-dependent safety mechanism causing positive covariation between "body size" and "risk-taking behaviour". Importantly, we also found that the two behavioural traits were negatively associated to the variation in body mass independent of the latent variable "body size" (i.e. energetic reserves). This finding is in line with predictions from the asset protection principle where individuals with higher assets (energetic reserves) were less risk-taking (Clark, 1994; Luttbeg & Sih, 2010). In our case, individuals that had on average low energetic reserves and therefore, less to lose, were relatively explorative and aggressive (i.e. took more risks), likely as a way to secure more resources. In contrast, higher assets allow individuals to behave more cautiously and avoid taking risks in order to protect their assets. An alternative interpretation of this finding is that birds that are heavy (independent of body mass) have a higher wing-loading (Bednekoff & Houston, 1994), and consequently, take less risk due to their greater vulnerability to predation. These two explanations cannot be disentangled with our study design. Yet, our findings do confirm the general notion that morphological and behavioural traits from different functional contexts covary. Our study therefore implies that phenotypic integration of behaviour and morphology may be more common among organisms than previously assumed (Araya-Ajoy & Dingemanse, 2014; Carter & Feeney, 2012; Dochtermann & Jenkins, 2007) and provides firm evidence for state-dependent personality.

The opposing effects of body mass (as a measure of both body size and energetic reserves) on behaviour highlights the benefits of using statistical approaches (such as structural equation modelling) that enable multiple relationships between traits to be estimated simultaneously. Doing so allowed us to conclude that a portion of the variation in one module was explained by associations with other modules. Our analyses suggest that empiricists interested in the relationships between body size, energetic reserves and behaviour should focus on quantifying latent variables instead of considering single traits such as total body mass. Our findings thus offer a solution to the long-running debate focussing on the question of whether body mass more strongly reflects energetic reserves or structural body size (Piersma & Davidson, 1991), by demonstrating that both components can be statistically quantified simultaneously. Theoretical work predicts that multiple state variables covary with risk-taking behaviour. However, previous studies did not account for the joint effect of several multivariate states acting on suites of correlated behavioural traits. Here we introduced an approach allowing the simultaneous study how multiple aspects of state covary with risk-taking. Only by doing so we were able to elucidate that asset protection and state-dependent safety models were both supported.

Overall, this study expands upon a classic body of research predicting that selection pressures generate correlations between morphology and behaviour, as a general example of state-dependent behaviour theory. We found that behavioural traits were linked to morphological traits by an overarching latent variable as part of a unique phenotypic character and to the single trait body mass as part of an “energetic reserves” module. Our study thus implies that an individual’s morphological and behavioural traits may represent expressions of a uniquely evolved character, ultimately having consequences for evolutionary trajectories. The modularity framework utilized here also emphasizes the broad applicability of multivariate analyses (e.g. SEM) in personality research and brings new exciting possibilities to behavioural ecologists studying complex relationships between phenotypic traits among individuals.

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Electronic Supplementary Material of Chapter 4

Table S1. Sources of variation in six morphological and behavioural attributes (standardized) measured in male great tit individuals. We present fixed (β) and random (σ^2) parameters with their 95% credible intervals (CI). Adjusted individual repeatability was calculate for each attribute as the proportion of the total phenotypic variance not attributable to fixed effects that was explained by individual identity.

	Body mass	Exploration	Aggressiveness	Tarsus length	Wing length	Bill length
Fixed effects	β (95% CI)	β (95% CI)	β (95% CI)	β (95% CI)	β (95% CI)	β (95% CI)
Intercept	-0.38 (-0.62, -0.13)	-0.31 (-0.54, -0.07)	0.01 (-0.10, 0.12)	0.12 (-0.09, 0.35)	-0.05 (-0.29, 0.19)	0.06 (-0.28, 0.40)
Time	0.06 (0.03, 0.09)	0.05 (0.02, 0.08)	--	-0.02 (-0.04, 0.01)	-0.00 (-0.03, 0.03)	-0.01 (-0.03, 0.02)
Random effects	σ^2 (95%CI)	σ^2 (95%CI)	σ^2 (95%CI)	σ^2 (95%CI)	σ^2 (95%CI)	σ^2 (95%CI)
Individual	0.63 (0.57, 0.69)	0.37 (0.33, 0.40)	0.27 (0.24, 0.31)	0.66 (0.61, 0.73)	0.39 (0.35, 0.43)	0.30 (0.27, 0.34)
Plot	0.02 (0.01, 0.05)	0.01 (0.00, 0.02)	0.01 (0.00, 0.02)	0.02 (0.01, 0.03)	0.00 (0.00, 0.01)	0.02 (0.01, 0.03)
Year	0.03 (0.01, 0.05)	0.01 (0.00, 0.02)	0.00 (0.00, 0.01)	0.00 (0.00, 0.00)	0.01 (0.00, 0.01)	0.01 (0.01, 0.01)
PlotYear	0.01 (0.00, 0.01)	0.00 (0.00, 0.00)	0.01 (0.00, 0.01)	0.00 (0.00, 0.00)	0.02 (0.01, 0.02)	0.00 (0.00, 0.00)
Observer	0.02 (0.01, 0.02)	0.02 (0.01, 0.03)	--	0.12 (0.08, 0.16)	0.14 (0.10, 0.19)	0.26 (0.18, 0.37)
Residual	0.33 (0.31, 0.36)	0.56 (0.51, 0.61)	0.72 (0.66, 0.79)	0.30 (0.28, 0.33)	0.49 (0.45, 0.53)	0.45 (0.42, 0.49)
Adjusted repeatability	*R* (95% CI)	*R* (95% CI)	*R* (95% CI)	*R* (95% CI)	*R* (95% CI)	*R* (95% CI)
Individual	0.61 (0.58, 0.63)	0.37 (0.35, 0.40)	0.27 (0.25, 0.29)	0.60 (0.56, 0.63)	0.38 (0.35, 0.40)	0.27 (0.24, 0.30)

Table S2. Results of model comparison using Akaike information criterion (AIC) to compare our 15 candidate models. Smaller AIC values are given to models that better fit the data. Models whose AIC values differ from that of the top model (ΔAIC) by more than 2 are considered to lack explanatory power relative to the top model. We also present the Akaike weight of each model, showing that a single model (Model 10) best explains the data and is 82 times more likely (i.e., weight = 0.82) than competing models.

Model	AIC	ΔAIC	Weight
Model 10	133.86	0.00	0.82
Model 11	136.85	2.98	0.18
Model 4	198.33	64.47	0.00
Model 12	200.32	66.45	0.00
Model 9	205.98	72.12	0.00
Model 7	206.42	72.56	0.00
Model 17	207.97	74.11	0.00
Model 18	209.61	75.74	0.00
Model 3	221.21	87.34	0.00
Model 16	222.96	89.10	0.00
Model 15	293.46	159.59	0.00
Model 13	295.10	161.23	0.00
Model 5	295.41	161.55	0.00
Model 8	296.74	162.88	0.00
Model 6	301.80	167.94	0.00
Model 2	306.81	172.95	0.00
Model 14	308.45	174.59	0.00
Model 1	855.98	722.12	0.00

General Discussion

My PhD thesis aimed at investigating how natural selection can give rise to repeatable among-individual differences in behaviour (i.e. animal personality). This question has attracted much attention from theoreticians and empiricists (e.g., Dall, Houston, & McNamara, 2004; Dingemanse & Wolf, 2010; Stamps, 2007; Wolf, van Doorn, Leimar, & Weissing, 2007; Wolf, van Doorn, & Weissing, 2008; Wolf & Weissing, 2010, **Chapter 1**). However, to date and despite the notable scientific input, the evolutionary origin of adaptive animal personality is still poorly understood. My thesis chapters were specifically planned to further our understanding of the adaptive cause of individual differences in labile traits such as behaviour. Below I provide a summary of the main findings of each Chapter.

Behavioural ecologists have mainly focused on studying patterns of phenotypic plasticity (i.e. within-individual variation). However, one should not ignore the multilevel structure of phenotypic variation in labile traits (i.e. variation among- and within-individuals). **Chapter 1** is an opinion paper where my colleagues and I discussed the application of state-dependent behaviour models to the study of animal personality, and expanded these ideas to broaden the conceptual framework of adaptive individual variation in behaviour. Particularly, our aim was to expand classic optimality models to specifically focus on among-individual differences in behaviour. Additionally, we presented new ideas about experimental design and provided insights into the statistical approach to empirically test the postulated models about among-individual differences in behaviour.

Life-history theory posits that trade-offs are a likely mechanism maintaining phenotypic variation among individuals, assuming that variation already exists among individuals. Life-history theory also specifies that trade-offs might exist at some but not other hierarchical levels (e.g. within- but not among-individuals). However, most empirical studies in behavioural ecology have focused, so far, on testing the existence of trade-offs using phenotypic data. In **Chapter 2**, we investigated whether a behavioural trade-off exists between decision-making traits, thereby explaining the maintenance of variation in cognition, a presumed driver of variation in animal personality. Furthermore, we placed special emphasis on testing whether the trade-off between the two cognitive traits was level-specific. To do so, we carried out a lab experiment to study the trade-off between two decision-making traits related to information use: accuracy in taking a decision and speed with which that decision was taken. We showed that speed-accuracy trade-offs were indeed level-specific: trade-offs between speed and accuracy existed among-individuals but not within-individuals. Our result thus demonstrated that birds that on average took faster decisions also were more often wrong in their decisions than birds that on average took slower decisions. Furthermore, we also demonstrated that failure to correctly account for level-specific trade-offs can lead to biased inferences about the existence of trade-offs (i.e. we found no trade-off at the population level). This study thus exemplified the importance of considering the hierarchical structure of labile traits when testing hypotheses involving trade-offs and supports the notion of trade-offs as mechanisms generating repeatable behavioural variation among individuals.

Following up with the notion of trade-offs as a cause of phenotypic variation, in **Chapter 3** we investigated the factors that determine energy management in wintering great tits. Great tits, as well other small passerines, face lower resource levels, shorter days and harsher climatic conditions as winter approaches. An extended number of theoretical models have aimed to explain how small birds survive in winter under such harsh conditions (Houston & McNamara, 1993; Houston et al., 1993; McNamara et al., 1994; Pravosudov & Lucas, 2001). Birds such as the great tit would face the bad winter conditions by increasing their fat reserves. However, birds must simultaneously avoid predation from aerial predators (e.g. hawks), giving rise to a trade-off between avoiding predation and avoiding starvation during periods of harsh environmental conditions. Several tests of models of fattening strategies in wintering birds have been carried out in the lab, very few in the wild, and almost no study attempted to measure both traits simultaneously in wild conditions (but see Macleod et al. 2005). In **Chapter 3**, we simultaneously studied the relationship between foraging activity at feeders and daily mass gain in wild wintering great tits. Our results demonstrated that birds foraged and gained mass early during the day, as predicted by theory when the starvation-predation risk trade-off is mass-dependent and starvation risk outweighs predation risk. We thus concluded that increased energetic demands experienced by small birds in winter might favour individuals avoiding risk of starvation rather than predation avoidance. Furthermore, the hypothesized trade-off did not explain the existence of among-individual variation in behaviour because individuals did not differ in how they resolved the starvation-predation risk trade-offs, i.e. all birds gained mass in the similar manner throughout the day. This result suggests a different process (e.g. another trade-off) as the underlying mechanism explaining the observed variation in foraging behaviour among individuals.

In **Chapter 4**, we jointly investigated the two bodies of theory explaining the maintenance of individual variation. On the one hand, evolutionary ecologists expect phenotypic integration in situations where correlational selection favours optimal combinations of functionally-related attributes. On the other hand, optimality models developed by behavioural ecologists predict that an individual’s behaviour will vary as a function of its state (e.g. body condition, size), thus also predicting that particular combinations of state and behaviour maximize fitness (see **Introduction**). Both the state-dependent personality theory and correlational selection concepts therefore imply that selection favours phenotypic integration and simultaneously leads to a flat fitness surface. In **Chapter 4,** we combined these two approaches and investigated patterns of phenotypic integration between morphology and behaviour based on predictions derived from two optimality models (i.e. "asset protection" and "state-dependent safety"). To test this hypothesis of state-dependent personality, we explored patterns of covariance for multiple morphological traits (body mass, wing length, tarsus length and bill length; encapsulating two dimensions of "state": structural size and energetic reserves) and two behaviours (aggressiveness and exploration) in free-living great tits in spring. Our results demonstrated the existence of a behavioural module "risk-taking behaviour" that covaried with each of two morphological (state) modules ("body size" and "energy reserves"), thereby providing support for both optimality models simultaneously (i.e. support for the "asset protection" and "state-dependent safety" hypotheses). Using for the first time a multivariate approach, we provided support for the existence of adaptive state-dependent personality. Furthermore, our results suggest that phenotypic integration in situations where correlational selection favours optimal combinations of functionally-related traits has indeed great potential as mechanism explaining among-individual variation in behaviour.

Generally, the relevance of my findings for ecology and evolution is implicitly addressed in each of the chapters of the thesis (**Chapters 1 - 4**). Therefore, in this General Discussion section I will frame the results presented throughout this thesis in a wider context. To do so, I will firstly discuss the need of reconciling theory on animal personality with empirical data and I will back up my arguments with ideas from **Chapter 1**. Second, I will highlight the importance of the variance-partitioning approach to study multi-level variation in labile traits such as behaviour. I will also expose the rationale and benefits of the use of the variance-partitioning approach by building up on the findings from **Chapters 2 and 3**. Third, I will discuss the multivariate nature of phenotypic traits and evoke for a more geometric view of phenotypic variation. While multivariate phenotypic variation is transversal to the entire thesis, I will develop my arguments focusing on **Chapter 4**. Fourth, I will discuss whether phenotypic traits are genetically unconstrained and discuss the assumption of the "phenotypic gambit". To conclude the General Discussion, I will provide some brief remarks on future avenues for behavioural and evolutionary ecologists interested in studying among-individual differences in behaviour.

Theoretical Modelling in Behavioural Ecology

> *"Essentially, all models are wrong but some are useful."*
>
> (Adage attributed to statistician George Box)

The goal of theoretical modelling in the field of behavioural ecology is to generate hypotheses that empiricists can experimentally test. One of the most prominent types of models in behavioural ecology involves optimality theory. Optimality models have been widely used to develop hypotheses about how nature works, providing quantitative predictions that can be tested with observational or experimental work. Models usually make obvious assumptions about the nature of the system (e.g. birds must gain more energy reserves when winter conditions are severe, **Chapter 3**); but these modelling exercises force researchers to identify important components of complex systems. These complex systems of optimal behaviour should be ideally underlined by simple mechanisms, as opposed to the more traditional approach of complex models developed in simple environments (McNamara & Houston, 2009).

While optimality theory is unequivocally a powerful tool in behavioural ecology, it is not exempt from criticism (e.g. reviewed by Parker & Maynard-Smith, 1990). Optimality models are based on the assumption that natural selection maximises the fitness consequences of the behavioural action (e.g. via reproductive output or survival). However, these models do not aim to demonstrate that natural selection indeed produces optimal solutions (i.e. models do not test whether nature optimizes). The ultimate goal of optimality theory is to help us understanding the biological constraints that shape adaptations. Thus, given a specific state and time, optimality models will inform researchers about the optimal behavioural response of an individual. For instance, models will predict how much foraging a bird should perform based on its energy reserves, predation risk and food availability (**Chapter 3**).

The application of optimality theory to the study of repeatable individual differences in behaviour (i.e. animal personality) has not been exempt from criticism either. The main critique is that models are not explicit about the level of variation they aim to explain (i.e. whether the model concerns individual- versus mean-population-level plasticity). This vague definition of their level-specificity has led to some misunderstanding about the suitability of the theory in explaining animal personality. When considering that models predict mean-population plasticity, all individuals of a population are expected to optimally adjust their behaviour in response to the environmental conditions in order to maximize fitness. In that scenario, all individuals of the population behave optimally and theory would predict a single mean optimum for the entire population. Hence, variation among individuals would be considered as statistical noise around the adaptive mean (Wilson, 1998). This view is, however, opposite to the actual rationale of optimality theory. The focus of the theory is usually at the individual level. That is, optimality theory is based on the notion that each individual makes specific behavioural decisions to optimize its fitness by trading-off the costs and benefits of such decisions and given its own state (Houston & McNamara, 1999). Thus, optimality theory explains individual differences in behaviour based on individual differences in state. State is broadly defined as any feature that affects the costs and benefits of an individual's behavioural actions (e.g., energy reserves, metabolism, predation risk, age, information state, social rank, etc.; Houston & McNamara 1999, **Chapter 1**).

Feedback dynamics between states and behaviours have been long assumed ((Houston & McNamara, 1999). However, those feedbacks were typically assumed to be negative (e.g. the balancing feedback between nestling begging behaviour and parental provisioning effort in many bird species). More recently, positive state-behaviour feedbacks have come to the foreground as part of the field of animal personality (**Chapter 1**). These models effectively explain the emergence of among-individual variation in behaviour; however they cannot explain or predict consistency in behavioural differences. In other words, most optimality models predict patterns of reversible plasticity (Fig 1 in **Introduction**). While there have been some attempts to describe how feedback dynamics between state and behaviour can lead to repeatable behaviour differences among individuals (reviewed in **Chapter 1**), the field of animal personality is lacking a general theoretical framework. Hence, future modelling work should focus on investigating under which conditions state-behaviour feedbacks give rise to consistent individual differences in behaviour. To investigate that question, theoreticians need to model whether it is possible that initial differences in state or behaviour have different equilibrium points and to determine how easily individuals can be moved from one equilibrium point to another (e.g. due to stochastic changes caused by a parasitic infection or windfall resources). Additionally, future empirical work should put more emphasis in hypothesis-testing. The goal of mathematical models is to determine which factors are capable of generating repeatable individual differences via feedbacks dynamics; and it is the turn of experimental biologists to accumulate empirical data supporting the notion that state-behaviour feedback can indeed predict repeatable individual differences in behaviour. To date, there has been scarce exchange between state-behaviour feedback theory and real-world data (but see Mathot, Dekinga, & Piersma, 2017).

Overall, the field of behavioural ecology and specially, behavioural ecological research on animal personality, will greatly benefit from an enhanced communication and collaboration between theoreticians and empiricists. Indeed, the aim of **Chapter 1** was precisely that one, to promote an active feedback between models and empirical data (see Mathot & Frankenhuis, 2018; Niemelä & Dingemanse, 2018 for similar arguments). Besides expanding the scope of classic optimality theory to specifically focus on models about among-individual differences in behaviour, in **Chapter 1** we also provided clear guidelines to empiricists on how to go about with experiments and statistical analyses. Thus, our ultimate goal was to encourage researchers to do more hypotheses testing and facilitate future research on the topic.

The Merit of the Variance-Partitioning Approach

Responses to selection are only expected if the covariance between behaviour and fitness is at the among-individual level and underpinned by an additive genetic covariance (Lynch & Walsh, 1998). Therefore, it is important to acknowledge the multi-level nature of labile traits when testing hypotheses about the adaptive causes of phenotypic variation among individuals. For this reason, in **Chapters 2-4** I made use of theory and methods developed in quantitative genetics to partition phenotypic variation at multiple levels.

Variance-partitioning approach refers to a statistical method developed to "partition" the relative contribution of the genetic (among-individual) versus environmental (within-individual) components to the total phenotypic variation in traits (and fitness). The relevance of the variance-partitioning approach is well acknowledged because the study of evolutionary responses to selection explicitly requires the partitioning of phenotypic variation into the among- and within-individual components (Falconer & Mackay, 1998). However, collecting repeated measures of the same behavioural traits for each individual and applying the "variance-partitioning" approach is not yet the norm in behavioural ecology.

Behavioural ecologists typically collect phenotypic observations, being forced to assume that phenotypic information is representative of the underlying among-individual architecture. Hence, researchers rely on the so-called "individual gambit" (i.e. to infer patterns of among-individual variation in labile traits based on unpartitioned phenotypic data) (Brommer, 2013). Empirical evidence has shown, however, that phenotypic behavioural data may or may not be representative of underlying patterns of among-individual differences of behaviour (Dingemanse et al., 2012). There are several reasons for that. First, the use of phenotypic data to describe individual (co)variation might be a conservative approach when residuals of behavioural traits are uncorrelated. This will lead to a biased estimation of individual-(co)variance compared to the actual ones (Brommer, 2013). Second, phenotypic data to describe individual (co)variation can be a deficient approach given the existence of level-specific mechanisms underlying individual patterns (e.g. **Chapters 2 and 3**). This will lead to an underestimation of individual-(co)variance compared to the actual ones. Lastly, phenotypic data to describe individual (co)variation can indeed be an appropriate approach given the good correspondence between patterns at different levels (reviewed in Brommer & Class, 2017). In sum, while in some specific cases it might seem a valid approach; it is likely that researchers are simply gambling when relying on the individual gambit. I will discuss our findings from **Chapters 2 and 3** to illustrate in more detail the importance of partitioning the phenotypic variance into among- and within-individual components, and consequently, study level-specific patterns.

In **Chapter 2**, we applied a variance-partitioning approach to investigate the hierarchical structuring of trade-offs between decision speed and accuracy. Quantifying trade-offs is generally challenging because their existence may often be obscured by other biological processes (van Noordwijk & de Jong, 1986, see **Introduction**). Indeed, we showed that decision speed and accuracy traded off among- but not within-individuals. Furthermore, when we re-ran our original statistical model to include the phenotypic effect of decision speed on accuracy instead of its among- and within-individual components, the strength of support for the existence of trade-offs decreased substantially to the extent that it was no longer significant. Thus, if we would have not partitioned the covariance between these two cognitive traits across the two hierarchical levels, we would have likely drawn the erroneous conclusion that there was no trade-off between decision accuracy and speed.

Similarly, in **Chapter 3** we applied a variance-partitioning approach to test predictions developed by starvation-predation risk trade-off theory for wintering great tits. By applying such a statistical framework, we showed that the part of our analyses focussing on the trade-off at the population level demonstrated a match between the temporal pattern of mass gain and foraging activity. So, overall birds foraged more intensively in the morning, and therefore, gained mass more rapidly in the first half of the day. By contrast, when focussing on individual differences we demonstrated that birds differed greatly in how often they visited the feeders. Strikingly, all birds in our population gained mass in the same manner. This means that even though all individuals acquired enough reserves before going to roost, their patterns of foraging were very different. Some individuals relied heavily on our feeders and other individuals visited the feeders but foraged for the bulk of the day somewhere else. This mismatch between population-level patterns and individual-level patterns was indeed one of the most exciting findings of **Chapter 3** and it would have remained hidden if we had relied on the “individual gambit”, and thus, applying a phenotypic approach.

In conclusion, the multi-level nature of behaviour (as of all labile traits) underlines the need to incorporate level-specificity in biological hypotheses explaining the maintenance of individual variation among individuals (Westneat, Wright, & Dingemanse, 2015b). Indeed, two of the empirical studies of this thesis **(Chapters 2 and 3)** demonstrated the need for such considerations, as level-specific mechanisms in the trade-offs between speed and accuracy, and between avoiding risk of predation and starvation, resulted in level-specific patterns of covariance between the traits studied. Furthermore, the “individual gambit” should not be taken for granted because it is more biologically meaningful, but also because statistically speaking is usually more appropriate to use mixed effects models than a phenotypic approach to investigate variation in traits that vary across multiple levels. The findings from PhD thesis thus showed that the use of mixed-effect models and variance-partitioning to study individual differences in labile traits is important because allowed the detection of the actual among-individual patterns that otherwise would have been hidden at the population level.

A Geometric View of Phenotypic Variation: Multivariate Traits

“Pigeons with short beaks have small feet, and those with long beaks large feet. Hence, if man goes on selecting, and thus augmenting, any peculiarity, he will almost certainly unconsciously modify other parts of the structure, owing to the mysterious laws of the correlation of growth.”

Darwin (1859)

Phenotypic variation is found in almost all labile traits even in the presence of strong natural selection; however selection should deplete such variation in phenotypes. The perceived incompatibility between these two common observations is likely a consequence of taking a trait-by-trait approach to study phenotypic variation in a single trait and its evolutionary consequences (reviewed in Walsh & Blows, 2009). Since Darwin (1859) it is clear that phenotypic traits are not independent. While Darwin in the quote at the beginning of the section was referring to allometric correlations between morphological traits, researchers have long debated about the degree of independence of many sorts of traits (reviewed in Walsh & Blows, 2009). For instance, several studies have already pointed out the multivariate nature of behaviour (e.g., Araya-Ajoy & Dingemanse, 2014; Carter & Feeney, 2012). The multivariate nature of phenotypes is, thereby, well known. Furthermore, empirical evidence also demonstrates that phenotypic correlations are indeed widespread (Lande & Arnold, 1983b).

Chapter 4 provided a fitting illustration of the relevance of using such a multivariate framework when investigating the causes of adaptive behavioural variation among individuals. In **Chapter 4**, we investigated patterns of among-individual integration between morphology and behaviour in free-living male great tits. We found evidence for quasi-independent modules; a morphological module linking the four morphological traits positively to a latent variable that one may dub “body size”; and a behavioural module linking the two behavioural traits positively to a latent variable that we may dub “risk-taking behaviour”. Importantly, we also found evidence for an overall integration between behaviour and morphology mediated by two distinct mechanisms: one integration mechanism between behaviour and morphology acted through the overarching latent variable “body size” while another integration mechanism was mediated by size-independent variation in body mass (i.e., an “energetic reserves” module). Our analyses therefore provided an important lesson for future research, suggesting that empiricists interested in the relationships between body size, energetic reserves and behaviour should focus on quantifying multivariate variables instead of considering single traits such as total body mass. Overall, the framework applied in **Chapter 4** allowed us to quantify the multivariate nature of the underlying (i.e., latent) evolutionary “character” (c.f. Houle, 2001) while testing for hypothesis of causal relationships among traits.

In conclusion, given the existing theoretical and empirical evidence, multivariate analyses should logically be favoured over univariate ones for describing the complex structure of multiple labile traits that will likely covary with each other. However, this approach is not the norm. Researchers still often inappropriately assume that selection acts on single traits, consequently applying univariate analyses. A plausible reason for such a preference towards univariate approaches is the difficulty of implementing multivariate analyses. However, one may argue that the benefits of applying multivariate analyses will likely exceed the challenges of implementing complex methods, and promise a deeper understanding on the evolutionary constrains of labile traits.

The “Phenotypic Gambit” and Evolutionary Constraints of Behaviour

The “phenotypic gambit” is an approach to the study of adaptations based on the assumption that patterns at the phenotypic level are not constrained by the underlying genetics (Grafen, 1984). Under this assumption, natural selection acts as an optimising process, being unconstrained by genetic architecture (Grafen, 1984). Behavioural ecology largely relies on the “phenotypic gambit” to make evolutionary inferences, both from the theoretical and empirical perspectives. From the theoretical perspective, optimality theory is largely a phenotypic framework (Grafen, 1984; Weissing, 1996). The underlying genetics of the behavioural traits in optimality models are unknown but assumed to be not constraining phenotypic patterns and under the general rules of natural selection (i.e. any required genetic mechanism will evolve and that any genetic constraint will be removed during long-term evolution, (Weissing, 1996). Thus, by assuming that the underlying genetics impose no constraints on natural selection; modellers can ignore the evolutionary dynamics and increase the tractability of their models. From the empirical perspective, behavioural ecology relies on the phenotypic gambit as researchers typically collect phenotypic observations of behavioural traits, and therefore, it is not possible to partition the genetic and environmental components from total phenotypic variation.

Is it valid, however, to assume that the genetic architecture does not constrain behavioural traits? The answer is not so obvious. To detect quantitative constraints, researchers must first examine both the amount and nature of the genetic variation for each trait. This is important because the amount of genetic variation will set an upper limit to the rate of evolution of each trait. In the case of behavioural traits, among-individual differences have been shown to be heritable (Réale et al., 2007; Stirling et al., 2002; Van Oers et al., 2005). Even though it is important to bear in mind that labile traits such as behaviours are in general expected to present large environmental (co)variance (Falconer & Mackay, 1998). Additionally, to predict a quantitative constraint, researchers need to measure the genetic covariance among traits. This is important because genetic correlations among traits have the potential to affect evolutionary responses of behaviours as correlated traits may not be able to respond to selection independently (Blows & Hoffmann, 2005; Lande, 1979; Lande & Arnold, 1983b; Walsh & Blows, 2009). These correlations might either speed or constrain the evolutionary potential of a population (Dochtermann & Dingemanse, 2013). In the case of behavioural traits, they are often correlated with each other or with other traits such as life-history or morphological traits (e.g. **Chapter 4**). Furthermore, there is also good evidence that genetic correlations between behaviours can indeed produce suites of correlated behaviours (reviewed by Dochtermann, 2011). Indeed, the results of a meta-analysis implied that there are stronger genetic correlations among behavioural traits than among life-history traits (Dochtermann & Dingemanse 2013). This suggests that among-individual correlations between behaviours impose greater evolutionary constraints than correlations between morphological or life-history traits (Dochtermann & Dingemanse, 2013). Hence, caution is needed when making inferences about the evolutionary responses of populations (Kruuk, Merilä, & Sheldon, 2003), especially for labile traits such as behaviour.

In conclusion, it is important to collect both phenotypic and genetic data for a full understanding of the evolutionary processes of behavioural variation (Roff, 1997). Thus, the subsequent question must arise: why some behavioural ecologists are still willing to take the phenotypic gambit? The answer is straightforward. Estimating genetic parameters (and then constructing a pedigree) is logistically-challenging in most natural systems. One of the reasons is that relatedness matrices in field studies are not easy to obtain because essentially every individual in the population needs to be known. Furthermore, estimating heritabilities and genetic correlations accurately requires large sample sizes. Both aspects make very difficult to obtain genetic information of individuals in natural populations. This is also the case in our own great tit population (Araya-Ajoy et al., 2016; Araya-Ajoy & Dingemanse, 2017). In this thesis I was able to partition phenotypic variation into among- and within-individual variance components because I had repeated behavioural observations for each individual. However, I did not further partition the among-individual variation into its genetic versus environmental components. This is because we currently lack a sufficiently deep pedigree from our population of great tits (but see Araya-Ajoy & Dingemanse, 2017). These impediments might be, however, alleviated with the introduction of genomics in the field of behavioural ecology (Bengston et al., 2018; Rittschof & Robinson, 2014; Zuk & Balenger, 2014). For instance, genetic mapping is the progressing genetics approach to relate molecular genetic patterns with phenotypes (Hoffman et al., 2014; Knief, Kempenaers, & Forstmeier, 2017; Lander & Schork, 1994), allowing researchers to study the genetics of phenotypic variation without information on the pedigree of a population.

Conclusions

The main findings of my PhD thesis lead to several important conclusions. On one hand, behavioural ecology theoreticians working in optimality models should develop models that generate quantitative predictions about the relative contributions of the different processes to phenotypic variation **(i.e., we need more level-specific predictions)**. On the other hand, empiricists should test the theoretical predictions of such models and in turn, inform theoreticians **(i.e., we need more hypothesis testing)**. Furthermore, researchers should also collect and use appropriate data and statistical tools to quantify the different sources of multilevel variation in labile traits **(i.e., we should not simply rely on the individual gambit)**. Additionally, my findings emphasize the importance of a “whole organism” (rather than “single trait”) approach, thus taking into consideration that organisms are integrated complex phenotypes **(i.e., we need to go multivariate)**. Lastly, I call for caution when ignoring the underlying genetics of phenotypic variation and making inferences about the evolutionary responses of populations **(i.e. we need to acknowledge the existence of genetic constraints)**.

Overall, this thesis presented a series of studies on the adaptive causes of among-individual differences in behaviour. These studies were developed with two main objectives. The first objective was to dive into the theoretical background on the maintenance of repeatable individual differences in behaviour. The second objective was to test and provide empirical evidence for the postulated theoretical framework. In general, my PhD work calls for the integration of different perspectives to study the adaptive causes of phenotypic variation among individuals in labile traits. While these questions were investigated in the context of behaviour, my work aimed at achieving a general understanding on the multilevel nature of labile traits. Therefore, the framework presented throughout my thesis could be readily applied to other phenotypic traits, such as physiological and life-history traits.

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Chapter 1 Animal personality and state–behaviour feedbacks: a review and guide for empiricists.

AS, MW and NJD conceived the study. Each co-author wrote a different part of the paper; MM conceived the overview of mechanisms, wrote the associated texts, tables, and figures.

Chapter 2 A multi-level approach to quantify speed-accuracy trade-offs in great tits (*Parus major*).

MM, KJM and NJD conceived and designed the study, MM collected and analysed the data, MM wrote the paper with input from and KJM and NJD.

Chapter 3 To eat and not be eaten: diurnal mass gain and foraging strategies in wintering great tits.

MM, KJM, and NJD designed the study. MM performed the field work and statistical analyses. MM and NJD wrote the manuscript with input from KJM.

Chapter 4 Evidence for phenotypic integration predicted by state-dependent behaviour theory in a wild bird population.

MM and NJD conceived and designed the study; MM, YAA, KJM, AM, NJD, and others collected the data; MM, YAA and NJD carried out the statistical analyses; and MM wrote the manuscript with input from all co-authors.

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Curriculum Vitae

MARIA MOIRON CACHARRON

Nationality: Spanish

EDUCATION

09/2013 – present	**PhD in Evolutionary and Behavioural ecology** International Max Planck Research School for Organismal Biology Max Planck Institute for Ornithology, Seewiesen, Germany Ludwig-Maximilian University (LMU), Munich, Germany
09/2011 - 09/2012	**MSc in Terrestrial Ecology** Autonomous University of Barcelona, Spain
09/2006 - 07/2011	**BSc in Biology** University of A Coruña, Spain

LANGUAGES:

Galician (native); Spanish (native); English (fluent); Catalan (fluent); German (spoken)

RESEARCH ACTIVITY

2013/present	**Max Planck Institute for Ornithology, Seewiesen, Germany** Evolutionary Ecology of Variation Research Group Supervisors: Niels J Dingemanse and Kimberley J Mathot
2011/2012	**Centre for Ecological Research and Applied Forestry (CREAF)** Autonomous University of Barcelona, Spain Supervisor: Daniel Sol
2010/2011	**Environmental agency, University of A Coruña, Spain** Biodiversity Department Supervisor: Elvira Sahuquillo
Jul-Sep/2010	**Marine Research Center (CIMA), Ribadeo, Spain** Supervisor: Dorotea Martinez
2009/2010	**Science Faculty, University of A Coruña, Spain** **Evolutionary Biology Research Group (GIBE)** Supervisor: Elvira Sahuquillo

GRANTS AND SCHOLARSHIPS

2017	IMPRS bridge funding (scholarship for PhD students)
2016	Travel grant to ISBE Conference, ISBE
2015	Travel grant to CogCom workshop, University of Vienna
2010/2011	Research collaboration Scholarship, Biodiversity Department, Environmental agency (OMA-UDC), University of A Coruña
2010	Internship in the Marine Research Centre (CIMA), Ribadeo
2009/2010	Research collaboration Scholarship, Evolutionary Biology Group (GIBE), University of A Coruña

PUBLICATIONS

Moiron M, Mathot KJ, Dingemanse NJ. 2018. *To eat and not be eaten: diurnal mass gain and foraging strategies in wintering great tits*. Proc. R. Soc. B. 285:20172868

Abbey-Lee RN, Araya-Ajoy YG, Mouchet A, **Moiron M**, Stuber EF, Kempenaers B, and Dingemanse NJ. 2018. *Does perceived predation alter extra-pair paternity? A field experiment in a passerine bird. Funct* Ecol. 00:1–10. https://doi.org/10.1111/1365-2435.13052

Moiron M, Mathot KJ, Dingemanse NJ. 2016 *A multi-level approach to quantify speed-accuracy trade-offs in great tits (Parus major).* Behav. Ecol. 27: 1539-1546

Sih A, Mathot KJ, **Moirón M**, Montiglio P-O, Wolf M, Dingemanse NJ. 2015. *Animal personality and state–behaviour feedbacks: a review and guide for empiricists.* Trends Ecol. Evol. 30(1):50-60

Moiron M, Gonzalez-Lagos C, Slabbekoorn H, Sol D. 2015. *Singing in the city: high song frequencies are no guarantee for urban success in birds*. Behav. Ecol. 26 (3): 843-850.

WORK IN PROGRESS

Moiron M, Araya-Ajoy YG, Mathot KJ, Mouchet A, Dingemanse NJ. Evidence for phenotypic integration predicted by state-dependent behaviour theory in a wild bird population. (submitted)

Adreani NM†, **Moiron M†,** Guedes E, Cavalli E, Tassino B, Mentesana L†. Defending as a unit: sex- and context-dependent aggressiveness in a duetting bird. †Shared first-authors. (submitted)

CONFERENCES

2017	poster	**ESEB**, Groningen
2016	Invited talk	**ISBE post-conference symposium**, Exeter
	talk	**ISBE**, Exeter
2015	talk	**EOU**, Badajoz
	talk	**ESEB**, Lausanne
	talk	**CogCom workshop**, Vienna
2014	poster	**ECBB**, Prague
2013	audience	**Individual differences Conference**, Groningen

SUPERVISION EXPERIENCE

2014/2015	MSc student: Lorena Heilmaier, TUM, Munich, Germany Co-supervised by: Niels J Dingemanse
2014/2015	Internship student: Bert Thys, European Lifelong Learning Programme – Leonardo da Vinci, University of Antwerp, Antwerp, Belgium Co-supervised by: Niels J Dingemanse

MEMBERSHIP AND VOLUNTEERING

2018- present	Member of American Society of Naturalists
2017- present	Member of European Society for Evolutionary Biology
2011- present	Member of SEO/BirdLife (Spanish Ornithological Society)
Jul-Aug/2011	SEO/BirdLife volunteer, Garajonay National Park, Spain
Jul-Aug/2009	Volunteer in Centre of Studies of Iberian Raptors, Toledo, Spain

WORKSHOPS AND COURSES

2013–17	Various statistical, presentation, writing and visualisation courses, IMPRS
2016	**Study design and sampling decisions in mixed-effect model analyses**, Seewiesen
2015	**Social Network Analyses**, Radolfzell **Statistical and Conceptual Approaches towards Multivariate Phenotypes**, Seewiesen
2014	**General and Generalized linear mixed-effect models**, Seewiesen
2012	**Bird vocalizations: song analysis and recognition**, La Garrotxa

Statutory Declaration and Statement

Eidesstattliche Versicherung

Ich versichere hiermit ein Eides statt, dass die von mir vorgelegte Dissertation von mir selbstständig und ohne unerlaubte Hilfe angefertigt worden ist.

München, den 28.06.2018 Maria Moiron Cacharron

Erklärung

Hiermit erkläre ich, dass die Dissertation nicht ganz oder in wesentlichen Teilen einer anderen Prüfungskommission vorgelegt worden ist. Im Weiteren erkläre ich, dass ich mich nicht anderweitig einer Doktorprüfung ohne Erfolg unterzogen habe oder ohne Erfolg versucht habe, eine Dissertation einzureichen oder mich einer Doktorprüfung zu unterziehen.

München, den 28.06.2018 Maria Moiron Cacharron