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The relationship between personality and cognition in the fowl, *Gallus gallus*

Josefina Zidar

IFM Biology

Department of Physics, Chemistry and Biology

Linköping University

SE-581 83 Linköping, Sweden

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To Askur

“Your soul can never grow old, it’s evergreen”

List of published papers outside of this doctoral thesis

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- Tsuboi M, Kotrschal A, Hayward A, Buechel S D, **Zidar J**, Løvlie H and Kolm N. 2016. Evolution of brain-body allometry in Lake Tanganyika cichlids. *Evolution*. 70:1559–1568.
- Favati A, **Zidar J**, Thorpe H, Jensen P and Løvlie H. 2016. The ontogeny of personality traits in red junglefowl, *Gallus gallus*. *Behavioural Ecology*. 27:484–493.
- Tsuboi M, Husby A, Kotrschal A, Hayward A, Buechel S, **Zidar J**, Løvlie H and Kolm N. 2014. Comparative support for the expensive tissue hypothesis: big brains are correlated with smaller gut length but greater parental investment in Lake Tanganyika cichlids. *Evolution*. 69:190–200.
- Jarnemo A, Minderman J, Bunnefeld N, **Zidar J** and Mansson J. 2014. Managing landscapes for multiple objectives: alternative forage can reduce conflict between deer and forestry. *Ecosphere*. 5:art97.
- Løvlie H, **Zidar J** and Berneheim C. 2014. A cry for help: female distress calling during copulation is context dependent. *Animal Behaviour*. 92:151–157.
- **Zidar J** and Løvlie H. 2012. Scent of the enemy: behavioural responses to predator faecal odour in the fowl. *Animal Behaviour*. 84:547–554.
- Eriksson P, **Zidar J**, White D, Westander J and Andersson M. 2010. Current husbandry of red pandas (*Ailurus fulgens*) in zoos. *Zoo Biology*. 29:732–740.

Popular science article (in Swedish)

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List of papers included in this doctoral thesis

The thesis is based on the following articles (I-VI).

- I. **Zidar J**, Balogh A, Favati A, Jensen P, Leimar O and Løvlie H. 2017. A comparison of animal personality and coping styles in the red junglefowl. *Animal Behaviour*. 130:209–220.
- II. **Zidar J**, Balogh A, Favati A, Jensen P, Leimar O, Sorato E and Løvlie H. The relationship between learning speed and personality is age- and task-dependent in red junglefowl. *In review in Behavioral Ecology*.
- III. **Zidar J***, Balogh A*, Favati A, Jensen P, Leimar O and Løvlie H. Generalisation to a novel cue covaries with behavioural flexibility in red junglefowl chicks. *Manuscript*.
- IV. **Zidar J***, Sorato E*, Malmqvist A-M, Jansson E, Rosher C, Jensen P, Favati A and Løvlie H. 2017. Early experience affects adult personality in the red junglefowl: a role for cognitive stimulation? *Behavioral Processes*. 134:78–86.
- V. **Zidar J**, Campderrich I, Jansson E, Wichman A, Winberg S, Keeling L and Løvlie H. Optimism endures: Environmental complexity buffers against stress-induced negative judgment bias. *In review in Scientific Reports*.
- VI. **Zidar J**, Sorato E, Jansson E, Jensen P and Løvlie H. The relationship between personality, affective state and judgment bias, in the red junglefowl. *Manuscript*.

* Indicates equal contribution to the manuscript

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Abstract

To cope with a changing environment, animals have traditionally been considered to behave adaptively to each situation faced. Yet, individual behavioural responses can both differ widely within populations, and show between-individual consistency (i.e. describing variation in animal personality). In this thesis, I focus on individual differences in animal personality and cognition (i.e. how animals perceive, process, store and act on environmental stimuli), and explore the possibility that they are interlinked. I use domestic- and red junglefowl (*Gallus gallus ssp.*), a species that is cognitively, behaviourally and socially complex, to explore these aspects of behaviour, through a series of studies.

Animal personality and coping styles are frequently used terms to describe within- and between-individual differences in behaviour, which are consistent over time and across various situations. The terms are often used as synonyms, even though they differ in some respects. In **paper I**, I show that animal personality and coping styles can be measured in red junglefowl, and that behavioural flexibility might be an important aspect for both. Further, I show that the terms should not be used as synonyms since they describe different aspects of behavioural variation.

In **paper II**, I observe large individual variation in both personality traits and learning speed in both chicks and adult red junglefowl. Interestingly, learning performance does not correlate across tasks, contrasting what has been found in humans and rodents. Thus, individuals that learn rapidly in one task are not necessarily fast learners in another task. I observe a relationship between personality and cognition that is task- and age-dependent, in which exploration relates to learning speed, but in opposite directions for chicks compared to adult females. In **paper III**, I show that red junglefowl chicks that are more behaviourally flexible have a stronger preference for new generalised stimuli, than less behaviourally flexible chicks. Behavioural flexibility was associated with fearfulness, indicating variation in reactive-proactive coping styles. In **paper IV**, I show that early cognitive stimulation to some extent can affect adult personality, thus showing a causal relationship between personality and cognition. Not all personality traits were affected, which might depend on the type of cognitive stimulation chicks were exposed to.

Important cognitive processes like perception and decision-making, can contain biases. One such bias is called judgment bias, which describes how individuals interpret ambiguous stimuli on a scale from positive to negative (optimism to pessimism). In **paper V**, I show that alteration of emotional state can influence such biases. Here, unpredictable stress influence judgment bias negatively, when individuals are housed in simpler, but not in complex environments, suggesting that there is an effect of additive stress that lead to reduced optimism. Complexity instead seems to buffer against negative effects of stress, since individuals in complex environments remained optimistic after stress exposure. Furthermore, increased dopamine activity was associated with optimism in chicks. In **paper VI**, I find that aspects of personality associate with how chicks judge ambiguity. Highly active individuals are more likely to approach cues than less active individuals, and when approaching, individuals that are slow to approach ambiguous cues are more vigilant when assayed in personality assays. Vigilant individuals might be more worried and reactive, which suggest that emotional traits can influence responses in a judgment bias task.

Taken together, I show consistent behavioural differences among individuals describing personality and coping styles, and variation in cognition. I show that these traits are related, and that there is an interplay between them, in which cognition can influence personality, and vice versa. I further show that judgment may be affected by the individual's current affective state and personality. Thus, I show a complex relationship between personality and cognition that in combination with environmental effects can help explain behavioural variation.

Introduction

Imagine a flock of chickens with newly hatched chicks. In the flock there are two sibling chicks, let us call them chick A and chick B. They grow up in the same social and ecological environment, and face similar challenges their first weeks of life. They follow their mother and learn what food is edible and what food they should avoid. Chick A learns very quickly these rules about food and sticks to eating that, while chick B samples a bit more before learning what food to avoid. After a few weeks, the chicks go further away from their mother and explore more of the surroundings on their own. Chick A quickly explores the environment and is making its excursions longer and longer. Chick B is staying much closer to the mother, and slowly explores the environment closer to her. One day a sparrow hawk flies over the flock when they are out exploring. Chick B runs underneath his mother's wing for protection and stays there for several minutes before emerging again, whereas chick A first runs under a bush, but shortly again enters the open and continues exploring. The following day a fox enters the area and kills one of the chickens in the flock. There is a lot of turbulence in the flock for a while, but slowly things get back to normal. Chick B again takes a long time to start exploring after the visit by the fox, while chick A is one of the first to start roaming round.

Despite sharing both genes and environmental conditions, chick A and chick B respond very differently from each other to these situations, but they respond consistently similar to themselves in comparable situations. We can therefore describe them to have different personality. Why do we observe these consistent behavioural differences among individuals within the same population? How are these differences maintained? Should there not be selection for the most optimal type? Do chick A and B differ because they see and respond differently to cues in the environment, in other words, do they differ in their cognitive traits as well as in personality? These are some of the questions that have driven the research I have carried out in this thesis.

Animal personality

In many species, individuals vary in the way they deal with potential risks, novelty and social encounters, as well as in their basal activity levels (Dall et al. 2004; Sih et al. 2004; Réale et al. 2007; Sih et al. 2012). At the same time, individuals can display relatively stable behavioural responses when faced with similar situations or when repeatedly experiencing the same type of situation, thus showing limited behavioural plasticity. For example, some individuals consistently display a bold or more aggressive behaviour in situations where other individuals are shy or timid (e.g. Huntingford 1976; Riechert & Hedrick 1993; Wilson et al. 1994). Such consistent between-individual variation in behaviour is observed even when individuals are of the same age, sex, and are being raised under similar conditions (Wilson et al. 1994; Groothuis & Carere 2005), and has been observed in species ranging from insects, to birds and mammals (e.g. Gosling 2001; Carere & Maestripietri 2013). In the relatively short period in which research has focused on consistent behavioural differences among individuals, various terms have been used to describe this phenomenon, such as animal personality (Gosling 2001), behavioural types (e.g. Sih & Watters 2005), temperament (Gosling 2001; Réale et al. 2007), coping style (Koolhaas et al. 1999), and behavioural syndromes (Sih et al. 2004; Huntingford 1967; Bell & Stamps 2004; Dingemanse et al. 2007). Animal personality has been defined as within-individual consistency and between-individual

differences in behaviour, consistent over time and/or across contexts (e.g. Dall et al. 2004; Sih et al. 2004), and is described for personality traits such as, activity, exploration, aggressiveness, boldness, and sociality (Réale et al. 2007). ‘Context’ can be defined as all external stimuli (including both social and physical environment) that influence an individual to express specific behaviours (Stamps & Groothuis 2010a). A single behaviour is considered ‘stable over time or context’ if the rank order between individuals is relatively consistent. That is, the absolute level of the behaviour may change over time or context, or be constant, but a similar rank order between individuals is maintained (Sih et al. 2004). In related concepts, a behavioural type is describing behavioural tendencies in individuals associated with ecological tasks, behavioural syndromes is describing correlations of suits of behaviours, and coping styles is describing suits of correlated traits often with links to physiology (Sih & Watters, 2005; Koolhaas et al. 2010). Here, it is the association between different behaviours that remain with similar rank order across time or context (see Bell & Stamps 2004 for review). Coping styles are describing consistent behavioural responses along a proactive-reactive gradient. Behaviours describing these coping styles are for proactive individuals a fight-flight response to stressors, fast and superficial exploration, and impulsive behaviour with high risk-taking, aggressiveness and boldness as well as social dominance (Koolhaas et al. 2010). Reactive individuals, on the other hand, explore more thoroughly and in a slower pace, accept or avoid stressors, and are less aggressive and shyer. Reactive individuals also seem to be more plastic in their behaviour (Koolhaas et al. 1999; 2010). Proactive-reactive phenotypes have so far mainly been described in male laboratory rodents, but the phenotypes have also been confirmed in other commonly studied species in animal personality research, such as the great tit (*Parus major*, Verbeek et al. 1994; Dingemanse et al. 2002; Cockrem 2007).

That animals respond differently to cues from the world around them, can have fitness consequences (Wolf & Weissing 2012). Bolder individuals may for example have increased access to recourses, but at the same time, may also be more susceptible to predation because they may be more risk-taking. Variation in aggression, boldness and activity often correlate and form a proactive behavioural syndrome (Huntingford 1976; Sih et al. 2004; 2012). In a situation where aggressiveness and boldness are linked, an increase in aggressiveness during sexual maturity (e.g. explained by increased testosterone levels), may have positive implications for reproduction. However, it might also influence boldness in a way that may result in maladaptive high-risk behaviour in risky situations that can be detrimental (Sih et al. 2004; 2012). For example, funnel-web spiders (*Atrax robustus*) that resume foraging quickly after disturbance and thereby take a greater risk of being predated, more often win antagonistic interactions with conspecifics (Riechert & Hedrick 1993). Similarly, sticklebacks (*Gasterosteus aculeatus*) that are aggressive towards predators, are successfully defending territories against intruders (Huntingford 1976). Selection for aggression might thus influence other traits, like boldness, and might explain why we sometimes observe apparently maladaptive behaviours. Although, what seem like maladaptive behaviour in the short-term, may have positive implications for fitness in the long-term (McNamara et al. 2012).

The observation that individuals can vary consistently in their behavioural responses raises some fundamental questions about behaviour. From an evolutionary perspective, and at least traditionally, we expect behaviour to be very plastic and that behavioural plasticity is selected for. Thus, it is therefore puzzling why we observe limitations to behavioural plasticity and that individuals behave in a consistent manner. Further, if there is an optimal way to behave in a certain situation, all individuals should be selected to act accordingly, minimising variation in behaviour between individuals and maximising behavioural plasticity for any given situation (Sih et al. 2004; Bell 2007). Why do then individuals vary in their behavioural responses and why does this variation persist? Variation is a prerequisite for selection and

studies aiming to understand individual variation are therefore fundamental in biology. The field of animal personality thus fills an important role in aiming to understand development and maintenance of consistent behavioural responses that vary among individuals within populations. Studies exploring personality in animals have skyrocketed the past decades (e.g. Gosling 2001; Dall et al. 2004; Sih et al. 2004; 2012; Groothuis & Carere 2005; Koolhaas et al. 2007; Réale et al. 2007; 2010; Dingemanse & Wolf 2010; Carere & Maestripieri 2013) and important theoretical models present how either inherent constraints or adaptive benefits are presumed to explain consistent behavioural variation among individuals (Dall et al. 2004; Stamp 2007; 2010; Wolf et al. 2007; Dingemanse & Wolf 2010). Mechanisms suggested to explain observed personality include life-history trade-offs (Smith & Blumstein 2008; Stamps 2007), and balancing selection such as negative frequency dependence favouring rare types (Dall et al. 2004; Nicolaus et al. 2016).

Many personality traits typically show heritability around 20-50 % (van Oers et al. 2004; 2005; 2010), which suggest that also environmental factors can influence personality traits. In fact, similar to other behavioural traits, genes, environment, as well as gene by environment interactions, are likely determining variation in personality (Dingemanse et al. 2010). Despite the abundance of theoretical models, the field is still largely biased towards descriptive empirical studies (DiRienzo & Montiglio 2015) and a holistic conceptual framework is still lacking (see David & Dall 2016 for review). Because animal personality is still a relatively young research field, at least within behavioural ecology, more empirical studies (both descriptive and hypothesis-driven) are encouraged, to improve our understanding of the evolution of personality (Bell 2017). Improved understanding of why individuals show limited behavioural plasticity and how behavioural responses co-vary with other traits, can offer a holistic view on this type of observed behavioural variation.

To compare personality across species, tests are encouraged to be designed to capture variation in similar traits that are of ecological relevance (Réale et al. 2007; Dall & Griffith 2014; Koski 2014). This has proven to be tricky because not all tests trigger the same response in all species. To further add confusion, authors sometimes use different labels on traits measured in one test, or the same trait can be labelled the same as traits obtained in other tests. This is known as the jingle-jangle fallacy, where ‘jingle’ refers to a single label used to describe functionally different traits measured with different tests, and ‘jangle’ when more than one label describes the same trait. The jingle-jangle fallacy presents a problem if comparisons are to be made between studies (Carter et al. 2013; Roche et al. 2016). There has been some attempts to streamline what personality traits to focus on, and how to design tests to capture this variation. In a seminal paper by Réale and colleagues (2007), 5 main categories of personality traits were suggested: boldness, exploration, activity, aggression, and sociality. These personality traits will probably capture the majority of the behavioural variation that individuals displays in various situations (Careau & Garland 2012). However, because animal personality is a field under development, we do not yet know if these categories are capturing all important personality traits for all species (Bell 2017). In addition, what is considered a personality trait will also depend on whether a broad sense or narrow sense definition is used. The broad sense definition includes all behaviour that is consistently differing among individuals (Réale et al. 2010), whereas narrow sense personality is limited to consistent behavioural variation in boldness, exploration, activity, aggression, and sociality and that is measured in specific tests (Réale et al. 2007; 2010).

Ontogeny of personality

Temporal stability, where personality traits are stable over relatively short periods of time, does not hinder that these traits change long-term, for instance, from young to adult (Stamps & Groothuis 2010a). Environmental and neuroendocrine factors can influence and alter brain circuitries, which could contribute to change in behaviour during development (Trillmich & Groothuis 2011). Ontogeny of personality could then potentially be explained by early reward sensitivity, where feedbacks (positive or negative) may influence personality through changes in the brain (Stamps & Groothuis 2010a). Although we know little about changes in personality during development, two periods in life are recognized as important in vertebrates for hormonal organization in neural structures; the perinatal period, and puberty (Koolhaas et al. 2010). Studying personality traits at several life stages can thus improve understanding of the development of personality.

Behavioural flexibility

Although individuals can display consistency in their behavioural responses over time and/or across contexts, individuals also seem to vary in their behavioural plasticity (Roche et al. 2016). Some individuals may be more uniform in their behaviour than and not as reactive to change as others (Dingemanse & Wolf 2010; Coppens et al. 2010), indicating that plasticity itself can be a personality trait (Koolhaas et al. 1999; 2010). A growing body of evidence show plasticity in personality traits within individuals (Dingemanse et al. 2010), particularly when linked to variation in coping styles (Carere et al. 2005; Coppens et al. 2010; Koolhaas et al. 1999; 2010). In rodents, differences in behavioural flexibility are for example displayed when proactive, inflexible individuals managed a maze better than reactive individuals only if the maze was not altered in any way (Benus et al. 1990). Then again, when the maze was regularly configured, reactive individuals did better (Benus et al. 1990). Even small changes, like turning the maze 90°, affected the behaviour of reactive individuals, suggesting that reactive individuals do better than proactive individuals in a changing environment. Thus, proactive individuals seem to base most of their decisions on internal cues or previous experiences, which can lead to inaccurate choices in a changing environment. However, reactive individuals may also lose valuable resources, as they take longer time exploring and do not seem to rely on previous experiences even in similar tasks (Coppens et al. 2010). There therefore seem to be differences in how individuals with different behavioural types may perceive and respond to cues in their surroundings, hence suggesting that there may be differences also in cognition among different personality types.

Animal cognition

Animal cognition describes the ways that individuals take in sensory information, store and recollect information, as well as process and use information (Shettleworth 2010). Cognition thus affect perception, learning and decision-making, which are important processes influencing behaviour in important aspects of an animal's life, such as during foraging and mate-choice (Shettleworth 2010). Historically, the field of animal cognition has largely focused on comparing cognitive abilities between species (comparative cognition) and understanding cognitive mechanisms (Pearce 2008; Shettleworth 2010). In more recent years, several new sub-fields have emerged, focusing on aspects of cognition within species, such as ethological cognition and ecological cognition (Shettleworth 2010).

An important aspect of cognition that has received a lot of research attention, is learning (Pearce 2008; Shettleworth 2010). A well-validated paradigm for measuring learning in experimental biology, is to measure how fast an association can form between a conditioned stimulus (CS) and an unconditioned stimulus (US), often using a discrimination task where two cues are presented simultaneously (e.g. Rescorla & Wagner 1972). If one individual quickly associate a colour cue with a reward, while another individual is taking much longer to make the same association, it might depend on individual differences in information acquisition. While the fast learner only learns to associate a colour with a reward, the other individual might learn about other properties of the cue, such as its size and shape and also sample the unrewarded cue more to learn about the value of both cues (Rowe & Healy 2014). Thus, variation in learning speed might reflect other aspects of cognition than ability *per se*. This is interesting, because variation in animal cognition has been hypothesized to link to variation in animal personality (Carere & Locurto 2011; Sih & Del Giudice 2012; Griffin et al. 2015). Empirical studies have found such a link (e.g. Amy et al. 2012; Guillelte et al. 2009; 2011; Titulaer et al. 2012), at least when exploring some aspects of personality and cognition (Griffin et al. 2015). The observed link has been suggested by theoretical models to reflect a speed-accuracy trade-off in which individuals with varying personality have different cognitive styles, describing cognitive traits, independent of cognitive ability (Sih & Del Giudice 2012). In this scenario, it is theoretically predicted that individuals that have a fast, proactive personality type may also be faster at using new information. These individuals may not pay attention to smaller details or changes in a task, and will therefore be fast at learning simple tasks, but at the same time start to struggle when learning requires them to pay attention to details (Carere & Locurto 2011; Sih & Del Giudice 2012). Individuals that have a slow, reactive personality type will instead take in more information and learn all details of a given task, which will make them slower at learning simple tasks, while better as tasks become more difficult; they pay attention and therefore make fewer errors (Carere & Locurto 2011; Sih & Del Giudice 2012). A speed-accuracy trade-off as an underlying mechanism explaining a link between personality and cognition still needs to be empirically validated. The observed relatedness between personality and cognition might also be explained by other underlying mechanisms or a more direct causal relationship where personality affects cognition or vice versa. In addition, there are other aspects of decision-making, than learning, that can be affected. For example, there are biases in cognitive processes (Sharot et al. 2009; Mendl et al. 2010; McNamara et al. 2012) that might be influenced by personality and/or more temporary emotions (i.e. excitement or sadness, Roelofs et al. 2016), a research topic that has received research interest the last couple of years.

Judgment bias

Emotions can influence cognitive processes, and cognitive processes can in turn initiate emotional responses (Mathews & MacLeod 2005; Gotlib & Joorman 2010). Roelofs and colleagues (2016) therefore suggest that emotions and cognition should not be regarded separately. Cognitive bias describes several different types of biases that include attention bias, memory bias and judgment bias. Attention bias describes increased attention to threatening stimuli when individuals are in an anxious state (Mathews & MacLeod 2005), memory bias that positive and negative events are more easily remembered than neutral events (Hamann et al. 1999), and judgment bias that ambiguous stimuli is interpreted as either positive or negative dependent on affective state (e.g. Harding et al. 2004; Paul et al. 2005; Gotlib & Joorman 2010; Roelofs et al. 2016). Humans tend to overestimate the likelihood of positive outcomes (i.e. have an optimistic bias, e.g. Carver et al. 2010; Sharot et al. 2011), unless they are depressed or suffering from other affective disorders (e.g. Mathews & MacLeod 2005; Gotlib & Joorman 2010). Overestimation of positive outcomes has been associated with success among humans in a variety of contexts (see Drozd et al. 2016 for review), but has also been related to increased risk-taking, which can have negative consequences (Tennan & Affleck 1987). Recent theoretical predictions and empirical studies suggest that affective states, such as anxiety or excitement, can influence judgment bias in animals in a similar way as in humans (Harding et al. 2004; Mendl et al. 2009; 2010; Doyzd et al. 2016; Roelofs et al. 2016).

Judgment bias in animals is typically measured using an experimental approach developed by Harding and colleagues (2004). Animals are trained to associate one stimulus with a reward and another stimulus with punishment or lack of reward. After associations are confirmed (meaning that animals have reached a stable learning criteria), ambiguous stimuli that are intermediate of the trained stimulus are presented and the animal's reaction to that stimuli is measured. The animal will presumably tackle the risk and uncertainty presented with the ambiguous cue using cognitive processes (Bateson 2016). If the individual is responding to the ambiguous stimuli with more similar behaviour as toward the learnt positive cue, the individual is considered relatively optimistic (Douglas et al. 2012). On the other hand, if the individual respond with similar behaviour towards the ambiguous cue as a learnt negative cue, it is considered pessimistic (Douglas et al. 2012). After the seminal study by Harding and colleagues (2014), positive and negative judgment biases have been measured in a range of species using a variety of experimental, although similar, set-ups (Roelofs et al. 2016). Treatments of both long (applied weeks before the test) and short (just prior to test) durations have successfully influenced judgment in animals (Mendl et al. 2010; 2011; Baciadonna & McElligott 2015, Roelofs et al. 2016). Some studies however show unclear or unexpected results, such as, increased optimism after shearing, neglect or owner absence (e.g. Doyle et al. 2010; Sanger et al. 2011; Müller et al. 2012; Briefer & McElligott 2013). Judgment bias tests where responses to ambiguous cues intermediate between learnt cues have been studied for little over a decade now, therefore tests procedures and protocols still need to be evaluated and validated. The methods currently used have to some extent been critiqued (McNamara et al. 2011; Roelofs et al. 2016). For example, when presenting the same ambiguous cue several times in a session, there is a risk of learning, which could influence interpretation of results (Roelofs et al. 2016). Additionally, it is difficult to know what an optimal response to an intermediate cue between two learnt cues should be and it is not clear that an optimal response that gives most gain in the short-term will do so in the long-term (McNamara et al. 2011). For results to be meaningful and interpretable, it is important that test paradigms are developed with a specific species in mind (Anderson et al. 2012). Further, when interpreting results, differences in study design must be considered. For example,

associating punishment with a negative cue, compared to associating a lack of reward with a negative cue, likely influence the expected responses in a test. Expectation of punishment will most likely lead to absolute avoidance of that stimulus, whereas a negative cue with only the absence of a reward more likely lead to a decreased response compared to the rewarded cue (Gygax 2014).

Judgment bias tests in animals have so far mainly been a tool to estimate animal welfare. Animals exposed to poor environmental conditions or stress tends to respond in a pessimistic way when presented with ambiguous cues (e.g. Bateson et al. 2007, 2011, Doyle et al. 2011, Destrez et al. 2013, Neave et al. 2013), whereas animals receiving enrichment, respond in an optimistic way (e.g. Brydges et al. 2011, Burman et al. 2011). Emotional traits that contrarily to temporary emotional states, refers to permanent emotional properties of the individual (Faustino et al. 2015), have recently been suggested to associate with judgment. This has stimulated a handful of studies, exploring a link between personality and variation in judgment biases (e.g. Cussen & Mench 2014; Lalot et al. 2016; Asher et al. 2016; d'Ettorre et al. 2017). The results so far suggest that personality can associate with judgment. For example, coping styles in pigs (*Sus scrofa domesticus*) and explorative behaviour in carpenter ants (*Camponotus aethiops*) were associated with variation in judgment bias (Asher et al. 2016; d'Ettorre et al. 2017). However, there are also studies that did not find an association between personality and judgment (Lalot et al. 2016).

The role of brain monoamines in judgment bias

Monoamines such as dopamine, serotonin and noradrenaline/norepinephrine are underlying emotional processes (Kandel et al. 2000; Sharot et al. 2012) and are suggested to influence variation in judgment (Sharot et al. 2009). Dopamine is an important part of the reward system that is involved in learning about rewards and seeking rewards (Wise 2004; Flagel et al. 2011), norepinephrine is involved in perception, learning and memory (Hu 2007; Berridge 2008), and serotonin is involved in many aspects of brain function and behaviour (Boureau et al. 2011). Until recently, only human studies had investigated the influence of monoamines on judgment bias (e.g. Sharot et al. 2009; 2012). These studies revealed that increased levels of dopamine led to an increased optimistic bias (Sharot et al. 2009; 2012). In humans, dopamine has been related to associating pleasure with future events (Sharot et al. 2009), and to further impair the ability to update information about negative events (Sharot et al. 2012). Recently studies have explored the influence of monoamines on judgment bias also in animals. Similar to the findings in humans, dopamine increased optimistic bias in rodents (*Rodentia*, Rygula et al. 2014; Kregiel et al. 2016) and bumblebees (*Bombus terrestris*, Perry et al. 2016). In rodents, there is some evidence that serotonin (Rygula et al. 2014; Anderson et al. 2013) and norepinephrine (Rygula et al. 2014; Enkel et al. 2010) also influence judgment bias. However, their role in influencing judgment biases is still unclear (Enkel et al. 2010; Anderson et al. 2013; Rygula et al. 2014; Kregiel et al. 2016). More studies on this topic should therefore hopefully increase our knowledge of monoaminergic systems involvement in judgment bias.

Aim of the thesis

Together, animal personality and animal cognition represent important phenotypic variation within species that can have consequences for individual survival and success. Further, animal personality and cognition were recently theoretically hypothesised to be interlinked. The general aim of this thesis was therefore to investigate the relationship between animal personality and animal cognition. For this, I used two breeds of fowl, the ancestor, the red junglefowl (*Gallus gallus*), and its domesticated decedent, the domesticated chicken (*Gallus gallus domesticus*).

First, I compared whether the commonly used terms animal personality and coping style are present and describe the same behavioural variation in the fowl (**Paper I**). Then I explored whether there is a link between animal personality and cognition, by focusing on learning and generalisation (**paper II, III**, respectively), and if there is a casual relationship between personality and cognition (**paper IV**). I continued by investigating if early experiences and environmental factors, representing emotional states, influence judgment (**paper V**), and whether biases in cognitive processes are associated with animal personality, representing emotional traits (**paper VI**).

Methods

The study system

The red junglefowl is a wild, ground living bird, native to Southeast Asia (Fumihito et al. 1994). In its natural habitat; semi-open landscapes and forests, it lives in small flocks consisting of one dominant male, one dominant female, subordinates of both sexes and their chicks (Appleby et al. 2004; Al-Nasser et al. 2007). Both males and females form strict hierarchies (Guhl 1968; Collias et al. 1994). Red junglefowl are sexually dimorphic; females are camouflaged and brown, while males have a conspicuous plumage with feathers in red/orange, black and shimmering green, blue and purple, with long tail feathers and a large fleshy red comb (Zuk et al. 1990, **Fig. 1**). Chicks are precocial, which means that they are fully developed at hatching. They follow their mother and learn about the world by observing her and their conspecifics. Under natural conditions, chicks stay in their flock for a long period, sometimes even after sexual maturation (Collias et al. 1994).

Figure 1. A group of domestic chickens of an old Swedish game breed, phenotypically very similar to red junglefowl.

Fowl eat a varied diet consisting of insects, seeds, berries and small vertebrates (Savory et al. 1978). They use several senses to experience their world. For example, the tip of the beak is used for tactile discrimination (Gentle & Breward 1986), olfactory cues used to detect cues from predators (Zidar & Løvlie 2012), and sounds used to communicate with conspecifics (Gleich & Langermann 2011). As in many bird species, their sight is well developed and their primary sense (Nicol 2015). They can see and focus on objects that are close, such as food on

the ground, and at the same time observe things at a distance, like predators high up in the air (Dawkins & Woodington 1997). They also see and can discriminate between a wide range of colours, including ultra-violet (Osorio et al. 1999; Zylinski & Osorio 2013).

Around 8000 years ago, the red junglefowl became domesticated (West & Zhou 1988) and is the main ancestor of today's domesticated chickens (Al-Nasser et al. 2007, Fumihito et al. 1994). Despite strong selection for production traits (eggs and meat), the domestic fowl still resembles their wild relative in behaviour and cognition (Nicol 2015; Marino 2017). In the wild, red junglefowl populations are decreasing due to habitat loss, over-hunting and hybridisation with chickens (BirdLife International 2016). Captive populations enables non-invasive behavioural observations. In this thesis, I have mainly worked with a captive population of red junglefowl, but also with a layer breed of domestic fowl, Bovans Robust.

Personality in chickens

It has recently been shown that both red junglefowl and domestic chickens display consistent behavioural differences among individuals, thus they have personality (Favati et al. 2014a,b; 2016). Personality traits show temporary consistency in chicks, but vary during development when chicks go through developmental stages, and then stabilise again after sexual maturation (Favati et al. 2016). Personality traits like exploration, vigilance, and aggressiveness can influence which male wins a social interaction and thus who becomes dominant in a flock when two morphologically matched males, duel (Favati et al. 2014a). Outside of the context of intra-sexual selection (Favati 2017), there is limited research carried out on personality in the fowl.

Cognition in chickens

Historically, people have assumed that chickens are cognitively simple (Marino 2017). This is despite that avian brains are functionally similar to mammalian brains, and that both birds and mammals show cognitive complexity (Emery 2006; Butler 2008). Research in large deviates from the general perception of simple and dumb chickens, and instead reveals chickens to be cognitively, behaviourally and socially complex animals (Nicol 2015; Marino 2017). For example, chickens use referential communication with a specific sound for ground predators as opposed to aerial predators, which triggers different responses in the receivers (Evens et al. 1993). They also recognize individuals within the social group and know their social rank (Bradshaw et al. 1992). Further, they adapt their behaviour according to present circumstances. For example, males use food display sounds and behaviour to attract females (Bradshaw et al. 1992), while in the presence of a dominant male, a subordinate male may not utter the sound, but only do the visual demonstration of this display. This may reduce attraction from the dominant male and avoid his interference. Once the dominant male is otherwise occupied, the subordinate male may add the sound aspect of this behaviour, to attract females (Smith et al. 2011). Females use distress calls contextually, and utter more distress calls when harassed by subordinate males when dominant males are close by, compare to in their absence (Løvlie et al. 2014). Domestic chicks have been used widely in cognitive studies of for example lateralisation, early learning and memory (Bolhuis & Honey 1998; Rogers 1995). Chickens have also shown good spatial ability, making them suited for investigations of spatial learning (Tommasi & Vallortigara 2000; Nicol 2015).

Study populations

For the majority of my papers in this thesis (**paper I-IV**), I have used a population of red junglefowl that originates from a captive population (earlier kept at Götala Research Station, Swedish Agricultural University, Skara). These birds have been randomly bred at Linköping University for over 12 generations (see Schütz & Jensen 2001 for more details) and pedigree-bred, the last 6 generations. Chicks were hatched in commercial incubators, in the hatchery, 'Krujit'. All chicks were individually tagged to enable identification (**Fig. 2a**). The first 6-8 weeks of life, chicks were kept at campus in pens with sawdust, perches and a dark brooder or heat lamp for warmth. Water and food were available ad libitum. Pens varied in size dependent of group size and experimental procedure. At 6-8 week, chicks were transported to our research facility for adult birds, 'Wood-Gush', which is situated 15 km from the university. There they were held in indoor pens (3 × 3 m) with access to outdoor aviaries. Chicks were housed in mixed-sex groups until sexual maturation, when they were separated according to sex.

Figure 2. Red junglefowl chicks (a), and domestic chicks (b). A metal identification-tag can be seen on the red junglefowl chick at the front.

In **paper V**, I used chicks from a commercial breed of layer hens, Bovan Robust (**Fig. 2b**). These were bought from a commercial hatchery (Swedfarm AB, Linköping) directly after hatching. Chicks were transported to the research station Lövsta, Swedish Agricultural University, Uppsala, where they were held in 8 pens (1.2 × 1.2 m). Due to the experimental design, half of the chicks were held in 'simple' pens that had sawdust, food and water-bells, as interior, whereas the other half were held in 'complex' pens that also had wooden blocks, perches and a shelf under which the birds could hide.

Cognitive tasks

To understand how animals process information, scientists typically either study the nervous systems directly, or study the behaviour of animals that are exposed to tasks that aim to capture different aspects of cognition (Pearce 2008). In this thesis, I have used an experimental approach observing behavioural responses of chickens, that have been exposed to commonly used cognitive tasks. Individuals were tested singly to reduce influence from the social environment and the behaviour of conspecifics.

Discrimination learning

Discrimination learning is important for most animals; animals for example need to learn what type of food that is edible or should be avoided, how predators look like, and who is part of their social group (Pearce 2008). To measure variation in discrimination learning, chicks were first habituated to being alone in a test arena ($28 \times 18 \times 37$ cm), and to eat mealworms out of bowls ($\varnothing$ 3 cm, **Fig. 3**). At three days post-hatching, chicks were presented with two colour cues. One of the colour cues was rewarded (a third of a mealworm), while the other was left unrewarded. The selected colours were colours that the chicks would be able to see and discriminate between, but that did not have a clear innate biological value to the chicks, since that could bias learning. For example, red is the colour of many berries that chickens eat and is also part of their sexual ornament, the comb. Therefore, red was avoided, and blue and green (**paper II**), and black or white (**paper II-VI**), were used.

For chicks, the colour cues (laminated coloured papers, behind same coloured bowls, **Fig. 3**) were presented at the end of an arena, with a cardboard divide that separated the cues. The cardboard was added to make it easier to see what a chick chose. In every trial, a chick was placed at the opposite side from the cues and where allowed to approach the cues to make its decision. Initially, chicks were helped by the experimenter to find the reward, who pecked at the bowl with a finger. Once the chick had made its choice, and eaten the worm if choosing the correct colour, it was picked up and tested again in a new trial. A trial thus started when a chick was put at the starting position and ended when it had chosen a colour cue and eaten a reward. The bowls changed places according to a predetermined schedule, except for in **paper II**, where the bowls changed sides every trial. Chicks were considered to have learnt to discriminate between the two cues once they reach a criterion of 5 (**paper II**) or 6 (**paper III-VI**) consecutive correct choices in a row. The criteria for learning changed across papers, and became more conservative after the first study. Number of trials until the set learning criteria was reached, was used as a measure of learning speed (**paper II-VI**).

When testing adults at 5 months of age (**paper II**), only females were tested. This is because males at this age are hard to motivate with food rewards. It would have been very time consuming, although not impossible, to test them at this stage. To minimise the risk that females would escape during training, the test was modified somewhat compared to how it was tested in young chicks, which are less able to fly. I used a three step learning procedure; shaping behaviour. In step one, the female was presented with the reward placed on top of a lid with the rewarded colour pattern. The lid was placed on top of a bowl. In step two, the reward was placed in the bowl, and the patterned lid was only half covering the bowl, enabling the female to see the reward inside the bowl. In the third step, the female had to peck at the lid to retrieve the reward that was in the bowl. Between every trial, a black shield was

held in front of the female while preparing for the next trial. The cues were presented in a random order (determined by rolling a die).

Reversal learning

Reversal learning (**Fig. 3**) is a more demanding task than discrimination learning, because it requires the individual to let go of an established association, and at the same time establish a new association between the previously unrewarded cue and a reward (Pearce 2008). Reversal learning was preformed directly following an established association between a reward and a colour cue in discrimination learning, or after a refresh session (i.e. a session following learning, where chicks again needed to reach learning criteria). Refresh sessions were sometimes used if time had passed between an established association in discrimination learning and reversal training, with the aim to keep the association fresh in mind of the individual when reversal training began. Reversal learning was performed in the same manner as described for discrimination learning, except that in reversal learning the previously unrewarded cue was now rewarded, and the previously rewarded cue was unrewarded. In addition there was no help offered during reversal learning. For adult females (**paper II**), only the third step of the learning procedure was used in reversal learning, since females already knew how to retrieve the reward.

Figure 3. Red junglefowl chick in associative- or reversal learning task.

Spatial learning

In spatial learning (**paper II**), individuals learn the location of a reward in an arena, based on spatial cues. Here a simple arena (76×114 cm) was used (**Fig. 4**), where the chick only needed to walk from a start box to the end of a straight runway and then turn a corner to locate the reward. The reward could not be seen from the start box. Because a chick could find the reward simply by exploring the arena, behavioural criteria on its performance in the test was added; for a trial to be counted as ‘correct’, the chick needed to find the reward without stopping or turning around along the way. A criterion of 5 correct responses in a row was used as learning criterion, and number of trials to reach this criterion was used as a measure of learning speed.

Figure 4. Schematic of the arena (76×114 cm) used to measure spatial learning and behavioural flexibility in red junglefowl chicks. X marks the starting position. A circle symbolises the location of a bowl containing a mealworm as reward. The black solid line symbolises the wall of the arena, and the patterned line symbolises the metal grid, that was opened in the behavioural flexibility test and presented a short-cut to the reward. A dashed line illustrates the correct path to the rewarded bowl.

Judgment bias

In judgment bias tasks (**paper V, VI**), ambiguous cues intermediate between previously learnt cues are presented to the animal and its behavioural response measured (Mendl et al. 2010). Since Harding and colleagues (2004), judgment bias has been measured in several species, and the tasks have been modified to suit the study species in question. For example, different types of cues (e.g. tactile, visual, olfactory, auditory) and a variety of positive and negative reinforcers, have been used. Because fowl are visually orientated, I used visual cues. At ca 1 week of age, a judgment bias task was performed directly after reversal learning. The rewarded and unrewarded colour cues from the reversal learning task (black and white) already had a value to the chicks and were therefore used as positive and negative cues in the judgment bias task. A refresh trial was used to make sure chicks associated the rewarded colour with a reward and the unrewarded colour with lack of reward. In addition to the learnt cues, three intermediate, ambiguous, grey cues were presented one at the time in a predetermined order. These cues were dark grey: 25 % white/75 % black, medium grey: 50 % white/50 % black, and light grey: 75 % white/25 % black. The cues were presented one at the time, but similarly to the learning tasks, they were presented at the far end of the arena (**Fig 5**). The probability for individuals to approach a cue, as well as latency to approach it, were measured. A response to an ambiguous cue similar to a positive cue is considered an optimistic response, whereas a response similar to a negative cue is considered a pessimistic response.

Figure 5. Red junglefowl chick during a judgment bias task.

Analysis of brain monoamines

In **paper V**, birds that had successfully completed a judgment bias task, were anesthetized by a hard hit to the head and euthanized by swift cervical decapitation. The brains of the birds were immediately removed and dissected into 7 parts. The left optic tectum, together with the left telencephalon, the mesencephalon and hypothalamus-thalamus were instantly frozen on dry ice and stored in -80°C until measuring monoamine concentrations.

Frozen samples were homogenised in 4 % (weight/volume) ice-cold perchloric acid containing dihydroxybenzylamine (DHBA) as an internal control. The samples were centrifuged and the supernatant was used for the analysis. To analyse concentrations of monoamines a high performance liquid chromatography with electrochemical detection (HPLC-EC) was used. Dopamine (DA), serotonin (5-HT), norepinephrine (NE), and the metabolite of dopamine; 3,4-dihydroxyphenylacetic acid (DOPAC) and the metabolite of serotonin; 5-hydroxyindoleacetic acid (5-HIAA), were analysed. The HPLC-EC separates and oxidises substances and the current produced during this chemical reaction is measured. Concentrations were analysed by comparing DA, 5-HT, NE and the metabolites DOPAC and 5-HIAA to standard solutions with known concentrations. The ratio of metabolite/monoamine were used as a measure of activity.

Personality assays

Personality is often observed by studying individual behavioural responses to somewhat stressful situations or events, and grading the observed responses along one of several personality gradients. In this thesis, I have exposed individuals to commonly used behavioural assays inspired by applied ethology (e.g. used for commercial chickens), and behavioural ecology (e.g. used for great tits) to measure personality and coping styles. All birds were tested singly.

Novel arena test

A novel arena test was used in **paper I-IV, VI**. A novel arena is typically used to measure activity, exploration (Réale et al. 2007), and fearfulness (Forkman et al. 2007). Familiar, but empty food and water bells were placed in the arena to prevent birds from observing the entire arena from their starting position, and encourage exploration. Latency to start moving and latency to explore the entire arena were measured. In addition, were locomotion and vigilance recorded with instantaneous sampling every 10 seconds for 10 minutes. To measure activity, the arena was divided into equally sized imaginary sections, allowing for measures of number of transitions between squares. I also measured number of escape attempts (i.e. when birds tried to fly out of the arena). To quantify consistency in behavioural traits, it is necessary to obtain repeated behavioural observations of the same individual. However, it is important to consider the risk of habituation and sensitisation when conducting repeated measures on the same individual (Greenberg & Mettke-Hofmann 2001; van Oers et al. 2005; Martin & Réale 2008). Thus, responses in a second test can depend on the individuals' experiences during the first test occasion. For instance, if an individual did not explore a novel environment the first time it was exposed to the test, the individual may be prone to do so in the second test. In contrast, if an individual explored the environment thoroughly the first time in the test arena, this individual may not be as eager to explore it again the second time, or may simply explore the environment faster (Greenberg & Mettke-Hofmann 2001). Therefore, with the aim to make the arena novel even for repeated tests, the familiar objects were moved around in the arena between tests, as well the substrate changed. As birds grew in size, larger arenas were used (e.g. for young chicks, 76×114 cm, and for adults, 2×2 m).

Novel object test

A novel object test was used in **I-IV, VI**. In a novel object test, an unfamiliar object is presented to the birds and their behaviour reaction is measured (Forkman et al. 2007; Réale et al. 2007; Greggor et al. 2015). Depending on the attractiveness or aversiveness of the novel object used, novel object test measure neophobia-neophilia, boldness, and/or exploration (Forkman et al. 2007; Réale et al. 2007; Greggor et al. 2015). The object needs to generate enough between-individual variation in the population to be able to capture statistical differences. The choice of a too frightening object may cause all individuals to become too scared, and the assay may not show variation among the test individuals, leading to ceiling and flooring effects. On the other hand, the choice of an object that generates weak responses

can generate similar problems, since no reaction or little variation in the response of individuals will lead to similar statistical problems (Réale et al. 2007). I used novel objects that resembled a potential predator (one of two differently coloured plush toys with large yellow and black eyes), thus it was not expected to attract individuals and instead to measure boldness, exploration and neophobia. The novel object tests were performed in the same arena and directly following the novel arena test. This meant that birds could be tested singly in an arena that they had had some time to familiarise themselves with, minimising the influence of behaviour reactions to a novel environment (Réale et al. 2007). The light was briefly switched off before placing the object in the arena as far away from the bird as possible. The behaviour of the individual was measured in the same way as described above for the novel arena test, and the test lasted for 10 min.

Tonic immobility test

To measure fear in birds a tonic immobility test was used in **I-IV, VI**. Tonic immobility is a commonly used test to measure fear in birds (Gallup 1979; Forkman et al. 2007). To induce tonic immobility, a bird was placed on its back and a hand placed on its chest, with a light pressure for 15 seconds. During these 15 seconds most individuals will go into a tonic state, a reaction thought to be an anti-predator response (Forkman et al. 2007). Latency to stay in a tonic state was used as a measure of fearfulness. Three attempts to induce tonic immobility were used. If the individual was not induced in tonic immobility after this, it received a score of 0 sec. Individuals that stayed in tonic immobility for 10 minutes received a max score.

Behavioural flexibility tests

To measure behavioural flexibility, two tests were used: i) alteration of a spatial arena (**paper I**), and ii) reversal latency (**paper II-III**). Alteration of a spatial arena has previously been used to measure behavioural flexibility in rodents (e.g. Benus et al. 1990). For the fowl I used the arena previously described to be used to measure spatial learning (see above; **Fig. 4**). First, the individual learned that there was a reward in a bowl around a corner. Once it had established a routine and walked directly to the reward after release five times in a row (i.e. had reached the set learning criteria), the arena was configured. A short-cut was opened near the beginning of the arena, and the normal route to the reward was cut-off by placing a grid across the path. Latency to find the reward was used to measure behavioural flexibility. An individual that was behaviourally flexible would observe the new entrance and retrieve the reward quickly, while an individual that had formed a set routine, would continue to try the learnt route several times and thus take longer before finding the new opening. Another measure of behavioural flexibility typically used, is latency for an individual to explore a previously unrewarded cue in the beginning of a reversal learning test (Coppens et al. 2010). Individuals that were more behaviourally flexible would sooner inspect also the other bowl, whereas less flexible individuals would continue to go to the previously rewarded cue for longer before abandoning it. All individuals were allowed 3 trials á 5 minutes to locate the reward. Individuals that did not approach within the time given to them, did receive a max score.

Multivariate behaviour test

In **paper V**, a multivariate behaviour test was used, designed to measure several behaviours in one single test. Multivariate tests have been used in rodents to allow animals to freely choose between arenas of different qualities (Meyerson et al. 2006). Similarly, a social versus foraging arena has been used in chickens to study social motivation (Väisänen & Jensen 2003). A chick was placed in a start-box and was left there to habituate for 3 minutes. The chick could observe 4 of its pen-mates who were placed in a small enclosure out of wire mesh in the centre of the arena (first test: Ø 0.30 m, second test: Ø 0.40 m), from the start box. To get to its pen-mates, the chick first had to solve a detour, which meant walking in the opposite direction from the pen mates and then turning around a corner. Latency until the chick started moving and latency until the chick had solved the detour, were recorded. The chick were allowed 7 minutes to solve the detour. Chicks that did not solve the detour within this timeframe, were allowed to walk directly into the arena without solving the detour (i.e. the wire mesh blocking the direct route into the arena was removed). Once a chick had entered the arena (first test: Ø 1.20 m, second test: Ø 1.60 m), it was given 5 minutes to explore freely. To encourage birds to explore the arena, four cardboard screens were placed opposite each other, forming a not fully closed circle. The arena was divided in 3 imaginary zones, aiming to measure how the chick used the arena. The proportion of time that the individuals spent in the different zones was measured.

Paper I

A comparison of animal personality and coping styles in the red junglefowl.

Several terms, mainly animal personality (e.g. Dall et al. 2004, Sih et al. 2004) and coping style (Koolhaas et al. 1999), have been used in animal behaviour to describe consistent behavioural variation among individuals. These terms are often used as synonyms even though both definitions and test paradigms differ. Coping styles are unlike animal personality often described as bimodal traits that covary, with links to physiological stress responses (Koolhaas et al. 1999), and including behavioural flexibility. It is therefore still unclear whether the terms describe the same or different phenomenon.

In **paper I**, I explored whether both animal personality and coping styles could be measured in red junglefowl. I further aimed to understand if the terms were describing the same or different aspects of consistent behavioural variation. For this, I exposed red junglefowl chicks and later adults to personality assays (responses to novel arena, novel object) and coping style tests (responses to induced tonic immobility, to altered maze, and reversal learning).

Behavioural responses measured in both personality and coping style assays showed continuous distributions. I observed high repeatability in behavioural responses measured in animal personality assays in chicks, thus confirming that animal personality was measured. The repeatability was lower when comparing responses in chicks to that after sexual maturation, confirming our earlier work (Favati et al. 2016). I also observed coping styles; latency in tonic immobility was negatively correlated to behavioural flexibility in both chicks and adults (**Fig. 5a,b**). However, I observed no correlations between behavioural responses measured in personality and coping style assays. This indicates that animal personality and coping styles can both be measured in red junglefowl, but is not measuring the same consistent behavioural variation and should therefore not be used as synonyms.

Figure 5. Behavioural responses obtained from coping style assays (**paper I**) of (a) chicks, and (b) adult female red junglefowl. Behavioural flexibility (measured as latency to explore a previously unrewarded colour cue in the beginning of a reversal learning task), was negatively correlated with fearfulness (measured as latency in tonic immobility) in both (a) male (black circles), and female (grey circles) chicks, and (b) adult females (grey circles). The figure shows transformed variables.

Paper II

The relationship between learning speed and personality is age- and task-dependent in red junglefowl.

Animal personality is suggested to associate with animal cognition (Carere & Locurto 2011; Sih & Del Giudice 2012; Griffin et al. 2015), and a speed accuracy trade-off is suggested to underlie this relationship (Sih & Del Giudice 2012).

In **paper II**, I explored if animal personality and an important aspect of cognition; learning, were related in red junglefowl, and whether such a relationship could be explained by a speed-accuracy trade-off. I exposed chicks and adults to behavioural assays (novel arena, novel object, tonic immobility), and learning tasks (discriminative-, reversal-, and spatial learning). To reduce aspects of anxiety and fearfulness hampering learning, chicks were gently handled and habituated to the test set up, directly after hatching.

I observed individual variation in both personality traits and learning speed in cognitive tasks. Interestingly, there was no correlation in learning performance across tasks, unlike what has been observed in humans and rodents. Furthermore, associative- and spatial learning were not related to any of the measured personality traits. Conversely, reversal learning, a more complex cognitive task, was related to exploration in both juveniles and adult females (**Fig. 6a,b**). This relationship was negative for chicks, and positive for adult females. I therefore found support for a speed-accuracy trade-off in adult females. However, since explorative chicks (**Fig. 6a**), as opposed to less explorative adult females (**Fig. 6b**), learned the reversal task faster, a speed-accuracy trade-off did not explain the observed relationship in chicks. These results show that personality and learning speed is linked in the fowl, although dependent on task and personality traits in focus and age when tested, and further suggests that a speed-accuracy trade-off may not underlie all observed relationships between personality and cognition.

Figure 6. The association between reversal learning speed (i.e. number of trials to reach the learning criteria) and a explorative personality trait (PC1 from a PCA analyses) was: (a) negative for red junglefowl chicks; more explorative individuals learned faster, and female chicks (grey circles, solid line) learned faster than male chicks (black circles, dashed line), and (b) positive for adult hens that where less explorative hens learned faster. A single female outlier was removed from the sample, which did not change the results (see **Paper II** for details).

Paper III

Generalisation to a novel cue covaries with behavioural flexibility in red junglefowl chicks.

Most studies to date that explore a relationship between animal personality and cognition, have focused on learning (e.g. Guillette et al. 2009; 2011; Exnerová et al. 2010; Light et al. 2011, Amy et al. 2012, Titulaer et al. 2012, **paper II, IV**). Other facets of cognition like generalisation, impulsiveness and memory are hypothesised to associate with personality, but have been less explored.

In **paper III**, I investigated the link between personality and generalisation. Generalisation describes how individuals use previously learnt rules when faced with new information with similar properties. To measure generalisation, I first taught red junglefowl chicks to associate two colours (red, and yellow) with a reward. Then I presented the intermediate colour (orange) together with one of the previously rewarded colours and an unrewarded colour (grey), and measured the chicks' preference for this new generalised colour. I also measured the chicks' behaviour in personality and coping style assays (novel arena, novel object, tonic immobility, reversal latency).

I observed that chicks preferred the generalised colour to both the previously learnt colour and the unrewarded colour. More importantly, there was individual variation in generalisation that was linked to behavioural flexibility. Individuals that were more flexible, also had a stronger preference for the generalised colour (**Fig. 7a**). In addition, behavioural flexibility was positively associated with fearfulness (**Fig. 7b**), indicating a coping style, described along a proactive-reactive gradient. Reactive individuals that were behaviourally flexible and more fearful thus generalised differently from proactive individuals, by showing a stronger preference for the generalised colour. This indicates that reactive individuals are more sensitive to new information, which is in accordance with theoretical predictions (Sih & Del Giudice 2012).

Figure 7. Association between generalisation to a novel colour cue and responses in behavioural assays by red junglefowl chicks. **(a)** Preference for orange correlated with behavioural flexibility (measured as reversal latency), and **(b)** behavioural flexibility correlated with fearfulness (measured as response to tonic immobility). The figure shows a log transformed behavioural flexibility-measure.

Paper IV

Early experience affects adult personality in the red junglefowl: A role for cognitive stimulation?

Following theoretical predictions (Carere & Locurto 2011; Sih & Del Giudice 2012, Griffin et al. 2015), relationships between animal personality and animal cognition has been observed in several empirical studies (e.g. Guillelte et al. 2009, 2011, Exnerová et al. 2010; Light et al. 2011; Titulaer et al. 2012; **paper II, III**). The directionality of this relationship is however still unclear, and could in principal be that: i) personality and cognition share common underlying mechanisms, such as a speed-accuracy trade-off (Sih & Del Giudice 2012), ii) personality either influences cognition, or the other way around; iii) cognition influences personality.

In **paper IV**, I tested the latter of these three scenarios, by exploring if early cognitive stimulation can influence future personality traits in adults. For this, I exposed one group of red junglefowl chicks to a battery of learning tasks (discriminative-, reversal-, and spatial learning) in their first weeks of life, and compare their behavioural responses as adults in behavioural assays (novel arena, novel object, induction of tonic immobility), to that of individuals from the same population lacking this experience.

I observed that individuals that had experienced cognitive stimulation were more vigilant in a novel arena and novel object test (**Fig. 8a**), and were less likely to perform escape attempts in a novel object test (**Fig. 8b**). This indicates that early cognitive stimulation can alter personality traits observed later in life. Not all personality traits were affected by the stimulation that was used. This indicates that the type of stimulation might affect different behavioural traits.

Figure 8. Early cognitive stimulation effects behaviour of red junglefowl. (a) Proportion of time that individuals were vigilant increased, and (b) number of escape attempts decreased, for individuals exposed to early cognitive stimulation (grey circles), compared to control individuals (white circles) in novel arena -, and novel object tests. Bars show marginal means $\pm$ SE. The circles show observed values, with size of the circles representing the proportion of observations.

Paper V

Environmental complexity buffers against stress-induced negative judgment bias.

Cognitive processes can include biases that will affect decision-making (Drozd et al. 2016). Judgment bias describes one such bias in which individuals interpret ambiguous stimuli on a scale from positive to negative (optimism to pessimism, e.g. Bateson 2016). Biases in judgment are often influenced by emotional states (Mendl et al. 2009; Baciadonna & McElligott 2015; Roelofs et al. 2016). In humans, anxiety and depression are associated with a negative judgment (Mathews & MacLeod 2005; Gotlib & Joormann 2010), and similar associations are recently observed also in animals (Salmeto et al. 2011; Brydges et al. 2012). How early life experiences and additive stress influence judgment bias is less explored.

In **paper V**, I explored how early cold stress and unpredictable stress, as well as environmental complexity, affect judgment bias in domestic female chicks. Further, I explore if the monoaminergic systems are associated with variation in judgment. Chicks were housed in simpler or more complex pens, and exposed to cold stress, or not. When 4 weeks old, they were all exposed to a week of unpredictable stress. A multivariate behaviour test and a judgment bias test were carried out before and after this week of unpredictable stress. At seven weeks of age the chicks were euthanized and the monoamine levels analysed.

Cold stressed chicks moved faster in the multivariate behaviour test than not stress chicks, which can be due to higher motivation for social reinstatement. Early cold stress did not influence judgment either before or after exposure to additional unpredictable stress (**Fig. 9d-f**). There were no behavioural differences between individuals housed in simpler vs. more complex environments before the unpredictable stress (**Fig. 9a**). Interestingly though, after being exposed to the unpredictable stressor, chicks in simpler environments decreased their approach latency in the judgement bias test (**Fig. a-c**). This indicates that additive stress influences judgment in domestic female fowl and that environmental complexity can buffer against negative effects of stress. Further, I observed higher dopamine activity in the brain of more optimistic chicks than less optimistic chicks, showing similarities to findings in humans and other animals.

Figure 9. Influence of stressors and environmental conditions on interpretation of visual cues in a judgment bias task in domestic female chicks. Latencies, (a, d) before and (b, e) after chicks were exposed to a battery of unpredictable stressors, as well as, (c, f) the change in latency from the first to the second test, are shown. (a) Environmental complexity did not affect latency to approach the colour cues before exposure to unpredictable stress. (b) Chicks in complex conditions had shorter latencies to reach the colour cues compared to chicks in simpler conditions, after exposure to unpredictable stress, and (c) there were a difference in latency between the first and the second test. Cold stress did not affect judgment bias in chicks (d) before or (e) after unpredictable stress, and (f) there were no difference in latencies from the first to the second task. Latency to approach colour cues was measured in seconds, and shown as mean $\pm$ SE.

Paper VI

The relationship between personality, affective state and judgment bias, in the red junglefowl.

Both temporary emotional states and more permanent emotional traits (e.g. personality) are theoretically predicted to influence judgment bias in animals (Faustino et al. 2015; Roelofs et al. 2016). Empirical studies exploring a link between personality and judgment bias are scarce and results inconclusive. An association between personality and judgment has been observed in some species (e.g. Asher et al. 2016; d’Ettorre et al. 2016), but not in others (Lalot et al. 2016), warranting further investigation of this possible association.

In **paper VI**, I investigate if individuals raised in a uniform environment differ in judgment bias and if such variation can be explained by affective state and personality, in red junglefowl chicks. To measure variation in judgment bias I used a similar judgment bias task as in **paper V**. I recorded both approach probability and latency to approach ambiguous cues. These cues were presented after either a rewarded or an unrewarded cue, enabling me to also look at how differences in affective state affected their responses (i.e. if individuals were more positive after having eaten a reward). Later, the same chicks were exposed to behavioural assays (novel arena, novel object, induction of tonic immobility).

I found that individuals in general showed an optimistic bias by approaching all ambiguous cues more often than chance-level. Recent reward resulted in a more optimistic response to the following cue. This confirms other studies on influences of affective state on responses to judgement bias tests (e.g. Harding et al. 2004; Baciadonna & McElligott, 2015; **paper V**). Further, the probability to approach a cue was linked to activity in the personality tests used, indicating an influence of personality where more active individuals were more likely to approach cues. Individual variation in latency to approach a cue was instead linked to vigilance; more vigilant individuals were slower to approach cues in the judgment bias task. This indicates that the probability to approach ambiguous cues and latency to approach cues when doing so, are measuring different aspects of the decision-making process. Further, these seem to be linked to different aspects of personality. That both personality and temporary emotional states were associated with judgment, suggest that individual differences in judgment may not only depend on variation in affective state, but may also represent emotional traits, that are more permanent characteristics of the individual.

Discussion

Thirty years ago, Bennett (1987) argued against the focus at that time on analysis of average responses, something he referred to as the ‘tyranny of the golden mean’. His message to focus on individual variation within populations, as opposed to focusing on averages, was well received and changed the focus in many research disciplines (see Williams 2008 for review). In animal behaviour research, as opposed to human personality research, consistent between-individual variation was still, ten years later, rarely seen as meaningful variation, but rather as variation surrounding a more useful mean (Wilson 1998). However, the last twenty years, the focus has changed also in animal behaviour research, and we now see an explosion of studies within behavioural ecology focusing on consistent behavioural variation within populations (Gosling 2001; Réale et al. 2007; 2010). This trend was closely followed by an increased interest also for individual variation in animal cognition (Rowe & Healy 2014). A few years ago, it was proposed that variation in animal personality and cognition might covary (Carere & Locurto 2011; Sih & Del Giudice 2012; Griffin et al. 2015). This intriguing possibility inspired me to focus my research on exploring individual variation in animal personality, animal cognition and the relationship between them.

In **paper I**, I show that two commonly used terms for consistent behavioural variation among individuals; personality and coping styles, can be measured in the fowl, but do not overlap and thus are not describing the same behavioural variation. In **paper II**, I observe individual variation in personality and cognition, and reveal a relationship between one important aspect of cognition, learning, and one important personality trait, exploration. In **paper III**, I observe another interesting relationship between behavioural flexibility and another aspect of cognition, generalisation. In **paper IV**, I show a directional relationship where cognitive stimulation in young chicks influences adult personality. In **paper V**, I observe that biases in cognitive processes can be affected by emotional states. Further, I reveal in **paper VI**, that also more permanent emotional traits (i.e. personality) can affect cognitive processes influencing judgment bias. Taken together, I show individual variation in personality, coping styles and cognition in the in red junglefowl. Further, I show that personality and cognition are related, and that there is interplay between them. Additionally, I show that biases in cognitive processes are influenced by both the individual’s current affective state, and its personality. Thus, I reveal a complex relationship between personality and cognition that in combination with environmental influences can help explain observed individual behavioural variation.

Personality and coping style – same-same or different?

As a newcomer into the research field of animal personality I was confronted with rather confusing terminology. The terms animal personality, temperament, behavioural syndrome and coping style, all describe consistent behavioural variation among individuals and are thus closely related. However, according to their definitions, they describe somewhat different aspects of consistent individual behavioural variation. Despite these differences, they are often used as synonyms in research papers and their differences and similarities are rarely discussed. If there are differences that are ignored, this can cause confusion and hamper our understanding of behavioural variation observed. In **paper I**, I therefore explored if two of the most frequently used terms; animal personality and coping style, could be measured in the fowl, and more importantly, whether they described the same phenomenon. For this I used an

experimental approach where I measured behavioural responses in both juvenile and adult red junglefowl, using commonly used personality assays validated also for the fowl (Favati et al. 2014a,b; 2016), and typical coping style assays (e.g. Benus et al. 1990, Koolhaas et al. 1999). I show that animal personality and coping styles could be measured in the fowl, but that behavioural responses measured under one term was not correlated to measures from the other. Thus, personality and coping styles does not seem to capture the same behavioural variation in the fowl. The terms should therefore not be used as synonyms, but rather be measured and interpreted in their own right. These results are important, because they suggest that comparisons between studies of personality and coping styles should not be made without caution. Further, studies should aim to specify whether they measure personality or coping styles, minimising the risk of confusion and misunderstandings. It is however important to consider that these results are based on one study population of fowl and that it might not apply to other species or even other populations. Nonetheless, until further studies explore the generality of these findings, researchers should be careful when labelling the behavioural traits under study and when making comparisons across studies that have focused on different aspects of behavioural variation.

Coping style research has, at least historically, focused on male lab rodents and the concept is defined and developed with rodents as model species (Koolhaas et al. 1999; 2010). Results from **paper I** suggest that coping styles in the fowl are not fully equivalent to coping styles in rodents. For example, while male lab rodents show a bimodal response in coping style tests (Koolhaas et al. 1999), fowl show a continuous response. Interestingly, there are studies that use the term coping style, which have created a bimodal distribution by directional selection for extreme personality types (e.g. great tits, Verbeek et al. 1994; Nicolaus et al. 2015). It is not clear if a bimodal response in coping style tests is specific for rodents, and only present in other species after selection on extreme phenotypes. The distinction between reactive or proactive copers may vary depending on species and for some species it should be thought of as a continuous gradient, rather than a separation of individuals into reactive and proactive types.

The relationship between personality and cognition

To explore if there was a relationship between personality and cognition in the fowl, I exposed both young and adult red junglefowl to a battery of cognitive tasks and personality assays. Importantly, I show individual variation in both aspects of personality (**paper I-IV, VI**) and cognition (**paper II-IV, VI**), enabling further investigation of this relationship. Learning speed in the different learning tasks was not correlated, suggesting that fowl, as opposed to rodents (e.g. Matzel et al. 2010; Light et al. 2011), do not show a general learning performance across tasks.

In line with predictions (Carere & Locurto 2011; Sih & Del Giudice 2012), I demonstrate a relationship between consistent behavioural variation and cognition (**paper II-IV**). In **paper II**, I demonstrate a relationship between learning speed in reversal learning and exploration in both chicks and adult hens. On the other hand, I observed no relationship between learning speed in discriminative learning and spatial learning, and any of the other personality traits measured. Thus not all types of learning were associated with personality. My results are in line with some of the previous studies exploring a relationship between learning speed and personality traits (e.g. Guillette et al. 2009; 2011; Titulaer et al. 2012). For example, Titulaer and colleagues (2012) observed a relationship between exploration and reversal learning in great tits, but not between any other aspects of learning that they measured. Thus, it seems

like only certain aspects of learning are related to certain personality traits. One aspect that separate reversal learning from discriminative learning and spatial learning, is the aspect of behavioural flexibility, which require individuals to pay more attention to details about the task. In reversal learning, rules that are established are suddenly changed, meaning that previously learnt associations need to be extinguished as well as new associations formed. The attention to changes that is required in reversal learning might explain why a relationship is found here and not for the other learning tasks (Titulaer et al. 2012). Individuals that pay more attention to changes learn faster in reversal learning, and differences in attention might also influence how fast individuals are to explore a novel environment. In **paper III**, I find a relationship between another aspect of cognition, generalisation, and variation in behavioural flexibility. Further, behavioural flexibility was correlated with fearfulness, suggesting variation in reactivity-proactivity (Koolhaas et al. 1999). Individuals that were more behaviourally flexible, generalised differently from less flexible individuals. Behavioural flexibility is often observed to be larger in reactive, fearful individuals (Benus et al. 1990) and reactive individuals are expected to pay more attention to changes in their environment (Sih & Del Giudice 2012). Reactive individuals might thus have paid more attention to a novel generalised stimuli compared to proactive individuals. On the other hand, proactive individuals, might have been more bound to their routines, and therefore sampled the new stimuli less (Sih & Del Giudice et al. 2012). Thus, both **paper II** and **III** reveal a link between personality and aspects of cognition that both might be linked to variation in attention. In mice (*Mus musculus*) selective attention (i.e. the ability of focusing on cues relevant for the task, while ignoring salient distracters), has been associated with working memory and general learning performance across a battery of learning tasks (Kolata et al. 2007; Matzel et al. 2010; 2011). Furthermore, it has been suggested that working memory and learning ability is dependent on selective attention (Matzel et al. 2010; 2011). Additionally, attention bias has been associated with personality in parrots (*Amazona amazonica*, Cussen & Mench 2014). Thus, variation in attention is a potentially contributing factor to both variation in cognition and personality and might explain the link between them. To learn whether aspects attention are influencing the relationship between personality and cognition, future studies might benefit from adding tasks that specifically measure variation in attention, in addition to measuring variation in aspects of cognition and personality.

Directionality of the observed relationship

Previous studies (e.g. Guillette et al. 2009; 2011; 2014; Titulaer et al. 2012; **paper II, III**) indicate that there are associations between personality and cognition, although the directionality of the relationship is less clear. This is because so far only correlative studies have been carried out, making it hard to infer causality. In principal, there are three possibilities that can explain the observed relationship: i) both personality and cognition could share the same underlying mechanism, ii) variation in personality could influence cognition, or iii) variation in cognition could influence personality. I discuss these three possibilities in the light of my results, below.

Speed-accuracy trade-offs

The current main theory put forward to underlie personality and cognition relationships, is a speed-accuracy trade-off (Carere & Locurto 2011; Sih & Del Giudice 2012). Individuals with a fast behavioural type (i.e. fast exploring, proactive) are expected to have a cognitive style where they adopt a speed over accuracy strategy. In this scenario, a slow behavioural type (i.e. through exploring, reactive) will instead adapt a strategy of accuracy over speed (Sih & Del Giudice 2012). The speed-accuracy trade-off hypothesis further predicts that individuals that adapt a speed over accuracy strategy will be fast at learning simple tasks. However, as soon as tasks become more complex and require individuals to slow down and think before acting, they will make more errors (Sih & Del Giudice 2012). The opposite is predicted for individuals adapting a strategy of accuracy, because they will spend time sampling even in simpler tasks, which will make them take longer to learn compared to fast behavioural types. At the same time, because they will spend more time and observe changes in tasks, they are predicted to make fewer errors in complex tasks, compared to faster explorers and will therefore learn faster in complex tasks (Sih & Del Giudice 2012). Additionally, because information storing can slow down decision-making, proactive individuals are predicted to store less information than reactive ones (Sih & Del Giudice 2012).

In line with the speed-accuracy trade-off hypothesis, I observe in **paper II** that slower exploring adult females were better at a more complex cognitive task, reversal learning, compared to faster exploring females. Thus, these results are consistent with slower exploring individuals being more accurate and therefore learning faster in complex tasks. Further, in **paper III**, I observe that reactive individuals that are more behaviourally flexible, have a stronger preference for a novel, generalised stimuli. Reactive individuals might be more prone to interrupt an established routine, and also less prone to form a routine from the start, than proactive individuals. Thus, it is possible that proactive individuals have a weaker preference for the generalised stimulus because they have formed routines that are hard to break up, focusing on the previously rewarded stimuli. They might also be less likely to evaluate a novel colour cue, which could also explain the lower preference for the generalised cue compared to reactive individuals. There has not yet been that many studies that have explicitly explored the influence of a speed-accuracy trade-off on the relationship between personality and cognition. However, several studies have observed links that could fit with the speed-accuracy trade-off hypothesis. For example, fast-exploring black-capped chickadees (*Poecile atricapillus*) learned a simple acoustic discrimination task in fewer trials compared to slow-exploring individuals (Guillette et al. 2009), while in a more demanding discrimination task slow-exploring individuals outperformed the fast-exploring individuals (Guillette et al. (2011). In a recent study, Guillette and colleagues (2014), investigated a speed-accuracy trade-off and observed that slow-exploring black-capped chickadees had higher performance in a complex learning task, supporting a speed-accuracy trade-off. Thus, a speed-accuracy trade-off might explain why some personality traits are linked to cognition. Guillette and colleagues (2014) trained individuals on acoustic tones and then tested their accuracy by presenting new variations of that tone. Their study design might therefore measure aspects of generalisation and made them give an alternative explanation to their findings; reactive individuals learn general rules and therefore are more accurate when presented with new similar cues to learnt cues, while proactive individuals learn more about the absolute properties of the cue and therefore are less accurate. What makes reactive individuals generalise differently from proactive individuals is not clear, but differences in the information the animal is encountering, how much of that information is processed and remembered, might explain the difference (Guillette et al. 2014). These suggestions need to

be further explored to be confirmed. How individuals respond to new stimuli may result in behaviour of individuals that can appear non-optimal. Observed behaviour in the short-term may on the other hand be an optimal way to behave long-term (McNamara et al. 2011), and since both slow and fast exploring behavioural types persist in populations there may be benefits associated with both types.

Even though my results show some support for the speed-accuracy trade-off hypothesis, I also have results that do not support it, suggesting that this trade-off at least is not underlying all observed links between personality and cognition. If a speed-accuracy trade-off do not explain all observed relationships between personality and cognition, it is possible that there are other underlying mechanisms that influence the relationship. For example, selection for personality traits have been shown to affect performance in cognitive tasks (Groothuis & Carere 2005), suggesting shared underlying mechanisms (Coppens et al. 2010). Another possibility is that there is a causal relationship. The ways in which an individual behave will affect what the individual experiences. An individual that is bold and explores a new environment fast might as a consequence interact more with its environment (Light et al. 2008) and encounter situations that a shy and slow exploring individual will never encounter. It is therefore possible that individuals that take in more information from their environment acquire more information than individuals that are slow to explore. On the other hand, fast explores may be fast because they process information faster than slower explorers. Personality affecting cognition, or cognition affecting personality may therefore explain some observed links.

Personality influencing cognition

The few previous studies investigating whether personality affect cognition have found limited support for this causal link (Matzel et al. 2003). For example, when mice were exposed to several new arenas in a battery of tests, individuals that were fast to explore were not better at learning, they only habituated faster to the new environment (Matzel et al. 2003). In **paper II**, I observed that chicks that were faster to explore a new environment were better at learning a reversal learning task, which could suggest that individuals that are fast explorers learn faster, but equally it could suggest that individuals that were fast to explore did so because they were better at taking in new information. However, because this study was not designed to test this directly, it is hard to disentangle whether the association is reflecting a causal link and in so case in which direction the causality goes, or if it is explained by some other factors. In **paper VI**, individuals that were more vigilant in a novel arena were slower to approach an ambiguous cue, whereas more explorative individuals were more likely to explore a negative cue. Individuals in this study were treated the same, raised in the same environment and exposed to the exact same tasks. Thus, variation in responses to the ambiguous cues should reflect the individuals' intrinsic personality traits and not be affected by emotional states. These results indicate that animal personality can affect cognition or at least biases in cognition. There are a handful of studies that have explored the relationship between personality and judgment biases in animals, none of which explored a causal relationship (Cussen & Mench 2014; Asher et al. 2016; Lalot et al. 2016; d'Ettorre et al. 2017). For example, in parrots, attention bias was associated with personality (Cussen & Mench 2014). In studies on humans, it has been suggested that children with a shy personality are more susceptible to negative biases than less shy children, which in turn leads to anxiety and depression later in life (Weeks et al. 2016). One of the arguments for personality affecting cognitive biases, and not vice versa, is that the development of cognitive biases is thought to

occur after development of other social and cognitive skills (see references in Weeks et al. 2016). In **paper VI**, chicks displayed variation in judgment bias already one week after hatching, suggesting that judgment biases are present early in chicks. Whether judgment biases are heritable, and how these biases develop and change during development, are still not studied in animals, but would shed light on these questions. In addition, to explore if personality is influencing judgment bias and not the other way around, selection lines with for example shy-bold individuals can be used and tested in judgment bias tasks.

Cognition influencing personality

Variation in cognition could influence personality (Matzel et al. 2003; Light et al. 2008). Individuals that process information faster may also as a result explore faster than individuals that are slower to process information (Light et al. 2011; Carere & Locuto 2011). For example, mice that were fast learners were more explorative and habituated faster to a novel environment (Light et al. 2011). In **paper IV**, I show that individuals that had been exposed to cognitive stimulation as chicks were both more vigilant and escaped less in a behavioural assays as adults, compared to individuals that had not been exposed to the same cognitive stimulation. These results suggest that cognitive stimulation influenced personality later in life, and thus that variation in aspects of cognition can affect personality. Vigilance is a personality trait in the fowl that is often associated with predator awareness (Zidar & Løvlie 2012; Favati et al. 2014a,b). Although, vigilance might also indicate increased attentiveness where individuals are gathering information from the environment. Vigilance is for example enhanced in dominant male fowl (Favati et al. 2014b), indicating that they increase information gathering about their social environment. Thus, that I observe increased vigilance in cognitively stimulated birds could indicate that they show increased attention to their surroundings as adult, which is as predicted. I also observed fewer escape attempts in cognitively stimulated individuals. If it had been the other way around, that escape attempts increased, that could in combination with increased vigilance have indicated increased fearfulness in these birds. Because cognitively stimulated birds escaped less, it could instead potentially reflect decreased fear or decreased motivation for social reinstatement (Forkman et al. 2007). Thus, early cognitive stimulation may lead to changes in sociality, but if and how such a relationship is mediated, needs further exploration.

By exposing individuals to the same amount of handling and by placing both test and control birds alone in the test arena, I aimed to remove other differences between the two groups. Even so, I cannot exclude that the observed effect was not caused by other mechanisms. For example, the experience of performing a task, independent of it being a cognitive task, might have caused the observed changes in behaviour, not because it was cognitive stimulation per se. This can be explored in future work by adding additional treatment groups of birds performing tasks of various types, and investigate the influence on their future behaviour.

Not all personality traits measured after cognitive stimulation was affected. The cognitive tasks that the chicks were exposed to only covered some aspects of cognition (mainly associative learning) and the exposure was during a brief period during development. It is possible that adding other cognitive tasks or exposing individuals for a longer period would have given other results. Here I used visual tasks that affected attentiveness and escape behaviour. Adding tasks that included more spatial alertness might have affected other personality traits, like activity and exploration. Indeed, in quail chicks, spatial stimulation

from living in complex environments increased exploration behaviour (*Colinus virginianus*, Lazic et al. 2007).

States and traits affecting judgment

Animals are often faced with ambiguity. A bird may know that the eyes of an owl represents a threat, but will it have the same reaction when it the first time encounters a butterfly with eye spots? Recent research suggests that individuals will interpret ambiguous stimuli differently dependent on their current affective state (i.e. dependent on experiences and environmental factors, Mendl et al. 2009; 2010; Baciadonna & McElligott 2015) and also depending on their personality, which can represent more permanent emotional traits (see Roelofs et al. 2016 for review).

Contrary to many studies where stress and environmental conditions have influenced judgment in animals (Mendl et al. 2010; 2011; Baciadonna & McElligott 2015, Roelofs et al. 2016), I found no such effects on domestic chicks exposed to early cold stress and simple environmental conditions. Interestingly though, after the same chicks were exposed to additional stress both behaviour and judgment bias were affected. More specifically, chicks that had been exposed to early cold stress and later to unpredictable stress were faster to start moving in a multivariate behaviour test, which could indicate increased motivation for social reinstatement. Furthermore, chicks that were housed in simpler environments were less optimistic after experiencing unpredictable stress when confronted with ambiguous stimuli, compared to individuals housed in more complex environments. This suggests that additive stress can influence both behaviour and judgment. Indeed, the additive effect of multiple stressors has proven to be significant and can have fitness consequences (Sih et al. 2004). Thus, even though I found no effect after only exposing chicks to cold stress and simpler environments, I found that multiple aversive events can affect judgment. Because the effect was detected first after adding additional stress, it seems like there is a threshold of how much stress that is needed to cause an effect on judgment. Interestingly, individuals that had been housed in more complex environments were just as optimistic when presented with ambiguous stimuli after the unpredictable stress as they had been before the stress, indicating that a complex environment has a buffering effect against stress effects. To my knowledge, this has not been reported before, although it is well known that enrichment can have positive effects on behaviour (Francis et al. 2002; Ashokan et al. 2016). In the same study I further show that dopamine levels in the brain is associated with judgment bias. This is not surprising because dopamine is involved in learning about rewards (Wise 2004; Flagel et al. 2011) and dopamine has recently been linked to judgment bias in other species (Sharot et al. 2009; 2012; Rygula et al. 2014; Kriegel et al. 2016; Perry et al. 2016). Here, I find support that levels of dopamine in the brain can influence judgment also in the fowl.

Personality has only recently, and only in a hand full of studies, been linked to judgment bias in animals. For example, proactive pigs interpreted ambiguous stimuli more optimistically than reactive pigs and were at the same time less plastic in their responses to ambiguous cues (Asher et al. 2016). While reactive pigs showed an optimistic bias in an enriched environment that was reduced in a less enriched environment, proactive pigs where instead optimistic independent of environmental conditions (Asher et al. 2016). In **paper VI**, I exposed individuals raised in the same environment to a judgment bias test. I found that the probability to approach stimuli was linked to exploration of a novel arena, thus personality was associated with judgment. Individuals that were faster at exploring an arena were also more likely to approach a negative cue. Contrarily, in carpenter ants, fast exploring

individuals were more pessimistic (d'Ettorre et al. 2017). Different ecology and social systems in these species might explain the observed differences between species, as it is currently not known how such differences affect responses to ambiguous cues. Inactivity has previously been linked to depression in rats (Weiss et al. 1998). That inactivity was associated with a less optimistic response might therefore indicate that these individuals were depressed. However, inactivity could also just reflect a slower behavioural type. I further observed that latency to approach cues was linked to vigilance, and not activity. Individuals that were more vigilant in personality assays were slower to approach ambiguous cues, which could reflect variation in anxiety (Salmato et al. 2011). This in turn may suggest that vigilance might reflect an emotional trait. These are interesting results, not only because it shows that personality can affect judgment, but also because it indicates that measures of probability to approach cues and latency to approach cues are measuring different phenomena. First, an individual will decide whether it will approach a cue or not, and then it will decide at which speed it will approach. Thus, the two measures seem to capture different aspects of the decision-making process, and this might explain why studies exploring associations between affective states and judgment bias have shown inconsistent results. Considering that the two measures most likely capture different aspects of the decision-making process, which also seem to relate to personality in different ways, comparisons between studies are better suited when studies have used the same measure. Taken together, these results show that individual variation in judgment may not exclusively arise from temporary variation in affective states, but may also describe more stable emotional traits, thus a more permanent feature of the individual. Further, traits and potentially also states influence different aspects of the decision-making process.

Concluding remarks and future challenges

So what have we learnt about the differences between chick A and chick B, described in the introduction? Chick A is bold, explorative and less flexible in its behaviour, consistent with describing a more proactive behavioural type. Conversely, chick B is shyer, less explorative and seem to pay more attention to changes in the environment, as predicted for a reactive behavioural type. Further, chick B seem to sample more information before learning what food is palatable and what food is distasteful or noxious, than chick A. It is quite likely that the differences between chick A and chick B are present because of an association between their behavioural type and variation in their cognitive processes. We can therefore further predict, based on the results of my thesis, that chick B, the more reactive chick, would generalise novel stimuli faster, and learn more complex tasks faster, compared to chick A.

In conclusion, I have in this thesis shown that aspects of cognition (i.e. learning speed and generalisation), associate with consistent behavioural responses describing personality and coping styles in the red junglefowl. I have shown that the association between personality and cognition can depend on both underlying mechanisms, such as a speed-accuracy trade-off and/or be explained by more direct casual relationships. Indeed, both the observed relationship between learning speed and exploration in adult female fowl, and the relationship between generalisation and coping styles in chicks, are consistent with expectations of a speed-accuracy trade-off. Although, I did also observe a reversed relationship between learning speed and exploration in young chicks compared to the one I observed in adult hens. This emphasise the possibility that a speed-accuracy trade-off does not explain all observed relationships between personality and cognition. Certainly, cognitive experiences that an individual had during early development influenced some personality traits later in life, proposing a causal relationship where cognition has the potential to alter personality. If cognition is affecting the personality of individuals, this might also influence how individuals handle a changing environment, with potential fitness consequences. Furthermore, I find that an animal's current affective state and its personality are associated with how individuals judge ambiguity. This offers the possibility that personality is influencing cognition, and is an important possibility for future studies to explore further. Moreover, to be able to draw more general conclusions about the association between personality and cognition and the mechanisms driving this association, future studies should include multiple measures of cognition and personality traits, as well as aspects of physiology. I observed that dopamine activity associate with optimism, suggesting that the monoaminergic systems are involved in influencing biases in cognitive processes. Given that additive stress and personality also associated with judgment bias, both internal and external factors are important possible mediators of judgment biases. A challenge for future studies is to explore the causality of these observed associations, and the significance of observed relationships for fitness. To conclude, I observe a complex relationship between consistent behavioural variation and cognition, results with implications for both animal welfare and behavioural ecology, and that lay the foundations for future studies aiming to better understand observed behavioural variation within populations.

Sammanfattning på svenska

Inom biologin har man traditionellt uttalat att individer bör anpassa sitt beteende och reagera optimalt i varje situation för att vara framgångsrika. Istället har det dock konstaterats att individer i samma population kan bete sig väldigt olika, och att individer har begränsad anpassningsbarhet. Individer beter sig på liknande sätt i liknande situationer gång på gång. I en situation där en individ är rädd, kan en annan individ vara modig. Detta kallar vi personlighet hos djur. Hur sådana beteendemönster uppkommer och varför de bibehålls i populationer är fortfarande oklart. Individer uppvisar dessutom stor variation i kognitiva egenskaper, som till exempel hur de uppfattar, bearbetar och agerar på information i sin omgivning, samt hur väl de minns vad de lärt. Teoretisk har variation i kognition bedömts, i alla fall till del, kunna förklara varför djur har personlighet. Den här avhandlingen utforskar sådana samband, och fokuserar på individuella skillnader i personlighet och kognition, samt hur dessa samverkar. Jag har använt mig utav djungelhöns och domesticerade höns för att studera detta.

Djungelhönan är en grupplevande, social art som är kognitivt och beteendemässigt komplex. Den lever naturligt i skogsmiljö i Asiens regnskogar och är beroende av att lära sig att hitta och känna igen föda och rovdjur direkt efter att den kläcks. Djungelhönan och dess domesticerade ättlingar tamhönsen är därför en perfekt art för studier av beteende och kognition. För att få en bättre förståelse för om och hur personlighet och kognition samverkar hos djungelhöns utfördes olika beteendetester samt kognitiva tester i en rad studier.

Terminologin som beskriver konsekventa beteendemönster hos djur är fortfarande otydlig. Dels har begreppet ”djurs personlighet” använts flitigt, samtidigt har det diskuterats kring djurets sätt att hantera stress, något som kallats ”stresshanteringsstrategi” (”coping style”, på engelska). Dessa två begrepp beskriver något olika aspekter av beteendevariation, men används ofta som synonymer. För att ta reda på huruvida man kan använda dessa termer för att beskriva djungelhönans beteende, testade jag kycklingar och vuxna i beteendetester som utformats för att fånga upp beteenden beskrivna under respektive term. Jag fann både personlighet och stresshanteringsstrategier hos djungelhönan, men observerade att de beskriver olika aspekter av beteendevariationen hos arten. Jag konkluderar därför att termerna inte bör användas synonymt.

Vidare observerade jag en stor individuell variation i både personlighet och inläring. Intressant var att individer som lärde snabbt i ett inläringstest nödvändigtvis inte lärde snabbt i ett annat inläringstest. Alltså fanns inget som tydde på generell intelligens hos mina försökshöns. Jag observerade också en koppling mellan inläring och utforskande beteende hos både kycklingar och vuxna höns. Intressant var att förhållandet var omvänt hos vuxna jämfört med kycklingar. När kycklingar som lärde snabbt i ett omvänt diskriminationstest, också utforskade en ny miljö snabbare, så var det istället de långsamt utforskande vuxna hönsorna som lärde sig snabbast. Det är mycket som händer under utvecklingen från kyckling till höna som potentiellt kan förklara att förhållandet mellan kognition och personlighet ändras över tid. Den koppling jag fann mellan inläring och personlighet var hos de vuxna hönsorna, men inte hos kycklingarna, överensstämmande med en teori där individer har en strategi av noggrannhet eller effektivitet/snabbhet (”speed-accuracy” på engelska). Individer som är mera noggranna, är långsammare på att utforska en ny miljö och undersöker saker länge, vilket gör att de tar tid på sig att lära, men de gör ofta saker noggrant och därför mer korrekt. Därför klarar dessa individer svåra kognitiva utmaningar bättre än individer som fokuserar på snabbhet. Individer som använder strategin där snabbhet är dominerande, är snabba på att utforska en ny miljö och lär snabbt så länge det inte krävs noggrannhet.

I en annan studie undersöktes om individer med känd personlighet på olika sätt använde information de lärt sig tidigare och generaliserade ny information med liknande egenskaper. Jag såg att individer som var mera flexibla i sitt beteende också använde tidigare information i större utsträckning och generaliserade mer än individer som var mindre flexibla. Flexibilitet i beteende var också kopplat till rädsla vilket tyder på en stresshanteringsstrategi, där flexibla, rädda individer beskriver reaktiva individer medan mindre flexibla och mindre rädda individer beskriver proaktiva individer. Att reaktiva individer generaliserade starkare än proaktiva kan förklaras av att reaktiva individer förväntas vara mer uppmärksamma på förändringar och detaljer i miljön än proaktiva individer, vilket kan förklaras med teorin om noggrannhet mot snabbhet.

Kopplingen mellan kognition och personlighet skulle även kunna bero på ett kausalt samband, där aspekter av kognition påverkar personlighet, eller tvärtom, att personlighet påverkar kognitiva processer. Jag utförde därför ett experiment där det undersöktes om kognitiv stimulering påverkade vilken personlighet individen utvecklade senare som vuxen. Jag jämförde individer som utsatts för kognitiv stimulering som små, med individer som endast hanterats, och såg att individer som hade fått lära som små var mer uppmärksamma som vuxna. Detta tyder på att tidiga erfarenheter kan påverka utvecklingen av personlighetsdrag.

Förutom stor individvariation kan kognitiva processer förvånande nog ofta innehålla feltolkningar av information. Dessa feltolkningar kan påverka de beslut en individ tar. Information kan till exempel tolkas mer eller mindre positivt på en skala från pessimistiskt till optimistiskt. För att undersöka om individer tolkar världen olika på grund av den sinnesstämning de befinner sig i, eller deras personlighet, gjorde jag två experiment. Först undersökte jag hur en individs sinnesstämning påverkade hur individerna tolkade tvetydig information i form av gråa symboler när de hade lärt sig att vit var belönad, medan svart var obelönad. Individer placerades i enklare eller mer komplexa miljöer och utsattes sedan för stressande faktorer. De individer som levde i en enklare miljö och utsattes för stress tolkade den tvetydiga information mer negativt efter att de utsattes för stress än individer som levde i en komplex miljö. Att utsättas för en ytterligare stress orsakade därmed att hönsen blev mindre optimistiska. Individer som levde i en komplexare miljö verkade däremot klara av stress bättre. En mer komplex miljö verkade därmed kunna motverka den negativa påverkan av stressen. Mer optimistiska höns hade också högre halter av dopamin i hjärnan, vilket är liknande som har hittats hos människan och andra djur. I det andra experiment undersökte jag hur personlighet påverkade hur hönsen tolkade tvetydig information. Jag fann att individer som var utforskande i en ny miljö tenderade att tolka information positivt, medan individer som var mer uppmärksamma och troligtvis mer ängsliga, tolkade informationen mer negativt. Individerna var dessutom mer positiva i varje testomgång där de i föregående testomgång fått en belöning. Både personlighet och rådande sinnesstämning verkar därför påverka hur individer tolkar tvetydig information, och därmed hur optimistiska de är.

Sammantaget visar dessa studier att (i) det finns konsekventa individuella skillnader i beteende som beskriver både personlighet och stresshanteringsstrategier, och stor individ variation i kognitiva egenskaper hos djungelhönan, (ii) att dessa är korrelerade, och (iii) att det finns ett samspel emellan där personlighet kan påverka kognition eller tvärtom att kognition kan påverka personlighet. Därtill har jag visat att (iv) feltolkningar i kognitiva processer påverkas av både personlighet och djurets sinnesstämning. I denna avhandling har jag därmed visat att personlighet och kognition har ett intrikat samspel, betydelsefullt för både djurvälstånd och beteendekologi, och som kan nyttjas i kommande studier som vill få bättre förståelse för variation i beteenden inom populationer.

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